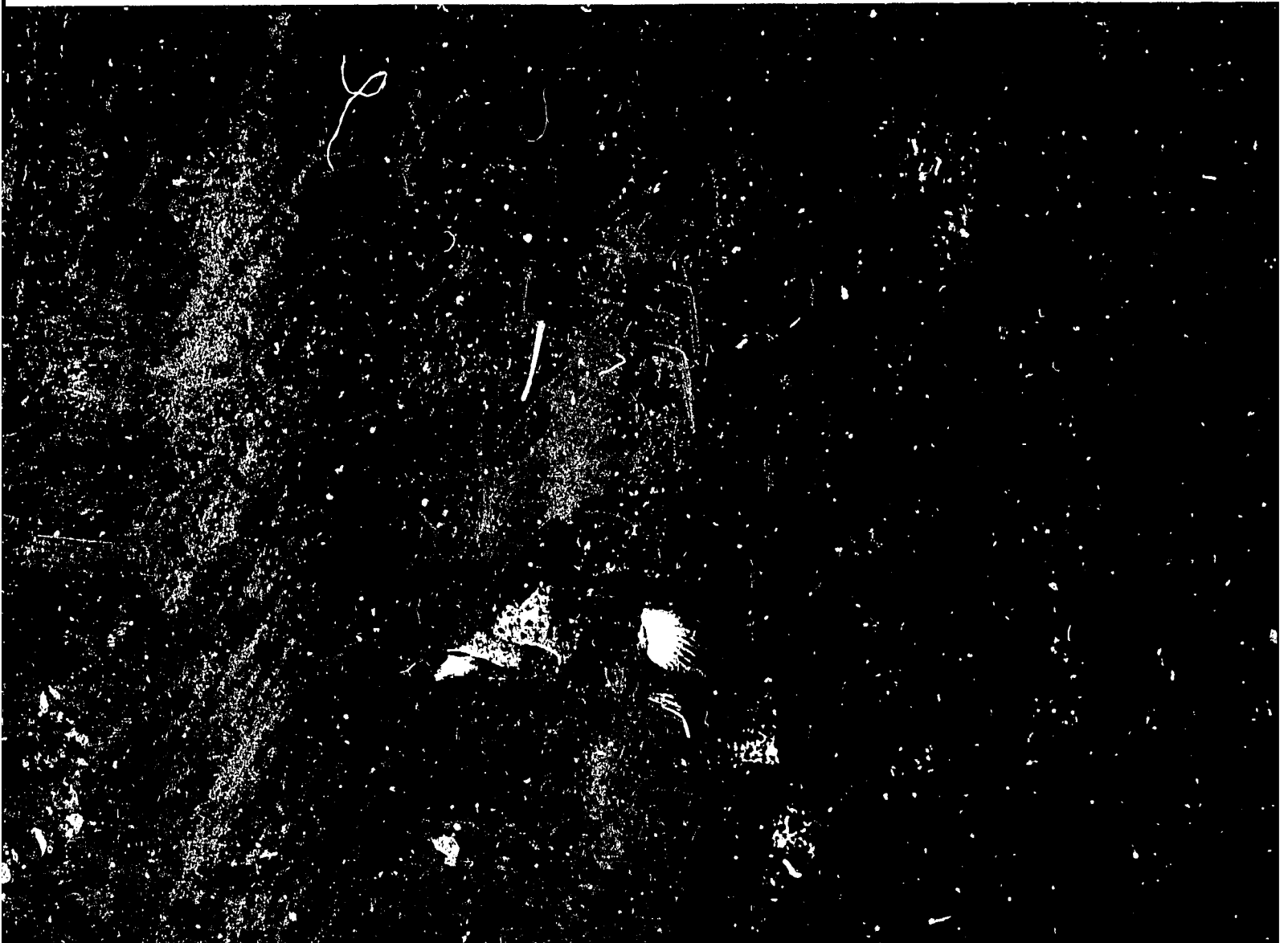


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ICLARM STUDIES AND REVIEWS 7

Caribbean Coral Reef Fishery Resources

Edited by J. L. Munro



Caribbean Coral Reef Fishery Resources



R. V. Caranx

Caribbean Coral Reef Fishery Resources

A second edition of
"The Biology, Ecology, Exploitation and Management
of Caribbean Reef Fishes: Scientific Report of the
ODA/UWI Fisheries Ecology Research Project
1969-1973:
University of the West Indies, Jamaica"

Edited by

J.L. Munro

1983



**INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES**

111

Caribbean Coral Reef Fishery Resources

Edited by

J.L. MUNRO

1983

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Front cover: The coney, *Cephalopholis fulva* (Serranidae)—one
of the principal components of reef fish catches. Photo by
Alex Kerstitch.

Back cover: Bar jack, *Caranx ruber* (Carangidae) and white
grunt, *Haemulon plumieri* (Pomadasyidae) in Nassau fish
market. Photo by J.L. Munro.

ICLARM Contribution No. 125

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PREFACE TO THE SECOND EDITION

The information presented in this volume was first published in 18 mimeographed parts over the period 1973-1981 as Number 3 in the series *Research Reports from the Zoology Department, University of the West Indies*. The full series is now reprinted by ICLARM, with the permission of all contributors, as a single volume. An epilogue reviewing progress in coral reef fisheries research over the period 1973-1982 has been added,

from which it is possible to make some appraisal of the accuracy of the original parameter estimates.

The scientific names used in this report follow those in Randall (1968) for the most part and recent changes or proposed changes in nomenclature have not been incorporated into this edition. Areas have been converted from square nautical miles to metric units.

PREFACE TO THE FIRST EDITION

At the end of 1968, a proposal for a Fisheries Ecology Research Project in Jamaica was submitted to the United Kingdom Ministry of Overseas Development (now the Overseas Development Administration). At that time it was apparent that various national and regional exploratory fishing programs, mostly sponsored by the UNDP and executed by FAO, had generated some interest in the possibilities of investment in modern offshore fishing vessels. It appeared likely that the nucleus of a modern fishing fleet might develop in Jamaica in the near future and that unexploited shelf and slope areas beyond the reach of the mechanized canoe fleet might be brought into production.

It was therefore considered desirable to undertake two major studies: (1) an investigation of the dynamic characteristics (age, growth, mortality and population density) of the main species of lutjanids, serranids and carangids comprising the incipient offshore line fishery and (2) a study of the effect of trap fishing upon the composition of reef-fish communities.

The results of these specific investigations would then be utilized to assess the maximum sustained yield which can be obtained from the most important elements of the exploited demersal fish populations in Jamaican seas, and to establish a valid biological basis for the regulation and management of these fisheries.

During the period 1 September 1969 to 31 March 1973, the ODA/UWI Fisheries Ecology Research Project was financed by very substantial grants (R2174 and R2174A) from the Overseas Development Administration, which included the cost of construction of a 17-m, 58-t, ferrocement-hulled research vessel, the *R. V. Caranx*. The scientific staff comprised a project manager, and four fisheries biologists or research assistants. Supporting staff comprised a fishing gear technologist/diving officer, ship's master, engineer, two deck hands and a part-time secretary.

The Project was based at the Port Royal Marine Laboratory of the Zoology Department, University of the West Indies.

ACKNOWLEDGMENTS

The staff of the Project benefited from the assistance of many individuals and agencies during the course of the investigations.

The scientific progress of the project was supervised by Dr. D.N.F. Hall, Fisheries Adviser of the U.K. Overseas Development Administration and Dr. I.M. Goodbody, Professor of Zoology at the University of the West Indies, to whom we are very grateful for their guidance and support. Mr. D.S. Foster, Mr. P.G. Ottewill and Mr. W.A. Brownlie of ODA successively and successfully dealt with the administrative problems raised by the Project. Mr. O.R. Davenport and his staff at the Crown Agents were of great assistance to the Project Manager in dealing with design specifications and supervising the construction of *R. V. Caranx*.

Mr. K. Deeming developed the computer programs for the analysis of trap catches and Mr. Peter Jutsum, Director of the U.W.I. Computing Center, was unfailingly helpful.

Mr. V. Khaleel and Mr. T. Khaleel of Khaleel's Deep Sea Fisheries permitted Project staff to regularly rummage through catches delivered to their plant and provided every assistance.

Mr. J. Dibbs, Project Manager of the UNDP/FAO Caribbean Fishery Development Project kindly gave permission for Project staff to participate in cruises of the *M.F.V. Alcyon* during the period preceding the delivery of our research vessel. We also derived much benefit from discussions with members of the CFDP staff, particularly Mr. G. Chislett, Mr. K. Kawaguchi, Mr. E. Oswald and Mr. W. Rathjen.

Many members of the Jamaica Branch of the British Sub-Aqua Club participated during 1970 in an *in situ* investigation of the composition of fish trap catches from which we derived an insight into the complexities of trap fishing.

Capt. J.M. Sutherland, Master of *R. V. Caranx*, contributed enormously to the success of the offshore operations. Mr. N.M. Simms, Gear Technologist/Diving Officer (subsequently Master of *R. V. Caranx*) diligently accepted the responsibilities of overseeing the scuba diving activities of the Project, and it is to his credit that no mishaps occurred during the course of these investigations.

Thanks are due to Dr. J. Graham of the Zoology Department, University of the West Indies, who identified zooplankton from stomach contents of grunts, Dr. D.I. Gibson of the British Museum of Natural History, London, for identification of parasites, and staff at the Bermuda Biological Station who enabled collection of scale samples of grunts from Bermuda.

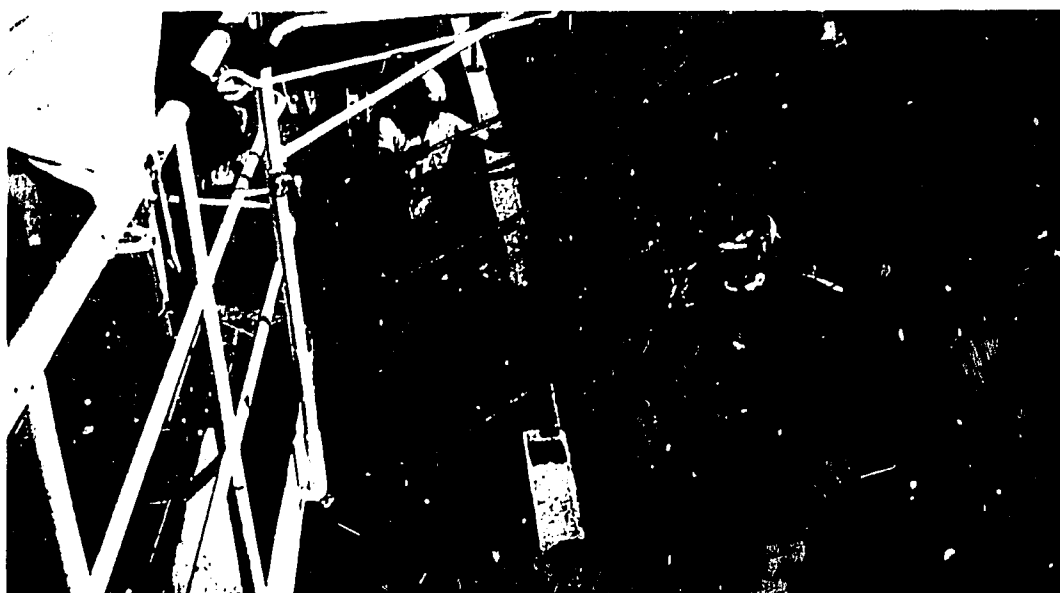
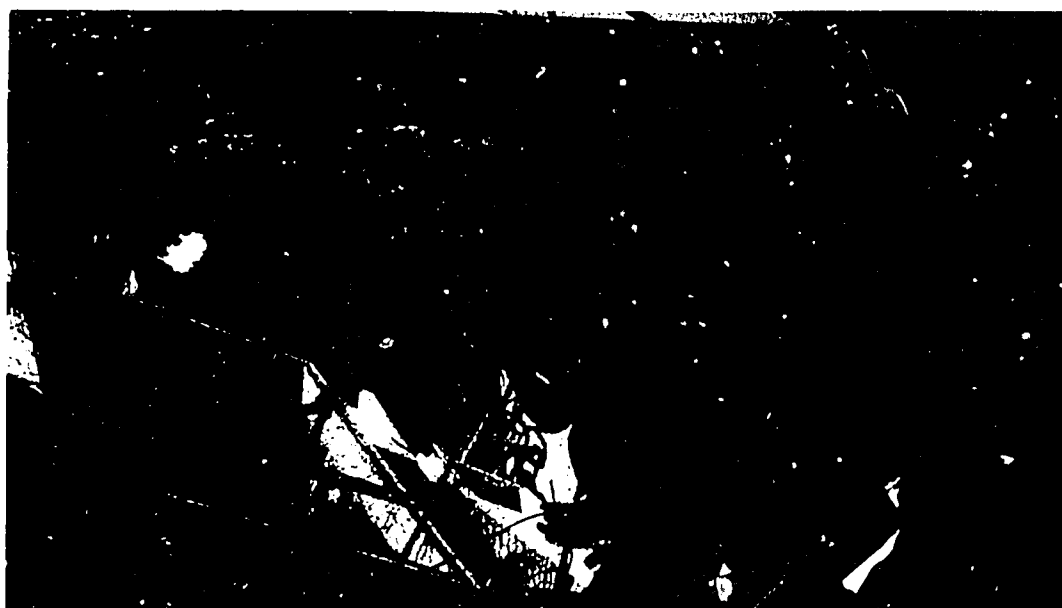
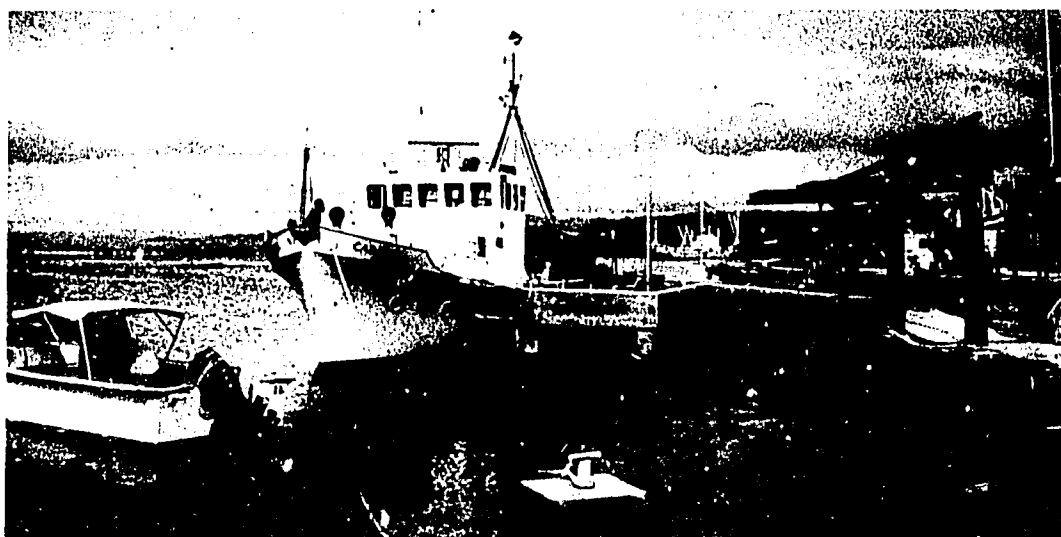
Mr. E. Hamblyn, ODA Fisheries Adviser in Jamaica, and Mrs. P.E. Munro provided helpful criticisms of the early drafts of many parts of this report. Mrs. C. Swift kindly prepared the reference list for this edition.

Chapters 7 and 11 have previously been published in condensed form in the *Journal of Fish Biology* (vol. 8: 79-97 and vol. 12:115-146). Permission to reproduce this material in this volume has kindly been granted by Academic Press Inc. (London) Ltd. and by the Fisheries Society of the British Isles.*

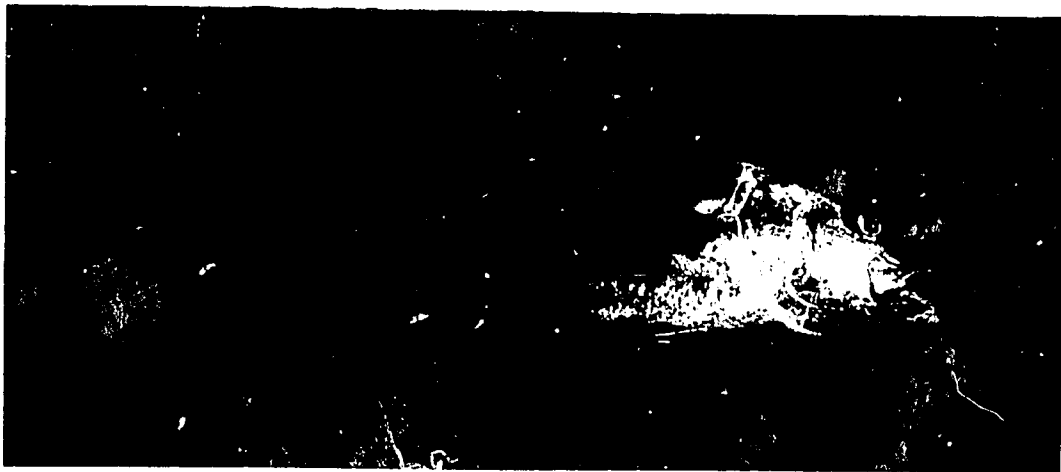
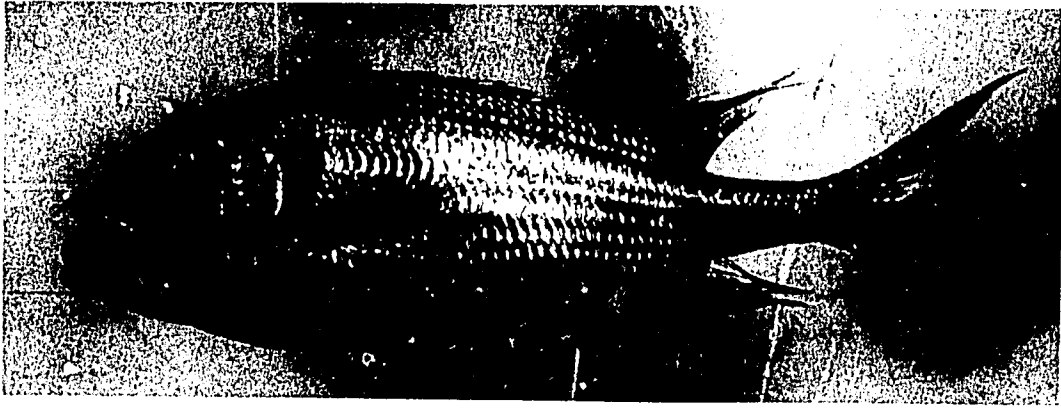
Several portions of this report were prepared by J.L. Munro during the course of a Fellowship (R 2866) sponsored by the Natural Resources Research Department of the U.K. Ministry of Overseas Development, during the tenure of which he was based at the Sea Fisheries Laboratory of the U.K. Ministry of Agriculture, Fisheries and Food at Lowestoft. The assistance of the Director and staff at that laboratory in providing facilities, services and valuable discussions is gratefully acknowledged.

J. L. MUNRO
P. H. REESON
R. THOMPSON
V. C. GAUT
K. AIKEN
J. R. WYATT

*Mr. J. Higman, Executive Director of the Gulf and Caribbean Fisheries Institute kindly gave permission to incorporate into Chapter 19 material presented at the 35th meeting of GCFI in November 1982.

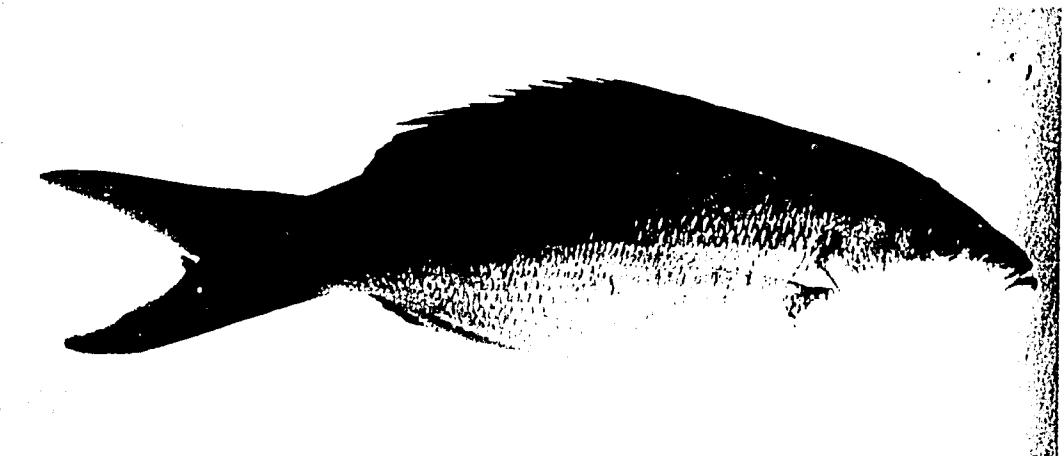
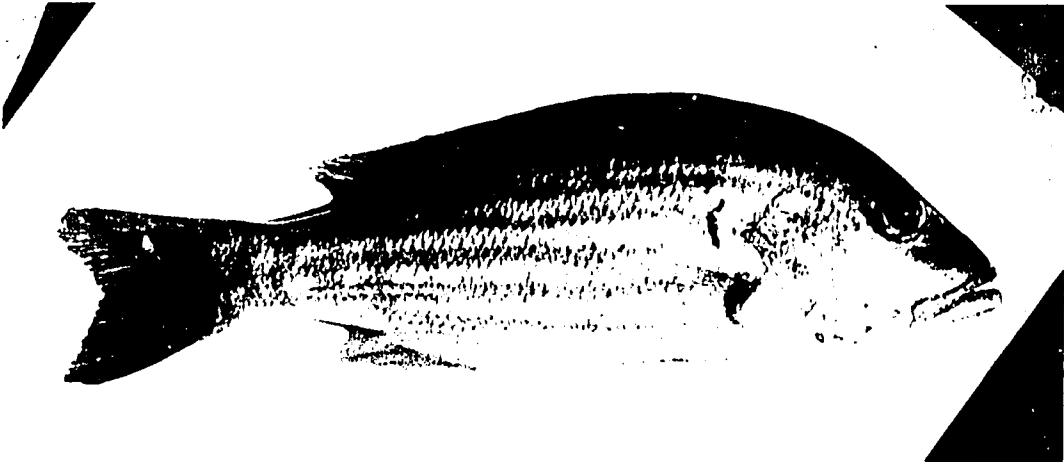
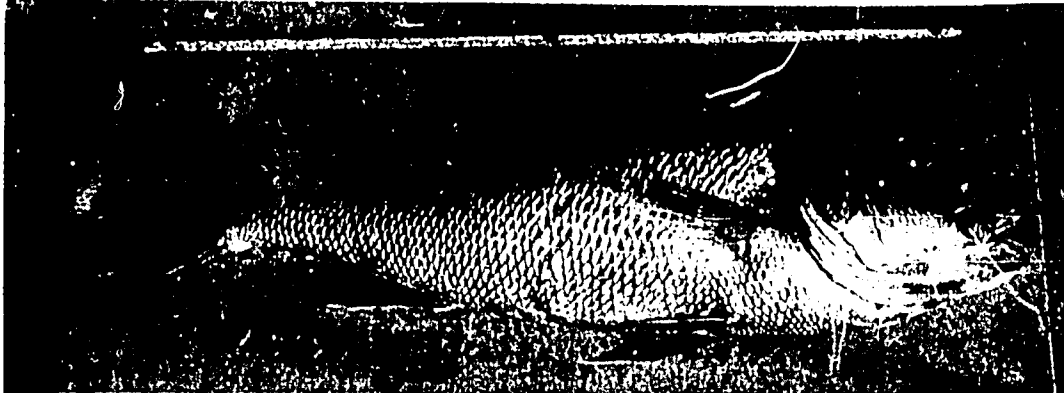
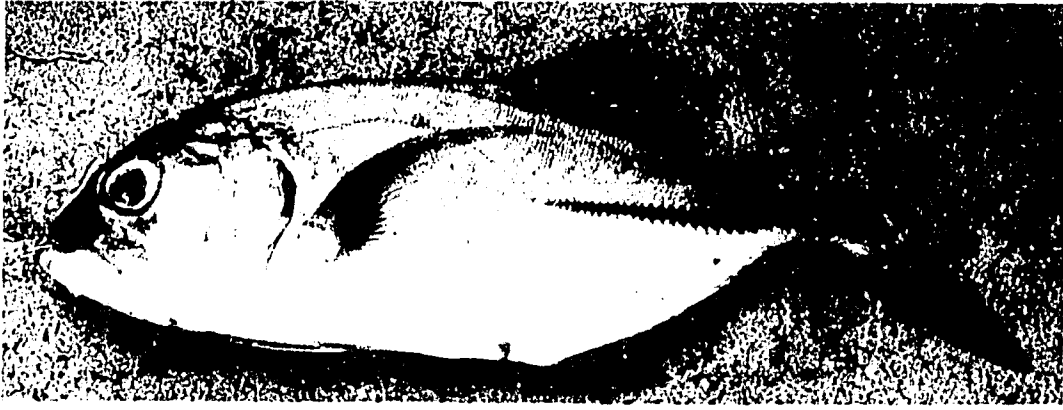


Top: R. V. Caranx, the project's 17-m ferrocement-hulled research vessel, at the Port Royal Marine Laboratory, Jamaica. Center: Hauling dollar traps in a heavy sea: R. V. Caranx. Bottom: A large Z trap being hauled by the M.V. Alcyon, of the UNDP/FAO Caribbean Fishery Development Project. Color photos by J. Munro, except where noted.



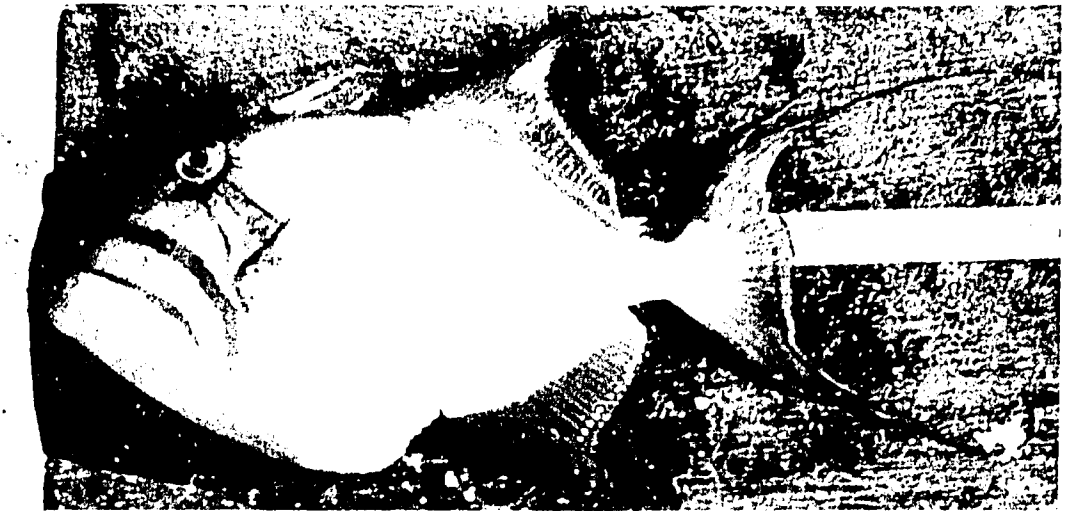
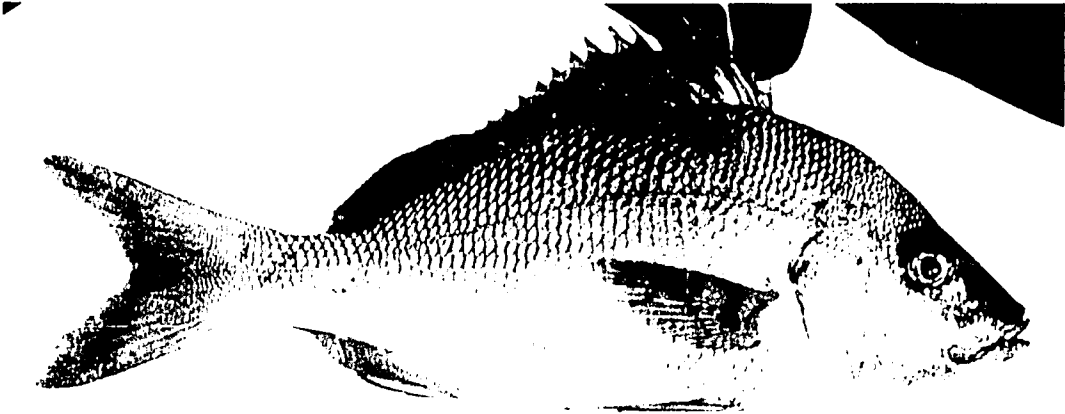
Commercial Caribbean reef fishes. *Top to bottom: Holocentrus rufus**, 18 cm TL (Holocentridae); *Myctoperca venenosa*, 75 cm FL (Serranidae); *Epinephelus guttatus*, 35 cm TL (Serranidae); and *Seriola dumerili*, 110 cm FL (Carangidae).

*Photo: K. Aiken



Commercial Caribbean reef fishes. *Top to bottom: Caranx latus**, 35 cm FL (Carangidae); *Lutjanus vivanus*, 60 cm FL (Lutjanidae); *Lutjanus synagris*, 25 cm FL (Lutjanidae); and *Ocyurus chrysurus*, 35 cm FL (Lutjanidae).

*Photo: K. Aiken



Commercial Caribbean reef fishes. *Top to bottom: Haemulon plumieri*, 70 cm FL (Pomadasyidae); *Haemulon album*, 25 cm FL (Pomadasyidae); *Balistes vetula**, 40 cm FL (Balistidae); and the spiny lobster *Panulirus argus**, 10 cm CL (Palinuridae).

*Photos: K. Aiken

**CHAPTER 1:
CORAL REEF FISH AND FISHERIES OF THE
CARIBBEAN SEA**

by
J.L. Munro
(November 1973)

Review of Caribbean Reef Fisheries

GENERAL EXTENT OF REEF FISHERIES

The fisheries exploited in the Caribbean region and adjacent areas, such as the Bahamas can, with a few significant exceptions, be defined as reef fisheries. That is, the exploited fish populations usually occupy or are associated with rocky or coralline areas in which the nature of the topography precludes or severely restricts the use of trawls or other nets.

The major exceptions to this general condition are found in the southeastern portion of the Caribbean Sea, particularly the eastern Venezuelan coast, the Gulf of Paria and the Gulf of Venezuela, where upwelling or the influence of major land drainage or the presence of extensive shelves provides the basis of several important pelagic fisheries and trawling industries (Griffiths and Simpson 1973). Also, some areas off the coasts of Nicaragua, Honduras, Belize (British Honduras), Cuba and Jamaica offer variable potential for trawl fisheries, particularly for penaeid shrimp; but the extent of trawlable areas in each case represents only a very small portion of the shelf areas of these countries.

In many of the Leeward and Windward Islands of the Eastern Caribbean, beach-seine fisheries for shoaling clupeids and carangids yield a significant portion of the total catch. Flying fish are captured by means of hooks, lift nets, gill-nets and purse nets at Barbados and some of the Windward Islands. Pelagic scombrids, mainly *Scomberomorus maculatus* (Spanish mackerel), *S. cavalla*

(king mackerel) and *S. regalis* (cero mackerel), *Thunnus atlanticus* (blackfin tuna), *Euthunnus alletteratis* (little tuna) and *Katsuwonus pelamis* (skipjack tuna) form a small but valuable part of total landings, particularly in the eastern Caribbean. With few exceptions, the scombrid fisheries are conducted on a seasonal basis when the fish are "running" or by trolling while en route to and from the demersal fishing grounds. Gill-net fishing for clupeids and shoaling carangids is also important in some areas.

Apart from the abovementioned exceptions, the reef fish communities constitute the only immediate source of supply of fresh fish for the populations of the continental coastal region and the islands of the Caribbean Sea. Spiny lobsters are a particularly valuable portion of this resource and in a number of countries form the basis of important export industries.

Previous reviews of Caribbean fisheries include the works of Hess (1961) and of Salmon (1958). A perusal of these works and of the review by Idyll (1971) and the present report will reveal that no significant changes have occurred in the past decade.

CARIBBEAN REEF FISHES

Prior to 1968, taxonomic works on the reef fishes of the Caribbean were to be found in scattered references and reviews or in the outdated, but valuable, volumes of

Jordan and Evermann (1896), and in the work of Cervigon (1966) on the fishes of Venezuela. However, with the publication of comprehensive works by Randall (1968) and by Bohlke and Chaplin (1968), problems of taxonomic detail were greatly simplified and the larger elements of the reef fish fauna to depths of 200 m can be said to be adequately documented. Beyond the 200-m level, in the upper bathyal zone, very little collecting has been done and identification of catches can become problematical.

Of the more than 350 species of reef or reef-associated fishes known to occur in the Caribbean region, approximately 180 species are known to be marketed by the fishermen. The species of major economic importance are included in at least 10 families comprising the herbivorous Acanthuridae and Scaridae, the invertebrate-consuming Holocentridae, Pomadasyidae, Mullidae, Chaetodontidae and Balistidae and the predatory Lutjanidae, Serranidae, Carangidae, Sphyrnidae and Carcharinidae.

METHODS OF EXPLOITATION OF REEF FISHES

The use of trawls and other nets in coralline tropical seas is precluded or severely restricted by the presence of hermatypic (reef-building) corals (Munro 1969, 1973). Even the use of bottom long-lines or traps affixed along the length of a setline is hazardous because the line is liable to become lodged under a coral ledge resulting in loss of all or much of the fishing gear. In most areas, fishing techniques are therefore restricted to the use of individually buoyed traps or vertical lines. In addition, spear-fishing is becoming an increasingly important harvesting technique, mostly for reasons related to the low capital outlay required, and to high rates of unemployment in many areas.

Traps

Traps for capturing reef fishes and crustaceans are the predominant feature of Caribbean reef fisheries. Basically, two types of trap can be recognized: 1) the "Antillean" trap, a generic term used by Munro, Reeson and Gaut (1971) to describe all wooden-framed traps covered with a mesh of galvanized wire and 2) traps constructed specifically for the capture of spiny lobsters.

Antillean traps have previously been described by Munro et al. (1971). The framework usually consists of sticks supporting a galvanized wire mesh structure. The traps are of three basic designs: Z-shaped, or S-shaped, with two entrance funnels, or chevron-shaped (otherwise described as arrowhead-shaped) with a single entrance funnel (Fig. 5.1). The Z-shaped traps are most popular in Jamaica, the S-shaped traps in Cuba (Buesa Mas 1962) and the single-funnelled chevron traps in the Eastern Caribbean islands. Rectangular traps with one or more entrances are used in the Bahamas, Bermuda and in Belize, and to a small degree elsewhere in the Caribbean

and might reflect the absence of a trap-fishing tradition in some of the former areas.

It appears that the use of "Antillean" traps in the Caribbean region dates back, at least, to the early Spanish occupations, for the arrowhead or chevron trap is identical in design and concept to those described by Hornell (1950) as being used in Madiera. Certain African and Asian designs are also similar (Burdon and Parry 1954). The maximum aperture of the wire mesh commonly used in the Caribbean is 2.5 to 5 cm.

An analysis of the mode of operation of Antillean fish traps is given by Munro (1974). Primary conclusions are that traditional designs afford very high rates of escapement and that the rate of escapement is proportional to the size of the inlet funnels and inversely proportional either to the area or to volume within which the fishes are contained. A simple mathematical model can be used to describe the processes involved.

Escapement from medium-sized (183 x 122 x 61 cm) Antillean traps averaged 11 to 12%/day and over 50% of the fishes which entered traps escaped during the course of a 10 to 19-day soak. S-shaped traps permit greater rates of ingress (entry into traps) than do Z-shaped traps, presumably as a result of their curved shape guiding fishes more readily to the entrance funnels (Munro et al. 1971).

Traps designed specifically for the capture of spiny lobsters (mainly *Panulirus argus*) are relatively uncommon in the Caribbean region, and their use appears largely to be confined to areas where the resources of lobsters are relatively large, and the marketability of trap-caught fishes is relatively low, either as a result of low population densities in the coastal regions or of relatively sophisticated market requirements. Three basic types of traps are used in the lobster fisheries:

1. Florida lobster traps are rectangular in shape and made of wide slats of wood, are heavily weighted and have a single short vertical entrance funnel in the top of the trap (Cope 1959). Similar traps are used in Cuba (Buesa Mas 1960).
2. The traps used in Belize are similar to Florida traps but of lighter construction and have a single horizontal entrance funnel at one end of the trap.
3. Corn Island traps, used in Nicaragua (Chislett and Yesaki 1974), are small rectangular structures made of welded, galvanized rectangular wire mesh with a single horizontal entrance funnel, these are usually set in gangs or strings along a bottom long-line.

It would appear that lobster traps have not attained popularity wherever trap-caught fishes are readily marketable, and it is likely that the selective properties of lobster traps (Feliciano 1958) are outweighed by the value of the catch of fishes which can be taken in Antillean traps.

During the course of this investigation, metal-framed stackable traps based on the Antillean design were developed and tested (Figs. 5.2, 5.3 and 5.4). The details of the traps and their design have been described by

Munro (1973). These traps developed out of the need to increase the trap-carrying capacity of our research vessel, thus increase fishing effort and mobility in offshore fishing areas. The metal-framed traps retain the desirable features of the Antillean traps (twin entrance funnels and large size), but are split in the vertical-longitudinal axis to yield two identical halves which can be stacked one upon the other. This resulted in a 10-fold increase in the trap-carrying capacity of the vessel (Fig. 5.4).

Two variants were developed and described (Fig. 5.2): 1) the "split-S" trap or "dollar" trap, essentially based upon the Cuban S trap (Buesa Mas 1962) in which the frame is curved to approximate to an S-shape and 2) the "split-hexagonal" trap in which the curved corners were discarded and replaced by angular framework (Fig. 5.2). The size of the trap was also increased when it was found that catch rates were directly related to the size of the trap.

Hook and Line

Hook-and-line fishing techniques are the second most important method of exploitation of reef fishes in the Caribbean region. Variations in technique appear very nearly to equal the number of proponents of the method and the degree of expertise displayed is often remarkable. While the basic technique of placing bait upon a hook and casting it upon or into the water is commonplace, the expertise in controlling the baited line and sensing the activities of fishes tends more towards an art when demonstrated by experienced line-fishermen. Kawaguchi (1974) found that experienced line-fishermen usually catch an average of 50% more than less-experienced individuals under identical circumstances and this is borne out by our own experience.

In Jamaica, the most common method used in relatively shallow waters (< 45 m) is to use a lightly weighted line, with one or two relatively small (3/0 and 2/0) hooks, which is fed into the water down-current until proximal to the bottom. When fish are found, additional bait is cast into the water and the lines are progressively shortened until the feeding fishes ascend to near the surface and can be hauled in with great rapidity.

In deeper waters (45 to 250 m), adequate weight is attached to send the monofilament nylon line almost vertically to the sea floor. Between 3 and 15 hooks may be placed on a single line. The hooks are of larger size (4/0 to 7/0) than those used in shallower depths and self-setting tuna circle hooks are popular in some areas. The line is not raised until the fisherman feels that no further fishes will strike the hooks. Electrically powered (12-24 V DC) or hand-powered reels are merely variants of this technique. They give added efficiency in terms of hauling time and are usually fitted with braided stainless steel line which is inelastic and gives greater control over the bottom rigs at extreme depths.

Bottom-set long-lines (called "palanka" in Jamaica) are also used in certain areas but cannot be used in areas

of frequent coral outcrops for fear of entanglement and consequent gear loss. In most true reef fisheries this gear is therefore of no significance.

Nets

Seine nets are frequently used in shallow back-reef areas, bays and harbors, but except where shoaling carangids occur, the catch is often composed largely of small demersal species and immature reef fishes. Seine nets are the principal method of exploitation of the stocks of sardines (*Sardinella anchovia*) in eastern Venezuela.

The use of bottom-set gill-nets is gaining popularity in some areas, although damage to nets as a result of contact with coral reefs or as a result of the presence of sharks appears to limit the possibilities for development of this technique. Floating gill-nets are fairly extensively used for capturing neritic pelagic clupeids and carangids and would appear to offer opportunities for further development in many areas.

Wickham (1971) has demonstrated that lights can be used to attract harvestable concentrations of several species which are relatively abundant in the Caribbean, but no commercial development has yet occurred in this respect. A pursed gill-net has been used to capture flying fish at Barbados (Wiles 1952). The concentrations of flying fish in the western Caribbean appear to be inadequate to sustain such a fishery.

As stated earlier, the use of trawls is greatly restricted to circumscribed areas of the Caribbean, where ecological conditions inhibit the development of hermatypic corals. It is possible that aimed mid-water trawling or pelagic seining techniques might become important, given the necessary technological innovations.

Spearfishing

In the Caribbean, spearfishing is becoming an increasingly important economic activity as a result of socio-economic factors related to underemployment and to the low capital outlay for equipment. In economic terms the method appears most attractive, offering income-earning capacity to otherwise unskilled or impoverished individuals. In terms of rational management of resources, spearfishing activities tend to harvest the oldest, largest, least-productive members of the fish community, thus promoting conservation of the stock.

In Belize (British Honduras), about 67% of the production of spiny lobsters is derived from spearfishing (Dres and Meyer 1965), and the spearfishing community appears to be one of the most prosperous sectors of the populace.

Other Methods

A minor proportion of the reef-fish catch of the Caribbean is taken by the use of dynamite and fish poisons or intoxicants. In some areas, the coral reef

Table 1.1. Yields of shelf-dwelling species (excluding oceanic pelagics) per unit area of shelf in the Caribbean Sea and adjacent coralline regions. Based on greatest reported annual catches during the period 1964-73 and calculated areas of shelf within the 200-m isobath.

Shelf	Area of shelf x 1,000 ha	Largest annual catch x 1,000 t	Year	% oceanic pelagic fish	Catch (kg) per ha of shelf per year	
Bermuda	171	1.0	1972	?	<5.8	
Bahamas Is. including Cay Sal Bank	18,311	6.1	1973	?	<0.3	
Turks and Caicos Is. including Mouchoir B.	760	0.7	1973	0	0.9	
Silver Bank	298	0	—	0	0	
Navidad Bank	77	0	—	0	0	
	19,446	6.8	1973	?	<0.3	
Cuba	10,287	72.5	1973	?	≤7.0	
Misteriosa Bank	34	0	—	0	0	
Pickle Bank	17	0	—	0	0	
Cayman Is.	17	+	—	+	?	
	10,355	72.5	1973	?	<7.0	
Mexico, E. coast of Yucatan	710	+	—	+	?	
Belize	694	2.0	1972	+	2.9	
Guatemala	+	0.3	1967	?	?	
Honduras	6,937	4.4	1971	?	<0.6	
Nicaragua	5,353	7.9	1973	?	<1.5	
Cos'a Rica	377	0.8	1972	?	<2.1	
Panama	1,269	?	—	?	?	
	15,340	>15.4	—	?	~1.0	
Rosalind Bank	494	0	—	0	0	
Thunder Knoll	135	0	—	0	0	
Alice Shoal	26	0	—	0	0	
Serranilla Bank	99)					
Serrana Bank	21)	137	1.4	1968	0	10.2
Bajo Nuevo	17)					
Quito Sueno Bank		110	?	—	?	?
Roncador Bank		4	?	—	?	?
Providencia Is.		27	?	—	?	?
San Andres and nearby banks		13	?	—	?	?
	946	>1.4	—	?	>1.5	
Jamaica, S. coast and nearby banks	292)	342	4.3) 6.6	1968	6) 11	13.8) 17.2
Jamaica, N. coast	50)		2.3)	1968	21)	37.0)
Pedro Bank, West	704)	804	+	1974	+	+
Pedro Bank, East	100)		0.756	1974	+	7.6
Morant Bank		17	0.095	1973	+	5.6
Salmon Bank		13	0	—	+	0
	1,176	7.5	—	<11	~5.7	
Hispaniola	2,640	11.1	1973	?	<4.2	
Puerto Rico and Virgin Is., including St. Croix	1,183	4.9	1972	12	3.6	
	3,823	16.0	—	?	<4.2	

Continued

Table 1.1. (continued)

Shelf	Area of shelf x 1,000 ha	Largest annual catch 1,000 t	Year	% oceanic pelagic fish	Catch (kg) per ha of shelf per year
Anguilla Bank; Sombrero Bank (Anguilla, St. Martin, St. Bart)	449	?	-	?	?
Saba Bank	225	~0	-	?	~0
St. Kitts Bank (St. Eustacius, St. Christopher, Nevis)	77	>1.0	1973	?	~13.0
Barbuda Bank (Antigua, Barbuda)	336	0.8	1973	?	<2.4
Montserrat	9	0.1	1973	>50	<5.6
	1,096	>1.9	-	?	<1.7
Guadeloupe and Marie Galante	211	4.8	1973	>50	<11.4
Dominica	46	0.5	1973	>50	<5.4
Martinique	127	4.8	1967	59	15.5
St. Lucia	55	1.7	1973	59	15.5
Barbados	34	4.0	1973	91	10.6
	473	15.8	-	~63	~12.4
St. Vincent and Grenadine Bank, including Grenada	360	2.4	1973	28	4.8
Colombia	3,875	60.8	1968	?	<15.7
Netherlands Antilles)		10.0)			
Venezuela)	9,087	162.4	1973	~2	~19.0
Trinidad)		13.0)			
	12,962	237.2	-	+	<18.3

Notes:

- + Significant quantities of oceanic pelagic fish are landed, but the magnitude of the landings is unknown.
- 0 No significant landings made.
- ? No information available.

infrastructure and the very basis of reef fish production have been severely damaged by the use of explosives, and controls over the acquisition of explosives are urgently required in a number of areas (Munro 1969).

LANDINGS AND STATISTICS

Table 1.1 shows reported catches by Caribbean countries during the period 1965-73, shelf areas (ha), percentage of oceanic pelagic species in the catches and estimated annual yields of shelf fishes (excluding oceanic pelagics) expressed in kg/ha. The catch statistics have been compiled from FAO (1974), supplemented by details derived from Kawaguchi (1974), Juhl (1971), Vidæus (1969a-d, 1970a-e, 1971a, 1971b), Nascimento and Rojas (1970), Simpson and Griffiths (1967), Suarez-Caabro (1973) and Hamblyn (pers. comm.) and for the most part are highly approximate and supported by very little detail. Of the countries involved, very few have permanent catch-monitoring systems and the reported catch is almost entirely undifferentiated. Nevertheless,

when the yields are calculated in terms of yields of neritic species (i.e., excluding oceanic pelagic species), per unit area of shelf within the 200-m isobath, a coherent pattern emerges. The calculated yields of shelf-dwelling species are lowest in the Bahamas, on the Central American shelf and the oceanic banks of the southwestern Caribbean, but this is a result of low, or inefficient fishing effort or non-reported catches. The greatest yields per unit area are obtained on the Jamaican shelf, in the Windward Islands (particularly Guadeloupe, Martinique and St. Lucia) and in the shelf area of Venezuela and Trinidad. Other areas, such as Cuba, Hispaniola, Puerto Rico, the Virgin Islands and the Leeward Islands give intermediate yields due to low technological development, difficult marketing conditions, sophisticated consumer preferences, presence of ciguatoxic fishes or orientation towards distant-water fishing.

The yields in areas with well-developed or intensive fisheries appear to vary between about 6.0 kg/ha in Cuba, to values exceeding 15 kg/ha in Jamaican waters and on the Caribbean coast of northeastern South America.

ESTIMATES OF POTENTIAL PRODUCTION

Gulland (1971) estimated that the potential fish production of the Bahamas region and of the Caribbean Sea amounted to 12 to 24 kg and 18 to 40 kg/ha, respectively, of shelf, of which production of demersal fishes might provide 2 to 4 kg/ha and 2 to 8 kg/ha, respectively. The bulk (75% to 88%) of the catch would be of pelagic species, presumably mostly neritic in habitat.

Moiseev (1971) estimated that the production of neritic and shelf species in the West Central Atlantic in 1966 averaged 2.9 kg/ha of shelf area and that total production in the Western Central Atlantic might be increased to approximately 8.1 kg/ha. However, most of the species he cites as possibly being underexploited do not occur in the Caribbean, and the bulk of the increase is presumably expected to come from the Gulf of Mexico and the eastern coast of the U.S.A. He also states that "there does not appear to be a possibility of including in the fishery in the near future such fishes as coral-reef fishes whose numbers are relatively great, but because of habitat and other reasons are unsuitable for fishing." The latter is clearly a misconception and might explain some of the disparity between Gulland's (1971) estimates of 12 to 40 kg/ha (taking the Caribbean and Bahamas together) and Moiseev's (1971) projected maximum for the region of about 8 kg/ha.

It is of interest to compare the foregoing estimates with the data given in Table 1.1. The overall Caribbean production of demersal and neritic pelagic species from waters within the 200-m isobath is less than 4.2 kg/ha, but production apparently exceeds 8 kg/ha in most areas which are intensively fished, including the Colombian-owned banks of the west-central Caribbean, the Jamaican shelf, the exploited parts of Pedro Bank and the Morant Bank and the shelf areas of Guadeloupe, Martinique, St. Lucia and Barbados and the entire shelf of northern South America.

The highest reported production rate is achieved on the very narrow, northern shelf of Jamaica. Unsubstan-

tiated evidence (Vidaeus 1970b) suggests that the demersal fish production in this area (which is almost entirely covered by living coral reefs) might amount to about 37 kg/ha/yr, despite being severely overfished (Munro 1969). The implication, which cannot be substantiated owing to poor statistical data, is that production of demersal fishes from coral reef areas might be much greater than envisaged by Gulland (1971) and Moiseev (1971).

Investigations have not produced evidence that very large unexploited stocks of pelagic species exist in the epipelagic region (Wolf and Rathjen 1971). Underexploited stocks of neritic clupeids and carangids can probably be identified and exploited in a number of areas, particularly along the South and Central American continental shelves, but no assessments of such stocks have been published up to the present time.

The estimates of production rates per unit area which are shown in Table 1.1 take no account of possible under- or over-reporting of catches. Nevertheless, it appears on the present evidence that rates of production of shelf-dwelling demersal fishes approaching 17.5 kg/ha are attained under unregulated but intensive fishing and a yield of 11.7 kg/ha is readily attained in many areas. Very much greater yields might be taken from areas of intensive coral growth.

Based upon these values the annual yield of demersal fishes from the entire shelf areas of the Caribbean and Bahamas totalling 66×10^6 ha might fairly easily be increased to about 750,000 t and under intensive exploitation might exceed 1,000,000 t. These production rates are respectively equivalent to about 11.3 and 15.1 kg/ha.

The above estimates should be compared with the 1968 yield of about 289,000 t (including oceanic pelagic species), which is equivalent to about 4.2 kg/ha, indicating that an increase in demersal fish production of between 260% and 350% is possible, given the necessary technological innovations or the development of fisheries in underexploited regions, such as the Bahamas and the Caribbean coast of Central America.

Previous Scientific Investigations in the Caribbean

CIRCULATION, BATHYMETRY AND PRODUCTIVITY

The history of scientific exploration of the Caribbean Sea has been reviewed by Bayer (1969). From the charts presented in Bayer's review, it is apparent that biological investigations have been concentrated in the eastern Caribbean. Even in recent years, surprisingly few research vessel cruise tracks have traversed the region lying southwest of Jamaica, including the wide shelf areas of Nicaragua and Honduras and the numerous oceanic banks of the Nicaragua-Jamaica Rise which separates the Colombian and Cayman Basins.

The general oceanographic features of the Caribbean are fairly well understood (Wust 1964) and were comprehensively reviewed by numerous authors in the

proceedings of the 1968 "Symposium on investigations and resources of the Caribbean Sea and adjacent regions" (UNESCO 1971).

Production cycles and the general features of phytoplankton and zooplankton production and distribution are by no means fully comprehended. Available data were reviewed by a number of authors (UNESCO 1971). According to Wood (1971), the Caribbean area "contains a relatively homogeneous phytoplankton assemblage, characteristic of tropical and sub-tropical waters." The amount of phytoplankton in the Caribbean Current increases as a result of turbulence-induced nutrient enrichment in the lee of the Lesser Antilles and increases again after passage over the Jamaica Rise. A similar enrichment is likely to occur in the zooplankton, but no

comprehensive account of the distribution and abundance of zooplankters is available at present.

Margalef (1971) states that in the most productive areas of the Caribbean, chlorophyll *a* is usually present in concentrations of 0.2 to 0.5 mg/m³ and production is 300 to 1,000 mg/m²/day. In contrast, the stable oceanic parts of the Caribbean lying in the path of the Caribbean Current would have chlorophyll *a* concentrations of 0.05 to 0.3 mg/m³ and carbon fixation is usually less than 200 mg/m²/day.

Gordon and Kelly (1962) stated that it has generally been concluded that coral reefs are among the most productive of marine communities. Odum et al. (1959) estimated the gross primary productivity of Puerto Rican reef communities to be 11 to 44 g dry organic matter/m²/day, and that of the adjacent seagrass (*Thalassia testudinum*) beds at 8 to 15 g/m²/day. The productivity of these areas is thus 8 to 220 times greater than that of the oceanic waters of the Caribbean.

ECOLOGY OF CORAL-REEF AREAS

The main features of the coral-reef communities which characterize the shallow regions lying in the paths of the Caribbean Current and the Antillean branch of the north Equatorial Current have been described by Goreau (1959), Goreau and Burke (1960), Goreau and Wells (1967) and Kuhlmann (1970, 1971), but these papers deal almost exclusively with Jamaica and Cuba. No attempt has yet been made to provide an account of regional variations in the morphology, zonation, and species composition of Caribbean coral reefs. It is apparent, from the fragmentary accounts in the literature and from observations made by the personnel of this project, that substantial variations occur, and that the morphology and zonation of Caribbean reefs are highly variable, even though a limited number of species of hermatypic corals usually predominate in the reef communities.

Taxonomically, the invertebrate and vertebrate faunas are fairly well known (although comprehensive accounts of many groups are not yet available), but the ecological interrelationships of the reef community as a whole, remain highly obscure. For example, there is not yet any adequate account of how hermatypic corals relate to the trophic structure of the reef community. Indeed, only a limited number of species of animals are definitely known to feed directly upon the tissues of Atlantic reef corals, and none of the coral predators appear to be of singular importance in the food chain. In particular, very few species of Caribbean reef fishes feed on coral polyps and coral tissues never constitute more than a small fraction of the foods ingested (Randall 1967). A fairly wide variety of Indo-Pacific species of fishes feed quite extensively on coral polyps (Hiatt and Strasburg 1960), but corals still do not constitute a major source of fish foods. On the basis of present evidence, it is likely that in terms of fish production, the

major role of hermatypic corals lies in the shelter that they afford for myriads of species of animals, resulting in development of high population densities and fuller utilization of the primary production by epiphytic algae and of the secondary production by sessile, filter-feeding invertebrates (Bakus 1964, 1966, 1967; Botros 1971) which find suitable habitats on the substratum provided by the corals. It is possible that energy transfer in the form of mucous and coral planulae is of some importance in the food web of coral communities.

BIOLOGY AND ECOLOGY OF REEF FISHES

Few attempts have been made to compile comprehensive accounts of the ecology and biology of reef fish communities or of particular families or groups of reef fishes. The notable works are those of Randall (see references) and Longley and Hildebrand (1941) who, respectively, studied the reef fish communities of the northeastern Caribbean and of the Dry Tortugas, at the southern end of the Florida peninsula. In Bermuda, Bardach and Menzel and their associates (see references) produced a number of highly significant papers on the ecological aspects of fish production on Bermudian reefs.

A question of the greatest importance which has not yet been extensively investigated is that of the standing crop of fishes in the coral-reef communities. Randall (1963) measured the standing crop of fishes on two shallow (less than 5.5 m) fringing reefs at St. John, U.S. Virgin Islands and obtained estimates of fish biomass of 158 g/m² and 160 g/m² (equivalent to 1,580 to 1,600 kg/ha) for the two reefs. Nagelkerken (unpublished presentation to 9th Meeting, Association of Island Marine Laboratories of the Caribbean, 1971) obtained similar values from fringing *Millepora* sp. and *Acropora palmata* reefs at Curacao. Bardach (1959) estimated the standing crop of fishes on a Bermuda patch reef to amount to a substantially lower value of 49 g/m² (490 kg/ha) and calculated that fish growth produced about 17.2 g/m²/yr (172 kg/ha/yr) of isolated shallow reef. These values have been compared (Randall 1963) with estimates obtained by Brock (1954) on Hawaiian reefs which harbored up to 185 g/m² (1,850 kg/ha). Fast and Pagan-Font (1973) recorded a standing crop of fishes of 218.0 g/m² on an artificial reef of car tires in Puerto Rico, and a biomass of only 23.3 g/m² on a nearby natural reef.

It is interesting to note that Randall's (1963) artificial reef harbored 1,740 g/m² (equivalent to 17,400 kg/ha). Randall ascribes this very high value to the fact that the reef was surrounded by seagrass beds which are the main feeding grounds of the grunts, mutton hamlets (*Alphistes afer*) and other species which constituted the bulk of the catch taken on the reefs. Presumably, if the biomass of fishes captured on the artificial reef had been divided by the area of seagrass beds nearest to the artificial reef, the calculated standing crop/m² would

have been very much less, and possibly substantially less than that obtained on the fringing reefs.

All of the reefs mentioned above are either unexploited or only lightly exploited. On the present evidence, admittedly scanty, it appears reasonable to believe that standing crops of unexploited reef fishes will commonly be found to exceed 2,000 kg/ha of shelf, provided that the amount of reef cover is not a limiting factor. Concomitantly, it can be expected that areas of shelf exceeding 15 to 20 m in depth (at which depth seagrasses disappear) may support very much lower standing crops and the primary trophic resource might be oceanic zooplankton, passing via the corals and filter-feeding invertebrates to the higher trophic levels. In such areas, the reefs might, in addition to providing shelter, also provide the major supply of food. Detritus derived from seagrass beds lying up-current together with soft green and red algae which grow at these depths might also be of significance in such areas.

Stevenson and Marshall (1975) have shown that the estimated standing crop of fishes on and around coral reefs may be 20 to 30 times greater than that found in temperate regions. Estimates that coralline areas could potentially produce annual fish catches in excess of 30 kg/ha of shelf (p. 14) are not incompatible with these standing crops of reef areas. Indeed, Bardach's (1959) estimate that fish growth on the Bermuda patch reef reached 172 kg/ha/yr suggests that an estimate of 30 kg/ha might be conservative, although it must be borne in mind that the population of a patch reef feeds over a wide surrounding area (Longley and Hildebrand 1941; Randall 1963). It is also important to note that the standing crop recorded in Bermuda is very much smaller than that recorded in the Caribbean by Randall and Nagelkerken (see above).

Studies by J. Randall (1963c) have covered aspects of the biology, ecology and taxonomy of species of Labridae and Scaridae (1963c; see also Randall and Randall 1963), Monacanthidae (Randall 1964a); the effects of grazing by herbivorous reef fishes (1961c, 1965b); growth and movements of reef fishes (1962 and 1963a) and studies of the density of fish populations on natural and artificial reefs (1963b). Investigations of the food habits of reef fishes (Randall 1964b, 1965a, 1967; Randall and Warmke 1967) have provided a significant insight to the competitive relationships of species of reef fishes.

The investigations of Bardach and Menzel (1957), of Randall (1962, 1963a) and of Springer and McErlean (1962) have clearly demonstrated that species of grunts, groupers and hinds, angelfish, butterflyfish, parrotfish, snappers, surgeonfish, squirrelfish, wrasses, filefish, triggerfish and trunkfish remain on the same reef, or even on the same portion of a reef, for their entire lives, and that even the least territorial species seldom cover distances of more than a few miles. It is interesting to note that few jacks (Carangidae) were tagged in these studies, and of those tagged, none were recovered. It is possible that the jacks are one of the few reef families

which are mostly free-ranging species.

Randall and Randall (1963) have made various observations on the breeding of scarids and labrids in the Virgin Islands and Puerto Rico. Munro et al. (1973) have described the spawning seasons of reef fishes in Jamaican waters (see Chapters 6-17 for further details). The basic conclusion was that for most species, the main spawning period coincides with minimal water temperatures in February, March and April, and many species might also spawn in September-October.

Singularly, little is known of the early life histories of reef fishes and the eggs and larval stages of most species are undescribed. Information on the early juvenile and adolescent stages is also very scarce and, in many cases, the main habitats of the juveniles are unknown.

Notes on general aspects of behavior and habits of a very wide range of reef fish species are given by Longley and Hildebrand (1941) and apart from behavioral papers (mostly concerned with demoiselles (Pomacentridae) by various authors, the former paper remains the most detailed source of information in this respect.

EXPLORATORY FISHING AND FISHERIES DEVELOPMENT

The earliest fisheries investigations (as opposed to fish collections and biological surveys) in the coralline Caribbean were those conducted by the United States Government vessels, *Albatross* and *Fish Hawk* between 1886 and 1899 (Bayer 1969), and the collections made by these vessels formed the foundation of much of today's knowledge of the region's fish fauna. However, subsequent to these investigations, there were very few large-scale attempts to investigate the fisheries potential of the Caribbean until 1950, when the U.S. Bureau of Commercial Fisheries vessel *Oregon* commenced its explorations of the Caribbean and the Gulf of Mexico. These efforts were supplemented by those of the *Silver Bay* and *Combat*, also of the U.S. Bureau of Commercial Fisheries (Berry and Drummond 1967). Unfortunately, as stated by Bayer (1969), "the results obtained have been so diverse that it is unlikely that any coordinated analyses of the distribution, abundance and composition of the bottom fauna can ever result." To a lesser extent, this comment also applies to the fish stocks, and no broadly based overview of the fisheries potential based upon these explorations has been published.

Between 1965 and 1971, the UNDP/FAO Caribbean Fishery Development Project attempted to make a regional survey of the catch rates obtainable by a variety of fishing techniques throughout the Caribbean (Idyll 1971). The extent of these investigations has been summarized by Wolf and Rathjen (1974), and the results of trap fishing, line fishing and fishing for lobsters are summarized in a series of reports (Wolf and Chislett 1974; Kawaguchi 1974; Chislett and Yesaki 1974).

Kawaguchi (1974) concluded that the areas with greatest commercial line fishing potential included the

Nicaraguan Shelf, Navidad Bank (north of Hispaniola), Barracuda Bank and Anguilla Bank (northeastern Caribbean) and the Guyana Shelf. Catch rates exceeding about 10 kg/line-hr were considered to be good, with lesser values having doubtful economic potential when exploited by hand-lines or electrically powered reels. Bottom long-lining gave discouraging results in most areas. Nearly all of the most promising areas are remote from land, and Kawaguchi concluded that vessels in the 45- to 50-ft (14- to 18-m) size range would be appropriate to the fishery, depending upon the distance of the fishing grounds from the home port.

Wolf and Chislett (1974) reported that trap fishing for snapper and other demersal species gave generally good results and showed that yields in excess of 9.1 kg per lift, for traps set overnight, were attainable in many areas, including most of the areas mentioned by Kawaguchi (1974) and, in addition, Pedro Bank and other oceanic banks near Jamaica. No trap fishing was done on the Nicaraguan Shelf, from which Kawaguchi (1974) reported best line fishing results, but it is to be expected that the area might likewise be productive. The trap fishing results reported by Wolf and Chislett (1974) can be criticized on the grounds that uneconomical amounts of imported bait (up to 11 kg of mackerel or herring per trap) were used, with the result that the value of the catch was often less than the value of the bait. Nevertheless, their results do show the potential initial catch rates in these areas and also suggest that efficient exploitation of the areas might be dependent upon the development of an inexpensive artificial bait. In most areas, very few of the species captured in traps are unmarketable, and there is generally insufficient "trash" captured for the traps to provide their own bait.

In addition to regional investigations, various national efforts in localized areas have done much towards obtaining a clearer picture of the probable lines of development and in some cases developed new or improved fishing techniques. Many such investigations have been reported, including studies of tuna, spiny lobster and shrimp resources in Cuban waters (Suarez Caabro and Duarte Bello 1961; Gonzalez Cardulis and

Guitart Manday 1969; Buesa Mas 1960, 1961; Perez Farfante, Acosta Jiminez and Alemany Proenza 1961), and general investigations of the economic feasibility of utilizing decked fishing vessels in Jamaica and Puerto Rico (Oswald 1963, 1962). In the eastern Caribbean, Wiles (1954) made significant advances in netting techniques for flying fish. The general progress of fisheries development work in the Caribbean is fairly well reflected in the annual proceedings of the Gulf and Caribbean Fisheries Institute issued between its inception in 1948 and the present time.

The marine resources of Venezuela are far better known than those of any other Caribbean country, largely as a result of the activities of the FAO/UNDP Fisheries Research and Development Project in that country. The results of these investigations are documented in an extensive series of publications issued by that project. Coralline shelf areas are limited by ecological conditions to the middle portion of the Venezuelan coastline and the resources do not compare with those of the eastern and western regions. Correspondingly, little research has been done in these coralline areas.

It is noteworthy that singularly little attention has been given the reef fish resource as a whole, and attention has centered upon the highly prized components, such as groupers and snappers and spiny lobsters, and questions pertaining to the potential catch of even such highly prized components as the carangids (jacks) or abundant groups, such as the grunts and triggerfishes, have largely been ignored (Carpenter and Nelson 1969).

In retrospect, it is unfortunate that great efforts have been expended in the past in attempts to locate stocks of oceanic pelagic species (mostly tunas) which, despite the evidence to the contrary, were thought to be present in the Caribbean (Whiteleather 1952). In no case have these efforts met with any significant success, but they have served to draw attention away from the demersal stocks. Even as recently as 1965-71, the UNDP/FAO Caribbean Fishery Development Project expended much effort on attempts to harvest tuna and other oceanic pelagic species with very little success (Wagner and Wolf 1974; Wolf and Rathjen 1974).

CHAPTER 2: THE JAMAICAN FISHING INDUSTRY

by

J.L. Munro and R. Thompson

(November 1973)

The Jamaican Fishing Industry

Various aspects of the Jamaican fishing industry have been described by Vidaeus (1970), Munro (1969) and Pecker (1972, unpublished). In common with many other Caribbean countries, the demand for fish and fish products far exceeds the supply and very large amounts of fish are imported to meet the demand. The procedures for distributing and marketing domestic catches are highly inefficient, being based upon the "higgler" system whereby large numbers of vendors purchase fish in small quantities at the source of supply and distribute it over limited areas. This results in inflated costs to the consumers and an inability to cope with unusually large catches, to the detriment of the fishermen. Conversely, however, the industry contributes to the support of a far greater number of individuals than would otherwise be the case. Storage and ice-making facilities are very limited and relatively expensive and this aspect has acted as a brake on development in some instances (Vidaeus 1970).

The Fisheries Division of the Ministry of Agriculture is responsible for the implementation of Government fisheries policy and for fisheries development and training schemes (Kirton 1967). To this end, the Division has operated three fishing vessels: the 21-m *M. V. Dolphin*, the 13-m *M. V. Blue Fin* and the 11-m *M. V. Albacore*. However, for reasons apparently related mostly to the shortage of trained staff, the latter two vessels were largely inactive during the period covered by this report.

The industry can be divided into several actual or potential sectors: the nearshore fishery, the cays fishery and the offshore fishery.

THE PRIMARY FISHERIES

The Nearshore Fishery

In 1973, approximately 3,100 canoes were based on 160 beaches distributed around the island. About 48% of the canoes operating on the fairly extensive southern shelf (Fig. 2.2) were equipped with outboard motors, whereas on the narrow northern shelf only 16% of the fleet were mechanized (Vidaeus 1970). The non-mechanized boats comprised about 66% of the total fleet. They are usually paddled and seldom use sails. Traditional Z traps, hand-lines, troll lines, seines, gill-nets and spearguns are the predominant fishing gears. The illegal use of explosives is prevalent (Munro 1969). The greatest part of the landings probably results from trap fishing (Vidaeus 1970).

Non-mechanized canoes have a radius of operations of only a few miles, but mechanized canoes can operate over the entire Jamaican shelf and to all the minor banks close to Jamaica (Fig. 2.2). In addition, some of the largest canoes based on the south coast of Jamaica travel to the northern edge of Pedro Bank and to the Pedro Cays, up to 110 kilometers from their bases. These operations, based on fish trapping supplemented by hand-lining, have been reported to be profitable in many cases. Unfortunately, a high degree of risk attaches to operating at such extreme distances in open canoes equipped with the minimum of safety equipment.

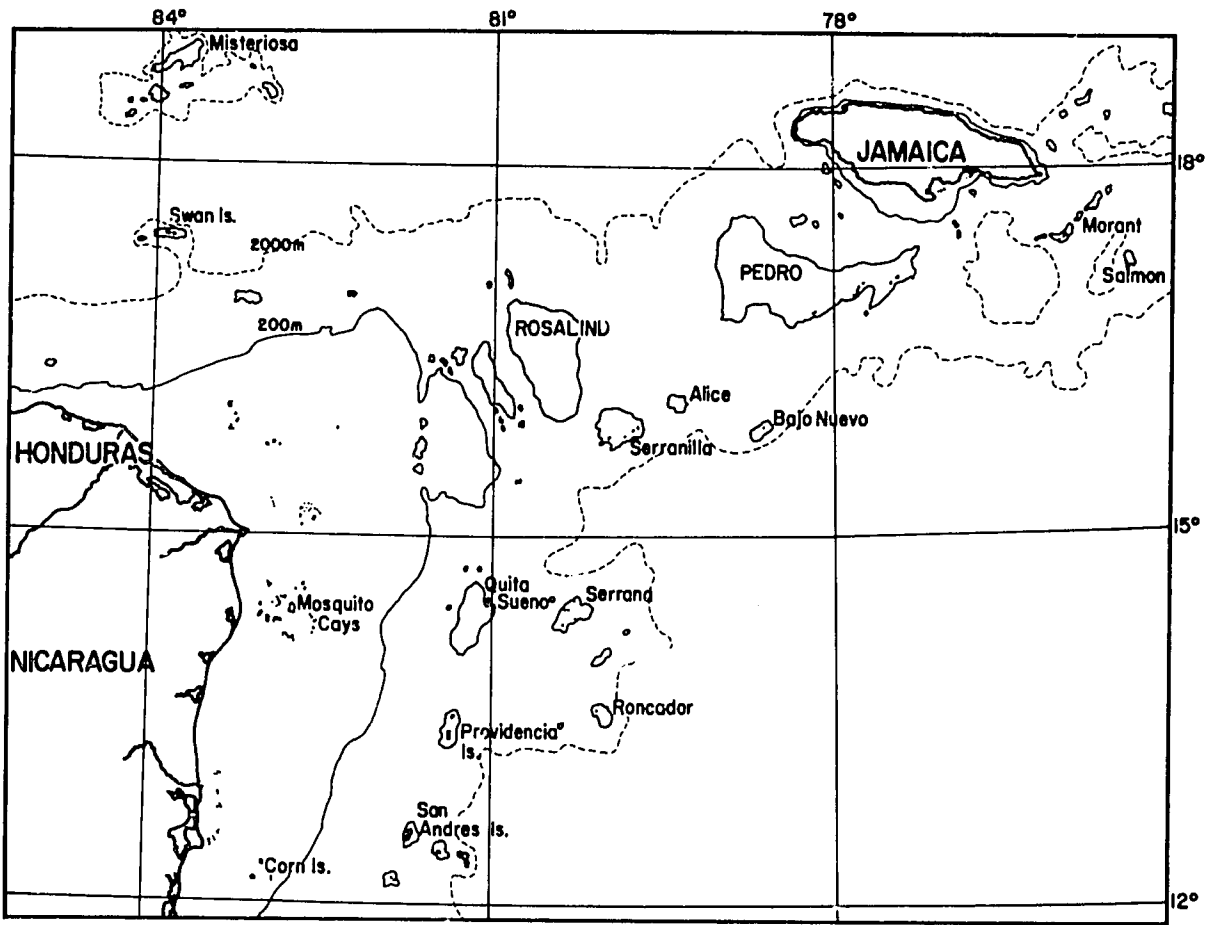


Fig. 2.1. Map of the west-central Caribbean, showing location and extent of oceanic banks, and place names mentioned in the text.

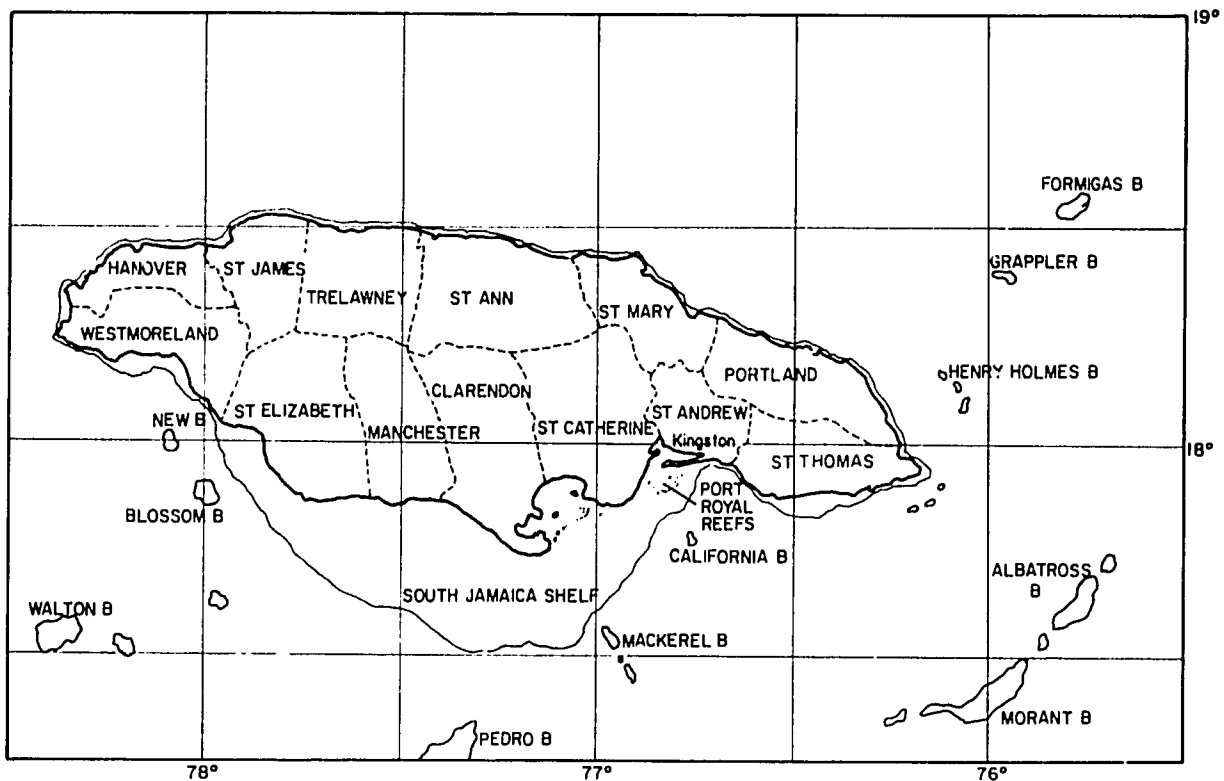


Fig. 2.2. Map of Jamaica showing extent of shelf areas (less than 200 m) and positions of proximal oceanic banks.

The Cays Fishery

In 1973, the landings of the nearshore fisheries were supplemented by the landings of a fleet of 150 to 200 mechanized canoes (Vidaeus 1970) based on the Pedro and Morant Cays, Bajo Nuevo, Serranilla and Serrana Cays and at the Mosquito Cays and other groups of islands on the Nicaragua-Honduras shelf (Fig. 2.1). Such operations are sustained by carrier vessels, usually in the 15 to 24 m (50 to 80 ft) size range, which ply between the cays and Jamaica, carrying supplies to the fishermen and returning with loads of iced fish.

The operation appears to have been first suggested by Thompson (1945) but did not succeed at that time owing to the lack of incentives to induce competent fishermen to live in these isolated areas. However, in response to rising market prices and the high profitability of the fishery (Vidaeus 1970), the number of carrier vessels increased to 21 active vessels in 1973, including 2 vessels which exceed 30 m in overall length. Poor berthing facilities, inadequate ice supplies and a poorly organized marketing system have impeded full development of the fishery. Claims by various Central American nations to exclusive fishing rights over rather wide areas also created uncertainty in the fishery and possibly impeded development to some degree.

The cays fishery utilizes Z traps almost exclusively, supplemented by occasional trolling for scombrids and barracuda. Hand-line fishing is seldom attempted. The range of operations of cays fishermen appears to seldom exceed 28 kilometers, this being the greatest distance from the Pedro Cays at which fishermen or trap buoys were observed during the course of these investigations.

The Offshore Fishery

For purposes of this report, the offshore fishery is defined as one in which the catch is taken aboard vessels operated independently of any land base for extended periods, in areas beyond the operating range of canoes.

Up to 1973, only two vessels operating from Jamaica fell exclusively within this classification; the *Chiquita* operated by the Manchioneal Fishermen's Cooperative, and the *Lady Blythe* operated by private interests. The *Chiquita* operated with hand-lines and hand-reels, mostly on the Nicaraguan shelf, and was reported to land about 70 t/yr (Vidaeus 1970).

The *Lady Blythe* fished the western portion of Pedro Bank, using traditional Z traps, and conducted line fishing on an opportunistic basis. The number of traps used was far in excess of the vessel's carrying capacity and its mobility was correspondingly limited. Landings were reported at 100 t/yr.

In addition, several carrier vessels were said to engage occasionally in limited trap and hand-line fishing, though most of these are not equipped for such work. The severe shortage of qualified captains and engineers (Munro 1969) and the difficulties of maintaining electronic and mechanical equipment when skilled tech-

nicians are generally unavailable appear to be a major factor limiting the development of this fishery.

CATCH STATISTICS

In 1962 and 1968, sample surveys were made of the Jamaican fishing industry, and the basic results have been reviewed by Vidaeus (1970). Unfortunately, the final results of the 1968 survey were never released by the Government of Jamaica and few details are available, other than those supplied to Vidaeus.

Pecker (1972), quoting Harris (1963), gives the following estimates of production by the nearshore canoe fishery:

1945-1949	5,450 t	(12.0 million lb)
1950-1954	4,995 t	(11.0 million lb)
1955	6,585 t	(14.5 million lb)
1956	7,720 t	(17.0 million lb)
1958	10,263 t	(22.6 million lb)
1959	9,900 t	(21.8 million lb)
1960	10,309 t	(22.7 million lb)
1962	10,990 t	(24.2 million lb)
1968 (Vidaeus 1970)	6,630 t	(14.6 million lb)

As stated in Chapter 1, the 1968 production of demersal and neritic pelagic species by the nearshore Jamaican canoe fishery amounted to 17.2 kg/ha, this being by a substantial margin the greatest rate of production reported for any area in the Caribbean. The claimed rates of production between 1956 and 1962 are therefore extraordinarily high and exceeded 29 kg/ha in 1962. Pecker (1972) has pointed out that the sampling technique adopted for the 1962 survey resulted in the enumerators usually visiting the fishing beaches on "fishing day," the day when most fish buyers attend a particular beach and on which there is consequently the greatest fishing effort. The recorded catch of each canoe was then raised by the number of fishing trips made in the preceding 7-day period, and the calculated average weekly landing then raised by the number of canoes stationed at the beach in question. It is also not clear from the account of the 1962 sampling program (Chuck 1963) that inactive canoes were excluded from the calculations. For the abovementioned reasons, the estimates for the period 1956-1962 are believed to be greatly inflated and are not further considered in this report.

In contrast, the 1968 survey does not appear to have suffered the abovementioned statistical deficiencies (Vidaeus 1972). As described below, the results produce (with one exception) a coherent pattern which lends much credence to the validity of the survey.

Bearing in mind the rather unsatisfactory statistical base, Table 2.1 has been compiled to show the 1968 shelf landings of demersal and neritic pelagic species (excluding oceanic pelagic species), the shelf areas adjacent to each Jamaican parish [data for Kingston and St. Andrew, St. Catherine, Clarendon, Manchester and St. Elizabeth, which abut on the South Jamaica Shelf (Fig. 2.2) have been combined], and numbers of canoes

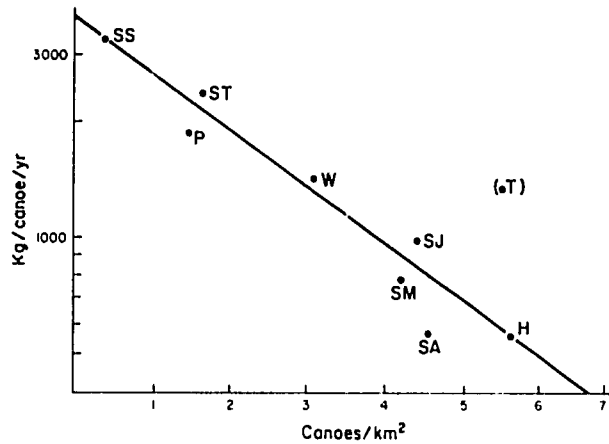


Fig. 2.3. Semi-logarithmic plot of relationships between annual catches of demersal and neritic pelagic species per unit of effort (kg/canoe/year) and fishing intensity (canoes/km²) for shelf areas adjacent to the Jamaican parishes of St. Thomas (ST), Portland (P), Westmoreland (W), St. James (SJ), St. Mary (SM), St. Ann (SA), Trelawney (T) and Hanover (H) and from the South Jamaica Shelf (SS). Trelawney is excluded from the regression.

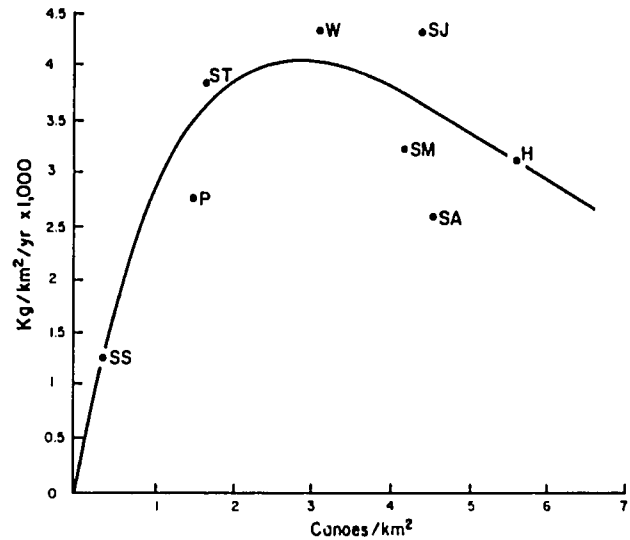


Fig. 2.4. Regression line of Fig. 2.3 translated to terms of annual yield per unit area (thousands of kg/km²/year) relative to fishing intensity (canoes/km²). Actual yields and fishing intensities (1968 statistics) for shelf areas adjacent to Jamaican parishes and for the South Jamaican Shelf are also included (abbreviations as given for Fig. 2.3).

Table 2.1. Yields of shelf-dwelling species (excluding oceanic pelagics) per unit area of the Jamaican shelf and proximal banks (but excluding Pedro and Morant Banks). Based on reported catches for 1968 (Vidaeus 1970b).

	Area of shelf and proximal banks km ² X	Number of canoes A	Number of mechanized canoes B	% of oceanic pelagic fishes C	Effective canoe effort on shelf D = A - (BC/100)	Effective canoes per km ² E = D/X	Total shelf landings (1968) kg x 1,000 F	Kg per canoe per year F/D	Kg of neritic species per ha per yr F/100X
St. Thomas	165	272	68	7.8	267	1.63	632	2,367	38.4
Kingston and St. Andrew, St. Catherine, Clarendon, Manchester and St. Elizabeth	2,760	1,079	656	5.4	1,044	0.38	3,423	3,279	12.4
Westmoreland	154	484	113	7.4	476	3.09	670	1,407	43.4
Hanover	48	295	54	46.5	270	5.63	150	556	31.2
St. James	34	152	21	0.9	152	4.43	148	974	43.2
Trelawney	31	177	21	34.6	170	5.51	222	1,306	71.9
St. Ann	51	236	17	1.8	236	4.58	133	564	25.9
St. Mary	48	210	59	13.2	202	4.20	155	767	32.3
Portland	130	204	39	31.1	192	1.49	360	1,875	27.6
South coast (St. Thomas to St. Elizabeth)	2,925	1,351	724	5.8	1,309	0.48	4,055	3,098	13.9
North coast (Westmoreland to Portland)	496	1,758	324	21.1	1,690	3.41	1,838	1,082	37.0
All areas	3,421	3,109	1,048	11.2	2,992	0.87	5,893	1,970	17.2

operating on the shelf. The number of canoes operating on the shelf of each parish has been derived by subtracting from the total number of canoes the estimated portion of the effort by mechanized canoes which is applied to fishing for oceanic pelagic species. In all cases, the resulting adjustment is very small. The last three columns of Table 2.1 show the estimated landings of demersal and neritic pelagic species of each parish, the calculated landings per canoe per year and the calculated landings per unit area of shelf. The reported production and calculated rate of production in the parish of Trelawney appear to be very greatly inflated, but there are insufficient data available to establish the source of the errors.

The relationship between catch per canoe per year and the number of canoes per km² of shelf of each Jamaican parish is shown in Fig. 2.3 in a semi-logarithmic plot. The basic assumptions are that the ecological regimes do not differ substantially around the island and that catch rates will decline exponentially in response to increases in fishing effort. These are borne out by the relatively good fit of the points to the regression, with the exception of that relating to the parish of Trelawney.

Figure 2.4 shows the regression line translated to terms of production per ha, and suggests that with the present fishing methods, maximum yields of around 4,100 kg/km² (41 kg/ha) are attained by a fishing intensity of about 3.2 canoes/km². The graph also implies that economic factors, such as the high operating costs of outboard motors or poor marketing facilities, limit the production on the South Jamaica Shelf where the density of canoes averages only 0.4 canoes/km². However, the assumption that productive regimes are similar on an island-wide basis precludes any definitive conclusions. Likewise, it cannot be assumed at this stage that a yield of 4,100 kg/km² is the maximum attainable, as this is largely achieved by intensive fishing with small-meshed (4.13 cm) fish traps supplemented by small-meshed beach seines and gill-nets and by hand-lines. It is important to note that the shelf areas referred to here include any areas which are within the 200-m isobath. For most areas, the largest extent is between 10-m and 30-m deep and is variously covered by coral reefs, seagrasses and sand or coral rubble. Fish yields in terms of harvests per unit area of actively growing coral reef are unknown.

CHAPTER 3: AREAS INVESTIGATED, OBJECTIVES AND METHODOLOGY

by

J.L. Munro and R. Thompson
(November 1973)

The Area Investigated

The main areas of interest to the ODA/UNEP Fisheries Ecology Research Project were the island shelf of Jamaica and oceanic banks within the operational range of the motorized canoes which characterize the fishing industry, plus oceanic banks lying beyond the operational range of canoes and which are virtually unexploited at present. The latter areas include the greater part of the 8,040 km² Pedro Bank (of which only some 1,000 km² proximal to the Pedro Cays are exploited with any degree of intensity), Rosalind Bank (4,940 km²) and the Nicaragua-Honduras Shelf (122,900 km²) and many other minor oceanic banks lying within the potential operational range of motorized fishing vessels operating out of Jamaica (Fig. 2.1).

For obvious practical reasons, sampling efforts were concentrated in three main areas:

- 1) The heavily exploited Port Royal Reefs lying south of Kingston and Port Royal. (Fig. 3.1)
- 2) The exploited and unexploited portions of Pedro Bank. (Fig. 3.2)
- 3) California Bank, a small (8.6 km²) oceanic bank lying some 20 km south of Port Royal, which is subjected to a moderate degree of exploitation. (Fig. 2.2)

The above was supplemented by varying degrees of effort in sampling the following areas:

- 1) Discovery Bay and the north coast of Jamaica (Fig. 2.2)
- 2) South Jamaica Shelf (Fig. 2.2)
- 3) Morant Bank (Fig. 2.2)
- 4) Lameshur Bay, St. John, U.S. Virgin Islands

In addition, prior to the arrival in Jamaica of *R.V. Caranx*, project staff participated in cruises of the *M.V. Alcyon* operated by the UNDP/FAO Caribbean Fishery Development Project, mainly on Pedro Bank but ranging as far afield as Navidad and Silver Banks to the north of the Dominican Republic, and Alice Shoal lying south of Pedro Bank.

Finally, commercial landings originating from Pedro Bank, the Serranilla Bank and the Mosquito Cays on the Nicaraguan Shelf were sampled at Khaleel's Deep Sea Fisheries between July 1971 and June 1972.

The limited amounts of oceanographic, bathymetric, and other ecological data which pertain specifically to the areas investigated are summarized below.

MORPHOLOGY OF THE REEFS AND SHELVES

Characteristically, the shelves and banks of the west-central and southwestern Caribbean are relatively flat, with depths seldom exceeding 45 m and averaging around 30 m. The depth increases abruptly at the edges, sometimes by a vertical or near vertical drop to depths exceeding 400 m. The edges of the banks and shelves are characterized by sill reefs of variable magnitude, which are best developed on shallow (less than 30 m) windward or up-current edges and may be absent on relatively deep (over 40 m) leeward edges. The landward margins of the shelf usually have well developed fringing reefs, particularly along the windward shores.

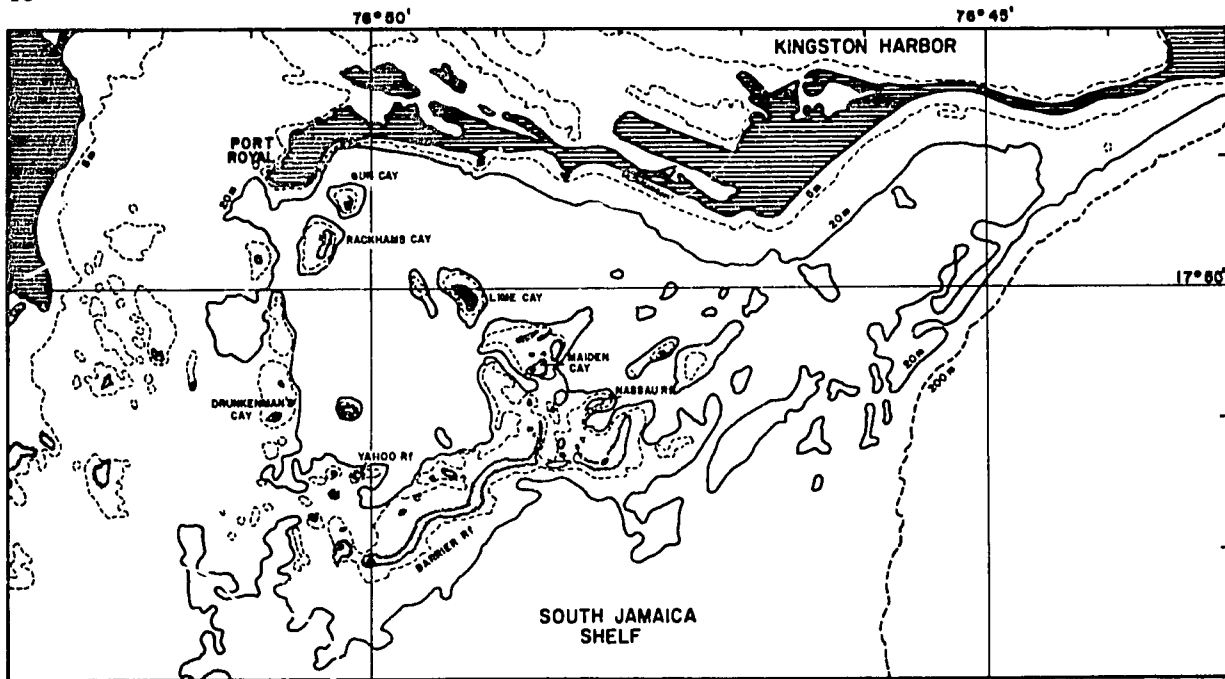


Fig. 3.1. Map of the Port Royal Reefs showing depths and the location of place names mentioned in the text.

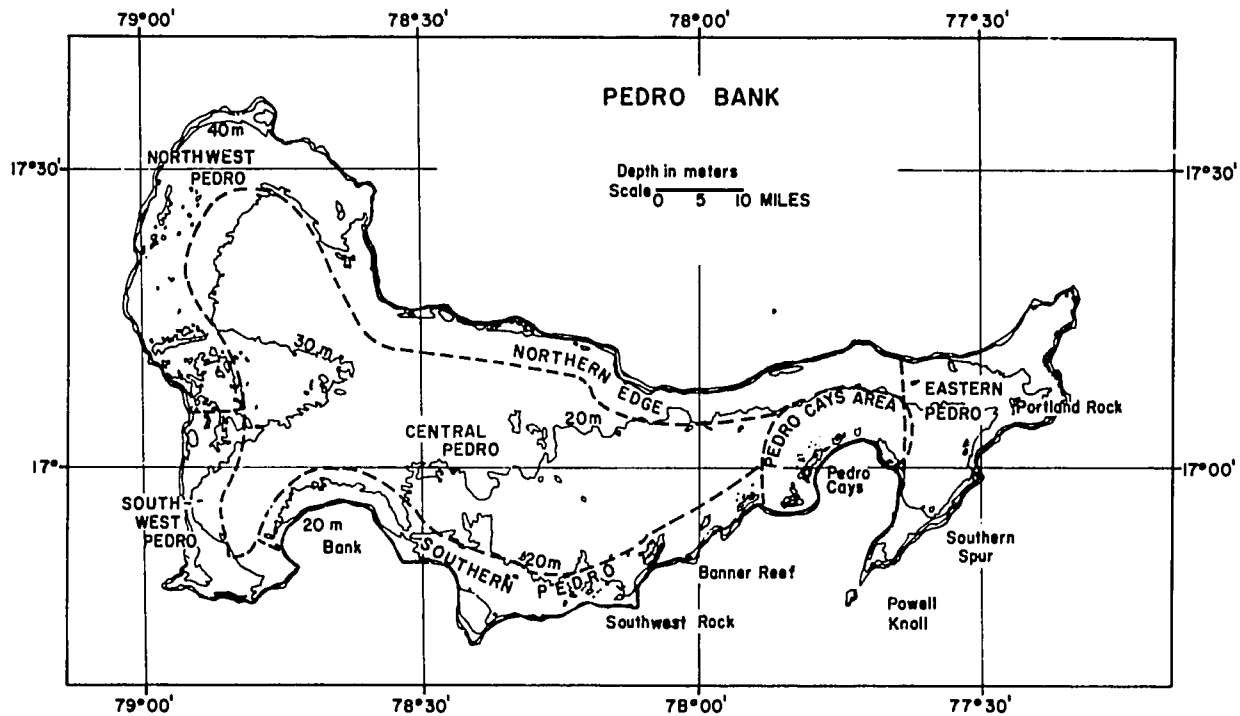


Fig. 3.2. Map of Pedro Bank showing place names mentioned in the text and the distribution of depth zones.

For purposes of this report, the plateau-lake shallow areas have been arbitrarily divided into three depth zones (10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m). The shallowest areas are usually located at the eastern or southeastern sides of the banks.

The central portions of the banks and shelves, remote from the well-developed sill reefs, are usually very flat

and appear to be sparsely covered with seagrasses and algae and infrequent, low, outcrops of coral. Isolated patch reefs occur in some areas.

Beyond the sill reef is the "drop-off", an abrupt increase in depth, starting at the outer face of the sill reef in as little as 12 m in the shallowest areas and around 45 m in the deepest areas, descending almost

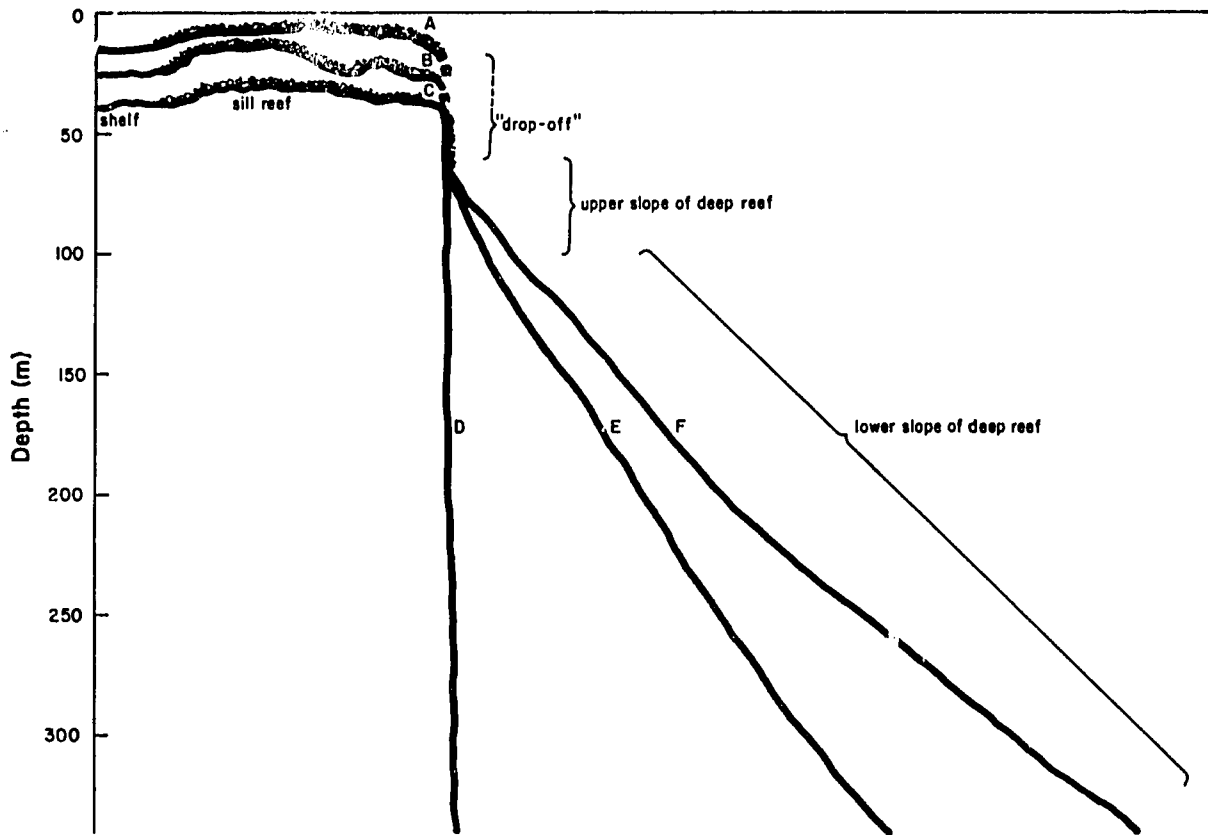


Fig. 3.3. Composite profile of sill reef and deep reef found at Pedro Bank and the South Jamaica Shelf. Sill reefs may (A) rise to within 10 m of the surface or be based in depths of as much as 45 m (B-C). The deep reef is often vertical (D) but sometimes has a slope of about 40° (F). The most usual slope is shown by profile (E).

vertically to at least 60 m, often continuing vertically to depths exceeding 400 m. The "deep reef" is defined as extending from about 60 m to the upper edge of the bathyal zone at about 250 m, and can be subdivided into two parts (60 m to 100 m and 101 to 250 m) on the basis of the composition of the fish catches. Owing to the extreme steepness of the slope, the basal area covered by the deep reef zone is extremely limited. The gentlest slopes encountered were of about 40° , always in depths exceeding 200 m, and slopes of 45 to 55° were considered to be "good" fishing stations. Vertical or extremely steep slopes appeared most common on the eastern and southeastern edges of Pedro Bank and the South Jamaica Shelf. A composite profile of the sill reef and deep reef zone is shown in Fig. 3.3.

Jamaica Shelf (Fig. 2.2)

Around most of Jamaica, the offshore shelf is relatively narrow so that the 40-m contour usually lies about 1,000 m from land. Between Kingston and Black River on the south coast, there is a large offshore shelf (the

South Jamaica Shelf) 28 km wide and approximately 150 km long. On the north coast fringing reefs extend, with few gaps, from Morant Point in the east to Negril in the west. On the south coast, large reefs are restricted to the eastern part of the South Jamaica Shelf, near Port Royal and the entrance to Portland Bight. Elsewhere on the south coast, reefs tend to be small, patchy and often senescent (Goreau 1959). The sill reef is well developed along most of the edge of the South Jamaica Shelf. On the north coast, the shelf is so restricted that the fringing reef and sill reef are almost contiguous. The sill reef and drop-off are characterized by massive corals, and Goreau and Wells (1967) have observed active reef growth to depths of 70 m on the Jamaican north coast. Below 70 m there is a reduction in coral population density, species diversity and colony size. Areas of open shelf remote from fringing reefs and sill reefs are not well known, but appear to be characterized by scattered patches of coral, gorgonians and seaweeds, interspersed with large sandy areas. Turtle grass (*Thalassia testudinum*) is present to depths of at least 15 m in some areas and eel grass (*Syringodium* sp.) and soft green algae occur to depths of at least 45 m.

The Port Royal Reefs

The Port Royal Reefs are situated south of Port Royal, at the eastern extremity of the South Jamaica Shelf (Fig. 3.1). The geological history of the Port Royal-Kingston area has resulted in the development of a rather unusual reef system differing from other areas in having a deep lagoon with a floor covered by fine calcareous sediments and few corals (Goreau and Burke 1960). The clarity of the water is not great and active growth of hermatypic corals ceases at a depth of about 15 m. The reefs cover an area of about 9 km wide by 15 km long. The lagoon is formed by a barrier reef and contains a complex of patch reefs and cays. The barrier reef, lying between South Cay and Southeast Cay is about 7.5 km long with a crest about 30 m wide. The lagoon has an uneven bottom with depths up to 35 m with many coral hillocks and irregular reef formations.

The major habitats found in the Port Royal reefs are briefly described below.

Thalassia flats. Shallow (down to 2 m) areas characterized by an abundant growth of *Thalassia testudinum* and small to medium-sized coral heads. There are extensive areas of this habitat in the lee of the barrier reef.

Coral and sand flats. Depth 2 to 4 m. Small patches of *Acropora palmata*, *A. cervicornis* and isolated coral heads, e.g., *Montastrea* spp. and *Diploria* spp. Large sandy areas with gorgonians and some *Thalassia testudinum* are also present.

Acropora cervicornis zone. Present on the upper slope from depths of 2 to 12 m, depending on the clarity of the water. Comprised of dense thickets of *A. cervicornis* with few other species present.

Mixed coral slope. Contains a little *A. cervicornis*, but is dominated by massive corals, e.g., *Montastrea* and *Porites* spp., sponges and gorgonians. Depth about 10 to 15 m.

Rubble slope. Composed of broken, dead coral and some live heads of *Madracis* sp. Depth distribution is around 10 to 18 m.

Reef base. Below the rubble zone flattens out to form a smooth, muddy bottom with isolated rocky outcrops and some coral growth. Depth about 20 to 30 m.

OCEANIC BANKS

Most oceanic banks rise abruptly from depths of well over 500 m to a submarine plateau with mean depths of 20 to 40 m. On some banks depths of less than 20 m are encountered in areas where reefs, cays and shoals are present.

The general bathymetric features of the Caribbean Sea are quite accurately documented, but precise details of the topography and depth of many of the oceanic banks are not yet available and the configurations of many banks are poorly represented in nautical charts.

Pedro Bank

Pedro Bank was surveyed in great detail by the British Naval Hydrographic ships *Fox* and *Fawn* during 1970

and very detailed charts were therefore available for the present investigation (Fig. 3.2). The Pedro Cays and associated features have been described by Zans (1958). The bank gradually deepens in a northwesterly direction and the shallowest, southern and southeastern portions of the bank, which face into the Caribbean current, have the best developed reefs.

The bank has a total area of about 8,040 km² with the various depth zones represented as follows:

0 -10 m	171 km ²	(2.1%)
10.1-20 m	2,219 km ²	(27.6%)
20.1-30 m	3,700 km ²	(46.1%)
30.1-40 m	1,742 km ²	(21.7%)
40.1-50 m	206 km ²	(2.6%)

The mean depth of the bank is thus about 24.5 m and the circumference is about 590 km.

The ecological features of the bank are practically unknown. Owing to the usually strong currents, high seas and abundant sharks, no diving observations have been made other than around shallow reefs. Viewed from the surface, the sill reefs do not in any way appear different to those on the north coast of Jamaica. Within several kilometers of the edges of the bank, coral outcrops decrease in frequency and the bottom configuration (as shown on echo sounders) becomes rather featureless. The extent of cover of algae or seagrasses, and hence, the relative primary productivity are entirely unknown.

California Bank (Fig. 2.2)

This small, 8.6 km², oceanic bank lies 22 km due south of the city of Kingston, and the northwestern end is 4.6 km from the nearest part of the South Jamaica Shelf. The intervening water has a minimum depth of over 700 m. The depth of the bank is 35 to 45 m and the sides are precipitous to depths of over 300 m. The bank has not been investigated by divers. Viewed from the surface, the bottom appears to have a sparse coral cover, and the sill reefs are not well developed.

Other Oceanic Banks

Other oceanic banks were investigated briefly, including Morant Bank and Mackerel Bank (Fig. 2.2). In addition, project personnel participated in cruises of the UNDP/FAO vessel *Alcyon* to Alice Shoal, Salmon Bank, Decca Ridge, Silver Bank and Navidad Bank. However, other than basic features given on ordinary nautical charts, nothing is known concerning these areas.

OCEANOGRAPHIC CONDITIONS

Jamaica and Pedro Bank lie in the middle of the zone of northeasterly trade winds and windspeeds of over 30 kt (15 m/sec) are not unexpected. Average windspeeds are in the region of 15 to 20 kt (8 to 10 m/sec). A season of relative calm usually extends from October to February, interspersed by rather violent northerly storms. The region is exposed to hurricanes between July and October, but records show that most hurricanes either traverse the entire Caribbean to the south of Jamaica or

take a more northerly course. As a result of the relatively windy conditions which prevail, and the consequent short, sharp seas, vessels of less than about 14 m (45') length are subjected to difficult, if not hazardous, working conditions.

Jamaica lies almost directly on the current shift axis between the Caribbean Current and a branch of the Antillean Current (or North Equatorial Current) which penetrates the Cayman Basin of the Caribbean through the passage between Cuba and Haiti (Perlroth 1971). A branch of the latter current periodically moves through the Jamaica Passage between Jamaica and Haiti and then turns westwards and runs along the south coast of Jamaica. The waters are easily identifiable, the Caribbean Current being warmer and of relatively lower salinity (Goodbody and Munro 1971). It appears that the current shift axis normally lies south of Jamaica between September and February and north of Jamaica between March and August (U.S. Naval Oceanographic Office 1969, 1970) and the extent of the shift might be related to the intensity of the trade winds. It also appears that pelagic fishes such as marlins and tunas might be associated with the shift axis. It is emphasized that the foregoing is based on scanty evidence. It is not known whether the axis ever shifts sufficiently far south for Pedro Bank to be bathed in the waters of the Antillean Current. The extent and timing of these shifts could have much influence on recruitment of larval and post larval fishes to Jamaican reefs (Munro et al. 1973).

Major efforts have not yet been made to investigate water circulation in the vicinity of the Jamaica Rise which lies directly in the path of the Caribbean Current. Emilsson (1971), in considering the upper layer circulation of the Cayman Sea, states that "the dominating feature of the surface current system is the Caribbean Current which enters (the Cayman Basin) from southeast

and flows in the direction of the Yucatan Channel." However, he also states that "this seems to be about the only point on which all current charts and descriptions agree." There are undoubtedly countercurrents and gyres on either side of the main current, but these might be subject to great seasonal or irregular variations in strength and direction. The presence of east-flowing surface and sub-surface countercurrents is also demonstrated by Emilsson (1971), not only at the margins of the basin, but also in mid-Caribbean. The passage of the Caribbean Current over the Mosquito, Rosalind and Pedro Banks causes intense lateral mixing (Emilsson 1971), and might possibly enhance the productivity of the area to a limited degree. Both the Antillean and the Caribbean Currents move at speeds between 0.4 and 1.0 kt (0.2 and 0.5 m/sec) with a mean of 0.5 to 0.6 kt (0.25 to 0.31 m/sec) (U.S. Naval Oceanographic Office 1969, 1970).

The effect of tides is slight, the range varying between 20 cm and 36 cm on the Jamaican coast. Tidal currents on Pedro Bank are sometimes sufficient to stop or reverse the flow of the prevailing westerly current.

Beers et al. (1968) showed that the upper 75 m of the oceanic waters south of Port Royal, Jamaica, were nearly isothermal and had an annual temperature range of 26.5 to 29.5°C. Salinity varied between 35.2 and 35.8‰. Goodbody and Munro (1971) found salinities of 34.50 to 36.42‰ in a series of stations transecting the current shift axis to the east of Jamaica.

Relatively high chlorophyll *a* concentrations of 0.15 to 0.36 mg/m³ have been recorded off the eastern end of Jamaica (Goodbody and Munro 1971) but Steven (1965) recorded an annual average of only 0.11 mg/m³ at a station south of Jamaica—indicating some variation in productivity.

Objectives of the ODA/UWI Fisheries Ecology Research Project

The objectives of the project were formulated against the background of general information available in 1969, which is outlined in the preceding parts of this report.

The stated objectives of the project were:

- 1) To study the effects of trap fishing upon the composition of reef-fish communities.
- 2) To investigate the dynamic characteristics (age, growth, mortality and population density) of the main species of Lutjanidae (snappers), Serranidae (groupers) and Carangidae (jacks) comprising the incipient offshore line fishery.

A full understanding of the effects of trap fishing also requires a comprehensive knowledge of the biology and ecology of the important components of the trap fishery, and an understanding of the mode of operation of fish traps.

Concurrent operations by the UNDP/FAO Caribbean Fishery Development Project eventually indicated that the prospects for a viable deepwater line fishery for groupers, snappers and jacks were not good in Jamaican waters (Kawaguchi 1974); thus, the trap fishery investigations were given the greatest emphasis.

Methods

FISHING METHODS

Fishing techniques were directed towards estimating catch rates and catch composition, gathering specimens for biological analysis and defining the operating characteristics of fish traps and were based on the use of traps

and baited hook and lines.

The methods employed varied according to the opportunities offered by the areas investigated and are described in detail in Chapters 4 and 5.

Nearshore Areas

Nearshore sampling was based entirely on the use of Antillean fish traps (described in Chapter 5) and the Port Royal Reefs were sampled for a period of 28 lunar months (November 1969 to January 1972). Additional areas sampled during this period included Discovery Bay on the north coast of Jamaica, and Lameshur Bay at St. John, U.S. Virgin Islands.

The basic technique involved setting traps (usually unbaited) in selected areas and depths using scuba-diving techniques. Buoyed traps were tried but soon abandoned as a result of thefts or interference with the traps. Most of the reefs at Port Royal were sampled but investigations concentrated on Nassau Reef and Yahoo Reef (Fig. 3.1).

Approximately half the traps hauled at the Port Royal Reefs were merely set in the desired locations and retrieved after a soak of variable duration. The remaining traps, set mostly on Nassau and Yahoo Reefs, were subjected to careful monitoring by divers. Traps to be observed underwater were numbered, thus identifiable, and were usually set in groups of five at depths between 7.1 m and 13.7 m, evenly spread diagonally down the reef slope over a distance of about 50 m. The traps were visited as often as possible and on each visit the contents of each trap were independently enumerated by two divers. All species of fishes and crustaceans were separately counted and further separated by sex or color phase wherever possible. Traps were usually hauled, emptied and reset at successive new and full moons. These techniques were also utilized on the reefs at Discovery Bay, St. John, U.S. Virgin Islands. Owing to weather conditions, technical problems and commitments to other aspects of the research program, it was seldom possible to visit traps daily, as would have been ideal, and the interval between successive observations varied between 1 and 6 days, with a mean of 2.33 days.

A total of 856 successive counts of the contents of 181 traps were accumulated between January and December 1970. The results and conclusions pertaining to the operating characteristics of fish traps have been published elsewhere (Munro et al. 1971; Munro 1974) and are not further dealt with in this report.

Offshore Areas

Offshore operations were conducted between January 1971 and February 1973, utilizing the project's 17-m research vessel, the *R. V. Caranx*. Traps of various types and hand-lines and electrically powered reels were normally used. The basic technique consisted of setting all traps on arrival at the sampling area and subsequently hauling and resetting the traps at one- to three-day intervals, depending upon the sampling design. Time not otherwise utilized, particularly at night, was devoted to hook-and-line fishing.

Traditional traps proved to be far too bulky relative to the carrying capacity of the research vessel, and metal-framed stackable traps (Figs. 5.2 to 5.4)

based on the Antillean design, were developed and successfully utilized (Munro 1973). These traps effected a 10-fold increase in the trap-carrying capacity of the vessel, and proved to be only slightly less effective than the traditional designs (Munro 1974).

All traps were set with the vessel drifting down-wind, or down-current, over the selected fishing area. Traps were individually set, the scope of the buoy line being twice or more the depth. Two polystyrene buoys were attached to the end of each line to facilitate recovery. The use of a bottom setline with numerous traps attached is impractical in most coralline areas. Traps were usually baited with 1 to 2 kg of trash fish but cans of cat food, merely punctured at each end, were used in the latter part of the project with equal success. All traps were covered with 3.17 cm (1¼") hexagonal "chicken-wire" mesh which has a maximum aperture size of 4.13 cm.

Traps were normally set on the shelf or sill reef in depths of 10 to 45 m, beyond which the slope becomes exceedingly steep. Several attempts were made to utilize the traps in deeper water (to 250 m) with promising results, particularly when metal-framed stackable traps were used as these have a greater on-bottom weight than traditional traps and are less liable to tumble down the slope. Unfortunately, the commitments of the established sampling program did not permit the deep trapping to be pursued.

For hand-line fishing, monofilament nylon lines were used with three or four Mustad straight 3/0 or 4/0 hooks surmounting a 100 to 300 g lead or steel weight. Frozen squid was normally used as bait. Electrically powered fishing reels were used for fishing to depths of 250 m, using braided stainless steel wire with up to five hooks on branch lines, and surmounted by a rubber snubber. Weights of up to 1 kg were used, depending upon current strength. Mustad 5/0 and 6/0 straight and circle hooks were normally used in deep water.

Bottom long-lines using tuna snaps and braided steel traces were used in deep water on several occasions, but were generally not successful in landing good quantities of fish. Trawls, gill-nets and lift nets were also used on occasions, mainly for the capture of bait.

VESSELS SAMPLED

The majority of the data pertaining to oceanic areas were collected aboard the project's research vessel *R. V. Caranx*. In addition, project personnel participated in cruises to oceanic banks during 1969-1970 aboard the 25 m exploratory fishing and training vessel, *Alcyon*, operated by the UNDP/FAO Caribbean Fishery Development Project, which was stationed in Jamaica at that time. The project also utilized data collected by Munro on *Alcyon* cruises before 1969. The fishing techniques were similar to those adopted on *R. V. Caranx*, except that stackable traps were not used.

During the early months of 1971 samples were taken from the *Tiki IX*, an American snapper fishing boat

chartered by the FAO/UNDP to investigate stocks amenable to commercial exploitation. Data were also obtained between July 1971 and June 1972 by sampling the landings of the carrier vessels that ply between Kingston and various oceanic cays which support the cays fishery (Chapter 2). One or two samples were collected per month at Khaleel's Deep Sea Fisheries where the catch from some carrier vessels was processed and stored before being sold.

BIOLOGICAL SAMPLING

The total sample obtained by all methods during the course of these investigations amounted to about 55,000 fishes of 130 species, weighing about 14,000 kg. Of this total, 39,924 fishes (about 120 species) weighing 10,793 kg were taken aboard *R.V. Caranx*. In the nearshore areas, about 13,500 fishes (120 species) weighing about 2,500 kg were obtained at the Port Royal Reefs. The remaining fishes were taken at Discovery Bay, St. John (U.S. Virgin Islands) and in fine-meshed mini-traps set near the Port Royal Marine Laboratory.

Almost all of the fish captured were measured, weighed and the sex and state of development of the gonads noted. Stomachs were usually everted when fishes were captured in any appreciable depth or if not everted, usually contained only bait. However, where food items were found their identity was noted. When catches of any one species were very large, or under adverse weather conditions, sub-sampling was resorted to. The minimum effort under the worst sea conditions constituted identifying, counting and collectively weighing each species represented in the catch from each station.

Samples of scales, otoliths and occasionally vertebrae and fin rays were taken. Entire gonads for fecundity estimates and ripe eggs for diameter measurements were taken at intervals.

All of the data are on file at the Port Royal Marine Laboratory and are available for inspection by interested parties.

Length and Weight Measurement

A standard fish-measuring board graduated in millimeters (mm) was used to measure lengths. All lengths were taken from the anterior end of the fish, with the mouth closed, *to the end of the middle caudal ray*. This equates with fork length (FL) in the case of species with forked tails or with total length (TL) in the case of species with truncated or rounded caudal fins. This procedure was adopted because the measurement of total length in the case of fishes with forked tails often needlessly introduces an additional degree of variability owing to variation in the development or loss of parts of the filiform upper or lower fin rays. Measurement of standard length (SL) is also unsuitable when dealing with large samples. Conversion factors for translating

measurements of FL, TL or SL are given for most of the important species dealt with in this report.

In sampling large numbers of fish to estimate length-frequency distributions, a measuring board with a flat surface of softboard was used. Graph paper marked off in millimeters was attached to this softboard and was covered by a polythene sheet. Fish lengths were then recorded by piercing the graph paper with a dissecting needle. The polythene sheet prevented excessive wetting and tearing of the graph paper. In this way a large number of fish could be measured in a short time.

Weights were measured to the nearest gram whenever possible, but when done at sea were not more accurate than 10 to 200 g, depending on the size of the fish and the sea state.

Length-weight relationships were calculated for all species for which adequate data were obtained by fitting a regression to the equation

$$\log W = \log a + b \log L$$

$$\text{or } W = aL^b,$$

where W is the weight in grams, L is the length in centimeters and a and b are constants.

Additionally, the relationships between maximum body depth (D), total length (TL) or fork length (FL) are given for most important species.

Gonads

Maturation stages. The gonads of each fish were examined macroscopically and the sex and state of activity was recorded. Gonad activity was recorded in accordance with the general criteria given below.

Stage 0	Immature	Gonads very small, frequently transparent and show no evidence of past spawning. Sex difficult to determine. This term applied only to small, obviously juvenile fishes.
Stage I	Inactive	Gonads larger in diameter than previous stage with a translucent appearance. Testes smaller than ovaries and usually less translucent. No eggs visible in ovaries.
Stage II	Maturing or recovering spent	Gonads slightly enlarged but still translucent. No sperm present. A few small eggs visible in ovary.
Stage III	Active or developing	Gonads are larger than above. Testes are opaque and no sperm is expelled by cutting testis and squeezing. Ovaries still translucent with small eggs visible macroscopically.
Stage IV	Active-Ripe or developed	Testes usually white, larger than Stage III and some sperm expelled from core when testis is cut. The ovary is

		opaque and solid. Eggs are fully formed and numerous, but not translucent.
Stage V	Ripe or gravid	Gonads are enlarged, occupying a large portion of the visceral cavity. Milt flows freely when testis is cut. Some of the eggs are translucent.
Stage VI	Spawning or ripe-running	Gonads enlarged to take up a major portion of the body cavity. Milt and eggs expelled from genital aperture on application of a slight pressure on both sides of the genital area. In later stages, the gonads are flaccid but numerous eggs and much milt still present.
Stage VII	Spent	Testes and ovaries flaccid. A few degenerating eggs present in ovary and testes almost empty.

For general descriptive purposes Stages I-II are referred to as "Inactive", Stages III-IV as "Active" and Stages V-VII as "Ripe."

A review of previous data and a preliminary account of the spawning seasons of Caribbean reef fishes based on data collected up to June 1971, is given by Munro et al. (1973).

Estimation of Fecundity

The method adopted is that described by Bagenal (1968). Whole ripe ovaries were preserved in Gilson's fluid (Simpson 1951) which hardens the eggs and helps separate them by breaking down the ovarian tissue. To facilitate this process the ovaries were split longitudinally and turned inside out to allow for quick penetration of the Gilson's fluid. Eggs were kept this way for several months. Cleaning involved decanting the Gilson's fluid and washing the eggs with water. Eggs still adhering to the ovarian tissue were removed manually and the tissue, free of eggs, was then discarded. By continually flushing with water and decanting the supernatant liquid, the eggs were freed of the remaining minute fragments of ovarian tissue. The eggs were then dried in air and kept in bottles until they were counted.

The cleaned, dried eggs from the ovaries of a single fish were weighed and one or two subsamples were then weighed and accurately counted. The proportionality equation $n/w = N/W$ was then used to calculate the total number of eggs present in the ovaries of the fish. In the equation,

n = number of eggs in the subsample

N = total number of eggs in the ovaries

w = weight of eggs in subsample

W = weight of eggs in the ovaries of the fish

This procedure was carried out for all of the gonads collected for fecundity estimates.

A Mettler H. 20 electric balance was used to weigh the eggs to the nearest 0.0001 g.

Egg Diameter

The diameters of eggs were measured by using the graduated screen of a microprojector and the mean diameter was recorded. Whenever possible the measurements were made on fresh eggs but otherwise ripe eggs which had been stored in a 2% solution of formalin, made up in seawater, were used.

Scales, Otoliths and Bony Parts

A limited program was undertaken of collection of scales, otoliths and other bony parts to be examined for evidence of annulus formation. In the case of tropical fishes, examination and interpretation of marks on bones and scales can be exceedingly difficult and time-consuming. The commitments of the project were such that scale or otolith examinations were made only for those species which showed fairly obvious and consistent rings or marks. Preliminary investigations (Thompson 1970, unpublished) showed that most species exhibited some marks on the scales and suggested that, given sufficiently large samples taken over the course of some years, it is likely that age and growth estimates could be made for many species. This is particularly feasible now that details of the spawning season, and thus the periodicity of spawning marks, are known.

Scales

Scales were taken from the areas which are covered by the pectoral fins when they are pressed against the body of the fish. This tends to nullify the variation in size and shape that is encountered if scales are taken from different areas on the body (Paul 1968). One or more unregenerated scales were taken from each fish. Regenerated (replacement) scales, characterized by having an opaque center, were very common on most fishes examined. In some instances, 100% regeneration was observed.

Ideally, scales from one fish were cleaned and stored in a single envelope. However, when a large sample of scales was collected, one unregenerated scale was taken from each fish and all scales were placed collectively in a sample bottle. Scales were cleaned by immersion in a detergent solution.

Temporary mounts were made by placing the scales in a film of water between two glass slides. The scales were then viewed microscopically or on a microprojector screen using transmitted light. The radius of each scale was measured and also the distances to each annulus along that same radius. This was done by using a microprojector screen graduated in millimeters. Results did not always warrant the calculation of a scale radius-fish length relationship. However, some calculations were made from scale marking. In these instances the body length-scale radius relationship was assumed to be linear

and the formula of Lea (quoted by Tesch 1968, and given below) was used:

$$L_n = \frac{S_n L}{S} \quad \text{where}$$

- L_n = length of fish when annulus "n" was formed
 L = length of fish at time scale sample was obtained
 S_n = radius of annulus "n" (at length ' L_n ')
 S = total scale radius

Otoliths and other bony parts

Otoliths were removed from small fishes by cutting a vertical section across the head from 0.6 to 1.3 cm behind the eye down to the mid-opercular region. The otoliths were then exposed by bending forward the cut section of the head. In large fishes, a longitudinal section was cut through the head between the eyes exposing the otoliths on either side in the otic capsules on the floor of the cranium. Three pairs of otoliths, the sagitta, lapillus and the asteriscus occur in the labyrinth of teleosts. The sagittae are the largest of the three and are the otoliths normally used in the aging of fish. The sagittae (hereafter referred to as the otoliths) were removed by using a pair of forceps. A thin envelope of connective, secretory and sensory tissue was usually removed from the labyrinth with the otolith and for best results the otoliths were cleaned by washing in water before they were stored.

A few opercular bones and fin spines were removed, cleaned by boiling in water and stored in envelopes. Vertebrae were also collected and cleaned by boiling.

Otoliths were examined from above by reflected light and for a translucent view by transmitted light. For reflected-light examination, the otoliths were placed in a black dish and covered with glycerine or xylene.

Various methods of preparation were used prior to viewing:

- 1) Otoliths were immersed in a clearing agent for up to two months. Clearing agents used were xylene, glycerine and cedar wood oil.
- 2) Burning, cutting, polishing and staining were tried independently and in combinations, e.g., burning then polishing. Staining reagents used were methyl violet B and alizarin red.

The methods used above for age determination from otoliths have been described by Albrechtsen (1968), Schott (1969) and Weidemann-Smith (1968). Bony parts other than otoliths were subjected to similar examinations.

ANALYTICAL TECHNIQUES

The data obtained at the Port Royal Reefs are the result of 28 lunar months of continuous sampling. As such, information on the relative abundance of each species is available for the full period, subject to normal chance variability or seasonal factors affecting the success of the sampling. In the case of the offshore

oceanic banks, our objective was to sample each of the main areas of interest once in every 10 weeks. Owing to variable weather conditions and mechanical problems, this objective was not entirely fulfilled and a full time series of data is not available for every species in every depth zone or area. An analytical format was therefore established with the objective of fully utilizing the available data and to arrive at the best possible estimates of biological parameters (growth rates, population structure and natural or fishing mortality rates applicable to each species). The basic plan is outlined below.

1. Length distributions of samples obtained from different areas or depth zones or using different fishing gear (traps or hooks) were first compared in terms of modal length, mean length and range in order to establish whether any differences existed between such samples. If no differences exist in size distribution, it then becomes possible, if necessary or desirable, to combine sample frequencies and treat, for example, a particular depth zone as a unit irrespective of the actual location of the sampling stations.

2. The samples were sorted into categories according to depth, area or gear or a combination thereof. The length distributions were then arranged in a time series to determine whether evidence of growth, in the form of modal progressions, was apparent. If samples of the species in question were small, frequencies were combined as necessary on a monthly, two-monthly or three-monthly basis.

Where modal progression was evident, growth curves (in terms of length) were prepared, and tested for conformity with the von Bertalanffy growth equation. Generally, the regression equation used was in the form

$$\text{Log}_e(L_\infty - L_t) = \text{Log}_e L_\infty + Kt_0 - Kt \quad (\text{Ricker 1958})$$

in which L_∞ is determined by trial regressions, L_t is the modal size, and t is the time interval between estimates of modal size (usually 1, 2 or 3 months).

Where age and growth estimates were possible on the basis of scale or otolith readings, the parameters of the von Bertalanffy equation were similarly estimated.

3. The overall annual average length composition of the catch of each species was estimated on the following basis:

- a. The unexploited portions of Pedro Bank, the exploited Pedro Cays area, California Bank and the Port Royal Reefs were treated as separate entities, and the length-frequency distributions of the catches were summed on a monthly, bimonthly, quarterly, four-monthly, half-yearly or annual basis in such a way that more than 100 fishes constituted the smallest summation.
- b. The percentage frequency of each length group was calculated for each time period and the mean of the periodic frequencies then calculated for each length group to obtain the best estimate of the annual mean length distribution of the catch.

- c. Estimates obtained in this manner clearly vary quite widely in the degree of confidence which can be attached to the resulting estimates of mean annual population length structure, according to the size of the samples, and the degree to which samples have had to be combined, e.g., an estimate of population structure based on a sample of at least 200 fishes in every month of the year will have a very much greater validity than an estimate based on samples so small that samples taken at irregularly spaced intervals during the year have merely been summed to obtain a gross estimate of the population structure.
- d. For descriptive purposes only useable estimates of population length composition have been graded into five groups, between "poor" and "excellent," according to the following format:

Total sample size	Time period (mo)					
	12	6	4	3	2	1
	Grade	Grade	Grade	Grade	Grade	Grade
1- 100	NU	NU	NU	NU	NU	NU
101- 500	0	0	0	1	1	1
501-1000	0	0	1	1	2	2
1011-1500	0	1	1	2	3	3
> 1500	0	1	2	3	4	4

NU = Not usable, 0 = Poor, 1 = Fair, 2 = Good, 3 = Very Good, 4 = Excellent

Those familiar with more developed fisheries might consider this grading to be over-optimistic. One should therefore bear in mind that approximately 130 species are dealt with in this report, and that no species is of overwhelming individual importance in the fisheries.

For many of the less common species dealt with in the following chapters, the sample sizes are far from being adequate owing to the vagaries of availability, weather and fishing effort. Nevertheless, for such species the analyses have been taken as far as is possible without exceeding the bounds of probability. Wherever possible, mean estimates are accompanied by confidence limits, even where the limits are extraordinarily wide.

Beverton and Holt (1956) showed that if fishes grew in accordance with the von Bertalanffy growth equation, and were subjected after recruitment to a constant mortality rate, then $Z = K(L_{\infty} - \bar{l})/(\bar{l} - l_c)$ where Z is the coefficient of the total mortality rate, K and L_{∞} are constants in the von Bertalanffy equation, l_c is not smaller than the smallest length-group fully represented in the length-frequency distribution of the catch and \bar{l} is the mean of all lengths equal to or greater than l_c .

In calculating mortality rates from the size composition of catches, it is important that calculations are based only on the fully recruited part of the population

and that elements of the stock within the recruitment ogive (the left side of the catch length-frequency distribution) are not incorporated into the calculations. However, in the case of the grunts and certain other groups discussed in this report, it appears that the populations exploited at the Port Royal Reefs are recruited at a smaller size than at Pedro Bank (possibly related to the shallow nearshore habitat) and that the largest elements of the populations at the Port Royal Reefs are either extinct or have migrated away from the nearshore reefs before they attain the full-retention size which is observed in catches from unexploited parts of Pedro Bank. For example, in the case of *H. plumieri* (Fig. 10.20) the mode of the length distribution of the catch at Pedro Bank is at 27.0 to 27.9 cm FL, but the modal size at the Port Royal Reefs is only 15.0 to 15.9 cm FL and the largest specimens captured at the Port Royal Reefs were only within the 28.0 to 28.9 cm FL group. In a technical sense, the stock at the Port Royal Reefs therefore becomes almost extinct while still within the length range covered by the recruitment ogive, and in order to make calculations of mortality rates, it is necessary to adjust the observed length-frequencies of the Port Royal stocks by dividing by the probability of capture as indicated by the recruitment ogive of the unexploited stocks.

Where necessary the length distribution of catches have been adjusted in this way (e.g., Tables 10.31, 10.32). As it is possible that systematic errors might arise in making such adjustments, the estimates of fishing mortality rates derived from such data should be regarded only as first approximations.

Given values of K and L_{∞} , it is therefore theoretically possible to calculate the value of Z from any reasonable representation of the annual average population length-frequency distribution and to compare values of Z obtained in different areas. Furthermore, if samples of a species are also available from an unexploited population, then $Z = M$ (the coefficient of the natural mortality rate) and the fishing mortality rate, F , in exploited areas can then be derived as $F = Z - M$.

In cases where the value of K is unknown, the equation in the form $Z/K = (L_{\infty} - \bar{l})/(\bar{l} - l_c)$ can be used to obtain estimates of the ratios Z/K or M/K (in the case of unexploited populations) provided that the asymptotic length L_{∞} can be reasonably estimated or bracketed. This is important insofar as the values of M and K appear in Beverton and Holt's (1964) yield equation only in the form of the ratio of M/K , and the actual magnitudes of M and K need not be known in order to make a preliminary assessment of the fishery potential of a species.

Finally, if the values of Z/K for an exploited population and M/K for an unexploited population are known, the value of F/K can be estimated and the rate of exploitation determined from Beverton and Holt's (1964) "Tables of Yield Functions for Fish Stock Assessment."

Assumptions implicit in the above equation are that throughout the exploited size range, the natural and fishing mortality rates remain constant and the patterns of

growth conform with the von Bertalanffy growth equation. For the species considered here, for which good estimates of growth and mortality are available, there is no evidence of any radical departures from the patterns of growth or mortality which have generally become accepted as the basis of fish population dynamics.

In the case of species for which estimates of mortality rates are available, an index of recruitment, R' , can be calculated as

$$R' = (C/f)Z$$

where C/f is the mean numerical catch per 1,000 trap nights and Z is the total mortality rate prevailing in the population. The resulting index, R' , is the theoretical number of recruits at the mean recruitment length, l_r , required to produce the observed catch rate.

Assessment of the potential fish production of the coral reef fish communities is discussed in Chapter 18.

PREPARATION OF ACCOUNTS OF THE BIOLOGY AND ECOLOGY OF IMPORTANT SPECIES AND FAMILIES

Accounts of the biology, ecology and bionomics of the important species and families of reef fishes are given in Chapters 6-16. To the greatest extent possible the arrangement of these chapters has followed version No. 2 of the outline given in the FAO publication on "Preparation of synopses on the biology of species of living aquatic organisms" (Rosa 1965), and every effort has been made to summarize or at least refer to all the relevant and important data available in previous publications and to relate these to the data collected and to the conclusions which have been formulated during the course of the present investigations. A particular effort has been made to draw attention to significant gaps in our knowledge of the species or groups involved.

CHAPTER 4:
THE COMPOSITION AND MAGNITUDE OF
LINE CATCHES IN JAMAICAN WATERS

by
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(January 1974)

Introduction

Hook-and-line fishing, a well established traditional technique throughout the world and in many parts of the Caribbean, including Jamaica, is practiced with a high degree of expertise. However, with few exceptions, the traditional line fisheries of the Caribbean are near-shore operations using small fishing vessels and simple, inexpensive monofilament nylon lines.

During the past decade, interest has been aroused in the possibilities of introducing new vessels and techniques in order to exploit fish resources in areas beyond the reach of small craft, and the possibilities of introducing techniques similar to those used in the Gulf of Mexico red snapper and grouper fishery have been investigated by various agencies and by master fishermen operating under the auspices of FAO. The objective has been to effectively exploit the stocks of snappers, groupers and jacks which occupy the steep slopes around the margins of banks and shelves, and which are not effectively harvested by handlines. The basic equipment of the Gulf of Mexico vessels has been described by Carpenter (1965) and consists of large, electrically, hydraulically or mechanically powered reels holding several hundred fathoms of braided stainless steel wire. The terminal rigs vary in arrangement, but basically consist of a weight (sufficient to ensure a rapid, near-vertical, descent of the line) surmounted by 3 to 15 hooks. Self-setting "tuna circle hooks" are popular in many areas, often with the barb removed to reduce the resetting time. A rubber "snubber" is often placed above the terminal rigs and serves to absorb shocks and reduce gear damage and fish loss.

In Jamaica, Oswald (1963) experimented with the use of a 13-m modified shrimp trawler for combination fishing with troll lines, shallow-water (less than 45 m) hand-lines and traps and, on the basis of his results, concluded that operations using multipurpose vessels would be economically viable.

AREAS INVESTIGATED AND FISHING METHODS

Line fishing investigations were conducted almost entirely on Pedro Bank (Fig. 3.2) where a total of 1,450 line-hours of effort were expended. A limited amount of fishing (57 line-hours of effort) was done on the edges of the South Jamaica Shelf and along the narrow northern shelf of Jamaica (Fig. 2.2). The 17-m research vessel, *Caranx*, was utilized throughout the investigations. Hand-line fishing was usually done at night with the vessel anchored on the sill reef or near to the edge of the bank in depths of 10 to 45 m. Monofilament nylon lines were used with three or four Mustad straight 3/0 or 4/0 hooks surmounting a 50 to 200 g lead or steel weight. Frozen squid was normally used as bait, being considerably more effective than trash fish, anchovies or shark which constituted the only alternatives.

The "drop-off" and deep reef were usually fished during the day, using electrically powered (24V) reels and stainless steel wire line. Up to five hooks (Mustad 5/0 or 6/0 straight or circle) baited with squid were set on branch lines and surmounted by a rubber snubber. Weights of up to 1 kg were used, depending upon the

strength of the currents. Most deep-reef fishing was done on the leeward or down-current edges of the banks, with the vessel anchored on the sill reef and the anchor line let out until suitable depths were found. Under calm

conditions, both the leeward and the windward slopes could be fished with the vessel maintaining position under power. High winds, however, usually precluded such operations.

Catch Composition and Catch Per Unit Effort

PEDRO BANK

Line fishing stations were distributed all around the margins of Pedro Bank, in all available depths and, in addition, several stations were also occupied in the central portion of the bank in areas remote from the edges (Fig. 3.2).

The success of fishing was highly variable, and was strongly influenced by wind and current strength. There were no significant differences (in terms of catch rate and catch composition) between stations of similar depth, and catch data from different parts of the bank have been combined to give an account of the magnitude and composition of the catches in the various depth zones (Fig. 4.1).

The line catch from the bank totaled 3,478 fishes, weighing 3,189 kg. At least 52 species were represented in the catch.

Table 4.1 summarizes the Pedro Bank catches and shows details of the numbers, weights, and the mean individual weights of the major species captured. Where sufficient numbers are available from several depth zones, there appears to be a general tendency towards an increase in mean individual weight with increasing depth. It must be borne in mind that catches from the deep reef were usually made by day using 5/0 or 6/0 hooks whereas the shelf and sill reef catches were made at night with 3/0 or 4/0 hooks, and the deep reef and shelf catches are therefore not comparable.

The general increase in size between 10.1 to 20 m and 30.1 to 45 m is shown by *Ocyurus chrysurus*, *Caranx latus*, *Haemulon album*, *H. plumieri*, *Balistes vetula*, and by the carcharinid sharks. This trend is not apparent in the hinds, *Epinephelus guttatus* and *Cephalopholis fulva*, or the squirrelfish *Holocentrus rufus*.

The mean size of fishes in the catch (excluding sharks) was greatest on the upper slope of the deep reef (60.1 to 100 m), mostly as a result of the presence of large species of carangids and of the black snapper, *Apsilus dentatus*.

Table 4.2 gives details of the average composition and catch rate (kg/100 line-hours) of all species captured in the various depth zones. Marked differences, discussed below, are apparent and are illustrated in Fig. 4.1.

The Shelf

FAO personnel operating in Jamaican waters had previously established that the central portions or shelf areas of Pedro Bank are very unproductive and that catch rates on lines or in traps are usually negligible (H.

Sperling, pers. comm.). Catches improve as the edge of the bank is approached, but it cannot yet be established whether this is related to the presence of actively growing corals or is simply an "edge effect" which occurs irrespective of the degree of development of the sill reef.

During this study, several stations were occupied in the central parts of the bank and yielded small numbers of sharks, squirrelfish and small grunts and confirmed that hand-line and trap fishing are very unproductive.

Sill Reef and Shelf Edge

Table 4.2 and Fig. 4.1 show that a limited number of species predominate in the catches throughout this zone. These species include *Caranx fuscus*, various carcharinid sharks, *C. latus*, *Epinephelus guttatus*, *Ocyurus chrysurus*, *Haemulon album*, *H. plumieri*, *Canthidermis sufflamen*, *Cephalopholis fulva*, *Balistes vetula*, *Sphyraena barracuda* and *Lutjanus buccanella*.

In the 10.1 to 20 m zone, 5 species constituted 70% of the catch: sharks (20%), *E. guttatus* (13%), *H. album* (12%), *O. chrysurus* (12%) and *C. latus* (12%). Sharks remained predominant (14%) in the 20.1 to 30 m zone, where 8 species comprised over 70% of the catch: *O. chrysurus* (11%), *E. guttatus* (10%), *H. plumieri* (8%), *C. latus* (7%), *B. vetula* (7%), *C. fulva* (7%) and *H. album* (7%).

In the 30.1 to 45 m zone, the catch rate for sharks decreased markedly and *Caranx fuscus* (20%) and *C. latus* (15%) yielded relatively high catch rates followed in relative abundance by *O. chrysurus* (15%), *E. guttatus* (12%), *H. album* (7%) and *C. sufflamen* (6%). The aforementioned species thus comprised over 70% of the catch.

The catch rate was greatest (283 kg/100 line-hours) in the 30.1 to 45 m zone, which also yielded the greatest proportion of highly valued snappers and jacks. While catch rates in this zone were highest they also tended to be highly variable and the catches in the shallower zones (161 to 192 kg/100 line-hours) tended to be more consistent. The deep sill reefs and edges are located mostly at the western side of Pedro Bank, with a few areas of limited extent on the southern, southeastern and eastern edges (Fig. 3.2).

The "Drop-Off"

The average catch from the drop-off zone was very small (98 kg/100 line-hours) but this is possibly a consequence of the extreme difficulty of fishing on the near-vertical face and not necessarily an indication of

Table 4.1. Summary of Pedro Bank line catches giving numbers (#), weight, W, (kg) and mean individual weights \bar{W}_c (g) of the important species captured in each depth zone.

Area Depth zone Effort (line-hours)	10-20 m 310			Sill reef and shelf edge 20-30 m 300			30-40 m 482			"Drop-off" 40-60 m 158			60-100 m 120			Deep reef 101-250 m 80		
	#	W	\bar{W}_c	#	W	\bar{W}_c	#	W	\bar{W}_c	#	W	\bar{W}_c	#	W	\bar{W}_c	#	W	\bar{W}_c
<i>Lutjanidae</i>																		
<i>Ocyurus chrysurus</i>	113	99.2	878	81	80.9	999	128	167.5	1,309	20	23.2	1,160	10	9.1	910	1	2.4	2,400
<i>Lutjanus buccanella</i>	18	11.3	628	31	18.9	610	70	36.4	520	10	4.8	480	51	52.6	1,031	13	9.8	754
<i>L. apodus</i>	3	3.2	1,067	3	2.4	800	21	16.3	776	15	6.8	453						
<i>L. vivanus</i>	1	.3	300							31	19.7	635	19	18.2	958	46	35.2	765
<i>Apsilus dentatus</i>				1	1.0	1,000				7	17.1	2443	83	142.9	1,722			
<i>Pristipomoides macrophthalmus</i>													1	.3	300	3	1.3	433
<i>Serranidae</i>																		
<i>Epinephelus guttatus</i>	116	74.0	638	58	45.8	789	239	135.2	566	39	16.7	428	17	8.2	482	3	3	1,000
<i>E. mystacinus</i>													1	15.0	15,000	3	28.5	9,500
<i>Cephalopholis fulva</i>	153	35.5	232	90	26.0	288	166	38.6	233	29	5.9	203	3	.7	233	5	2.4	480
<i>Carangidae</i>																		
<i>Caranx latus</i>	70	121.0	1,729	31	57.5	1,855	103	225.5	2,189	10	23.5	2,350	55	113.3	2,060			
<i>C. lugubris</i>	1	2.2	2,200	2	8.9	4,450	7	12.5	1,786				6	16.2	2,733			
<i>C. fusus</i>	1	.9	900				182	269.5	1,481									
<i>Alectis crinitus</i>				4	24.0	6,000				1	2.5	2,500						
<i>Seriola dumerili</i>	2	3.8	1,900				3	20.4	6,800				2	3.7	1,650			
<i>S. rivoliana</i>										1	1.2	1,200	1	1.1	1,100			
<i>Pomadasyidae</i>																		
<i>Haemulon album</i>	60	40.1	668	43	32.8	763	88	93.4	1,061	3	2.6	867	5	3.9	780			
<i>H. plumieri</i>	73	35.6	487	83	41.2	496	64	37.4	584	4	3.2	800	6	4.1	683	2	1.1	550
Other families																		
<i>Sphyræna barracuda</i>	4	22.9	5,725	8	40.8	5,100	11	65.6	5,964				1	6.0	6,000			
<i>Balistes vetula</i>	48	23.3	485	67	38.2	570	47	35.0	745	15	10.1	673	3	5.9	1,967	1	1.1	1,100
<i>Calamus sp.</i>	16	6.7	419	9	4.3	478	16	8.6	538									
<i>Holocentrus rufus</i>	50	6.0	120	32	3.5	109	37	4.8	130	7	.7	100	1	.1	100	3	.3	100
<i>Canthidermis sufflamen</i>	20	7.4	370	13	18.1	1,392	25	40.7	1,628	8	12.5	1,562						
<i>Malacanthus plumieri</i>	4	2.2	550	17	6.4	376	11	4.5	409	2	.9	450	1	.4	400			
<i>Melichthys niger</i>	13	7.7	592	16	10.1	631	3	1.6	533	1	.7	700						
<i>Scomberomorus cavalla</i>							1	2.3	2,300	1	15.0	15,000						
Other minor species	62	15.7	253	45	29.1	647	97	19.1	197	9	2.2	244	4	1.0	250	2	.3	150
Sharks	59	130.7	2,215	49	118.3	2,414	19	57.8	3,040				3	63.3	21,100	2	18.0	9,000
Totals	887	649.7	732	683	608.2	890	1,338	1,292.7	891	213	169.3	794	273	466.0	1,707	84	103.4	1,231
Totals excluding sharks	828	519.0	627	634	489.9	773	1,319	1,234.9	860	213	169.3	794	270	402.7	1,491	82	85.4	1,041

Table 4.2. Average composition of catches and mean catch rates (kg/100 line-hours) in the depth zones at Pedro Bank. Proportions of commercial grades are also given: Q, "quality" fish; C, "common" fish; T, "trash" fish and U, unmarketable fishes.

Area Depth (meters) Effort (line-hours)	Sill reef and shelf edge			"Drop-off"	Deep reef	
	10.1-20 310	20.1-30 300	30.1-45 482	45.1-60 158	60.1-100 120	100.1-250 80
<i>Carcharinidae</i>						
Unidentified species	38.8	22.9	7.7		67.4	18.7
<i>Muraenidae</i>						
<i>Gymnothorax moringa</i>	U	.2				
<i>Holocentridae</i>						
<i>Holocentrus ascensionis</i>	T	1.1	.7	2.3	.2	
<i>H. rufus</i>	T	2.2	1.4	.7	.2	.3
<i>Myripristis jacobus</i>	T	.1	+		+	
<i>Sphyraenidae</i>						
<i>Sphyraena barracuda</i>	C	6.5	9.2	10.9		2.8
<i>Serranidae</i>						
<i>Petrometopon cruentatum</i>	C		.3	.3		
<i>Cephalopholis fulva</i>	C	16.4	11.4	8.8	1.7	1.0
<i>Mycteroperca venenosa</i>	C		.7			
<i>Epinephelus guttatus</i>	C	25.2	16.9	34.3	9.5	8.8
<i>E. striatus</i>	C		1.4	1.7		
<i>E. mystacinus</i>	C				22.2	29.7
<i>Priacanthidae</i>						
<i>Priacanthus arenatus</i>	C	.3				
<i>Branchiostegidae</i>						
<i>Malacanthus plumieri</i>	U	.9	3.9	1.4	.2	.2
<i>Echeneidae</i>						
<i>Echeneis naucrates</i>	U		.3			
<i>Carangidae</i>						
<i>Caranx latus</i>	Q	23.0	11.7	43.6	6.3	64.7
<i>C. lugubris</i>	Q		1.9	1.4		9.7
<i>C. fusus</i>	Q	.2		57.1		
<i>C. bartholomaei</i>	Q	1.1	.7	.2		
<i>Seriola rivoliana</i>	Q	.8			1.2	.7
<i>S. dumerili</i>	Q			4.3		3.2
<i>Selar crumenophthalmus</i>	Q					.1
<i>Elegatis bipinnulatus</i>	Q	.1	.6			
<i>Alectis crinitus</i>	Q		6.2		1.3	
<i>Scombridae</i>						
<i>Euthynnus alleteratus</i>	C	.6				
<i>Scomberomorus cavalla</i>	Q		.3		4.1	
<i>Lutjanidae</i>						
<i>Ocyurus chrysurus</i>	Q	23.1	18.3	42.3	7.2	6.9
<i>Lutjanus buccanella</i>	Q	2.5	4.7	6.7	6.8	45.6
<i>L. apodus</i>	Q	.7	1.1	4.1	1.8	
<i>L. analis</i>	Q	.2				
<i>L. griseus</i>	Q			.4	.2	
<i>L. vivanus</i>	Q	.1			34.7	31.1
<i>Apsilus dentatus</i>	Q		.3		11.9	91.5
<i>Rhomboplites aurorubens</i>	Q					.8
<i>Pristipomoides macrophthalmus</i>	Q					.1
<i>Etelis oculatus</i>	Q					.2
<i>Pomadasyidae</i>						
<i>Haemulon album</i>		23.8	11.3	18.8	1.3	1.8
<i>H. plumieri</i>		12.0	13.7	7.2	1.6	4.8
<i>H. striatum</i>		+				
<i>H. aurolineatum</i>		.7	.3	.2		.1
<i>H. flavolineatum</i>		+	.2	.3	.1	
<i>H. melanurum</i>			1.0	.3		
<i>H. carbonarium</i>				+		

Continued

Table 4.2 (continued)

Area Depth (meters) Effort (line-hours)	Sill reef and shelf edge			"Drop-off"	Deep reef	
	10.1-20 310	20.1-30 300	30.1-45 482	45.1-60 158	60.1-100 120	100.1-250 80
<i>Sparidae</i>						
<i>Calamus pennatula</i>	C					
<i>C. calamus</i>	C	2.4	1.3	2.3		
<i>C. spp.</i>	C					
<i>Labridae</i>						
<i>Halichoeres maculipinna</i>	T		.2			
<i>H. radiatus</i>	T			.3		
<i>Balistidae</i>						
<i>Balistes vetula</i>	T	5.3	11.6	7.6	4.4	5.7
<i>Canthidermis sufflamen</i>	T	1.5	4.3	16.4	3.3	1.2
<i>Melichthys niger</i>	T	1.8	2.6	.2	.2	
<i>Diodontidae</i>						
<i>Diodon holacanthus</i>	U			.5		
<i>Palinuridae</i>						
<i>Panulirus argus</i>	Q		.4	.5		
Total "Quality" Fish	51.8	45.9	160.4	75.5	254.4	62.7
Total "Common" Fish	51.4	41.2	58.3	11.2	34.8	38.0
Total Grunts	36.5	26.5	26.8	3.0	6.6	1.3
Total "Trash" Fish	10.2	18.0	27.0	7.9	6.0	1.5
Total Sharks	38.8	22.9	7.7	0	67.4	18.7
Total Unmarketable	2.7	6.9	2.7	.4	.2	0
Total All Groups	191.4	161.4	282.9	98.0	369.4	122.2

low stock densities. In particular, hooks tend to become snagged on the shingle-like layers of corals (mostly *Agaricia* and *Montastrea* spp.) and much time is lost in replacing terminal rigs.

Figure 4.1 shows that five species comprised over 70% of the catch: *Lutjanus vivanus* (35%)—usually small specimens, *Apsilus dentatus* (12%), *Epinephelus guttatus* (9%), *Ocyurus chrysurus* (7%) and *Lutjanus buccanella* (7%). The catch is thus a mixture of species which predominate in other zones. The absence of sharks from the catch is of interest.

Upper Slope of the Deep Reef (60.1 to 100 m)

This zone provided by far the greatest catch rates (369 kg/100 line-hours), with *Apsilus dentatus* (25%), sharks (19%), *Caranx latus* (18%), *Lutjanus buccanella* (12%) and *Lutjanus vivanus* (8%) providing over 80% of the catch (Fig. 4.1). Sharks are particularly abundant, yielding about 67 kg/100 line-hours.

Unfortunately, this zone is virtually nonexistent in many areas where the drop-off continues to extreme depths, and the fishable area is correspondingly limited (Fig. 3.3).

Lower Slope of the Deep Reef

The lower slope of the deep reef starts at about 100 m. Most of the species of *Caranx* and *Seriola* and the black snapper, *Apsilus dentatus* which characterize the upper slope of the deep reef do not venture into this zone, and silk snapper (*Lutjanus vivanus*) (36%), misty grouper (*Epinephelus mystacinus*) (24%), and various sharks (15%) predominate in the catch (Table 4.1 and Fig. 4.1). The community persists to depths of about 250 m, beyond which it merges into the upper portion of the bathyal zone where large eels, brotulids and small sharks appear to predominate.

The catch rate was only about 122 kg/100 line-hours, but this is at least partly a function of the extreme depth and not necessarily an indication of low stock densities. Indeed the rapidity with which strikes are felt when a line reaches the bottom suggests that stock densities are not insignificant. Very steep inclines limit the extent of this zone, but not to the same degree as the upper slope of the deep reef (Fig. 3.3).

THE JAMAICAN SHELF

The limited amount of line fishing (57 line-hours of

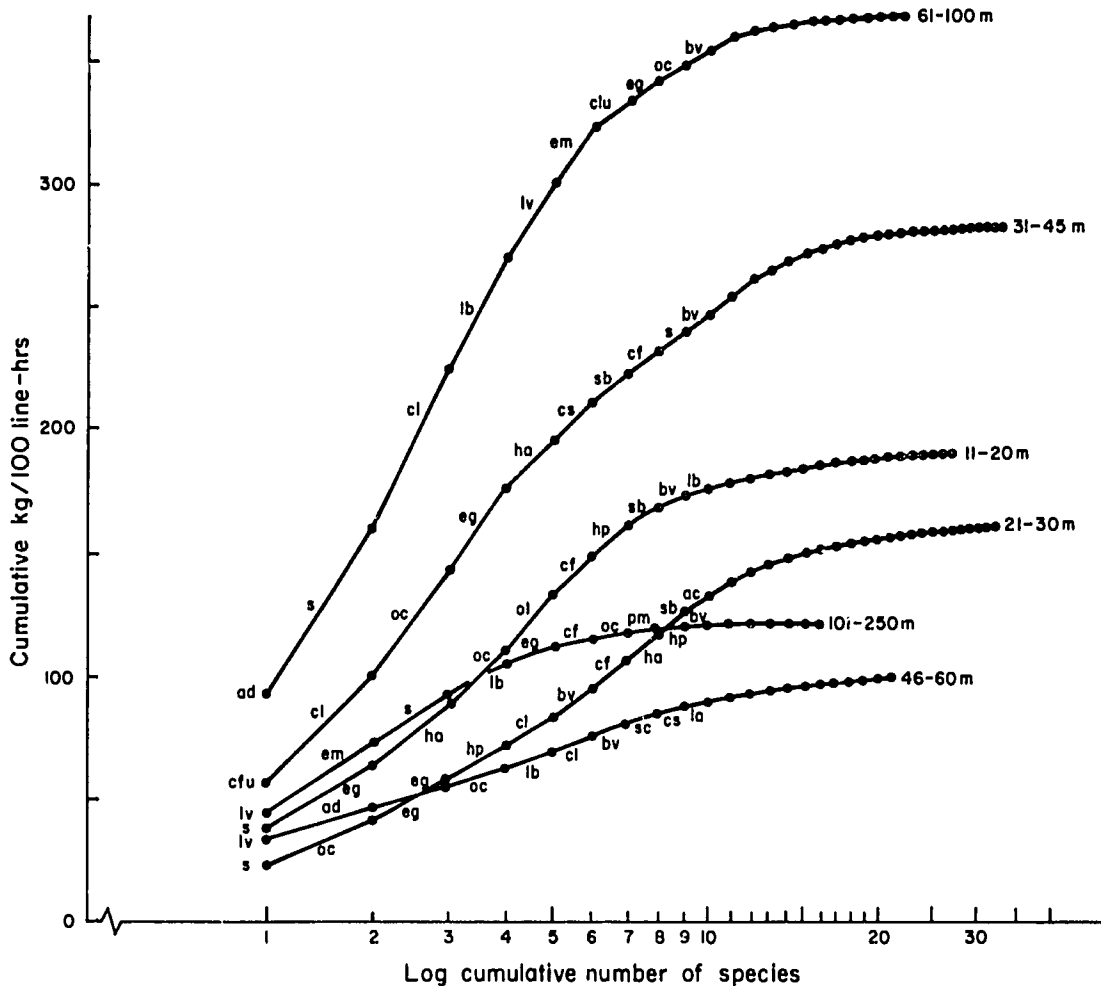


Fig. 4.1. Semi-logarithmic plot of cumulative catch per unit effort against the logarithm of the cumulative number of species represented in the catch from the six major depth zones at Pedro Bank. The logarithmic scale on the X-axis is used for illustrative purposes only and has no other significance. Abbreviations are as follows: ac, *Alectis crinitus*; ad, *Apsilus dentatus*; bv, *Balistes vetula*; cf, *Cephalopholis fulva*; cfu, *Caranx fusus*; cl, *C. latus*; clu, *C. lugubris*; cs, *Canthidermis sufflamen*; eg, *Epinephelus guttatus*; em, *E. mystacinus*; ha, *Haemulon album*; hp, *H. plumieri*; la, *Lutjanus apodus*; lb, *L. buccanella*; lv, *L. vivanus*; oc, *Ocyurus chrysurus*; pm, *Pristipomoides macrophthalmus*; s, unidentified carcharinid sharks; sb, *Sphyraena barracuda*; sc, *Scomberomorus cavalla*.

effort) done in the edges of the South Jamaica Shelf and along the narrow northern shelf of Jamaica yielded a total of only 12 fishes (10 species) weighing 9.2 kg and 9 out of 12 stations occupied yielded no catch at all. The catch rate ranged from zero to 0.55 kg/line-hour with a

mean of 0.16 kg/line-hour. The successful stations ranged in depth between 70 m and 300 m. Too few fishes were captured for the composition of the stocks to be defined, but the species encountered were the same that occur at similar depths at Pedro Bank.

Discussion

Kawaguchi (1974) reported on the results of exploratory line fishing for snappers and other demersal species by the UNDP/FAO Caribbean Fishery Development Project. The investigations of that project encompassed most of the Caribbean region and very large differences in catch rates (between zero and 62.2 kg/line-hours) were reported. This fishing was almost entirely conducted

on the drop-off and deep reef, usually in depths of 50 m to 250 m.

In Jamaican waters, the catch rates reported by Kawaguchi (1974) ranged between zero on parts of the Jamaican shelf to 10.6 kg/line-hour at northwest Pedro Bank. The catch composition at Pedro Bank was 39 to 92% snappers, 3 to 19% jacks, 2 to 22% groupers, 1 to

9% grunts and 1 to 26% other fishes, according to depth and locality. Exploited banks within the operating range of the Jamaican nearshore canoe fishery yielded a mean catch rate of 0.45 kg/line-hour; small, lightly exploited or unexploited oceanic banks yielded 3.0 kg/line-hour and Pedro Bank yielded an average of 3.1 kg/line-hour (Kawaguchi 1974). These values are very close to those obtained in similar depths during the present investigation (Table 4.2). In contrast, Kawaguchi reported much greater catch rates from the shelf areas of Nicaragua, the Guyana shelf and the banks of the northeastern Caribbean.

The reasons for the relatively low catch rates obtained at Pedro Bank are not fully understood. Munro et al. (1973) have suggested that the various catch rates reported for unexploited oceanic banks might be related to the patterns of oceanic currents and the lengths of the larval lives of the important species. At present, there is no evidence which suggests that the potential natural productivity of oceanic banks is very variable. The families of major importance include the snappers, jacks, groupers and hinds, grunts, triggerfishes and sharks. It has been well established (Berry 1959) that carangids have long-lived pelagic post-larval stages which are subject to very extensive dispersal by ocean currents. It appears that groupers and hinds and triggerfishes might also be widely dispersed through long-lived larval stages. However, very few larval or pelagic post-larval snappers or grunts have been reported from ichthyoplankton samples or from tuna stomachs in the western Atlantic. In particular, the larvae and early juvenile stages of the most important species such as *Lutjanus vivanus*, *L. buccanella* and *Apsilus dentatus* appear to be entirely unknown.

The relatively low line-catch rates recorded in Jamaican waters during the present investigations and by Kawaguchi (1974) appear to indicate rather unpromising prospects for a viable hook-and-line fishery using modern fishing vessels. In nearshore areas, Jamaican canoe fishermen undertake line fishing mostly on an opportunistic basis, when wind and sea conditions and moon phase appear to be favorable, and very few of such fishermen depend entirely on hand-lining for their livelihood. The very low catch rates reported for the Jamaican shelf presumably indicate that the stocks are quite heavily exploited by the present hand-line fishery and it is also possible that recruitment of certain species to the fishery is adversely affected by exploitation of the adolescent stages (which may tend to congregate on the sill reefs) by the trap fishery. However, the latter obser-

vation is only known to be true in the case of *Lutjanus buccanella*.

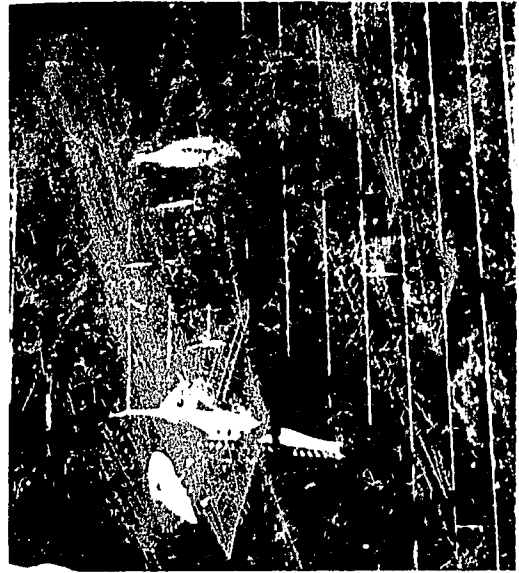
With the exception of sharks, most of the species which can be taken on lines can also be taken in traps. Several trial sets of stackable traps (Munro 1973) in depths of 150 to 300 m off the South Jamaica Shelf yielded modest hauls of *Lutjanus vivanus*, *Epinephelus mystacinus*, *Pristipomoides macrophthalmus*, and of caridean shrimps, and suggest that further deep-trapping trials might be warranted, particularly if the traps could be affixed to a bottom setline in order to increase the speed of deployment and retrieval of traps. Wolf and Chislett (1974) reported consistently good trap fishing results in depths of 79 to 210 m around the Northern Leeward Islands, but unfortunately did not attempt trap fishing in similar depths in Jamaican waters. The slopes of the deep reefs in Jamaican waters might be too acute in most areas, but it is possible that trap fishing in deep waters might be an economically viable alternative method of exploiting deep-reef communities which yield insufficient catch rates for exploitation by hook and line.

If a market for sharks (which are presently unsaleable in Jamaica) can be developed, the feasibility of bottom longlining would also warrant closer examination. Sharks formed a substantial fraction of the catch in most of the depth zones at Pedro Bank and predominated in the catches from the otherwise unproductive central portions of the bank which has a sparse coral cover and would therefore be particularly suited to this technique. Bottom longlining was also attempted on one occasion in the lower deep-reef zone at Pedro Bank, but without success.

Carpenter and Nelson (1969) estimated that the potential annual production of snappers and groupers from the Caribbean region (including the Guyana Shelf) amounts to 41,000 t. No details are available of the methods used in computing this value or of the methods to be used in taking this catch. As shown in Chapter 1, the total annual Caribbean demersal and neritic pelagic production might amount to 750,000 to 1,000,000 t under intensive exploitation. The aforementioned estimate of potential production of snappers and groupers from the Caribbean and adjacent regions amounts to not more than 5.5% of the estimated potential total production of all species from the Caribbean proper and the estimates are therefore not incompatible. However, as indicated above, it appears that economic and technological factors will have to be overcome if the deep-living snappers and groupers are to be fully exploited.

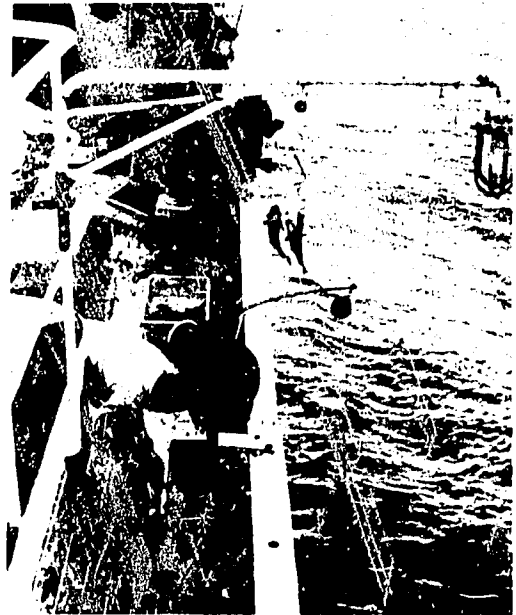


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1. Fishes of the upper part of the deep reef. Clockwise from top: *Seriola dumerili*, *Epinephelus guttatus*, *Apsilus dentatus*, *Cephalopholis fulva* and *Lutjanus buccanella*.
 2. A handline catch from the "drop-off" including (top to bottom) *Caranx lugubris*, *Lutjanus buccanella*, *Apsilus dentatus*, *Mycteroperca* sp. and *Sphyaena barracuda* (in basket).
 3. Fishing the deep reef with electrically powered fishing reels. *R. V. Alcyon*.
 4. Weighing a catch taken with electrically powered reels on *R. V. Alcyon*.
 5. A substantial catch of *Apsilus dentatus* taken with electrically powered reels from a feeding school, which rose off a ridge at 80-m depth at Northwest Pedro Bank. *R. V. Alcyon*.
 Photos by J. Munro



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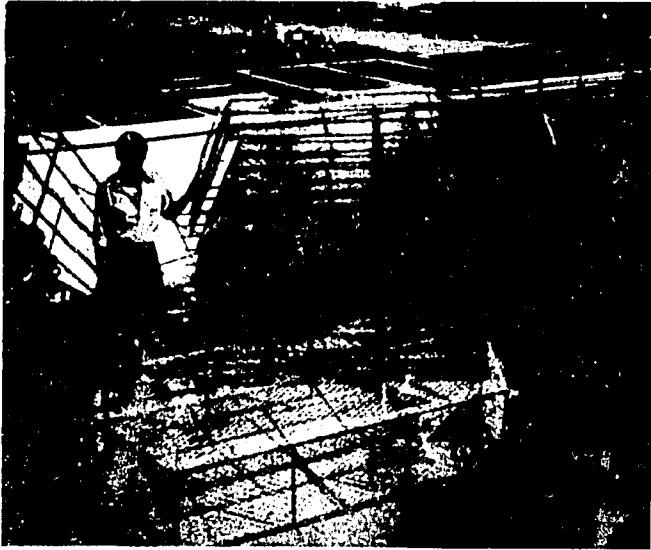


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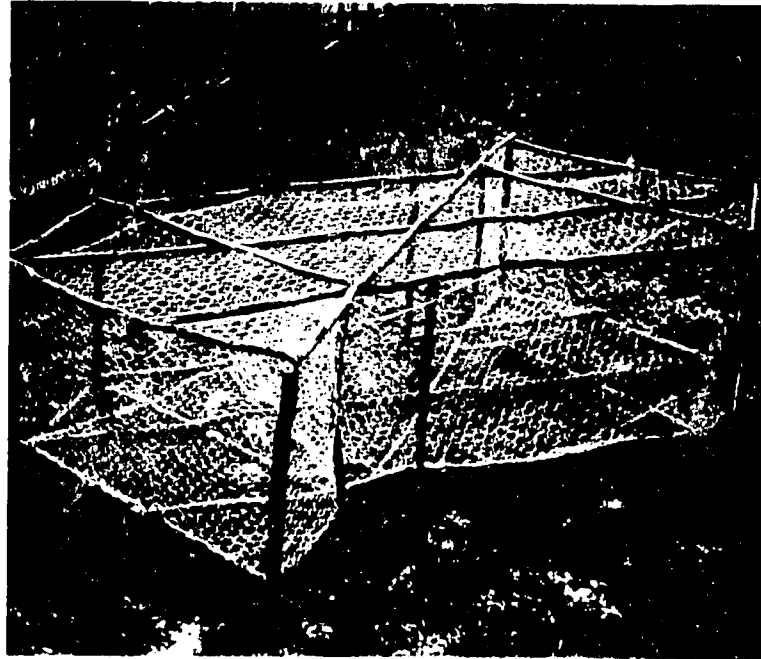
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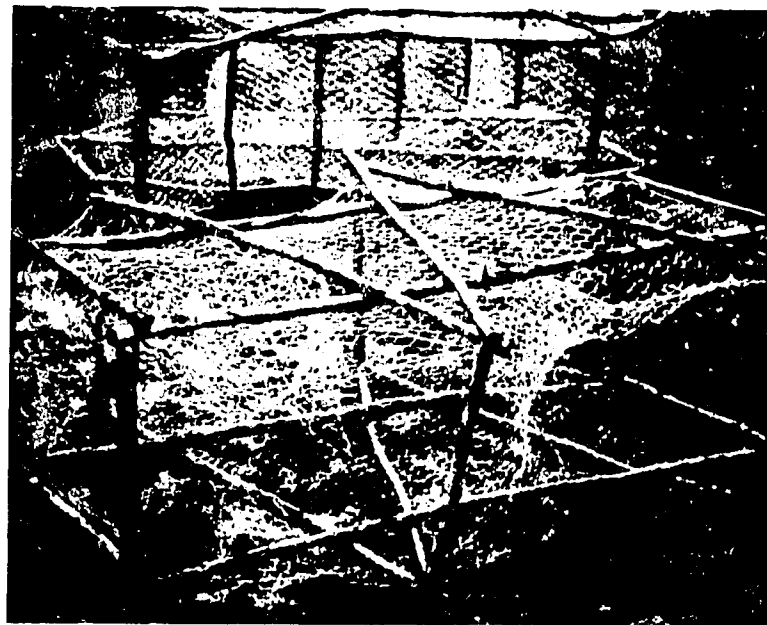
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Principal traps used during the investigations. 1. Stackable hexagonal traps. 2. Jamaican Z trap. 3. Cuban S trap. 4. Stackable split-S or dollar trap. Photos by J. Munro



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Chapter 5:
THE COMPOSITION AND MAGNITUDE OF
TRAP CATCHES IN JAMAICAN WATERS

by
J.L. Munro
(1980)

Introduction

Coral reefs and adjacent shallow areas support diverse fish communities which form the basis of fisheries in most tropical seas. In the Caribbean Sea these communities are mainly exploited by means of fish traps (also called fish pots) and handlines.

There is little available literature regarding the exploitation of coral reefs by the use of traps. The various designs of traps commonly used in the Caribbean have been described (Buesa Mas 1962; Munro et al. 1971) and studies of the mode of operation of traps have been reported (Munro et al. 1971; Munro 1974; High and Beardsley 1970). Wolf and Chislett (1974) reported on the exploratory trap fishing activities of the UNDP/FAO Caribbean Fishery Development Project during 1969-1971. Trap fishing studies have also been reported from the U.S. Virgin Islands (Dammann 1969; Brownell and Rainey 1971; Sylvester and Dammann 1972). Munro et al. (1971) have discussed the major factors affecting the performance of fish traps and have shown that the rates at which fishes enter Antillean traps are influenced by lunar phase (or tides), trap design and conspecific attraction.

The double-chevron or Z trap (Munro et al. 1971) is the most popular type of trap in Jamaican waters. Normal dimensions are 229 x 122 x 61 cm. Large variants of the Z trap, sometimes up to 183 cm high, are referred to as "jack-pots" and reportedly yield higher catches of jacks than the smaller Z traps. A small rec-

tangular trap called a "gang trap" is also used. These traps are linked with ropes and set as a fleet, usually on seagrass beds or where the sea bed is flat.

The setting of Z traps is accomplished by casting them overboard horizontally, with the entrance funnels downwards, so that they settle to the bottom in that fashion. One or two buoys may be attached to the traps, especially in deep waters with strong currents, but in areas where trap theft is prevalent the traps are unbuoyed and are located by taking land bearings and sometimes with the aid of a glass-bottom at box or face mask. These traps are hauled with a grapnel line and in murky waters, the grapnel may be dragged on the bottom until it hooks the trap. The traps are hauled over the side of the canoe, a procedure that is facilitated by the rolling motion of the canoe. At the surface, the trap is laid across the gunwales and the trap contents are emptied through a wired door in the trap. If necessary, traps may either be repaired at sea or brought back to land, depending upon the extent of damage or necessity of replacing parts of the frame.

The traps may or may not be baited, but where bait is used, it takes the form of small unmarketable fishes, stale bread, vegetables, fruits or pieces of white crockery. The soak (the length of time the traps are left underwater) is variable and very much dependent upon weather conditions and upon an individual's alternative opportunities for earning an income.

Areas Investigated and Methodology

AREAS INVESTIGATED AND FISHING TECHNIQUES

The trap fishing investigations were carried out at locations representing different levels of exploitation. The principal study areas were the nearshore reefs at Port Royal (Fig. 3.1) and the oceanic California and Pedro Banks (Figs. 2.2 and 3.2). Supplementary studies were made at nearshore areas around Discovery Bay, Jamaica, and Lameshur Bay, St. John, Virgin Islands.

Several designs of fish traps were used during the course of the project and those most commonly employed fall into two categories, as discussed below. The hexagonal wire mesh used to cover all the traps had a mean maximum aperture of 4.13 cm.

1. Wooden-Framed Traps (Fig. 5.1)

The traditional Jamaican Z trap and the Cuban-designed S trap (Buesa Mas 1962) were used extensively by the project at the Port Royal Reefs. The Z traps had typical dimensions averaging 229 cm long, 122 cm wide and 61 cm deep and the respective measurements for the S traps were 183 x 122 x 61 cm. Midi-traps (a small version of the S trap) with dimensions of 122 x 122 x 61 cm and chevron traps (122 x 100 x 61 cm) were also used by the project on occasions.

2. Stackable Metal-Framed Traps (Fig. 5.2)

Metal-framed traps of two designs, the "split-S" or "dollar" trap and the "split-hexagonal" trap were developed during the course of the project (Munro 1973). Their design allows the traps to be stacked in halves, increasing the number of traps that can be carried by offshore trap fishing vessels and thus increasing the potential catch as well as the mobility of the vessel. These traps were largely used during the offshore operations of the project.

Most of the nearshore fishing effort during this investigation was expended at the Port Royal Reefs (Fig. 3.1) where trap catches were made every month between November 1969 and February 1972.

Sampling was accomplished by the use of motor-powered skiffs or launches. Traps were carried to the desired locations and set individually by scuba divers at suitable sites on the reef slope. The depth of each trap was measured with a depth gauge. Traps were set in various reef habitats, usually on sand patches amongst corals so that the trap rested as firmly and close to the bottom as was possible without physically damaging the coral (it had been noted that traps rarely caught fish if they were set so that the bottom surface of the trap was not close to the substratum). Traps were also set on top of coral thickets such as are commonly found in the *A. cervicornis* zone. At the base of the reef, traps were never set more than 2 m away from the nearest coral

cover. Most trap fishing effort was expended on the slopes of patch reefs contained within the barrier reef (see Fig. 3.1). It was not possible to obtain sufficient comparative data from the seaward side of the barrier reef owing to the difficulty of operating from a small boat in the usually rough seas at this locality. The Port Royal Cays are popularly used by swimmers and boat owners and only a few traps were set on the reefs immediately surrounding the cays themselves, because of the likelihood of human interference and the general disturbance of the reef environment in these areas. The traps were set in depths of 1.5 to 15.9 m (5 to 85 ft) but as thefts were sometimes a problem, they were usually set below 7.6 m (25 ft), at which depth they were usually not visible from the surface.

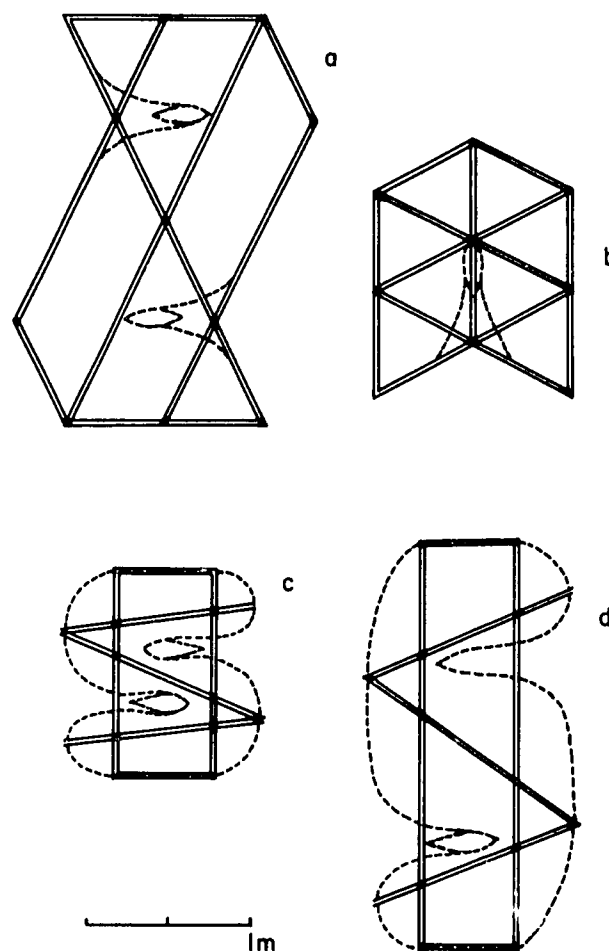


Fig. 5.1. Plan views of Antillean fish traps. The Z trap (a), the chevron trap (b), the midi-trap (c) and the S trap (d) are the trap types used during these investigations. The most usual dimensions are in multiples of 122 cm (4 feet), dictated by the usual dimensions of rolls of wire mesh. Traps are normally 61 cm high. Broken lines are mesh work and solid lines represent the wooden framework, usually constructed of mangrove poles. Wire mesh is most often of 4.13 cm maximum aperture.

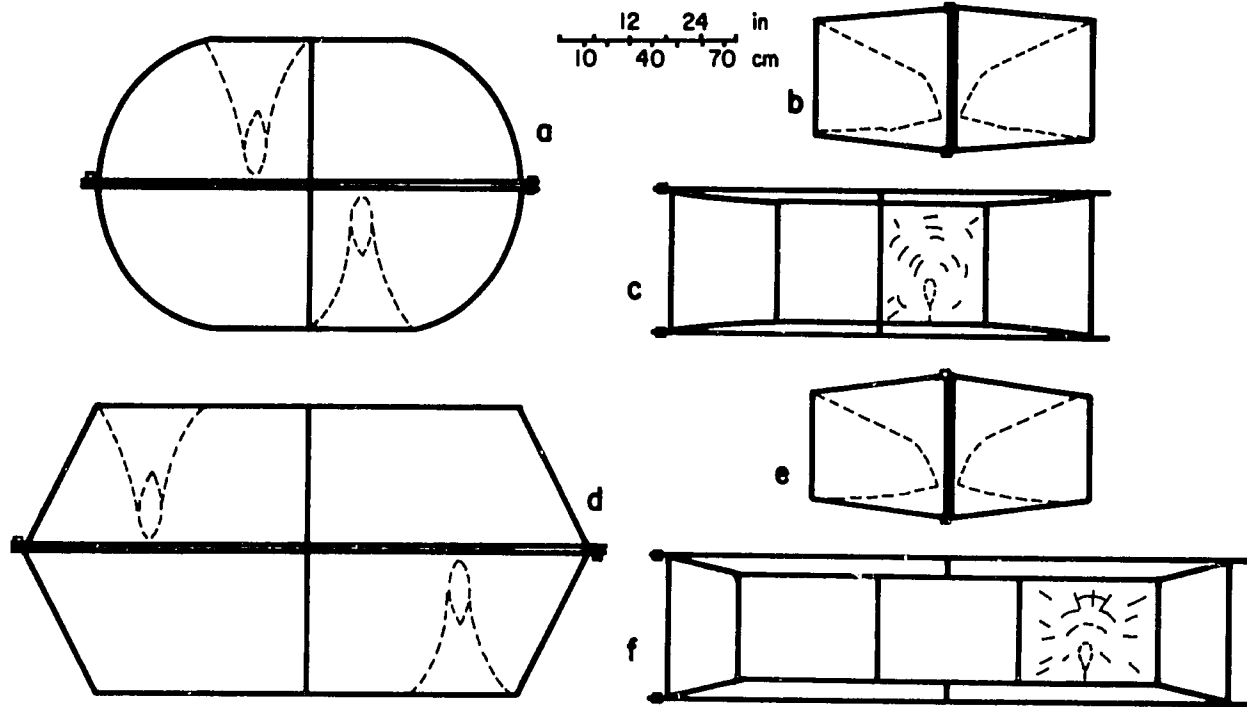


Fig. 5.2. Configuration of stackable traps. Plan (a), end (b) and lateral (c) views of split-S or dollar trap. Plan (d), end (e) and lateral (f) views of hexagonal trap.

Two particular reef complexes (Yahoo Reef and Nassau Reef) were selected for detailed studies and most experimental work was concentrated there (Fig. 3.1).

Offshore Areas

Between January 1971 and February 1973, 38 offshore trap fishing cruises were accomplished aboard the *R. V. Caranx*. Z, S, midi and dollar traps (Figs. 5.1 and 5.2) were used during the initial cruises but the wooden-framed traps were gradually phased out and replaced by stackable dollar and hexagonal traps. Only the stackable traps were used after May 1972.

Traps were set along transects by allowing the vessel to drift with the current and/or wind. The traps, individually buoyed, were set approximately 50 m apart and usually within 1,000 m of the edge of the bank. Stale bread, tins of catfood or trash fish were used as bait and the traps were soaked from 1 to 3 days. They were hauled to the surface by means of a capstan and the catches were accumulated into fish boxes, arranged so that catches, similar in terms of trap type, bait and soak, could be examined and recorded separately.

UNDERWATER OBSERVATIONS

A study of the effect of soak on the size and composition of trap catches was devised in which series of

unbaited Z traps or S traps were set on the slopes at Nassau Reef and Yahoo Reef (Fig. 3.1), near Port Royal, in depths of 7.6 to 16.8 m (25 to 55 ft) for two-week periods. Traps were set or hauled at, or within 2 days of, the new moon or the full moon and the trap contents were identified and counted underwater as often as possible over each two-week period. Observations were made on 62 traps set on Nassau Reef from March 1970 to December 1970 and on 50 traps set on Yahoo Reef between May 1970 and December 1970. Over each biweekly period, the traps were observed on average 5.1 times on Nassau Reef and 5.7 times on Yahoo Reef, giving a total of just over 600 separate counts of contents of individual traps.

Comparable data were obtained from observing unbaited S traps set on the reef slopes on the north coast of Jamaica at Discovery Bay, and at Groot Pan Bay, St. John, U.S. Virgin Islands.

The trap observation procedure gave rise to sets of data on the numbers and species of fishes observed in the traps on successive occasions over a period of up to 2 wk. It was not possible to make daily observations on each individual trap used during the experiment and the catch, for those days when observations were not made, was estimated by linear interpolation. Data from traps in which the interval between observations was greater than six days were not used. The cumulative number of fishes known to have entered each trap after each successive day was estimated and is referred to as ingress. Ingress is

a minimum estimate as it ignores losses due to death, predation or escapement and does not account for fishes which are counted and then die or escape from the traps and are then replaced by conspecifics during the interval between observations.

Results of these observation dives have been reported by Munro et al. (1971) and Munro (1974) and are not further discussed in this report.

DATA ANALYSIS

The inshore and offshore trap catches were analyzed with two major objectives in mind:

1. To determine the catch rates and species composition of samples taken from different areas, and
2. To collect data pertaining to the biology of individual species.

The data from trap catches from both Port Royal and offshore areas were coded and stored on magnetic disc. Data retrieval and computations were done on an I.B.M. 1620 computer at the Mathematics Department, U.W.I., Mona. The coded information included location fished, data on hauling, soak time, trap type and units of gear used, depth, and the numbers and weight of each species caught. At Port Royal, catches from individual traps were recorded separately and were thus coded. On the other hand, traps hauled from individual locations offshore had been set in fleets and the catches taken each day from similar trap types set for the same soak were recorded and coded together. Data from traps that had been damaged by large fish, e.g., sharks, or holed by any other means were not used.

AVAILABILITY AND EXPRESSION OF FISHING EFFORT

The model developed by Munro (1974) to describe the build-up of the catch in traps states that daily escapement of fishes from traps is a fixed proportion of the number of fishes contained within a trap and that, provided the daily rate of ingress is constant, the catch will reach an asymptote at which time ingress is equalled by escapement. Values of catch per day soaked (used as a measure of effort) are meaningless because of the asymptotic curve, and an index of availability equal to the mean daily ingress into traps, can be calculated to provide a useful comparative index of stock densities.

The availability value for each species in each trap catch was computed using the formula

$$\bar{A} = \frac{pC_s}{r(1 - e^{-Rs})}$$

where C is the catch taken after a soak of s days, p = probability of escape and R = coefficient of the rate of retention (r). The values p = 0.116 and r = 0.884 were used in the computations, derived from the underwater

observations of catch and ingress of *all* species combined (c.f. Munro 1974).

For example, if an unbaited Z trap soaked for 6 days produced a catch of 30 fishes, the availability would be

$$\begin{aligned} \bar{A} &= \frac{0.116 \times 30}{0.884 \times (1 - e^{-0.123 \times 6})} \\ &= \frac{3.48}{0.994 \times 0.523} \\ &= \frac{3.48}{0.4621} = 7.53 \text{ fishes/day} \end{aligned}$$

Thus, an average of about 7.5 fishes would enter the trap each day, giving a total ingress of 45 fishes, of which 15 will escape before the trap is hauled.

There was some interspecific variation in retention rates which appeared to vary between r = 0.970 and r = 0.777. The value of r = 0.884 is merely the average rate of retention of members of the fish community at Port Royal, and would only be an approximation for other communities. Also, as some species are more adept than others at escaping, the availability of species with high escapement rates will be underestimated when the average value of r = 0.884 is used in the above equation. Similarly the availability of species with low escapement rates will be overestimated.

The availability is the most accurate expression presently available for describing the abundance of the catchable component of trap fish stocks, and all data for the nearshore reefs are given in these terms.

In offshore areas, in which baited traps of various types were used, the rates of ingress are also influenced by the amount of bait used and the rate at which it is consumed (see Munro 1974 for further details). The rates of escapement might also differ owing to the different species composition and will differ according to trap designs. Availability indices therefore cannot be calculated and all results are given in terms of the catch of a hexagonal trap (Fig. 5.2) set for 24 hours. Effort data have therefore been adjusted on an empirical basis derived from comparative fishing trials. Table 5.1 shows the relative catching powers of various trap types soaked for one to three days. These data are derived from Munro (1974) and from previously unpublished data pertaining to the performance of baited hexagonal traps and to the effects of soak.

Thus, a Z trap soaked for 24 hours will be expected to produce a catch 1.45 times greater than a hexagonal trap soaked for the same period. An S trap soaked for 3 days would produce a catch 2.53 times greater than a hexagonal trap soaked for 24 hours. For example, the effective effort of a fleet of 20 Z traps soaked for two days, is equivalent to 20 x 2.61 = 52.2 hexagonal traps set for 24 hours.

All catch per unit effort and fishing effort data pertaining to offshore areas are given in terms of hexagonal traps soaked for 24 hours.

Catch Composition and Catch Per Unit of Effort

The trap fishing effort of the project yielded a catch of 48,040 fishes and crustaceans weighing 9,311 t. About 25% of the tonnage was taken using small craft in nearshore areas and 75% by the *R. V. Caranx* at oceanic banks and other offshore areas.

Approximately 120 species of fish and crustaceans were represented in the catches.

NEARSHORE AREAS

The 995 traps set at the Port Royal Reefs for various soak periods and in depths between 1.5 m and 25.9 m, caught 12,449 fishes weighing 1,910 kg, as well as 814 crustaceans weighing 467 kg. The fishes were represented by 106 species and the crustaceans comprised 4 species. In addition, two unidentified fishes weighing 2.53 kg were caught.

A substantial portion of the effort was devoted to experimental fishing with traps of various types, unbaited and with different baits and in a variety of areas. In order to reduce the possible bias in the catches from different trap types and to standardize the effort, further consideration is given only to data obtained from 547 unbaited Z and S traps set on Nassau and Yahoo reefs. These 547 traps were hauled after an average period of 15.7 days.

Catch Composition

A total of 8,068 fishes and crustaceans weighing 1,439.84 kg were caught in S and Z traps at Nassau and Yahoo reefs. The catch was made up of 97 species of fish weighing 1,117.25 kg and 4 crustacean species weighing 322.59 kg. The numbers, weight, mean availability and percentage composition of all species caught are given in Table 5.2.

The families comprising more than 1% of the total weight caught are shown in Table 5.3. The Scaridae (parrotfishes), Pomadasyidae (grunts) and Acanthuridae (surgeonfishes) made up 45.0% of the total weight caught, while the Palinuridae (spiny lobsters) and Majiidae (spider crabs) comprised an additional 22.4% of

Table 5.1. Catching power of various types of traps soaked for periods of 1 to 3 days, relative to hexagonal traps set for 24 hours. Data taken in part from Munro 1974, Table 6.

Trap type	Soak (days)		
	1	2	3
Hexagonal	1.0	1.80	2.30
Dollar	0.82	1.48	1.89
Midi trap	0.69	1.24	1.59
S trap	1.10	2.00	2.53
Z trap	1.45	2.61	3.34

the total weight. Eighteen species each comprised more than 1% of the total weight of fishes and crustaceans available to the traps and 21 species each comprised more than 1% of the total numbers available (Tables 5.4 and 5.5). No single species comprised more than 12% of the total catch.

Catch Per Unit Effort and Availability

Monthly trap catches and fishing effort are summarized in Table 5.6. The mean catch per trap varied between 1.17 kg and 3.81 kg, mostly in response to variations in soak.

Table 5.6 also shows the mean monthly availability, calculated in accordance with methods described previously. Several monthly peaks are apparent and the greatest availability is generally from December to March and May to July, and lowest in August to November. Individual monthly peaks are usually generated by the influx of particular species, either as recruits or as a general movement into the area. Changes in availability of particular species are discussed, where appropriate, in Chapters 6-16.

The average of all monthly values is 435 g/day. Average availability in 1970 was 443 g and declined only slightly to 426 g in 1971, suggesting that the project's fishing activities were not having a significant impact on the overall biomass of reef fish at Yahoo and Nassau Reefs.

The asymptotic catch, C_{∞} , is the catch which will accumulate in a trap which is soaked for an extended period of time and is given by the equation

$$C_{\infty} = A r/p \quad (\text{Munro 1974})$$

The average value of C_{∞} is thus $435 \times 0.884/0.116 = 3,315$ g.

The average catch after a 7-day soak is given by the equation

$$C_s = \frac{Ar(1 - e^{-Rs})}{p} \quad (\text{Munro 1974})$$

and amounts to only 1,917 g, a considerable portion of which will be composed of small fishes of negligible value.

OFFSHORE AREAS

The 38 trap fishing cruises were conducted between February 1971 and February 1973. The areas fished (see Figs. 2.2 and 3.2) were Pedro Bank (25 cruises), California Bank (6 cruises), South Jamaica Shelf (5 cruises), North Jamaica Shelf (1 cruise) and the Morant Cays (1 cruise). The results of these cruises are summarized in Table 5.7.

Table 5.2. Summary of catches made at Nassau and Yahoo Reefs near Port Royal, Jamaica, between January 1970 and December 1971. Data are derived from 547 Z or S traps soaked for an average of 15.7 days each, giving a total of 8,596 trap-nights. Availability is calculated according to the methods of Munro (1974) and gives an estimate of the number (A_n) or weight (A_w) of each species which will enter 1,000 traps in one night. The average daily rate of retention of fish in the traps is 0.884.

Species	Catch				Availability		Mean weight W_c (g)
	by number C	% by number %C	by weight W(kg)	% by weight %W	by number A_n	by weight A_w	
<i>Ginglymostoma cirratum</i>	1	.01	1.69	.11	.3	.51	1,690
<i>Urolophus jamaicensis</i>	49	.60	11.81	.82	13.7	3.30	241
<i>Synodus intermedius</i>	2	.02	.85	.05	.6	.26	425
<i>Gymnothorax funebris</i>	5	.06	6.40	.44	1.4	1.79	1,280
<i>G. moringa</i>	6	.07	5.26	.36	1.7	1.49	876
<i>G. vicinus</i>	1	.01	.80	.05	.3	.24	800
<i>Holocentrus ascensionis</i>	14	.17	1.66	.11	3.9	.46	118
<i>H. rufus</i>	188	2.33	16.29	1.13	52.7	4.56	86
<i>Myripristis jacobus</i>	3	.03	.15	.01	.8	.04	50
<i>Aulostomus maculatus</i>	5	.06	1.52	.10	1.4	.43	304
<i>Sphyrna barracuda</i>	3	.03	2.66	.18	.8	.71	886
<i>Polydactylus virginicus</i>	1	.01	.14	+	.3	.04	140
<i>Bothus lunatus</i>	1	.01	.11	+	.3	.03	110
<i>Cephalopholis fulva</i>	6	.07	1.24	.08	1.7	.34	206
<i>Petrometopon cruentatum</i>	88	1.09	14.73	.99	24.7	4.02	162
<i>Epinephelus striatus</i>	10	.12	9.30	.64	2.8	2.60	930
<i>E. guttatus</i>	107	1.32	30.17	2.09	30.0	8.46	281
<i>E. itajara</i>	1	.01	28.93	2.00	.3	8.68	28,930
<i>Mycteroperca bonaci</i>	7	.08	11.97	.83	2.0	3.42	710
<i>M. cidi</i>	1	.01	2.96	.20	.3	.83	2,960
<i>Hypoplectrus indigo</i>	15	.18	.81	.05	4.2	.23	54
<i>H. puella</i>	1	.01	.04	+	.3	.01	40
<i>H. nigricans</i>	1	.01	.04	+	.3	.01	40
<i>Priacanthus cruentatus</i>	8	.09	.89	.06	2.2	.24	111
<i>Caranx ruber</i>	129	1.59	15.45	1.07	36.2	4.33	119
<i>C. hippos</i>	1	.01	2.30	.15	.3	.69	2,300
<i>C. bartholomaei</i>	9	.11	1.35	.09	2.5	.38	150
<i>Selene vomer</i>	1	.01	.23	.01	.3	.07	230
<i>Lutjanus mahogoni</i>	13	.16	1.91	.13	3.6	.53	146
<i>L. synagris</i>	27	.33	4.50	.31	7.6	1.27	166
<i>L. analis</i>	2	.02	4.91	.34	.6	1.47	2,455
<i>L. jocu</i>	15	.18	6.97	.48	4.2	1.95	464
<i>L. apodus</i>	66	.81	13.11	.91	18.5	3.67	198
<i>L. griseus</i>	7	.08	2.88	.20	2.0	.82	411
<i>Ocyurus chrysurus</i>	73	.90	8.53	.59	20.5	2.39	116
<i>Haemulon aurolineatum</i>	11	.13	.61	.04	3.1	.17	55
<i>H. flavolineatum</i>	168	2.08	12.18	.84	47.1	3.42	72
<i>H. album</i>	1	.01	.14	+	.3	.04	140
<i>H. plumieri</i>	910	11.27	128.33	8.91	255.1	35.97	141
<i>H. carbonarium</i>	5	.06	.68	.04	1.4	.19	136
<i>H. sciurus</i>	220	2.72	42.21	2.93	61.7	11.83	191
<i>H. parra</i>	1	.01	.20	.01	.3	.06	200
<i>H. bonariense</i>	68	.84	7.26	.50	19.1	2.03	106
<i>H. macrostomum</i>	46	.57	11.44	.79	12.9	3.21	248
<i>Anisotremus virginicus</i>	73	.90	8.94	.62	20.5	2.51	122
<i>A. surinamensis</i>	16	.19	7.82	.54	4.5	2.20	488
<i>Calamus penna</i>	2	.02	.58	.04	.6	.17	290
<i>C. calamus</i>	6	.07	1.63	.12	1.7	.46	271
<i>C. pennatula</i>	22	.27	4.18	.29	6.2	1.17	190
<i>Calamus spp.</i>	1	.01	.20	.01	.3	.06	200
<i>Archosargus rhomboidalis</i>	1	.01	.18	.01	.3	.05	180
<i>Bairdiella batabana</i>	47	.58	6.11	.42	13.2	1.71	130
<i>Gerres cinereus</i>	68	.84	9.62	.66	19.1	2.69	141
<i>Equetus acuminatus</i>	4	.04	.32	.02	1.1	.09	80

Continued

Table 5.2 (continued)

Species	Catch				Availability		Mean weight W _c (g)
	by number C	% by number %C	by weight W(kg)	% by weight %W	by number A _n	by weight A _w	
<i>E. punctatus</i>	7	.08	1.20	.08	2.0	.34	171
<i>Mulloidichthys martinicus</i>	49	.60	8.46	.58	13.7	2.37	172
<i>Pseudupeneus maculatus</i>	80	.99	10.59	.73	22.4	2.97	132
<i>Chaetodipterus faber</i>	61	.75	32.59	2.26	17.1	9.13	534
<i>Holacanthus tricolor</i>	21	.26	2.62	.18	5.9	.73	124
<i>H. ciliaris</i>	46	.57	13.08	.90	12.8	3.67	284
<i>Pomacanthus paru</i>	1	.01	.24	.01	.3	.07	240
<i>P. arcuatus</i>	131	1.62	49.33	3.42	36.7	13.81	376
<i>Chaetodon ocellatus</i>	1	.01	.07	+	.3	.02	70
<i>C. capistratus</i>	381	4.72	9.63	.66	106.8	2.69	25
<i>C. striatus</i>	26	.32	1.00	.06	7.3	.28	38
<i>C. sedentarius</i>	5	.06	.14	+	1.4	.04	28
<i>Dactylopterus volitans</i>	4	.04	.91	.06	1.1	.26	227
<i>Eupomacentrus fuscus</i>	5	.06	.13	+	1.4	.04	26
<i>Abudefduf saxatilis</i>	546	6.76	32.27	2.24	153.0	9.04	59
<i>Lachnolaimus maximus</i>	26	.32	9.32	.64	7.3	2.61	358
<i>Bodianus rufus</i>	4	.04	.69	.04	1.1	.19	172
<i>Clepticus parrae</i>	1	.01	.12	+	.3	.03	120
<i>Halichoeres radiatus</i>	3	.03	.88	.06	.8	.25	293
<i>Scarus vetula</i>	8	.09	1.21	.08	2.2	.34	151
<i>S. taeniopterus</i>	4	.04	.68	.04	1.1	.19	170
<i>S. croicensis</i>	89	1.10	7.63	.52	24.9	2.14	85
<i>S. coeruleus</i>	42	.52	8.19	.56	11.8	2.29	195
<i>S. guacamaia</i>	5	.06	5.66	.39	1.4	1.59	132
<i>S. coelestinus</i>	45	.55	11.28	.78	12.6	3.16	250
<i>Sparisoma rubripinne</i>	2	.02	.34	.02	.6	.09	170
<i>S. chrysopterym</i>	369	4.57	62.97	4.37	103.4	17.64	170
<i>S. aurofrenatum</i>	333	4.12	30.95	2.14	93.3	8.67	92
<i>S. viride</i>	628	7.78	111.50	7.74	176.0	31.25	177
<i>Acanthurus coeruleus</i>	638	7.90	63.03	4.37	178.8	17.65	98
<i>A. chirurgus</i>	520	6.44	68.04	4.72	145.8	18.95	130
<i>A. bahianus</i>	414	5.13	26.34	1.82	116.0	7.38	63
<i>Balistes vetula</i>	26	.32	9.66	.67	7.3	2.71	371
<i>Cantherhines pullus</i>	37	.45	2.72	.18	10.4	.80	73
<i>Alutera scripta</i>	13	.16	7.78	.54	3.6	2.18	598
<i>A. schoepfii</i>	13	.16	5.31	.36	3.6	1.49	408
<i>Acanthostracion quadricornis</i>	83	1.02	12.29	.85	23.3	3.44	148
<i>A. polygonius</i>	13	.16	3.13	.21	3.6	.88	240
<i>Lactophrys triqueter</i>	74	.91	4.88	.33	20.7	1.37	65
<i>L. bicaudalis</i>	73	.90	7.85	.54	20.5	2.20	107
<i>Diodon hystrix</i>	16	.19	13.25	.92	4.5	3.71	828
<i>D. holacanthus</i>	142	1.76	22.58	1.56	39.8	6.33	159
<i>Chilomycterus antennatus</i>	10	.12	1.92	.13	2.8	.54	192
<i>Panulirus argus</i>	298	3.69	147.93	10.27	83.5	41.47	496
<i>P. guttatus</i>	65	.80	9.13	.63	18.2	2.56	140
<i>Mithrax spinosissimus</i>	160	1.98	158.97	11.04	44.8	44.56	993
<i>Scyllaroides aequinoctialis</i>	13	.16	6.56	.45	3.6	1.84	504
Totals	8,068	99.99	1,439.84	99.99			
Means					2,261.5	403.46	178

Species Composition

Eighty-eight different species of fish were caught on Pedro Bank and 47 species on California Bank. Altogether a total of 92 species were caught on these two banks.

Table 5.3. Major families represented in the catches of unbaited Z and S traps set at Nassau and Yahoo Reefs, Port Royal.

Family	% Weight	% Numbers
1. Scaridae	17.4	19.1
2. Pomadasyidae	15.6	18.1
3. Acanthuridae	12.0	20.0
4. Palinuridae	11.5	4.4
5. Majiidae	10.9	1.8
6. Chaetodontidae		
Angelfishes	5.0	2.5
Butterflyfishes	0.8	5.3
7. Serranidae	4.7	2.9
8. Pomacentridae	2.6	7.3
9. Lutjanidae	2.6	2.4
10. Diodontidae	2.5	1.9
11. Ostraciontidae	2.1	3.0
12. Ehippidae	1.9	0.6
13. Balistidae	1.6	1.0
14. Mullidae	1.4	1.6
15. Holocentridae	1.4	2.6
16. Carangidae	1.3	1.8
17. 14 other families (no species comprising more than 1% of total catch by weight).	4.4	3.3

Table 5.4. Species comprising more than 1% of the total weight of fishes and crustaceans available to unbaited S and Z traps at Nassau and Yahoo Reefs, Port Royal.

Species	Availability x 1,000 (kg)	%
1. <i>Mithrax spinosissimus</i>	44.6	11.0
2. <i>Panulirus argus</i>	41.5	10.3
3. <i>Haemulon plumieri</i>	36.0	8.9
4. <i>Sparisoma viride</i>	31.3	7.7
5. <i>Acanthurus chirurgus</i>	19.0	4.7
6. <i>S. chrysopterum</i>	17.6	4.4
7. <i>A. coeruleus</i>	17.7	4.4
8. <i>Pomacanthus arcuatus</i>	13.8	3.4
9. <i>H. sclurus</i>	11.8	2.9
10. <i>Chaetodipterus faber</i>	9.1	2.3
11. <i>Abudefduf saxatilis</i>	9.0	2.2
12. <i>S. aurofrenatum</i>	8.7	2.1
13. <i>Epinephelus guttatus</i>	8.5	2.1
14. <i>Acanthurus bahianus</i>	7.4	1.8
15. <i>Diodon holacanthus</i>	6.3	1.6
16. <i>Holocentrus rufus</i>	4.6	1.1
17. <i>Caranx ruber</i>	4.3	1.1
18. <i>Petrometopon cruentatum</i>	4.0	1.0

The list of species and their occurrence in traps at different locations is given in Table 5.8.

Those species comprising more than 4% by weight of the overall catch from locations visited on three or more occasions are listed in Table 5.9.

Balistes vetula was the dominant species in catches from the offshore banks, comprising between 15% (SW Pedro) and 50% (Pedro Cays) of the total weight caught. Twelve other species comprised more than 4% of the trap catches in one or more of the offshore areas as shown in Table 5.9.

Table 5.10 shows the percentage composition of the catch (by weight) according to families and includes all fish families which contributed 1.0% or more of the weight of the catch taken in any one area. Also included in the table is an indication of the market category to which the various families belong. The Balistids are overwhelmingly preponderant in all areas except California Bank and the South Jamaica Shelf (where Holocentrids predominate) and the Southeast Spur of Pedro Bank where Pomadasyids are the largest component of the catch.

Catch Per Unit Effort

The catch rates of individual cruises to California Bank, the South Jamaica Shelf and the nine locations on Pedro Bank have been plotted in Fig. 5.3. Although there was a high degree of variability between individual

Table 5.5. Species comprising more than 1% of the total numbers of fishes and crustaceans available to unbaited S and Z traps at Nassau and Yahoo Reefs, Port Royal.

Species	Availability x 1,000 (number)	%
1. <i>Haemulon plumieri</i>	255	11.3
2. <i>Acanthurus coeruleus</i>	179	7.9
3. <i>Sparisoma viride</i>	176	7.8
4. <i>Abudefduf saxatilis</i>	153	6.8
5. <i>Acanthurus chirurgus</i>	146	6.4
6. <i>A. bahianus</i>	116	5.1
7. <i>Chaetodon capistratus</i>	107	4.7
8. <i>Sparisoma chrysopterum</i>	103	4.6
9. <i>S. aurofrenatum</i>	93	4.1
10. <i>Panulirus argus</i>	84	3.7
11. <i>H. sclurus</i>	62	2.7
12. <i>Holocentrus rufus</i>	53	2.3
13. <i>Haemulon flavolineatum</i>	47	2.1
14. <i>Mithrax spinosissimus</i>	45	2.0
15. <i>Diodon holacanthus</i>	40	1.8
16. <i>Pomacanthus arcuatus</i>	37	1.6
17. <i>Caranx ruber</i>	36	1.6
18. <i>Epinephelus guttatus</i>	30	1.3
19. <i>Scarus croicensis</i>	25	1.1
20. <i>Petrometopon cruentatum</i>	25	1.1
21. <i>Acanthostracion quadricornis</i>	23	1.0

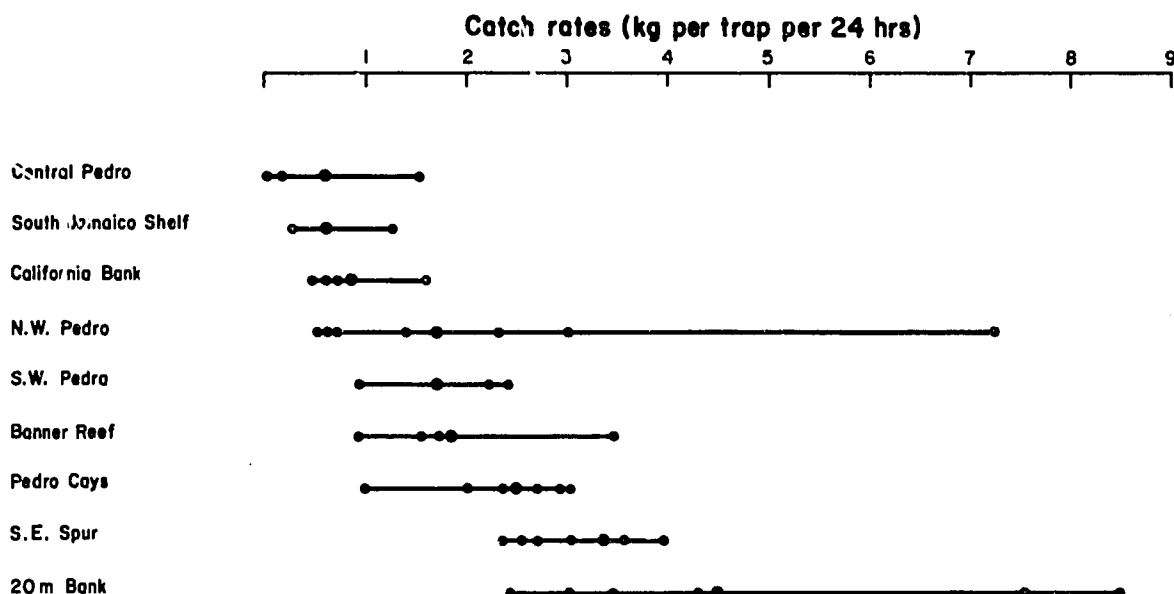


Fig. 5-5

Fig. 5.3. Mean catch rates in traps for various cruises (small points) and mean rates for all cruises (large points) at various offshore locations (see Figs. 2.2 and 3.2). Rates are expressed as kg per baited hexagonal trap (Fig. 5.2) soaked for 24 hours.

Table 5.6. Summary of monthly trap catches of unbaited Z and S traps set on Nassau and Yahoo Reefs, Port Royal Reefs, Jamaica.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
1970												
No. of traps	6	13	13	33	57	36	41	25	47	53	50	32
Total soak (days)	12	112	170	305	739	564	577	431	603	718	757	474
Mean soak (days)	2.0	8.6	13.1	9.2	13.0	15.7	14.1	17.2	12.8	13.5	15.1	14.8
No. of species	10	35	27	52	66	48	53	49	59	53	57	48
No. of fish	26	246	186	494	1,311	553	495	496	750	709	665	414
Wt. of fish (kg)	7.05	38.56	30.42	73.67	216.95	80.99	96.07	72.11	103.54	109.32	116.06	75.29
No. per trap	4.3	18.9	14.3	15.0	23.0	15.4	12.1	19.8	16.0	13.4	13.3	12.9
Wt. per trap (kg)	1.17	2.97	2.34	2.23	3.81	2.25	2.34	2.92	2.20	2.06	2.32	2.35
Availability (kg)	703	596	383	431	626	345	373	435	364	333	360	368
1971												
No. of traps	13	3	8	9	19	5	12	7	13	6	23	13
Total soak (days)	273	45	121	140	275	81	382	182	176	155	599	241
Mean soak (days)	21.0	15.0	15.1	15.5	14.5	16.2	31.8	26.0	13.5	25.8	26.0	18.5
No. of species	36	20	26	24	41	22	24	16	38	28	41	34
No. of fish	245	61	134	107	142	96	144	43	168	73	188	159
Wt. of fish (kg)	44.24	10.00	25.49	23.05	61.54	14.77	44.46	15.37	30.67	13.09	57.49	40.07
No. per trap	18.8	20.3	16.7	11.9	7.5	19.2	12.0	6.1	12.9	12.2	8.2	12.2
Wt. per trap (kg)	3.40	3.33	3.19	2.56	3.24	2.95	3.70	2.19	2.36	2.18	2.50	3.08
Availability (g)	482	519	496	394	510	448	495	300	382	298	342	450

Table 5.7. *R. V. Caranx*. Summary of trap catches, effort expended and catch per unit effort, by area and cruise. Effort is expressed in terms of hexagonal trap-nights.

Date	Number of traps	Soak (days)	Effort (trap-nights)	Number of fishes caught	Weight of fishes caught (kg)	Mean weight \bar{W}_c (g)	Numbers per (trap-night)	Weight per trap-night (kg)
(a) Pedro Cays								
8.2.71	20	1	21.5	545	66.33	121	25.4	3.08
21.4.71	37	1-2	51.1	302	52.10	173	5.9	1.02
1.12.71	98	1	91.1	2,309	286.36	124	25.3	3.14
25.7.72	58	1-3	80.2	1,206	220.44	183	15.0	2.75
9.10.72	20	2	36.0	589	109.99	187	16.4	3.06
4.12.72	47	1-3	75.1	1,095	179.16	164	14.6	2.39
22.2.73	27	2	48.6	525	102.82	196	10.8	2.12
Totals			403.6	6,572	1,017.2			
Means						155	16.3	2.52
(b) Banner Reef								
8.2.71	10	1	10.1	36	17.81	495	3.6	1.76
31.1.72	89	1	79.5	1,670	277.57	166	21.0	3.49
28.8.72	88	1-3	118.5	1,043	185.26	178	8.8	1.56
6.11.72	49	2-3	99.5	546	92.96	170	5.5	0.93
Totals			307.6	3,295	573.6			
Means						174	10.7	1.87
(c) 20 M. Bank								
6.5.71	32	1	22.1	685	188.71	275	31.0	8.54
13.12.71	87	1	70.3	2,519	531.77	211	35.8	7.56
11.5.72	106	1-2	116.0	2,994	505.56	169	25.8	4.35
17.8.72	69	1-2	76.7	1,025	188.25	184	13.4	2.45
23.10.72	20	3	46.0	259	140.05	541	5.6	3.04
8.1.73	39	1-2	56.2	1,124	194.84	173	20.0	3.47
Totals			387.3	8,606	1,749.18			
Means						203	22.2	4.52
(d) N.W. Pedro								
6.11.72	32	2	55.3	744	167.18	225		
21.5.71	87	1	60.0	683	436.21	639	11.4	7.27
14.2.72	95	1	85.2	390	197.53	506	4.6	2.32
27.6.72	60	1	52.8	103	33.46	325	2.0	.63
24.9.72	78	2-3	151.5	318	97.69	307	2.1	.64
6.11.72	32	2	55.3	744	167.18	225	13.4	3.02
19.11.72	68	1-3	128.0	251	72.61	289	2.0	.57
25.1.73	69	1-3	115.8	316	161.55	511	2.7	1.40
Totals			703.9	3,549	1,166.24			
Means						416	4.3	1.80
(e) S.W. Pedro								
11.5.72	42	1	36.0	325	80.22	247	9.0	2.23
17.8.72	55	1-2	75.4	387	70.60	182	5.1	.94
23.10.72	30	3	59.0	351	141.91	404	5.9	2.41
Totals			170.4	1,063	292.73			

Continued

Table 5.7. (continued)

Date	Number of traps	Soak (days)	Effort (trap-nights)	Number of fishes caught	Weight of fishes caught (kg)	Mean weight \bar{W}_c (g)	Numbers per (trap-night)	Weight per trap-night (kg)
Means						0.275	6.2	1.72
(f) S.E. Spur (incl. Eastern Pedro)								
16.1.72	75	1	62.1	670	161.25	240	10.8	2.60
25.5.72	70	2	112.0	3,323	456.78	137	29.7	4.08
10.7.72	121	1-3	183.5	2,073	433.94	209	11.3	2.36
9.10.72	50	2-3	120	1,699	325.81	192	14.1	2.72
4.12.72	29	2	33.4	542	104.10	192	16.1	3.12
22.2.73	30	3	66.7	1,183	239.99	203	17.7	3.60
Totals			577.7	9,490	1,721.87			
Means						181	16.4	2.98
(g) Central Pedro								
23.10.72	33	1	31.7	217	48.53	224	6.8	1.53
9.11.72	33	1	32.1	28	6.06	216	0.9	.19
8.1.73	28	1	28.0	6	0.50	83	0.2	.02
Totals			91.8	251	55.09			
Means						219	2.7	0.60
(h) California Bank								
8.11.71								
24.11.71	87	1	82.7	988	135.07	137	11.9	1.63
3.3.72	59	1	64.4	366	50.65	138	5.7	.79
20.6.72	55	1-2	64.8	399	47.63	119	6.2	.73
13.9.72	78	1-3	115.9	560	52.95	94	4.8	.46
19.12.72	39	1-2	62.2	191	40.69	213	3.1	.65
Totals			390	2,504	326.99			
Means						131	6.4	0.84
(i) South Jamaica Shelf								
25.1.71	4	1	2.8	30	5.08	169	10.7	1.81
-3.71	12	1-13	71.7	94	18.70	199	1.3	.26
13/28.3.72 & 6.4.72	79	1	47.6	266	61.09	230	5.6	1.28
Totals			122.1	390	84.87			
Means						218	3.2	0.62
(j) Other Areas								
11.1.71 (Morant Cays)	14	1	19.6	143	21.85	153	7.3	1.11
30.3.71 (Dis- covery Bay North Jamaica Shelf)	25	1-4	62	60	16.04	267	1.0	0.26

catch rates from certain areas, the 20-m Bank and SE Spur appeared to be more productive than the other areas, but good catches were taken in all other parts of Pedro Bank on occasions. The catch rates on the South Jamaica Shelf and at California Bank reflect the high fishing intensity in these areas.

Table 5.11 gives details of the average catch rates, together with the proportions of the various market categories. Catch rates on Pedro Bank varied very widely, particularly at NW Pedro and 20-m Bank.

DISCUSSION

Distribution of Stocks and Availability

The data presented in the preceding pages indicate that there is little uniformity in the distribution of available stocks for trap fishing. The overall impression gained from the data (Fig. 5.3 and Table 5.11) is that the abundance of coral cover is the main feature determining the distribution of exploitable stocks. Thus Banner Reef, the Pedro Cays, 20-m Bank and the South-eastern Spur, all areas of rugged bottom, provided the greatest catch rates. The areas fished at these locations are almost entirely within the 30-m isobath and all lie on the southern and eastern edges of Pedro Bank (Table 5.11). The SE Spur and 20-m Bank produced the most valuable catches (Table 5.11). Good catches of grunts and spiny lobsters (*Panulirus argus*) were a major feature of the SE Spur.

The deeper areas of the bank, lying on the western and northern margins produced fairly modest catches, but with a greater admixture of "quality" and "common" fish than Banner Reef and the Pedro Cays. The latter areas are relatively shallow (most depths fished were less than 15 m) and produced large catches of low-value fish, particularly *Balistes vetula*.

The central portions of Pedro Bank appear to be uniformly flat and sandy and with very sparse coral. Catches were extremely low and of poor quality. Catch rates at California Bank were about half those obtained at SW and NW Pedro (which are of similar depths) and lacked significant quantities of the more valuable species of fishes. It is believed that this reflects the quite heavily exploited state of California Bank. Catch rates on the South Jamaica Shelf equivalent to 618 g/hexagonal trap/day were more than twice as great as those taken at the Port Royal Reefs (equivalent to about 300 g/hexagonal trap/day), reflecting the extreme fishing pressure on the nearshore reefs. Nevertheless, catch rates are much larger than those obtained on the narrow northern shelf of Jamaica where catch rates of less than 100 g/trap/day are the norm.

VIABILITY OF OFFSHORE COMMERCIAL FISHERIES

Catch Rates

The results given in Table 5.11 and Fig. 5.3 give some indication of the *initial* catch rates which might be

expected by commercial vessels fishing the shallow (less than 50 m) shelves and banks near to Jamaica. It is emphasized that because of the exploratory and experimental nature of the work done during this project, no attempt was made to remain in areas which offered good fishing, nor to return to areas which had previously yielded good catches. It would be expected that commercial vessels might concentrate their efforts, at least initially, on the most productive areas (20-m Bank or the SE Spur) where average catch rates of about 4 kg/trap/24 hours could be expected.

Traps which were holed by sharks or other agencies were not included in our analyses. A commercial operator would have to take such factors into account, but this is definitely not a factor of major importance.

Commercial vessels would probably need to use stackable (Munro 1973) or collapsible (e.g., High and Beardsley 1970) traps to have any chance of hauling sufficient traps to meet operating costs. Clearly, the smallest possible vessel relative to trap-carrying capacity is required if profits are to be maximized.

Use of Bait

The traps used during this project were normally lightly baited with unmarketable fish or with punctured cans of cat food. There was little obvious difference between the catches in unbaited traps and those which were lightly baited.

Wolf and Chislett (1974) used 2.3 to 11.4 kg (5 to 25 lb) of imported bait in each Z trap fished on Pedro Bank and obtained daily catches (one-day soak) of 7.7 to 25.4 kg (17 to 56 lb). Most of their fishing was done with limited numbers of traps set on the upper slope of the deep reef (see Chapter 3 for details of bank morphology). Under such conditions, the value of the bait might well have been greater than the value of the catch, but the data do suggest that catch rates might be dependent to a large extent upon the amount of bait used. Table 5.11 shows that traps on Pedro Bank yielded only 106 to 227 g of unmarketable fish per trap/24 hours. If the undersized elements of the trash fish catch were not marketed and were also retained as bait, the traps might just sustain the bait requirements of the fleet. Increased catches of better-quality fish would have to outweigh the value of the trash fish used as bait if such an operation were to be successful. Additionally, Wolf and Chislett (1974) commented that they found trash fish relatively ineffective as bait.

The foregoing highlights the need for an inexpensive source of bait.

The Economics of Trap Fishing

Munro (1974) has described the mode of operation of Antillean-style fish traps by means of a simple mathematical model. The important points are that escape-ment of fishes from traps is quite high (about 12%/day for Z traps) and is inversely proportional to the size of

the traps and that catches will build up in traps until daily ingress of fishes balances escapement and thereafter remain static. If traps are baited, the ingress rates will be improved as long as bait remains in the trap but the rate of escapement will remain constant. This results in the catches reaching a peak around the time when the bait is exhausted (usually about 3 days) and thereafter declining. It is therefore essential that a vessel should operate sufficient traps to enable it to be fully occupied during each working day, without having to haul traps which have not been soaked for the optimum time.

If stackable traps are used, an efficiently operated vessel can haul and reset 100 traps per day in depths of 40 m or less. Considerably fewer traps can be operated if the deep-reef slopes are fished, owing to the difficulty of positioning the traps on the very steep and narrow sector of the 100 to 250-m zone (see Wolf and Chislett 1974).

In order to retain an optimum degree of mobility, a commercially operated vessel would need to be able to carry about 150 traps, enabling it to set a fleet of 300 traps in two return trips from shore and thereafter haul the traps on a 3-day cycle. This would suggest that vessels in the 18 to 23 m class would be required.

It is suggested that all vessels should also be equipped for hand-line or reef fishing and for trolling in order that benthic and pelagic species can be harvested when the opportunities arise. That is, bottom hand-lining or reef fishing could be done under calm or otherwise suitable conditions and trolling when schools of pelagic fish are sighted, or if weather conditions preclude hauling traps, and en route to and from the fishing grounds.

The foregoing points are emphasized because by any standards, the stock densities of trapable fish on the oceanic banks of the W. Caribbean are not large. Profitable commercial operations will be dependent upon careful advance planning, efficiently controlled operations, and upon operators making full use of opportunities for additional harvests of pelagic and line-caught fish. Fish and fuel prices, operating costs, wages and depreciation of vessels are relatively inflexible.

If vessels haul their traps on a 3-day cycle, average catches of at least 7.8 to 10.4 kg/trap should be attained at SE Spur and 20-m Bank, respectively. The least productive areas, NW and SW Pedro, should produce about 4.0 kg/trap. Thus, a vessel hauling 100 traps per day should produce an average minimum catch of 400 kg/day and an average of up to 1,040 kg/day in the most productive areas. Catch rates will decline as the fishery develops but the decline would need to be set against the higher average catch rates which would be attained by commercial vessels. From the analyses given in Chapter 18, it appears likely that maximum harvests would be attained when the catch/boat had fallen to about 75% of the initial catch rates, and that entry into the fishery beyond that point should be prohibited.

Munro (1977, and Chapter 18) has calculated that the maximum potential production by the offshore trap fishery would be 6,200 t and that the overall basic catch rate would be 2.725 kg/hexagonal trap/24 hours. This

rate would yield 6.25 kg/trap if hauled on a 3-day cycle. Thus, hauling 100 traps/day would produce 625 kg vessel/day. If the boats averaged 250 days fishing/year, each vessel would land 156.25 t/year and 40 vessels would give the calculated total catch. If, by virtue of greater efficiency, higher commercial catch rates are obtained, and the average catch per boat was greater than that cited above, the number of vessels permitted to enter the fishing should be proportionately reduced.

FUTURE RESEARCH REQUIREMENTS

Design and Development of Fish Traps

The stackable traps utilized by this project (Munro 1973) made it possible for the *R.V. Caranx* (a multi-purpose research vessel with a laboratory, trawl winch, electric fishing reels, etc), to carry up to 80 traps without undue difficulty, in limited deck and hold space. A more specialized vessel could carry much greater numbers of traps. The traps worked well, but for unknown reasons were 21% less efficient relative to their size than traditional designs. It has been suggested that the visual complexity of the traps' outlines might be a factor but this has not been investigated.

Escapement rates of 12%/day from Z traps (and possibly slightly higher for stackable traps) mean that a substantial portion of the catch escapes before a trap is hauled. Various devices to prevent fishes from escaping through the entrance funnels were tested, but all reduced the ingress of fish to an unacceptable level. Parlor traps, in which fishes enter two successive chambers, would reduce escapement dramatically (i.e., to 12% of 12% = 1.4%) but a stackable parlor trap remains to be devised. However, large parlor traps built on traditional lines (Munro, in prep.) are entirely feasible and should be tested for use in the nearshore fishery.

Damage to traps caused by sharks was not a major problem on Pedro Bank or in the nearshore fisheries but the possibilities of using less robust synthetic mesh materials have not been tested. Durability, ease of handling, construction and repair would appear to be the main advantages.

Hexagonal chicken-wire mesh with maximum apertures of 3.30 or 4.13 cm is used for trap construction in Jamaica. As the mesh is rigid, mesh selection is close to knife edge. A larger mesh size (6.60-cm max. aperture) has been advocated as a conservation measure (Chapter 18). It is fairly clear that this would not present any problem in the case of baited traps, but unbaited traps in which the smallest fishes act as bait for larger predators *might* suffer decreased catch rates. The Barbuda trap fishery uses 2-in (6.60-cm) maximum-aperture mesh with apparent success (Peacock 1976), but as a cautionary measure this might be investigated if it is intended that mesh-size regulations be introduced by the Jamaican authorities.

Table 5.8. Occurrence of species in trap catches at various sectors of Pedro Bank and at California Bank between January 1971 and February 1973.

	Pedro Cays	S.E. Spur	Banner Reef	20m Bank	S.W. Pedro	N.W. Pedro	Central Pedro	Portland RK and E. Pedro	Northern Edge	California Bank
<i>Ginglymostoma cirratum</i>	+	+	+		+	+		+		
<i>Urolophus jamalcensis</i>		+	+	+						
<i>Synodus intermedius</i>					+					
<i>Gymnothorax funebris</i>	+			+				+		
<i>G. moringa</i>	+		+	+	+	+		+	+	+
<i>G. vicinus</i>	+		+	+						
<i>Holocentrus ascensionis</i>	+	+	+	+	+	+	+	+	+	+
<i>H. rufus</i>	+	+	+	+	+	+		+	+	+
<i>Myripristis jacobus</i>	+	+		+	+	+			+	
<i>Aulostomus maculatus</i>				+	+	+				
<i>Sphyaena barracuda</i>	+	+		+			+	+		
<i>Bothus lunatus</i>		+		+	+					
<i>B. ocellatus</i>							+			
<i>Cephalopholis fulva</i>	+	+	+	+	+	+		+	+	+
<i>Petrometopon cruentatum</i>	+	+	+	+	+	+		+	+	+
<i>Alphestes afer</i>		+		+						
<i>Epinephelus striatus</i>			+	+	+	+		+		
<i>E. adscensionis</i>				+						
<i>E. guttatus</i>	+	+	+	+	+	+		+	+	+
<i>Mycteroperca tigris</i>		+	+					+		+
<i>M. venosa</i>	+		+	+	+	+				+
<i>Paranthias furcifer</i>										+
<i>Priacanthus cruentatus</i>				+						+
<i>P. arenatus</i>	+									+
<i>Malacanthus plumieri</i>	+	+	+	+	+			+		+
<i>Echeneis naucrates</i>						+				
<i>Caranx ruber</i>	+	+	+	+	+	+	+	+		+
<i>C. fusus</i>					+	+		+		
<i>C. latus</i>	+		+		+	+		+		
<i>C. bartholomaei</i>	+	+	+	+	+	+	+	+	+	+
<i>Seriola dumerilli</i>			+	+		+				
<i>Lutjanus vivanus</i>									+	
<i>L. buccanella</i>		+			+	+				
<i>L. jocu</i>					+	+				
<i>L. apodus</i>		+		+	+	+		+		+
<i>Ocyurus chrysurus</i>	+		+	+	+	+	+	+		
<i>Haemulon aurolineatum</i>	+		+	+	+	+	+	+		
<i>H. striatum</i>				+						+
<i>H. flavolineatum</i>	+	+	+	+		+		+	+	+
<i>H. melanurum</i>	+	+	+		+			+		
<i>H. album</i>	+	+	+	+		+	+	+		+
<i>H. chrysargyreum</i>	+	+							+	
<i>H. plumieri</i>	+	+	+	+	+	+	+	+	+	+
<i>H. carbonarium</i>	+	+						+		
<i>Calamus</i> spp.	+	+	+	+	+	+	+	+	+	
<i>Equetus acuminatus</i>	+	+		+				+		
<i>E. lanceolatus</i>										+
<i>E. punctatus</i>		+			+					
<i>Mulloidichthys martinicus</i>	+	+	+	+		+		+	+	+
<i>Pseudupeneus maculatus</i>	+	+	+	+	+	+		+	+	+
<i>Holocanthus tricolor</i>	+	+	+	+	+	+		+	+	+

Continued

Table 5.8 (continued)

	Pedro Cays	S.E. Spur	Banner Reef	20m Bank	X S.W. Pedro	N.W. Pedro	Central Pedro	Portland RK and E. Pedro	Northern Edge	California Bank
<i>H. ciliaris</i>	+	+	+	+	+	+		+		
<i>Pomacanthus paru</i>	+	+	+	+		+		+		+
<i>P. arcuatus</i>	+	+	+	+	+	+	+	+	+	+
<i>Chaetodon ocellatus</i>	+	+	+	+	+	+	+	+		+
<i>C. capistratus</i>	+	+	+	+	+	+		+	+	+
<i>C. striatus</i>	+	+	+		+	+	+	+	+	+
<i>C. sedentarius</i>		+		+		+		+		+
<i>Prognathodes aculeatus</i>								+		
<i>Microspathodon chrysurus</i>	+		+							
<i>Bodianus rufus</i>	+									
<i>Clepticus parrae</i>			+							+
<i>Halichoeres garnoti</i>								+		
<i>H. bivittatus</i>										+
<i>H. radiatus</i>	+	+								
<i>Scarus vetula</i>	+		+	+						
<i>S. taeniopterus</i>	+	+	+	+	+	+		+	+	+
<i>S. croicensis</i>	+			+						+
<i>S. coeruleus</i>	+	+			+	+				
<i>S. coelestinus</i>	+									
<i>Sparisoma chrysopterygum</i>	+		+							
<i>S. aurofrenatum</i>	+	+	+	+	+	+		+	+	+
<i>S. viride</i>	+		+							
<i>Acanthurus coeruleus</i>	+	+	+	+	+	+		+		+
<i>A. chirurgus</i>	+	+	+	+	+	+		+		+
<i>A. bahianus</i>	+	+	+	+	+	+		+	+	+
<i>Balistes vetula</i>	+	+	+	+	+	+	+	+	+	+
<i>B. capricornis</i>			+				+			
<i>Xanthichthys ringens</i>		+								+
<i>Melichthys niger</i>			+							+
<i>Canthidermis sufflamen</i>										+
<i>Cantherhines macrocerus</i>	+	+		+		+				+
<i>C. pullus</i>	+	+	+	+	+	+		+	+	+
<i>Aleutera scripta</i>	+	+	+	+	+	+				
<i>A. schoepfii</i>					+	+	+			
<i>Acanthostracion quadricornis</i>	+	+	+	+	+	+	+	+	+	+
<i>A. polygonus</i>	+	+	+	+	+	+	+	+	+	+
<i>Lactophrys triqueter</i>	+		+	+	+	+	+	+	+	
<i>L. bicaudalis</i>	+			+		+				
<i>Diodon hystrix</i>		+			+			+		
<i>D. holacanthus</i>	+		+	+	+	+				+
<i>Chilomycterus antillarum</i>		+								
Number of fish species	59	51	51	57	44	53	18	51	29	47
<i>Scyllaroides aequinoctialis</i>	+				+					
<i>Pinnulirus argus</i>	+	+	+	+	+	+		+		
<i>P. guttatus</i>	+		+							
<i>Mithrax spinosissimus</i>			+	+		+	+			+
Queen crab	+	+	+		+	+	+	+		
Box crab							+	+		
Number of crustacean species	4	2	4	2	3	3	3	3	0	1
Total number of species	63	53	55	59	47	56	21	54	39	48

Munro et al. (1971) found that Cuban-style S traps captured 25% more fish (by weight) than traditional Z traps, but insufficient data were available to establish the statistical validity of this difference. Subsequent investigations (Munro 1974) showed that efficiency of traps of equal height was proportional to the area covered by the trap (all traps had two identical entrance

funnels). At some stage it would, therefore, be desirable to compare sets of Z and S traps of identical volume and area. If the increased efficiency is demonstrable, a strong case exists for their introduction to the Jamaican fishery. Furthermore, S traps are easier and cheaper to construct and should increase profitability of the fishery.

Table 5.9. Percentage species composition of trap catches in various offshore areas fished between February 1971 and February 1973. List includes species which comprised more than 4% of the weight of the catch in any one area.

Species	Pedro Cays	SE Spur (incl. E. Pedro)	Banner Reef	20 m Bank	SW Pedro	NW Pedro (incl. N. edge)	California Bank	South Jamaica Shelf
<i>Holocentrus ascensionis</i>	3.6	3.4	8.0	1.8	4.2	5.0	9.1	3.2
<i>H. rufus</i>	3.4	6.4	2.5	4.4	0.7	0.2	15.6	10.1
<i>Cephalopholis fulvus</i>	5.9	3.4	3.7	8.3	2.8	1.9	7.8	2.4
<i>Epinephelus guttatus</i>	2.7	4.2	2.5	11.0	2.8	6.8	10.4	1.5
<i>Caranx ruber</i>	0.9	1.9	4.9	0.5	2.8	0.6	1.3	0.8
<i>C. bartholomaei</i>	0.9	+	0.3	0.	7.1	3.7	0.5	0
<i>Haemulon flavolineatum</i>	6.7	14.0	1.8	0.8	0	+	1.3	3.3
<i>H. plumieri</i>	1.6	4.5	7.4	5.2	8.5	1.2	0.2	2.6
<i>Pseudupeneus maculatus</i>	1.0	3.4	0.3	0.8	9.2	0.6	1.3	1.5
<i>Pomacanthus arcuatus</i>	3.2	2.6	6.2	3.6	2.1	2.5	+	0
<i>Acanthurus bahianus</i>	2.3	11.0	3.7	5.0	2.1	0.1	1.3	2.6
<i>Balistes vetula</i>	50.4	19.3	21.6	36.3	14.9	35.4	22.1	13.4
<i>Panulirus argus</i>	+	3.4	0.5	0.8	10.6	3.1	0	8.2
All other species	17.4	22.5	36.6	20.7	35.9	38.9	29.1	50.4
Number of species caught	63	53	55	59	47	56	48	44

Table 5.10. Percentage composition, by families, of trap catches in various offshore areas between February 1971 and February 1973. Catch rate is expressed in terms of lightly baited hexagonal traps fished for one night. Market classification is shown in the first column: U, unmarketable; T, trash; G, grunt; C, common; Q, quality; X, spiny lobsters.

Family	Market Group	Pedro Cays	Eastern Pedro and SE Spur	Banner Reef	20 m Bank	SW Pedro	SW Pedro	Calif. Bank	South Jamaica Shelf
Sharks & rays	U	.3	.5	1.1	+	.7	1.2	0	0
Muraenidae	U	2.3	0	.7	.5	1.6	.1	1.1	6.8
Holocentridae	T	8.0	9.7	13.8	7.3	3.7	5.4	28.7	14.0
Sphyraenidae	C	1.4	.2	0	.6	0	0	0	0
Serranidae	C	7.5	7.7	10.9	20.9	17.5	29.0	18.8	6.9
Carangidae	Q	2.1	1.9	9.5	3.4	11.4	8.0	1.8	.8
Lutjanidae	Q	.1	.8	.5	.4	4.7	1.8	.1	2.1
Pomadasyidae	G	7.8	25.5	10.2	7.9	12.9	3.5	2.2	8.5
Sparidae	C	.1	0	.3	.9	1.5	.6	0	.1
Sciaenidae	C	+	+	0	+	+	0	+	3.3
Mullidae	Q	3.2	6.0	1.4	1.1	10.5	1.1	2.5	2.0
Holacanthinae	T	4.3	6.5	7.8	6.1	3.9	3.7	.9	.2
Chaetodontinae	U	.8	4.5	3.8	1.7	1.7	1.0	2.8	1.2
Scaridae	T	3.1	.7	3.4	3.2	2.7	2.1	4.6	3.3
Acanthuridae	T	4.0	15.3	10.4	8.9	5.5	1.3	3.0	3.2
Balistidae	T	52.2	16.0	22.7	33.9	11.4	33.9	27.7	13.4
Monacanthidae	T	.9	.4	.6	1.1	1.2	.4	.6	.7
Ostraciontidae	U	.6	.4	.3	.5	2.2	1.7	.3	0
Palinuridae & Scyllaridae	X	.2	2.9	1.1	.8	6.4	3.3	0	8.2
Crabs	G	0	0	.2	.1	0	+	1.4	3.0
Other	U	0.7	0.6	1.1	0.6	0.2	1.9	1.9	22.2
Mean catch/trap-night (kg)		2.52	2.98	1.87	4.52	1.72	1.80	0.84	0.62

Table 5.11. Relative value of trap catch per unit of effort in various offshore areas. Approximate relative price structure is as follows: Unmarketable Fish (but useful as bait), 0; Trash Fish, 1.0; Grunts, 1.7; Common Fish, 2.2; Quality Fish, 3.3; Palinurids and Scyllarids, 5.0. Catch rates (C_w/f) in grams per trap-night. Value (V/f) in relative units.

Area	Mean total catch rate C_w/f (g)	Unmarketable fish		Trash fish		Grunt		Common fish		Quality fish		Lobsters		Total relative value V/f
		C_w/f	V/f	C_w/f	V/f	C_w/f	V/f	C_w/f	V/f	C_w/f	V/f	C_w/f	V/f	
S. Jamaica Shelf	618	191	0	211	2	52	1	83	2	30	1	51	3	9
California B.	838	65	0	844	8	18	+	174	4	37	1	0	0	13
Pedro Cays	2,520	146	0	1,804	18	197	3	231	5	136	4	5	+	30
N.W. Pedro (incl. N. edge)	1,798	113	0	833	8	63	1	532	11	196	6	60	3	31
S.E. Spur (incl. E. Pedro)	2,980	199	0	1,436	16	760	15	242	6	259	10	86	5	45
Banner Reef	1,865	145	0	1,083	11	190	3	213	5	213	7	21	1	27
20 m Bank	4,516	203	0	2,683	27	357	6	1,016	22	221	7	36	2	64
S.W. Pedro	1,718	139	0	467	5	216	4	328	7	457	15	110	5	36

**CHAPTER 6:
THE BIOLOGY, ECOLOGY
AND BIONOMICS OF THE
SQUIRRELFISHES, HOLOCENTRIDAE**

by
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(March 1976)

Identity

The north Atlantic Holocentridae are characterized by having an overall reddish color, big eyes and spiny scales. Head bones also bear spines (Bohlke and Chaplain 1968). The Atlantic species have been described by Jordan and Evermann (1896), Bohlke and Chaplin (1968) and Randall (1968).

The taxonomy of the Holocentridae according to Berg (1955) is as follows:

- Order - *Beryciformes*
- Family - *Holocentridae*
- Genus - *Holocentrus* Scopoli 1777
Flammeo Jordan and Evermann 1898
Adioryx Starks 1908
Myripristis Cuvier and Valenciennes 1829
Ostichthys Jordan and Evermann 1896
Plectrypops Gill 1826
Corniger Agassiz 1831

The nomenclature of the holocentrids is uncertain and has been subject to much grouping and splitting. The genera given above are those used by Bohlke and Chaplin (1968) who recognize five genera, but with the addition of *Corniger spinosus* and *Ostichthys trachypomas*. Members of the family are commonly referred to as squirrelfish or soldierfish. Table 6.1 gives the common and scientific names of the Caribbean species.

Morphological descriptions are given by Jordan and Evermann (1896).

Table 6.1. Scientific and common names of squirrelfish of the Caribbean Sea.

Scientific names	Jamaican common name/s
1. <i>Holocentrus ascensionis</i> (Osbeck) 1765	Welchman; Wenchman
2. <i>Holocentrus rufus</i> (Walbaum) 1792	Longspine squirrelfish
3. <i>Flammeo marianus</i> (Cuvier and Valenciennes) 1829	Long-jaw squirrelfish
4. <i>Adioryx vexillarius</i> (Poey) 1860	Dusky or spotfin squirrelfish; Welchman
5. <i>Adioryx coruscus</i> (Poey) 1860	Reef squirrelfish
6. <i>Adioryx bullisi</i> (Woods) 1955	Deepwater squirrelfish
7. <i>Adioryx poco</i> (Woods) 1965	Saddle squirrelfish
8. <i>Myripristis jacobus</i> (Cuvier) 1829	Blackbar soldierfish; Bigeye squirrelfish
9. <i>Ostichthys trachypomas</i> (Gunther) 1859	—
10. <i>Plectrypops retrospinus</i> (Guichenot) 1853	Cardinal soldierfish
11. <i>Corniger spinosus</i> (Agassiz) 1829	—

Distribution

Most of the western Atlantic Holocentrids are distributed from Bermuda to the Lesser Antilles and are usually associated with reefs. *Adioryx coruscus* is found in water of between 10 to 30 m, with most fish at around 22 m. *Adioryx bullisi*, *Ostichthys trachypomas* and *Corniger spinosus* are found in deeper water.

Adioryx poco has only been recorded from the Bahamas and Grand Cayman, in shallow water, though it is possibly more abundant than this but has not been recognized by some collectors. *Adioryx vexillarius* is another shallow-water species. It is found around shallow reefs throughout the Caribbean and West Indies from Bermuda to Panama.

Myripristis jacobus occurs in shallow reef water down to 20 m from Bermuda to Panama, including the coast of Florida. Further south, offshore from Guyana and northern Brazil, its depth range increases to 25 m.

M. jacobus also occurs in the eastern Atlantic along the W. African coast.

Of the two species in the genus *Holocentrus*, *H. ascensionis* has the greater geographic and depth range. It is found from Bermuda (30°N) to Santos, Brazil (25°S). In the Caribbean, it is commonly found between 12 to 30 m, whereas further north in American waters, it is more usually found at 8 to 12 m and very rarely ranges as deep, or deeper than 30 m.

H. rufus has a more restricted distribution. It has been recorded from Bermuda and throughout the Caribbean from Cuba and the Misteriosa Bank north to Quita Sueno Bank (14°N). It is not known from the Florida Cays or the Gulf of Mexico. During these studies, *H. ascensionis* and *H. rufus* were recorded from all areas sampled and at all depths down to 100 m.

Bionomics and Life History

Owing to their small size, species of squirrelfishes other than *Holocentrus ascensionis* and *H. rufus* are not normally retained by the 4.13-cm mesh commonly used for fish traps in Jamaican waters. Neither are they taken on the sizes of hooks employed by commercial fishermen. Consequently, only *H. ascensionis* and *H. rufus* are considered in the following account.

REPRODUCTION

Gonads

The gonads are easily identified and show no unusual features. Superficial examination shows no difference between *H. ascensionis* and *H. rufus*.

Sexuality

No evidence has been recorded of hermaphroditism, heterosexuality or intersexuality in species of squirrelfish. There is slight sexual dimorphism in growth and mortality rates.

H. rufus: Fig. 6.1 shows the size distribution of male and female *H. rufus* caught by traps at the Port Royal Reefs. There was a slight difference in the means, the males having a mean length of about 17.5 cm, the females 16.5 cm. Male and female *H. rufus* caught offshore are of about the same size (Fig. 6.2a). Mean length of both sexes was around 17.5 cm.

H. ascensionis: Fig. 6.2b shows the size distribution of male and female *H. ascensionis* caught by traps and lines on the oceanic banks (Pedro and California Banks). Although the females are slightly smaller, the size ranges of the sexes are not very dissimilar. Around Port Royal

Reefs, *H. ascensionis* was caught only by traps and the mean length of the males (19.5 cm FL) was about 3.0 cm longer than the females.

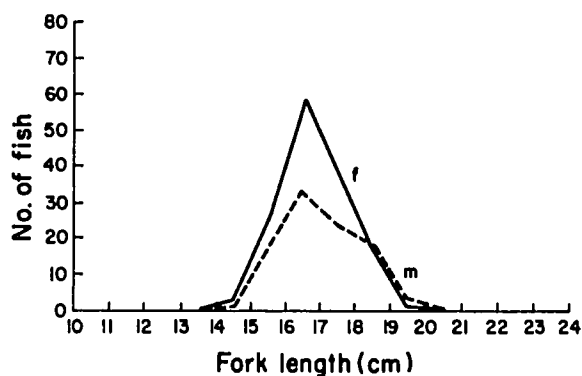


Fig. 6.1. Length-frequency distribution of trap catches of male (m) and female (f) *Holocentrus rufus* from the Port Royal Reefs.

Maturity

Table 6.2 shows that a substantial proportion of the smallest size groups of female *H. rufus* were mature. Maturity of females is therefore attained at or before 13 to 14 cm FL. The males might mature at a slightly larger size.

The percentage of ripe *H. ascensionis* in the sample increased with increasing size and full maturity appears to be attained by 18 to 20 cm FL. The smallest mature fishes were in the 14.0 to 14.9-cm length group.

Fecundity

Estimates of fecundity were not made during the present study. No estimates have been found in the literature.

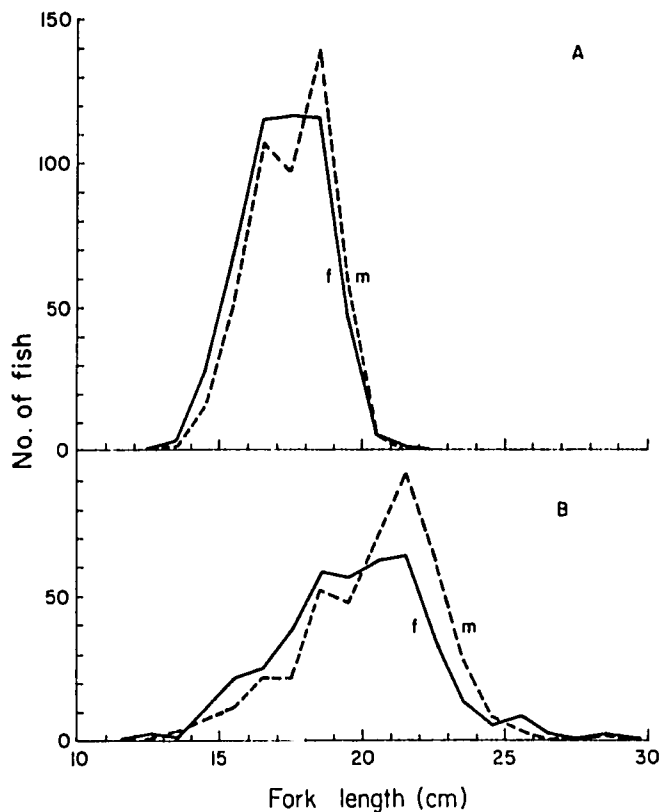


Fig. 6.2. Length-frequency distribution of trap and line catches combined of male (m) and female (f) holocentrids from all sampling areas offshore. (a) *Holocentrus rufus*, (b) *H. ascensionis*.

Mating and Fertilization

Mating has not been observed and there is no information on fertilization.

Spawning Seasons

H. ascensionis: Samples from Port Royal (N=44) and from Pedro Bank (N=868) were combined on a monthly basis (Fig. 6.3a). Ripe fish were collected in all months except June and only one ripe fish was found during July (in a sample of 48 fish). Most spawning appears to occur from January to March with a slightly smaller peak in October. The level of sexually "active" fish remained more or less constant (14 to 37%) between September and May.

H. rufus: Samples of *H. rufus* (Fig. 6.3b) showed seasonal spawning activity similar to *H. ascensionis*, with the greatest proportion of ripe fishes in October (44%) and in February (32%). "Active" fish were found in all months except July.

Further north from the Caribbean, the breeding season apparently shifts. Winn et al. (1964) report breeding in *H. ascensionis* and *H. rufus* from June to August in Bermuda in water of 4 to 8 fathoms (8 to 16 m). This shift in the breeding season corresponds to that suggested by Gaut (1971, mimeo) for *Haemulon sciurus* and other species.

Table 6.2. Proportions of male and female *Holocentrus rufus* and *H. ascensionis* in successive length groups. All specimens captured in traps at the Port Royal Reefs or at oceanic banks.

Median fork length (cm)	<i>H. rufus</i>				<i>H. ascensionis</i>			
	Males		Females		Males		Females	
	No. examined	% ripe	No. examined	% ripe	No. examined	% ripe	No. examined	% ripe
12.5	—	—	—	—	—	—	2	0
13.5	2	0	4	50	3	0	1	0
14.5	17	35	31	32	8	13	14	21
15.5	70	14	95	16	13	8	26	31
16.5	140	16	174	9	24	13	27	15
17.5	121	22	155	17	23	13	47	21
18.5	157	30	133	28	54	39	61	33
19.5	62	42	48	48	57	33	57	39
20.5	6	17	6	50	73	47	62	56
21.5	—	—	1	0	93	43	64	39
22.5	—	—	—	—	65	52	36	47
23.5	—	—	—	—	28	54	13	31
24.5	—	—	—	—	9	66	5	80
25.5	—	—	—	—	4	25	8	75
26.5	—	—	—	—	—	—	2	50
27.5	—	—	—	—	—	—	—	—
28.5	—	—	—	—	1	100	1	100
Totals	575		647		455		426	

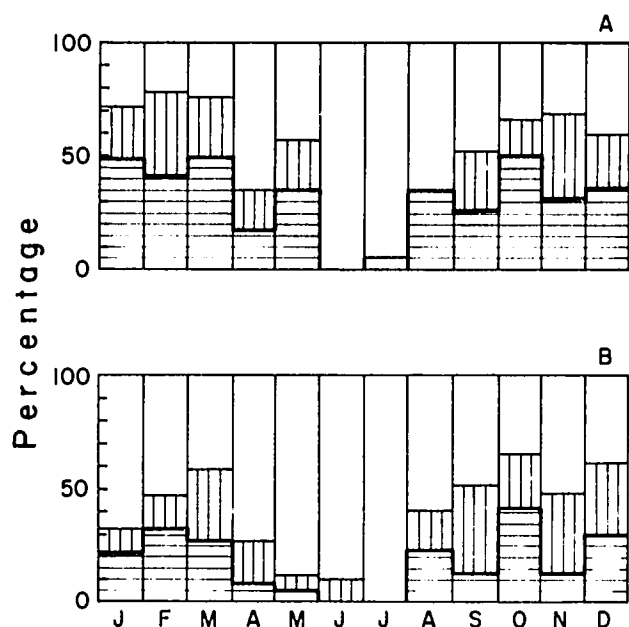


Fig. 6.3. Seasonal variation in the percentage of ripe (cross-hatched), active (vertically-hatched) and inactive (unshaded) holocentrids in Jamaican waters, sampled during 1969-1973, and combined on a monthly basis. (a) *Holocentrus ascensionis* (sample size = 912), (b) *H. rufus* (sample size = 1,331).

Spawn

The unfertilized and fertilized spawn of *H. ascensionis* and *H. rufus* have not been described.

PRE-ADULT PHASE

There is little information on the embryonic stages of squirrelfish, but more is known of their early life history due to the distinctive form of the young. Young squirrelfishes are planktonic, the post-larval stages, known as "Rhynchichthys" stage (McKenney 1959) are elongate, silvery, long snouted and have spiny heads. The spines diminish during growth. Holocentrids in this stage are common in plankton collections made around Jamaica.

The post-larval designation is based on the nominal genus *Rhynchichthys* (Valenciennes 1831), established as a true genus by Cuvier and Valenciennes for an Indian Ocean specimen. Other post-larvae earlier described as genera of *Rhinoberyx* and *Rhamphoberyx* are now recognized as being young stages of the genus *Myripristis*. Despite several descriptions of young holocentrids in the literature the only comprehensive life history series covering a considerable size range is that of McKenney (1959). This paper has a detailed bibliography covering young holocentrids.

ADULT PHASE

Competitors

Crabs and shrimps are the principal food of holocentrids. According to Randall (1967) crabs and crab

Table 6.3. Predators of Holocentridae determined by stomach content analysis (derived from Randall 1967).

Family	Predator Species	Prey
Aulostomidae	<i>Aulostomus maculatus</i>	<i>Adioryx coruscus</i> <i>H. rufus</i>
Serranidae	<i>Epinephelus striatus</i>	<i>Myripristis jacobus</i>
		<i>Holocentrus</i> sp.
		<i>H. rufus</i>
Lutjanidae	<i>Lutjanus jocu</i>	<i>M. jacobus</i>
		<i>Holocentrid</i>
		<i>Holocentrus</i> sp.
Carangidae	<i>L. mahogani</i> <i>Caranx latus</i>	<i>A. coruscus</i>
		<i>Holocentrus</i> sp.
		<i>M. jacobus</i> (juvenile)

larvae comprised 50% or more of the gut contents in only 12 of the 212 species of reef fishes he studied. Of these, only two serranids (*Alphistes afer* and *Epinephelus adscensionis*), a moray eel (*Echidna catenata*) and a snapper (*Lutjanus synagris*) might be considered competitive and, even so, the habitat overlap is probably slight.

Predators

Squirrelfish probably fall prey to the more common medium-sized predators, such as sharks, snappers and groupers. Randall (1967) recorded four families of fish (seven species) that preyed on holocentrids (Table 6.3). Dragovich (1970) sampled skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) and analyzed their stomach contents. Sampling was done in two areas in the Western Atlantic: 1) off the Carolinas in the northwest sector and 2) around the southern Caribbean and Guyanese coast (the southwest sector). Both species of tunas preyed upon post-larval holocentrids. In the northwest sector, holocentrid post-larvae were the fifth most important family of fish in the diet of yellowfin tuna (excluding unidentified fish which were the majority). The sample consisted of three *Holocentrus* spp. and one *A. vexillarius*. In the southwest sector, holocentrids were the seventh most important family in the diet of skipjack tuna and the sample comprised 61 *Holocentrus* spp., 4 *A. vexillarius*, 1 *Myripristis jacobus* and 3 "other holocentrids."

In the same area, holocentrids were the tenth most important family in the diet of yellowfin tuna and the sample was composed of 1 *M. jacobus*, 1 *Holocentrus* sp., 1 *H. ascensionis*, 1 *A. vexillarius* and 1 "other holocentrid."

By comparison, similar studies in the eastern Atlantic off west Africa did not reveal any holocentrids eaten by skipjack tuna and only a single *Holocentrus* sp. (40th

Table 6.4. Stomach contents of some Holocentridae shown as % of volume (derived from Randall 1967).

Food item	Species	<i>Holocentrus ascensionis</i> ¹	<i>Holocentrus rufus</i> ²	<i>Adioryx coruscus</i> ³	<i>Adioryx vexillarius</i> ⁴	<i>Flammeo marianus</i> ⁵	<i>Myripristis jacobus</i> ⁶	<i>Plectrypops retrospinis</i> ⁷
Shrimps + larvae		10.6	15.0	70.0	20.8	51.7	30.3	
Crabs + larvae		73.3	59.6	27.3	26.9	30.6	14.9	50.0
Stomatopod + larvae			0.4			3.3	17.4	
Gastropods		1.0	7.8		25.1			
Mysids			1.4				11.2	
Chitons			0.6		10.3			
Ophiuroids			7.1					
Polychaetes		3.9	4.5				7.0	50.0
Fish + larvae			1.2		5.2		5.4	
Amphipods							3.2	
Copepods						1.1	2.4	
Isopods		0.6	1.5		5.7		1.8	
Cephalopod larvae							1.5	
Hermit crab larvae							0.9	
Scyllarid larvae							0.9	
Ostracods			1.2				0.3	
Unidentified crustacea		10.6	2.4	2.7		13.3	2.7	
Unidentified animal matter							0.1	

¹Forages over grass flats more than other listed species. Sample: 31.

²Sample: 55.

³Sample: 24.

⁴Fish eaten were larvae of *Acanthurus* sp. Sample: 55.

⁵Sample: 13.

⁶Mainly plankton feeders. Fish eaten were chaetodontidae larvae. Sample: 46.

⁷Sample: 10.

family in order of frequency of occurrence in the diet) in the sample of food of the yellowfin tuna.

Parasites, Diseases, Injuries and Abnormalities

Few details are available on parasitized holocentrids. *M. jacobus* is frequently parasitized by an isopod which usually rests between the eyes [pl. 4 (d) Bohlke and Chaplin 1968].

Holocentrus spp. with missing or abnormal pelvic and anal fins have been caught on Pedro Bank on several occasions.

Saunders (1966a) examined 40 *H. ascensionis*, 42 *H. rufus* and 13 *M. jacobus* for blood parasites, especially *Haemogregarina bigemina*, but none was found.

Hardiness

Squirrelfishes have been found to survive for several days in traps. They have also been kept in aquaria at the laboratory for 2 to 3 mo with minimal attention and would appear to be quite hardy fish.

Both *H. rufus* and *H. ascensionis* have been caught in the shallow nearshore enclosed waters of Kingston harbor which receive sewage effluent and so must have some tolerance to pollution.

Longevity

Estimates of longevity are not available.

NUTRITION AND GROWTH

Feeding

Feeding occurs mainly at night (see section on behavior).

Food

Apart from casual observations indicating that squirrelfish are carnivorous, little is known about their diet. The most comprehensive work to date is that of Randall (1967). His findings on squirrelfish are summarized in Table 6.4.

No information on food or feeding was collected during the present study.

Growth Rates

Relative growth patterns

H. ascensionis: The length-weight relationship of males and females within the range 14 to 19 cm FL is described by the equation:

$$W = 0.05646L^{2.66}$$

The relationship of fork length (FL) to maximum body depth (MD) between the lengths 16.0 to 27.0 cm FL is

expressed by the equation:

$$MD = 0.2914 FL \text{ or } FL = 3.40 MD$$

The smallest *H. ascensionis* were caught in traps offshore, at California Bank and Banner Reef; both fish were 12.2 cm FL. A fish retainable by the 4.13 cm mesh would have an average FL of about 14.0 cm.

H. rufus: The length-weight relationship within the range 14 to 19 cm FL is described by the equation:

$$W = 0.01778L^{3.00}$$

The maximum body depth (MD) between the sizes 15 to 18 cm FL is equal to 0.237 FL or FL = 3.61 MD. Fishes of about 14.9 cm FL would be retained by the 4.13 cm wire mesh of traps.

The maximum size

The average asymptotic length (L_{∞}) of species of Holocentridae cannot be estimated from the present data.

Holocentrus ascensionis: According to Bohlke and Chaplin (1968) *H. ascensionis* is "said to reach two feet" (60 cm) although none of their specimens are over one foot. From references in the literature and our own experience, the figure of two feet would seem to be improbable. Randall (1968) records a maximum length of 13.6 in (34.5 cm). In the present study, the largest fishes were collected offshore and were 28.4 cm FL (male) and 28.2 cm FL (female). The largest caught at the Port Royal Reefs was 22.0 cm FL. If the asymptotic length for males and females is taken as 26.5 cm FL the calculated equivalent weight (extrapolating from the conversion equation, is around 345 g.

Holocentrus rufus: Randall (1968) states that *H. rufus* reaches at least 12.5 in (31.7 cm) or, according to Bohlke and Chaplin (1968), "at least one foot" (30.5 cm). In the present study, the largest fish was caught offshore and measured 23.3 cm FL (unsexed). The largest from the Port Royal Reefs was a female of 19.5 cm FL. The (four) largest males from the same area ranged from 19.0 to 19.2 cm FL.

It appears that the asymptotic size of *H. rufus* is in

the region of 23.5 cm FL, and the calculated equivalent weight is around 230 g.

Age and growth

This study did not produce any data which can be used to estimate the growth rates of squirrelfish.

Randall (1962) marked and measured squirrelfish and found that growth was very slow. However, despite negligible signs of wounds from tags, the fish were undoubtedly affected by tagging. Several fish did not grow at all. From a sample of 11 marked *H. ascensionis*, Randall obtained 21 recoveries. Size increases ranged from zero to 5.46 mm TL/month, with a mean value of 1.47 mm.

In the case of *H. rufus*, 19 recoveries were made from a sample of 15 fish. Tagging/recapture interval ranged from 37 to 591 days. Increases ranged from zero to 1.24 mm TL/month, with a mean value of 0.34 mm.

BEHAVIOR

Several workers have shown that this group is largely nocturnal (Hiatt and Strasburg 1960; Hobson 1965; Longley and Hildebrand 1941; Randall 1963; Starck and Davis 1966).

Starck and Davis (1966), working in Florida, state that both *H. ascensionis* and *H. rufus* are found individually in holes on the deep reef and reef top. *A. vexillarius* and *A. coruscus* occur in groups in coral crevices and under ledges from the reef top shoreward. *M. jacobus* is also found in groups on the reef top, but has a more restricted foraging range than other squirrelfish.

Squirrelfishes are probably territorial at least by day and less so at night. Territorial behavior is probably modified by the habitat, and where crevices are plentiful territories are contiguous. Habitat differences may also account for differences reported by Starck and Davis (1966) and Randall (1967), who described foraging in adjacent grass beds, whereas Winn et al. (1964) state that although territorial conflict is reduced at night, there is no evidence of nocturnal migration or dispersal.

Territorial behavior patterns are described by Winn et al. (1964) with an account of sound production. Two types of sounds are recognized: 1) "grunts" which are aggressive and 2) a "staccato" call which is associated with the escape reaction.

Populations

POPULATION STRUCTURES

Sex Ratios

The sex ratio of *H. ascensionis* caught in traps at the Port Royal Reefs was M:F = 1:1.57, whereas in offshore areas the ratio was M:F = 1:0.93. The sex ratio of *H. rufus* at the Port Royal Reefs was M:F = 1:1.48, while in

offshore areas the ratio was M:F = 1:1.05.

The differences found between the sex ratios in offshore areas and those at Port Royal are most likely the result of selective capture of the larger males by the intensive fishery in the Port Royal Reefs. It could also be the result of a size-related offshore migration with increasing size. There is however no evidence of such a movement.

Age and Length Composition

The absolute ages of squirrelfish cannot be determined at the present time; hence there is no information on the age composition of the stock.

The size compositions of samples of *H. ascensionis* caught at Pedro Bank, in depths of 10.1 to 20 m, 20.1 to 30 m, and 30.1 to 45 m are shown in Fig. 6.4. The modes and the ranges vary slightly, although the differences are probably not significant. The mean fork length for all three zones is around 19.5 cm.

Figure 6.5 shows the size composition of samples of *H. rufus* within the same depth zones. There is no change with depth in the modes; at 10.1 to 20 and 20.1 to 30 m, the mean is around 17.5 cm and at 30.1 to 45 m it is one cm less (circa 16.5 cm).

It is concluded that mature fish occur at all depths on the shelf.

Figures 6.6 and 6.7 show the size composition of *H. ascensionis* and *H. rufus* from Pedro Cays and California Bank. Insufficient data were obtained on these species at the Port Royal Reefs. In both cases, the sample sizes are

small and give "poor" estimates of population structure. Nevertheless, the greater relative abundances of larger fishes at unexploited parts of Pedro Bank and at the lightly exploited Pedro Cays are apparent in the samples. The occurrence of relatively large numbers of large individuals at the Pedro Cays is believed to result from a decrease in natural mortality rates which in turn results from selective exploitation of the major predatory species (see Chapter 17).

MORTALITY AND MORBIDITY

Major causes of mortality are fishing and predation. From the data on size composition, the relative mortality rates can be estimated for holocentrids at Pedro Bank, Pedro Cays and California Bank. Insufficient fish were caught at Port Royal Reefs for estimates to be made. The sexes are combined for analysis.

Table 6.5 shows the relative rates of decline in abundance of successive length groups of *Holocentrus ascensionis* beyond full recruitment at length, l_c , of 21.0

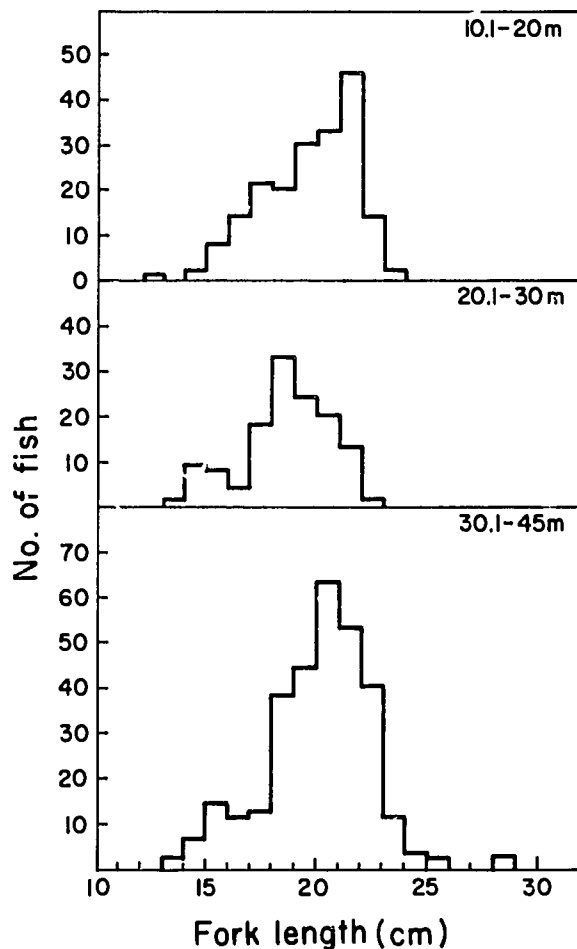


Fig. 6.4. Length-frequency distribution of trap catches of *H. ascensionis* from the 10.1-20 m, 20.1-30 m and 30.1-45 m depth zones of Pedro Bank.

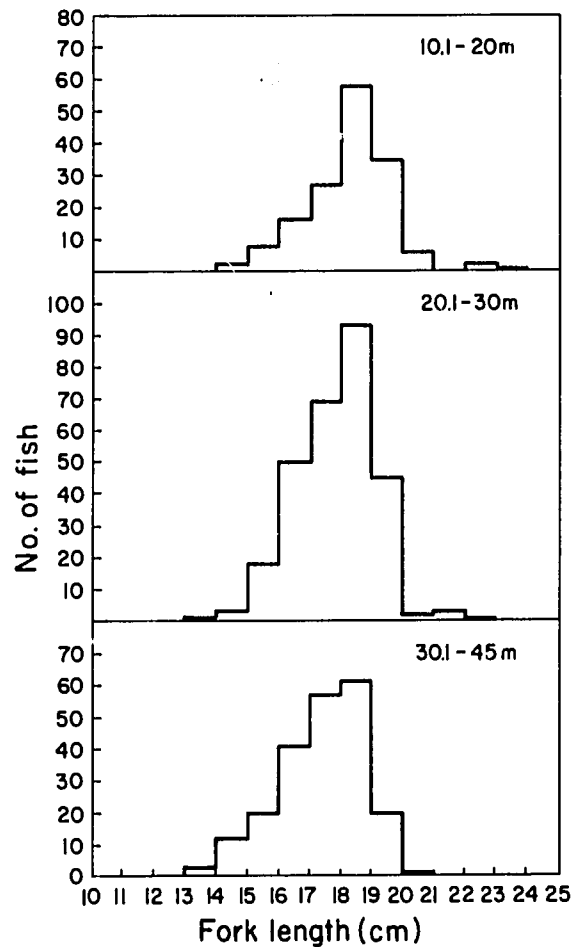


Fig. 6.5. Length-frequency distribution of trap catches of *H. rufus* from the 10.1-20 m, 20.1-30 m and 30.1-45 m depth zones of Pedro Bank.

Table 6.5 . Comparison of the relative abundance of successive length groups of *Holocentrus ascensionis* beyond full recruitment at 21.0 cm FL from Pedro Bank, Pedro Cays and California Bank.

Length group cm FL	Pedro Bank (unexploited)		Pedro Cays		California Bank	
	No. caught	Relative abundance	No. caught	Relative abundance	No. caught	Relative abundance
21.0-21.9	121	1.00	43	1.00	32	1.00
22.0-22.9	72	.59	31	.72	6	0.19
23.0-23.9	18	.14	10	.23	5	0.16
24.0-24.9	5	.04	6	.14	0	0
25.0-25.9	2	.02	5	.12	0	0
26.0-26.9	1	.01	1	.02	0	0
27.0-27.9	0	0	0	0	0	0
28.0-28.9	2	.01	0	0	0	0
Mean FL	= 22.18 cm		= 22.48 cm		= 21.87 cm	
If $L_{\infty} = 26.5$ cm						
Z/K	= $\frac{26.50 - 22.18}{22.18 - 21.0}$		= $\frac{26.50 - 22.48}{22.48 - 21.0}$		= $\frac{26.50 - 21.87}{21.87 - 21.0}$	
	= 3.66 (M/K)		= 2.72		= 5.32	

cm. If the asymptotic FL is estimated at 26.5 cm, then

$$Z/K = M/K = 3.66$$

at unexploited parts of Pedro Bank, whereas Z/K was 2.72 at Pedro Cays and 5.32 at California Bank.

The relative rates of decline in abundance of *Holocentrus rufus* beyond the full retention size, l_c , of 18.0 cm are shown in Table 6.6. The mean length of the fully retainable fishes is 19.04 cm at Pedro Cays compared to 18.94 cm at Pedro Bank (unexploited). Neither the growth rate nor the asymptotic length are known, but the latter is estimated to be 23.5 cm FL as a conservative figure. The value of Z/K is in the region of 4.3 for the Pedro Cays population, 4.9 for the unexploited population (where Z/K = M/K) and 7.2 at California Bank.

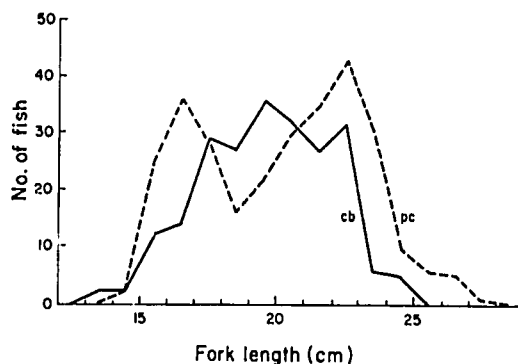


Fig. 6.6. Length-frequency distributions of trap catches of *H. ascensionis* from California Bank (cb) and Pedro Cays (pc).

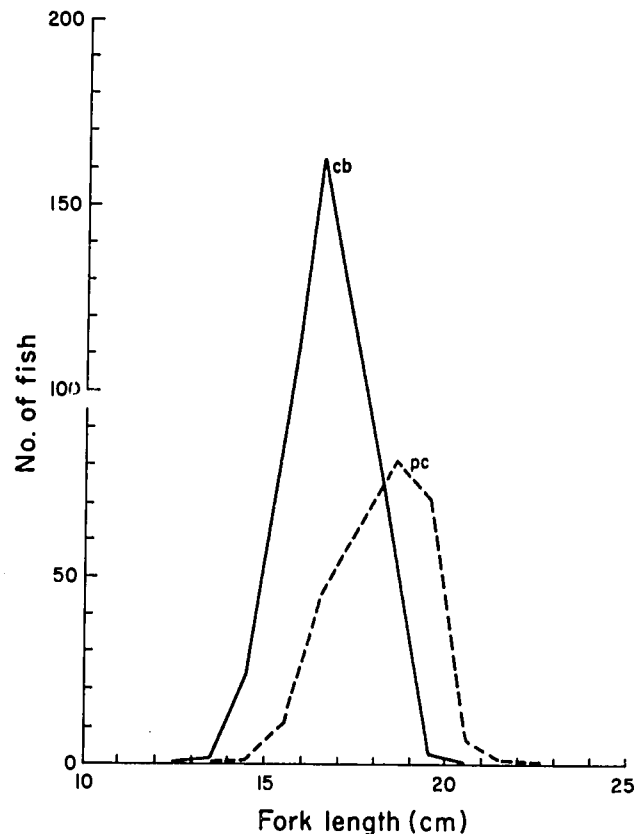


Fig. 6.7. Length-frequency distributions of trap catches of *H. rufus* from California Bank (cb) and Pedro Cays (pc).

Table 6.6. Comparison of the relative abundance of successive length groups of *Holocentrus rufus* beyond full recruitment at 18 cm FL from Pedro Bank, Pedro Cays and California Bank.

Length group cm FL	Pedro Bank (unexploited)		Pedro Cays		California Bank	
	No. caught	Relative abundance	No. caught	Relative abundance	No. caught	Relative abundance
18.0-18.9	212	1.00	82	1.00	95	1.00
19.0-19.9	100	.44	70	.85	14	.15
20.0-20.9	9	.03	7	.09	2	.02
21.0-21.9	3	.01	1	.01	0	0
22.0-22.9	3	.01	0	0	0	0
23.0-23.9	1	.003	0	0	0	0
Mean FL	= 18.94 cm		= 19.04 cm		= 18.67 cm	
If $L_{\infty} = 23.5$ cm						
Z/K	= $\frac{23.50 - 18.94}{18.94 - 18.00}$		= $\frac{23.5 - 19.04}{19.04 - 18.00}$		= $\frac{23.5 - 18.67}{18.67 - 18.00}$	
	= 4.85 (=M/K)		= 4.29		= 7.21	

ABUNDANCE AND DENSITY

Nothing is known about the absolute size or density of the populations studied.

Fig. 6.8 shows that at Port Royal Reefs, "availability" of *H. rufus* was greatest from November to April and least during the summer months. It is probable that peak availability is related to the spawning season.

H. ascensionis was not sufficiently common at the Port Royal Reefs for any conclusions to be drawn.

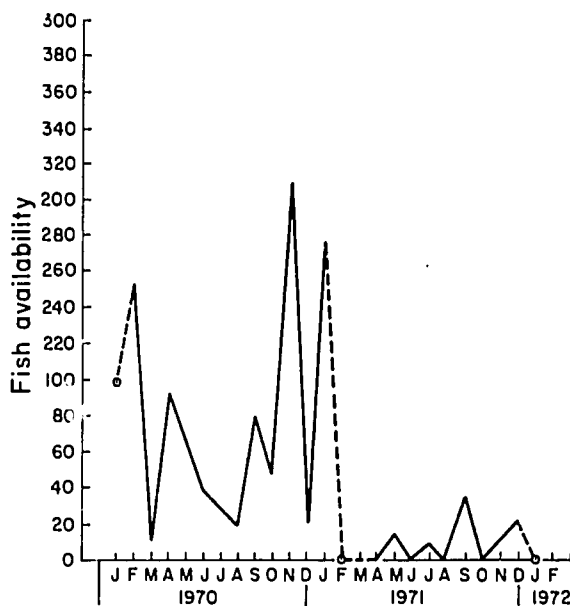


Fig. 6.8. Seasonal availability of *H. rufus* at the Port Royal Reefs. Availability is the theoretical number of fishes which would enter 1,000 traps set for 24 hours. Circled points connected by dashed lines indicate months in which less than 5 traps were set.

DYNAMICS OF THE POPULATIONS

The biological and population parameters estimated for males and females (combined sexes) of *Holocentrus ascensionis* and *H. rufus* are summarized in Table 6.7.

The value of M/K is high for both species as would be expected from the steep rates of decline of the right hand side of the catch length-frequency distributions.

Table 6.7. Summary of estimated population parameters for *Holocentrus ascensionis* and *H. rufus* exploited by traps with 4.13 cm wire mesh. All lengths are fork lengths in cm. Males and females are combined.

	<i>H. ascensionis</i>	<i>H. rufus</i>
Minimum retainable length	14.0	14.9
Mean retention length, l_r	18.8	17.29
Full retention length, l_c	21.0	18.0
Asymptotic length, L_{∞}	26.5	23.5
Asymptotic weight (g) W_{∞}	344.7	230.8
Coefficient of growth, K	1.18	0.94
Coefficient of natural mortality, M	4.32	4.56
M/K	3.66	4.85
Length at maturity, l_m	14.0-14.9 cm	13-14.0 cm
l_m/L_{∞}	1.89-1.78	1.81-1.68

**CHAPTER 7:
THE BIOLOGY, ECOLOGY
AND BIONOMICS OF THE
HINDS AND GROUPERS, SERRANIDAE**

by

R. Thompson* and J.L. Munro

(March 1974)

Identity

TAXONOMY

As the relationships of many of the species now placed in the family Serranidae are poorly known, Smith's (1962) definition of "groupers" is adhered to in this report. Thus, groupers are defined as large serranid fishes of the genus *Epinephelus* and of the allied genera *Mycteroperca*, *Dermatolepis*, *Cephalopholis*, *Alphestes* and *Paranthias*. The genus *Gonioplectrus* (not mentioned by Smith), which Jordan and Evermann (1896) consider to be related to *Alphestes*, is also included.

As defined above, the groupers are a group of closely related species. Smith (1971) divides the American groupers into three genera: *Paranthias*, *Epinephelus* and *Mycteroperca*. The nominal genera *Petrometopon*, *Cephalopholis*, *Epinephelus*, *Promicrops*, *Dermatolepis* and *Alphestes* are treated as subgenera, except for *Petrometopon*, which Smith considers a synonym of *Cephalopholis*. *Mycteroperca* seems to be a well-defined genus and *Paranthias* bears the same relationship to *Epinephelus* that *Ocyurus* bears to *Lutjanus* in the family Lutjanidae.

According to Smith, the lineage most remote from the main stem of Western Atlantic groupers gave rise to *Paranthias*, as this genus is extreme in nearly all characters. The genus *Mycteroperca* appears to be the result of an early split of the *Epinephelus* stem, and the subgenus *Cephalopholis* seems to be an offshoot of the main *Epinephelus* line. The subgenera *Promicrops*, *Dermato-*

lepis and *Alphestes* are also believed to be offshoots of the main *Epinephelus* line. Within the subgenus *Epinephelus*, Smith recognizes the following species-groups:

- the *Epinephelus striatus* group consisting of *striatus*, *guttatus* and *morio*;
- the *Epinephelus niveatus* group of which only *mystacinus* was collected during the present study;
- the *Epinephelus guaza* group of which no representatives were collected during the present study; and
- the *Epinephelus adscensionis* group represented by *adscensionis* during the present study.

The subgenus *Mycteroperca* is divided into two species-groups:

- the *Mycteroperca venenosa* group represented by *venenosa*, *bonaci* and *tigris* during the present study; and
- the *Mycteroperca interstitialis* group represented by *interstitialis*, *cidi* and *rubra* during the present study.

*A substantial portion of this chapter is derived from a thesis submitted to the University of the West Indies by R. Thompson for the degree of Master of Science. The thesis was based on data collected by the Fisheries Research Project up to May 1972. The sections on growth, sexuality, population structure, mortality and recruitment have been prepared by J. Munro, and incorporate all data collected by the project between November 1969 and March 1973.

Smith's (1971) divisions of the genera of groupers do not yet appear to be widely accepted and the nomenclature used by Randall (1968) and Bohlke and Chaplin (1968) is used throughout this report.

NOMENCLATURE

Seven genera and 16 species of groupers were collected during this study and are listed in Table 7.1. All these, with the exception of *E. mystacinus*, *M. rubra*, *M. cidi* and *G. hispanus* have been listed by Caldwell (1966) as occurring in Jamaican waters. *E. niveatus* (Valenciennes 1828), was recorded from Jamaica by Smith (1961), but it is quite possible that Smith's record is really *E. mystacinus*. *E. flavolimbatus* (Poey 1965), was also listed by Smith (1961) from Jamaica, but this species was not collected during this study. If *E. niveatus* and *E. flavolimbatus* occur in Jamaican waters, they are probably very rare.

MORPHOLOGY

The morphological features of the species listed in Table 7.1 are described by Randall (1968), Bohlke and Chaplin (1968), Smith (1971) and Jordan and Evermann (1896).

Table 7.1. Scientific and common names of groupers caught in Jamaican waters.

Scientific names	Standard common names
1. <i>Paranthias furcifer</i> (Cuvier and Valenciennes) 1828	Creole fish
2. <i>Epinephelus striatus</i> (Bloch) 1792	Nassau grouper
3. <i>E. morio</i> (Cuvier and Valenciennes) 1828	Red grouper
4. <i>E. guttatus</i> (Linnaeus) 1785	Red hind
5. <i>E. mystacinus</i> (Poey) 1852	Misty grouper
6. <i>E. adscensionis</i> (Osbeck) 1771	Rock hind
7. <i>E. itajara</i> (Lichtenstein) 1822	Jewfish
8. <i>Dermatolepis inermis</i> (Cuvier and Valenciennes) 1833	Marbled grouper
9. <i>Cephalopholis fulva</i> (Linnaeus) 1758	Coney
10. <i>Petrometopon cruentatum</i> (Lacepede) 1802	Graysby
11. <i>Alphistes afer</i> (Bloch) 1793	Mutton hamlet
12. <i>Mycteroperca venenosa</i> (Linnaeus) 1758	Yellowfin grouper
13. <i>M. bonaci</i> (Poey) 1860	Black grouper
14. <i>M. tigris</i> (Cuvier and Valenciennes) 1833	Tiger grouper
15. <i>M. interstitialis</i> (Poey) 1860	Yellowmouth grouper
16. <i>M. rubra</i> (Bloch) 1793	Comb grouper
17. <i>M. cidi</i> (Cervigon) 1966	White grouper
18. <i>Gonioplectrus hispanus</i> (Cuvier and Valenciennes) 1828	Spanish flag

Various workers, including Bardach et al. (1958), Longley and Hildebrand (1941), Norman (1963) and Smith (1961 and 1971) have described color variations in groupers. Bardach (1958) noted that there are three known types of variation which are a) individual variation in the location and extent of bars, stripes and spots; b) instantaneous color change and c) color variation due to environmental conditions.

Two color phases have been noted for *Mycteroperca venenosa* (Smith 1971). During this study, only the red, deep-water form was caught at California Bank (Fig. 2.2) which has a minimum depth of about 40 m, whereas both the red, deep-water, and the brownish, shallow-water forms were caught on Pedro Bank (Fig. 2.1) at depths of 40 to 60 m. Juvenile *M. venenosa* collected during this study were more red than adults caught at comparable depths, and a gradation in ground color (from red to dark brown) with increase in size was noted occasionally in catches from the same area. This is possibly a developmental trait or indicates a movement of juveniles from deep to shallow water.

A *Mycteroperca tigris*, 45.5 cm TL (37.6 cm SL), caught on California Bank at a depth of 44 m during 1972 showed a color phase distinct from the ordinary dark-greenish to brown and black ground color description given by Smith (1971). In this specimen, the hexagonal spots were of a bright orange-red color. These spots were particularly prominent on the dorsal surface and gave the fish a bright orange-red ground color.

Three distinct color phases have been described for the coney, *Cephalopholis fulva* (Smith 1961). These are the brownish-olive phase of shallow water; the bright red phase of deep water and the less common, bright yellow (xanthic) phase. In addition, a fourth color phase is occasionally encountered in which the ground color is bluish-black, and the dorsal surface of the body is darker than the ventral surface. The bases of the anal and soft dorsal fins are light blue, whereas the distal portion of these fins and the entire caudal, pelvic and pectoral fins are dusky-blue. Iridescent spots are present on the head and upper half of the body. These are about 0.7 mm in diameter and vary in color from light to dark blue. The dark blue spots are almost invisible against the ground color and are not surrounded by a dark ring. The caudal and soft dorsal fins have narrow, white distal margins. The two black spots on the dorsal surface of the caudal peduncle and the two at the top of the lower jaw are almost invisible against the general background color.

HYBRIDIZATION

One hybrid combination has been recorded by Smith (1966) for groupers in the western Atlantic. This is the combination of *Cephalopholis fulva* and *Paranthias furcifer*. Two specimens were collected from the vicinity of Havana, Cuba and form the types of *Menophorus dubius* and *Menophorus punctiferus*, although as stated by Smith, they are both probably the same.

HABITAT AND DEPTH DISTRIBUTION

Most species are secretive and occupy crevices, ledges and caves on reefs and wrecks (Smith 1961). Adult *Petrometopon cruentatum* and juvenile *Mycteroperca venenosa* and *M. rubra* have been collected on *Thalassia testudinum* beds in 2 to 4 m of water in Kingston Harbour. Juvenile *Epinephelus itajara* have been collected in the mangrove swamps in Kingston Harbour in depths of about 2 m among the mangrove roots, and in the Great Salt Pond, on the south coast of Jamaica (P. Reeson, pers. comm.). Large adults are quite often seen or captured in Kingston Harbour.

Most Jamaican groupers are caught in depths of 2 to 60 m with the exception of *Epinephelus mystacinus* and

Gonioplectrus hispanus which can be described as slope species. *E. mystacinus* has been caught at a depth of 70 m on Pedro Bank, but is more commonly caught at depths around 200 m. Brownell and Rainery (1971) give a depth range of 55 to 160 fathoms (100 to 289 m) for *E. mystacinus* in the Virgin Islands, with a mean depth of 114 fathoms (208 m). One *G. hispanus* was caught at a depth of 160 m on the southeastern coast of Jamaica (Cruise report 69/8, *M.F.V. Alcyon*, UNDP/FAO Caribbean Fishery Development Project, 1969) and P. Colin (pers. comm.) captured two at 200 m at Discovery Bay on the north coast of Jamaica.

The largest individuals of a particular species usually occur in the lower part of depth range.

Bionomics and Life History

REPRODUCTION

Gonads

The ripe gonads of all of the common species are similar and occupy a major portion of the body cavity. The structure of the protogynous epinephelid gonad has been described by Smith (1965) and the species considered here all conform with his description of the gonadal structure of *Cephalopholis fulva*.

The weight of ripe gonads relative to the total weight of the fish is small. Smith (1965) found that ripe ovaries of *Cephalopholis fulva* accounted for less than 5% of the total body weight. The ripe testes of a *Mycteroperca venenosa* (69.5 cm TL) collected during the present study accounted for 6.3% of the total body weight.

Sexuality

Protogynous hermaphroditism

Protogynous hermaphroditism is known to occur in several species of groupers (Lavenda 1949; Moe 1969; Smith 1959, 1961), although in related serranids synchronous hermaphroditism is also encountered. A broad overlap of the length distributions of the sexes is encountered in most species and suggests that there is no close correlation of age or size with sexual transition. Moe (1969) found that red groupers (*Epinephelus morio*) do not all transform into males and that the size of most transforming fish ranges from 450 to 650 mm SL.

Histological and field evidence obtained by Smith (1959) showed definite or strongly suggestive indications of sex reversal in the following species: *Epinephelus striatus*, *E. guttatus*, *E. itajara*, *Cephalopholis fulva*, *Petrometopon cruentatum*, *Alphesthes afer*, *Mycteroperca venenosa*, *M. bonaci*, *M. tigris* and *M. interstitialis*. In the case of *Paranthias furcifer*, results were inconclusive, and Smith suggested that this species may be gonochoritic. Evidence of the protogynous condition in the above-mentioned species was that no small males were found

even when gonads were examined histologically and, in the case of mature fish, the proportion of males increased with increasing size.

The sex of groupers cannot be determined with any degree of certainty by macroscopic means unless the gonads are in an active, ripe or early spent state. No histological work was done during the present study, and evidence of protogynous hermaphroditism is based upon comparative length distributions of males and females captured during the spawning seasons.

Length-frequency distributions of male and female *Epinephelus guttatus* and *Cephalopholis fulva* (Tables 7.3 and 7.4) show that the males are of larger average size than the females, although there is a broad overlap in the length distribution of the sexes. In both species, the percentage of males increases steadily with increases in total length. The mean size at sex reversal appears to be in the region of 38 cm TL in the case of *E. guttatus* and about 27 cm TL in the case of *C. fulva*.

Samples of mature specimens of other species of groupers and hinds were either numerically inadequate or covered too restricted a length range and therefore did not yield any information on sex reversal.

The factors triggering transition are largely unknown. However, Fishelson (1970) regulated protogynous sex reversal in *Anthias squamipinnis* (fam. Anthiidae) by the presence or absence of a male fish. Liem (1963) and Harrington (1967) demonstrated that environmental conditions, such as temperature, crowding and starvation can greatly influence sex ratios, sexual succession and the development of primary male gonochorists in clones of homozygous hermaphrodites. These pressures may also be influential in stimulating sexual transition in groupers. The sex ratios of mature *Epinephelus striatus* and *Mycteroperca venenosa* taken from relatively unexploited oceanic banks during the present study were M:F = 1:0.72 and 1:0.85, respectively. On the intensively exploited Port Royal Reefs the sex ratios of *Epinephelus guttatus* and *Petrometopon cruentatum* were M:F = 1:5.6 and 1:6.0, respectively. In an area with high fishing intensity the largest, mostly male, individuals became relatively less abundant. According to Fishelson (1970)

Table 7.3. Length-frequencies of mature male and female *Epinephelus guttatus* and the percentage of males in successive length groups. Samples from unexploited oceanic banks.

Length group cm TL	Number of fishes			Percent males
	female	male	total	
21.0-21.9	1	0	1	0
22.0-23.9	2	0	2	0
24.0-25.9	4	0	4	0
26.0-27.9	19	1	20	5
28.0-29.9	15	1	16	6
30.0-31.9	32	0	32	0
32.0-33.9	27	5	32	16
34.0-35.9	27	8	35	23
36.0-37.9	22	15	37	41
38.0-39.9	16	14	30	47
40.0-41.9	7	15	22	68
42.0-43.9	5	4	9	44
44.0-45.9	2	0	2	0
46.0-47.9	1	0	1	0
48.0-49.9	0	2	2	100
	180	65	245	

this should induce earlier transformation in an area such as Port Royal, but this is not reflected in the Port Royal catches. The smallest recognizable male *E. guttatus* at Port Royal was 26 cm TL whereas on oceanic banks the smallest male was 27 cm TL. Sustained high fishing pressure probably decreases the rate of transition thereby increasing the reproductive potential of the population by increasing the number of females (Moe 1969). However, as was suggested by Moe, continued exploitation could decrease the male component, beyond a critical minimal number, causing a rapid decline in numbers of the population.

Synchronous hermaphroditism

Smith (1959) discussed the relationship between the protogynous groupers and the synchronous hermaphroditic species, and mentioned the possibility that protogyny has been derived from synchronous hermaphroditism. Evidence of synchronous hermaphroditism in groupers was obtained from a specimen of *Cephalopholis fulva* collected during February 1971, on Pedro Bank. This individual measured 23.9 cm TL and was caught along with "normal" males and females with active to ripe gonads. It had a ripe ovotestis similar to the general description of ripe gonads of groupers. Eggs and sperm could be forced out of the ovotestis by the application of pressure to the gonad. This ovotestis is illustrated in Fig. 7.1.

The right lobe measured 3.5 cm in length and 1.4 cm in diameter. The left lobe was smaller, measuring 3.1 cm in length and was 1.6 cm wide at the widest portion. The gonadal tissue was primarily ovarian, interspersed with streaks of testicular tissue. Testicular tissue was

Table 7.4. Length-frequencies of mature male and female *Cephalopholis fulva* and the percentage of males in successive length groups. Samples from unexploited oceanic banks.

Length group cm TL	Number of fishes			Percent males
	female	male	total	
16.0-16.9	1	0	1	0
17.0-17.9	2	0	2	0
18.0-18.9	4	0	4	0
19.0-19.9	13	0	13	0
20.0-20.9	17	0	17	0
21.0-21.9	30	0	30	0
22.0-22.9	33	4	37	11
23.0-23.9	41	15	56	27
24.0-24.9	32	11	43	26
25.0-25.9	29	22	51	43
26.0-26.9	19	16	35	46
27.0-27.9	8	13	21	62
28.0-28.9	10	18	28	64
29.0-29.9	1	11	12	92
30.0-30.9	0	2	2	100
	240	112	352	

found on the ventral surface in a greater concentration than on the dorsal surface of the ovotestis. The testicular tissue penetrated the gonad to the lumen and was similar to testicular tissue in a normal testis.

This ovotestis raises the possibility of self-fertilization in hermaphroditic groupers. This specimen would evidently have spawned within a short time and as sperm and eggs were well developed, it is possible that external self-fertilization could have occurred if male and female

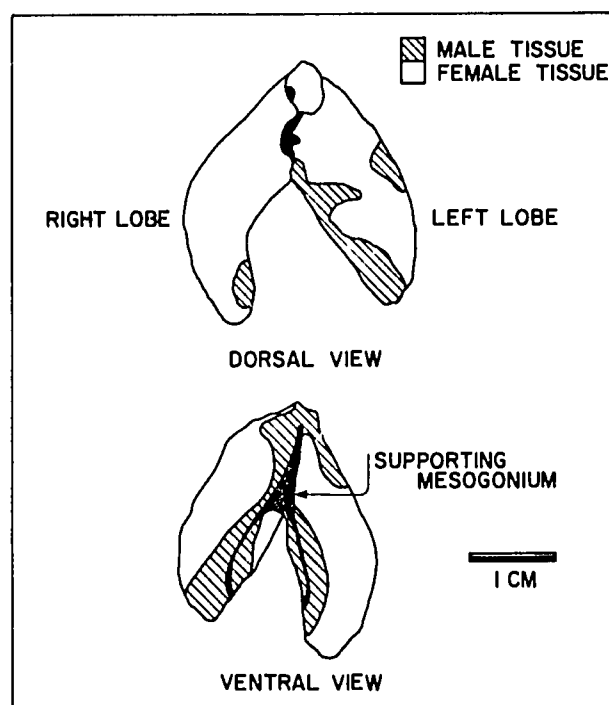


Fig. 7.1. Ovotestis of hermaphroditic coney, *Cephalopholis fulva*.

gametes were released simultaneously. Apparently, this is the first record of a synchronous hermaphroditic grouper and this condition must therefore be uncommon as numerous gonads have been examined.

Maturity

The sizes at which groupers first mature cannot be established from the present data. In all cases, the smallest length-groups contained a substantial proportion of mature fishes and the size at maturity is therefore probably less than the minimum size retained by the fishing gear. On this basis, it can only be stated that *C. fulva* matures at or before 16 cm TL (92 g), and *E. guttatus* at or before 25 cm TL (242 g). *Epinephelus striatus* first matures at or before about 48 cm TL (about 1,800 g) and *M. venenosa* and *P. cruentatum* at or before 51 cm and 16 cm (60 g), respectively.

Fecundity

Smith (1961) made the following estimates of the fecundity of four species of groupers:

	Standard length (cm)	No. of eggs
<i>Epinephelus guttatus</i>	35.8	233,273
<i>E. striatus</i>	44.5	785,101
<i>Mycteroperca venenosa</i>	-	1,425,443
<i>M. bonaci</i>	80.5	5,035,240

The contents of the ovaries of four species of groupers were counted during this study (Table 7.5). The numbers of eggs in the ovaries of similar-sized *Cephalopholis fulva* varied greatly, although all ovaries were ripe and firm when collected, suggesting that no eggs had been recently released prior to collection.

Indications are that different species of groupers produce comparable numbers of eggs per gram body weight.

Mating and Fertilization

Little information is available on the actual mating process in groupers. Ukawa et al. (1966) described the spawning behavior of *Epinephelus akaara* (Temminck and Schlegel) as the interaction between a single male and female. Manday and Fernandez (1966) noted no selection of pairs in the mating of *Epinephelus striatus* in tank-held individuals. Apparently, there is no coupling during spawning of groupers, and fertilization is external. The fact that no intromittent organ is present would support this assumption. Under natural conditions, in the Caribbean, at Bermuda and in the Bahamas, groupers apparently aggregate during the spawning season (T. Khaleel, pers. comm., Cayman Islands; W. Miller, pers.

Table 7.5. Estimated egg numbers and eggs per gram of body weight for (a) *Alphesthes afer* (4); (b) *Petrometopon cruentatum* (1); (c) *Cephalopholis fulva* (4) and (d) *Epinephelus guttatus* (6).

Species and total length (cm)	Total weight (gm)	Estimated no. of eggs	Eggs/gram weight
(a) <i>Alphesthes afer</i>			
23.2	225*	165,119	734
24.3	275	157,512	573
24.8	275	162,336	590
24.9	300	223,706	746
(b) <i>Petrometopon cruentatum</i>			
29.0	411**	262,604	639
(c) <i>Cephalopholis fulva</i>			
23.2	233**	160,366	688
23.5	233	67,883	291
23.7	233	149,363	641
24.3	260	282,389	1,086
(d) <i>Epinephelus guttatus</i>			
26.0	271**	96,982	358
31.0	456	139,070	305
34.1	599	288,096	481
35.0	654	329,532	504
36.3	711	526,358	740
41.0	1,047	379,350	362

*observed weights

**calculated weights from length-weight relationship data.

comm., British Honduras; Bardach 1958; and D. Beales, pers. comm., Bahamas).

Spawning Seasons

Erdman (1956) reported that *Cephalopholis fulva* spawned in Puerto Rican waters in December, *Epinephelus guttatus* in January, *Mycteroperca bonaci* in February and *M. venenosa* in March. Bardach et al. (1958) noted that the spawning season of most species in Bermuda extends from late April to late August. Smith (1961) observed *Mycteroperca bonaci* in spawning condition on the Campeche Bank during July and August. Moe (1969) noted that the red grouper, *Epinephelus morio*, spawned in the Gulf of Mexico from March to July, with peak spawning activity in April and May.

Randall and Brock (1960) noted that peak spawning activity of certain Indo-Pacific species occurred a few days before full moon. Ukawa et al. (1966) noted that *Epinephelus akaara* always spawned between 1530 and 1630 hr in culture ponds. Manday and Fernandez (1966) observed that *Epinephelus striatus* spawned at night.

Table 7.6. Monthly variations in the proportions of inactive (I), active (A), ripe (R) and spent (S) gonads of mature *Epinephelus guttatus* (exceeding 25 cm TL) at oceanic banks.

Month	Number in sample	I	Percentage		
			A	R	S
January	140	17.1	51.4	30.0	1.4
February	167	31.7	28.7	17.4	22.2
March	20	75.0	5.0	20.0	0
April	46	2.2	34.8	0	63.0
May	110	88.2	0	0	11.8
June	18	100.0	0	0	0
July	69	100.0	0	0	0
August	84	100.0	0	0	0
September	76	100.0	0	0	0
October	78	100.0	0	0	0
November	97	92.8	7.2	0	0
December	145	86.9	11.0	2.1	0
Total	1,050				

Seasonal variations in the proportion of sexually inactive, active, ripe and spent groupers captured at oceanic banks are given in Tables 7.6 to 7.9. Sampling activities on oceanic banks could not be conducted on an entirely regular basis, and samples taken during the period August 1969 to February 1973 have been combined on a monthly basis. Sampling was also done at Port Royal Reefs for a period of 28 lunar months, from November 1969 to January 1972. However, groupers were rather uncommon in the area and during the latter half of the sampling program, the abundance of groupers at the Port Royal reefs decreased to very low levels, possibly as a direct result of the sampling program. Very few sexually active groupers were caught and it appears likely that most species move to the shelf edge to spawn. Maturation stages are defined in Chapter 3.

Epinephelus guttatus: A sample totalling 1,050 fishes was taken on oceanic banks (Table 7.6). Ripe fishes were taken only in December-March and the greatest number of ripe or active fishes were taken in January. No active or ripe fishes were taken between May and October. About 50% of the fishes captured at the Port Royal reefs between December 1969 and May 1970 were sexually active but no ripe fishes were ever captured.

Epinephelus striatus: Samples of this species were not obtained in every month, but the high percentage of recently spawned fishes found during February and April (Table 7.7) indicates a spawning period extending from January to April. G. Chislett (pers. comm.) noted that almost all specimens taken at Navidad Bank during January 1970 were ripe.

Cephalopholis fulva: Ripe fishes were found between November and July, with peak spawning in January to March, and a subsidiary peak in June and July (Table

Table 7.7. Monthly variations in the proportions of inactive (I), active (A), ripe (R) and spent (S) gonads of mature *Epinephelus striatus* (exceeding 48 cm TL) at oceanic banks.

Month	Number in sample	I	Percentage		
			A	R	S
January	0		No data		
February	36	11.1	0	16.7	72.2
March	0		No data		
April	14	0	0	14.3	85.7
May	30	83.3	0	0	16.7
June	0		No data		
July	42	100	0	0	0
August	3	100	0	0	0
September	5	100	0	0	0
October	10	100	0	0	0
November	9	100	0	0	0
December	2		100	0	0
Total	151				

Table 7.8. Monthly variations in the proportions of inactive (I), active (A), ripe (R) and spent (S) gonads of mature *Cephalopholis fulva* (exceeding 16 cm TL) at oceanic banks.

Month	Number in sample	I	Percentage		
			A	R	S
January	129	20.2	26.4	49.6	3.9
February	211	16.1	33.2	47.4	3.3
March	53	13.2	30.2	52.8	3.8
April	39	0	56.4	17.9	25.7
May	149	87.9	2.0	4.7	5.4
June	51	56.9	7.8	35.3	3.9
July	127	53.5	15.0	22.0	9.4
August	75	94.7	1.3	0	4.0
September	110	98.2	0.9	0	0.9
October	87	100	0	0	0
November	127	93.7	3.9	1.6	0.8
December	151	74.8	22.5	2.6	0
Total	1,309				

7.8). The greatest proportion of spent fishes was taken in April.

Mycteroperca venenosa: The data given in Table 7.9 indicate that most spawning occurs between February and April.

Petrometopon cruentatum: Insufficient numbers were collected on a regular basis to define the spawning period of this species. Specimens with ripe gonads were captured at the Port Royal Reefs in April-May 1970. In April 1972, some fishes with active gonads were taken at Pedro Bank and during June 1972, most of the fishes in the commercial catch from Pedro Bank had ripe gonads.

Table 7.9. Monthly variations in the proportions of inactive (I), active (A), ripe (R) and spent (S) gonads of mature *Mycteroperca venenosa* (exceeding 51 cm TL) at oceanic banks.

Month	Number in sample	I	Percentage		
			A	R	S
January	0		No data		
February	37	2.7	0	94.6	2.7
March	0		No data		
April	16	0	0	68.8	31.2
May	34	20.6	0	2.9	76.5
June	0		No data		
July	38	94.7	5.3	0	0
August	2	100	0	0	0
September	11	100	0	0	0
October	0		No data		
November	8	100	0	0	0
December	1	0	100	0	0
Total	147				

Epinephelus mystacinus: Two ripe females were captured, one in November and one in August.

Mycteroperca interstitialis: Four ripe individuals were examined during April 1972. This species was reported as spawning from May to August in Bermuda (Smith 1958).

Alphistes afer: Found in spawning condition during December 1971 (4 ripe, 4 active and 2 inactive specimens seen). One active male was seen during May 1972. Smith (1958) recorded one ripe female from Bermuda during July.

Paranthias furcifer: Two ripe fishes (1 male and 1 female) were collected during January 1972, and three active males were collected during March 1972. Ripe individuals were reported from Bermuda during May (Smith 1958).

Spawning Grounds

On the eastern shelf of Cayman Brac and Grand Cayman spawning aggregations of groupers, mostly *Epinephelus striatus*, are found yearly during late January to early February (T. Khaleel, pers. comm.). These aggregations last up to 2 wk. Smith (1972) described spawnings aggregations of *E. striatus* near Bimini, Bahama Islands. Spawning aggregations have also been noted by W. Miller (pers. comm.) on the British Honduran shelf, by D. Beales (pers. comm.) in the Bahamas and by Bardach et al. (1958) on the Argus and Challenger Banks, off Bermuda.

Spawn

The eggs of the red grouper, *Epinephelus morio*, were described by Moe (1969) as being less than 1 mm in

diameter, containing an oil droplet and having no filaments or other appendages. Ukawa et al. (1966) described the eggs of *Epinephelus akaara* as pelagic, spherical in shape and measuring 0.70 to 0.77 mm in diameter. Bardach (1958) and Manday and Fernandez (1966) reported egg diameters ranging from 0.9 mm to 1.024 mm.

During this study, egg diameters of *Epinephelus guttatus* were found to vary between 0.70 mm and 0.90 mm and those of *Cephalopholis fulva* between 0.50 mm and 0.65 mm. No large transparent eggs were encountered in any of the ripe gonads examined and, as suggested by Smith (1965), the final maturation processes probably take place immediately before ovulation.

PRE-ADULT PHASE

Manday and Fernandez (1966) described the embryonic development of the Nassau grouper, *Epinephelus striatus*, up to the absorption of the yolk sac. Ukawa et al. (1966) described the early life history of *Epinephelus akaara* in the western Pacific. Presley (1970) described 16 larval specimens of *Epinephelus niveatus* which were collected in the Florida straits.

Virtually nothing is known of the early life history of western Atlantic groupers and our experiences and a review of the literature show that post-larval and early adolescent groupers are very rarely seen or collected. Early adolescent specimens of *P. cruentatum* and *E. guttatus* have been observed by divers on rare occasions, but no specimens smaller than about 5 cm TL were ever seen during the course of these investigations. Extensive searching revealed a few juveniles on the reefs, on seagrass beds and mangrove swamps. However, these numbers are insignificant when compared to the number of adults seen and caught. Moe (1969) reported that juvenile red groupers occur in low densities over rocky bottoms in the Gulf of Mexico to depths of at least 20 fathoms. These groupers secrete themselves in crevices and shells and thus would not be available to most collecting gear. The traps used throughout the West Indies could retain groupers down to sizes of about 15 cm TL. However, during the present study, individuals smaller than 20 cm TL were very rarely caught, indicating that if they are present in the fishing areas, their density must be low or that for some unknown reason, they are not prone to entering traps at this stage. Small specimens were also not taken on hook-and-line, nor were any taken in several traps fitted with 1.7 cm mesh which were capable of retaining groupers in the 6 to 9 cm TL size range.

ADULT PHASE

The amount of previous information concerning the adult phase is limited, and there is very little information on aspects such as longevity, hardiness, parasitism and

diseases, predators, competitors, or general physiological factors.

Competitors and Predators

It appears possible that a high degree of interspecific competition exists between most species of groupers which are mostly quite similar in food habits, size, habitats and distribution. Various snappers (Lutjanidae), jacks (Carangidae) and sharks are probably also competitors for food.

There appears to be no published information on predation on groupers, but they presumably fall prey to sharks and other large fishes.

Parasites and Infection

Parasitic isopods are commonly found clinging to the nostrils of *Epinephelus striatus* and *Mycteroperca venenosa*. Encysted larval tapeworms are very common in the viscera of many species, including *E. guttatus*, *E. striatus*, *E. mystacinus*, *M. venenosa* and *Cephalopholis fulva*. The entire viscera of a specimen of *E. mystacinus* (90 cm TL) was completely filled with these parasites and it is possible that such a degree of infection could lead to death. Ovaries of *E. striatus* and *M. venenosa* have been found infected with a reddish-brown nematode on several occasions. Heavy infection by this parasite can drastically reduce the number of eggs produced by an individual. No gonadal infection was noted for males.

In nature, groupers probably rely heavily on "cleaners" to help rid themselves of external parasites. In March 1971, an *E. guttatus* was observed resting on a coral head while being cleaned by a small wrasse (V. Gaut, pers. comm.).

Injuries to the snout and/or caudal fin of groupers obtained while trying to escape from fish traps showed no signs of healing if these fish were kept in aquaria and deterioration was accelerated as the injuries became infected. It is not known whether infections of this nature are common under natural conditions.

Abnormalities

Two pug-headed individuals of *C. fulva* were seen in a commercial catch from Serranilla Bank during February 1972. To help offset the difference in length between the upper and lower jaws, the premaxillaries of the pug-headed specimens were permanently protruded.

Many of the otoliths examined during this study showed excrescences on the concave surface. Usually these appeared as small bulbous growths, as described by Moe (1969), but in some cases as elongated mounds almost 1 cm long. Excrescences were most common in larger otoliths, their size increasing with the size of the otolith. Generally found on both otoliths of a particular fish, excrescences were noticed on otoliths of *E. guttatus*, *E. striatus*, *M. venenosa*, *P. cruentatum* and *C. fulva*. The otoliths of one *E. striatus* (58.3 cm TL) were completely

malformed, with the whole of the concave surface being overgrown with a large excrescence. The pair weighed 1.23 g as compared with the average weight of about 0.6 g for normal otoliths from fishes of a comparable size.

Injuries and Survival

During September 1970, a specimen of *E. guttatus* was collected with the tail, caudal peduncle and part of the soft dorsal fin missing. Eight soft dorsal fin rays were present (15 to 16 normally) and these had grown down over the "stump" to the region of the lateral line. The most posterior ones were in a horizontal position. They were longer than normal and along with the anal fin functioned as an inefficient tail. The total length of this fish was 16.0 cm (estimated normal total length about 22 cm) and it weighed 105 g. The injury was an old one as the damaged area was completely healed over and was covered with small regenerated scales.

During February 1972, a specimen of *Alphistes afer* (estimated TL 18.5 cm) was collected at Pedro Bank with half of the caudal peduncle missing and most of the caudal fin. A small central bit of the caudal fin remained.

Decaudate fishes are apparently the result of unsuccessful attacks by predators. The handicapped fish apparently survives for a time although swimming ability must be impaired, reducing their food capturing ability and also making them easy prey to faster-moving predators. Mortality in these fishes is therefore probably very high and only a small percentage would survive. The number of cases which have been recorded would suggest that the total number of decaudated fishes must be high.

Hardiness

Commercial fishermen operating at Pedro Bank have reported that hinds and groupers often die in traps, particularly in the summer months, and consider this to be an important problem affecting their livelihoods. This phenomenon was observed on several occasions during the present study and on a cruise to northwestern Pedro Bank at the end of September 1972, only three of the catch of 32 *E. guttatus* were alive when the traps were hauled from 40 m after a soak of 3 days. No other species were affected, suggesting that the mortality is not related to any oceanographic phenomenon or that this species might be more sensitive to environmental change than most other reef fishes. It is possible that the mortalities might result from shock, induced by behavioral traits being upset when the fishes are trapped.

Longevity

On the basis of otolith studies, Moe (1969) estimated that *E. morio* attained ages of up to 25 yr in the Gulf of Mexico. McErlean (1963) also used otoliths to estimate that *M. microlepis* attained ages of up to 13 yr in Florida.

Table 7.10. Relationships between total lengths (TL) and standard lengths (SL) of five species of groupers from Jamaican waters.

Species and formula	Number of measurements	Length range TL cm
<i>Epinephelus guttatus</i> TL = 1.8 + 1.19 SL	36	21-42
<i>E. striatus</i> TL = 3.0 + 1.09 SL	26	43-75
<i>Cephalopholis fulva</i> TL = 0.7 + 1.18	45	20-30
<i>Petrometopon cruentatum</i> TL = 0.5 + 1.20 SL	34	18-32
<i>Mycteroperca venenosa</i> TL = 1.0 + 1.16 SL	36	26-77

NUTRITION AND GROWTH

Feeding and Food

The groupers are unspecialized carnivores feeding mainly on fishes and crustaceans. Work on the food habits of groupers was done by Randall (1967) in Virgin Islands. Moe (1969) reported on the feeding of *Epinephelus morio* in the Gulf of Mexico.

During this study, little information was gathered about food habits as stomachs were frequently empty when examined. Small grunts (*Haemulon aurolineatum* and *H. melanurum*), crabs (notably small *Mithrax* sp.) and scyllarid lobsters were among the stomach contents of specimens of *E. guttatus* captured at oceanic banks. *E. striatus* were occasionally caught with spotted morays, *Gymnothorax moringa*, in their stomachs. One misty grouper, *Epinephelus mystacinus*, taken from 200 m had eight caridean shrimps and one partially digested eel in its stomach.

Groupers feed both by day and by night but according to Randall (1967) are more active at dawn and at dusk. Bardach et al. (1958) noted that the food is generally engulfed whole. The fish opens its mouth and dilates the gill covers rapidly to draw in a current of water and literally inhales the food.

Growth

Relative growth patterns

The relationships between total length and standard length, maximum body depth and weight were established for the most abundant species, and are summarized in Tables 7.10 to 7.12.

The total length-standard length relationship is linear in all instances (Table 7.10), and the small numbers of

Table 7.11. Relationships between total lengths (TL) and body depths (D) of three species of groupers from Jamaican waters.

Species and formula	Number of measurements	Length range TL cm
<i>Epinephelus guttatus</i> TL = 2.5 + 3.43 D	22	18-43
<i>Cephalopholis fulva</i> TL = 4.2 + 3.09 D	20	19-30
<i>Petrometopon cruentatum</i> TL = 0.5 + 3.47 D	33	17-26

Table 7.12. Relationships of total lengths (TL) to weights of four species of groupers from Jamaican waters. All lengths are expressed in cm and weights in grams.

Species and formula	Number of fish	Length range (TL) (cm)
<i>Epinephelus guttatus</i> $\log W = -1.754 + 2.960 \log L$ $W = 0.0176 L^{2.960}$	189	21.0-41.0
<i>Epinephelus striatus</i> $\log W = -1.971 + 3.112 \log L$ $W = .0107 L^{3.112}$	112	32.5-82.5
<i>Cephalopholis fulva</i> $\log W = -1.137 + 2.574 \log L$ $W = 0.0729 + L^{2.574}$	100	18.0-30.0
<i>Petrometopon cruentatum</i> $\log W = -2.118 + 3.237 \log L$ $W = 0.00762 L^{3.237}$	153	16.0-29.0

measurements taken are considered to be adequate.

The total length-maximum body depth relationship, as measured from the origin of the spinous dorsal fin to the insertion of the pelvic fins, can vary significantly depending upon individual variations in the shape of the body, the contents of the stomach and the state of activity of the gonads. Total length-body depth relationships for *Epinephelus guttatus*, *Petrometopon cruentatum* and *Cephalopholis fulva* are given in Table 7.11. Fishes with stomachs distended with food are not included.

The maximum aperture of the wire-mesh usually used in fish traps in the Jamaican fishery is 4.13 cm and the total lengths of *E. guttatus*, *C. fulva*, and *P. cruentatum* at this body depth are 16.7 cm, 17.0 cm and 14.8 cm, respectively. About 50% of the fishes of these sizes that enter such traps will be retained. Equations describing the length-weight relationships of four species of groupers are given in logarithmic and exponential terms in Table 7.12.

Maximum size

Maximum observed lengths and maximum lengths recorded in the literature are given in Table 7.13 for 17 species of groupers caught during this study. Unless otherwise stated, all lengths from past literature are taken from Bohlke and Chaplin (1968) or Randall (1968).

Age and growth

Few age and growth estimates have been made for groupers of the western north Atlantic. Moe (1969) and McErlean (1963) used otoliths to determine the ages of *Epinephelus morio* and *Mycteroperca microlepis* from the sub-tropical Florida waters of the Gulf of Mexico. Bardach and Menzel (1957) studied the growth of common grouper species in Bermuda and indications of growth were also obtained by Randall (1962, 1963) in the Virgin Islands and by Beaumariage (1969) in Florida, during the course of tagging experiments.

During the course of the present study, estimates of age and growth have been based upon analyses of length-frequency distributions and examination of scales and otoliths. The applicability of the methods varied with the species.

Analyses of modal progressions in length-frequency distributions of samples were possible for *E. guttatus*, *C. fulva* and *P. cruentatum*. Samples of other species were too small or irregularly spaced to produce coherent results. Grouper scales are generally small, rectangular, with rounded edges, and are ctenoid and most of the

scales which were examined showed irregular areas of resorption which resembled annuli and extended around the entire lateral and anterior sections. These areas were sometimes associated with the ending of old radii and/or the formation of new radii in the anterior field. However, scales showing these characters appeared haphazardly and no correlation could be made between the markings and increase in size of the fish. These markings were present only on some of the scales collected from a single fish and their formation is possibly related to the replacement of nearby scales. Some scales from large individuals of *Mycteroperca venenosa* and *Epinephelus striatus* showed a broad area of resorption in the anterior field and an increased number of radii anterior to this area. Possibly the resorption of circuli in these instances reflects the transition phase from male to female. *Alphes-tes afer* is the only species which appeared to show interpretable scale annuli.

Otoliths from specimens of *P. cruentatum*, *C. fulva*, *E. guttatus*, *E. striatus*, *E. morio*, *M. venenosa* and *M. bonaci* were examined. The otoliths of these species are similar to those of *E. morio*, described by Moe (1969), and those of *Mycteroperca microlepis*, described by McErlean (1963). The otoliths of *Mycteroperca* spp. are thinner and clear more easily than those of *Epinephelus* spp. Otoliths were treated as described in Chapter 3. With the exception of otoliths of *M. venenosa*, none of the methods produced satisfactory results, and cleared otoliths usually appeared uniformly translucent or showed numerous light and dark bands (e.g., those of *C. fulva*) but no interpretable markings. In contrast to results obtained by Moe (1969) in Florida waters,

Table 7.13. Observed maximum total lengths of groupers from Jamaican waters compared with measurements from past literature.

Species	No. of measurements	Observed max. length cm	Max. length literature (cm)
<i>Paranthias furcifer</i>	6	20	30.0*
<i>Epinephelus striatus</i>	382	84	90-120
<i>E. morio</i>	1	82	90.0
<i>E. guttatus</i>	954	48	53.7
<i>E. itajara</i>	9	Approx. 150	240
<i>E. mystacinus</i>	18	107	113**
<i>E. adscensionis</i>	1	51	60
<i>Dermatolepis inermis</i>	2	69	80
<i>Cephalopholis fulva</i>	2,881	33	37.5
<i>Petrometopon cruentatum</i>	639	33	30
<i>Alphes-tes afer</i>	10	26	30
<i>Mycteroperca venenosa</i>	198	86	90
<i>M. bonaci</i>	11	133	120
<i>M. tigris</i>	22	67	100
<i>M. interstitialis</i>	5	62	75
<i>M. cidi</i>	3	57	112.5
<i>M. rubra</i>	1	20	68.7

*Smith (1958)

**Brownell and Rainey (1971)

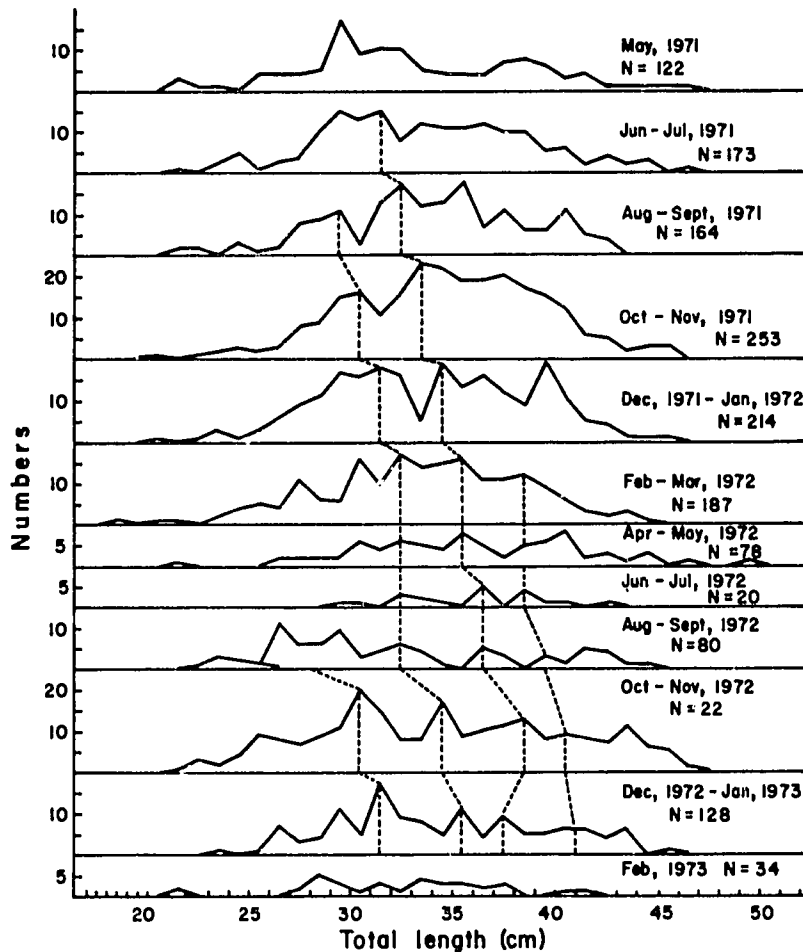


Fig. 7.2. Bimonthly length-frequency distributions of samples of *Epinephelus guttatus* from Pedro Bank, May 1971 to February 1973. Broken lines show the modal progressions utilized in estimating the growth rate.

otoliths of *E. morio* (collected from the Mosquito Cays on the Nicaraguan Shelf), cleared in glycerol and viewed by reflected light, showed no annuli.

Randall (1962, 1963) reported on the results of marking a wide range of species of reef fishes, including seven species of groupers. Results were expressed in terms of average increases in length per month. Where relevant, some of Randall's data have been re-analyzed using the regression equation

$$\log_e (L_\infty - l_a) - \log_e (L_\infty - l_b) = K(a - b)$$

in which l_a is the length at tagging at time a , and l_b is the length at recapture at time b (Munro 1982). Trial values of L_∞ have to be used to obtain the best fit of the points, which are usually widely scattered.

Epinephelus guttatus: Scales and otoliths of this species showed no discernible periodic marks or rings although otoliths of specimens taken in Florida and Bermuda waters are reported to show clear rings (J. Burnett-Herkes, pers. comm.).

Bimonthly length-frequency distributions of samples taken at Pedro Bank between May 1971 and February

1973 show clear modal progression (Fig. 7.2) and four discrete modes are apparent in most samples. A regression of values of $\log_e (L_\infty - l_t)$ against a two-monthly time scale gives three nearly parallel regressions (Fig. 7.3), using a value of $L_\infty = 52.0$ cm TL. The mean slope of the regression lines is 0.04 and on an annual basis the coefficient of growth, K , is 0.24.

Only five of the *E. guttatus* recaptured by Randall (1962) showed appreciable growth and were free for more than 100 days and calculated values of K for these specimens range between 0.12 and 0.26, with a mean of 0.18.

Cephalopholis fulva: Otoliths of this species showed numerous light-and-dark bands, but these marks did not appear to be related to seasonal factors. Scales showed no markings.

Length-frequency distributions of samples taken in traps and on hook and line at Pedro Bank between December 1971 and February 1973 are shown in Fig. 7.4. One additional sample is available for May 1971. Recruits in the 18 to 21 cm TL range appeared in the catches between June and September 1972, and reached about 24.5 cm TL by February 1973. Fishes in the

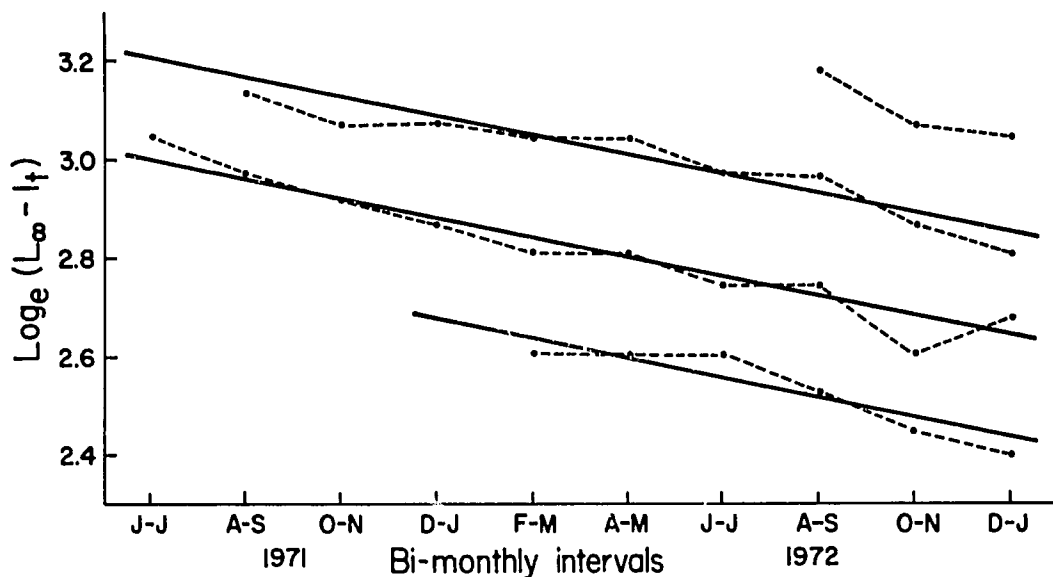


Fig. 7.3. Modal lengths of bimonthly samples of *Epinephelus guttatus* from Pedro Bank expressed as values of $\log_e (L_\infty - l_t)$. Data from Fig. 7.2. Best fit of regression is obtained when $L_\infty = 52$ cm TL. Mean slope, $K = 0.24$ per 12 months.

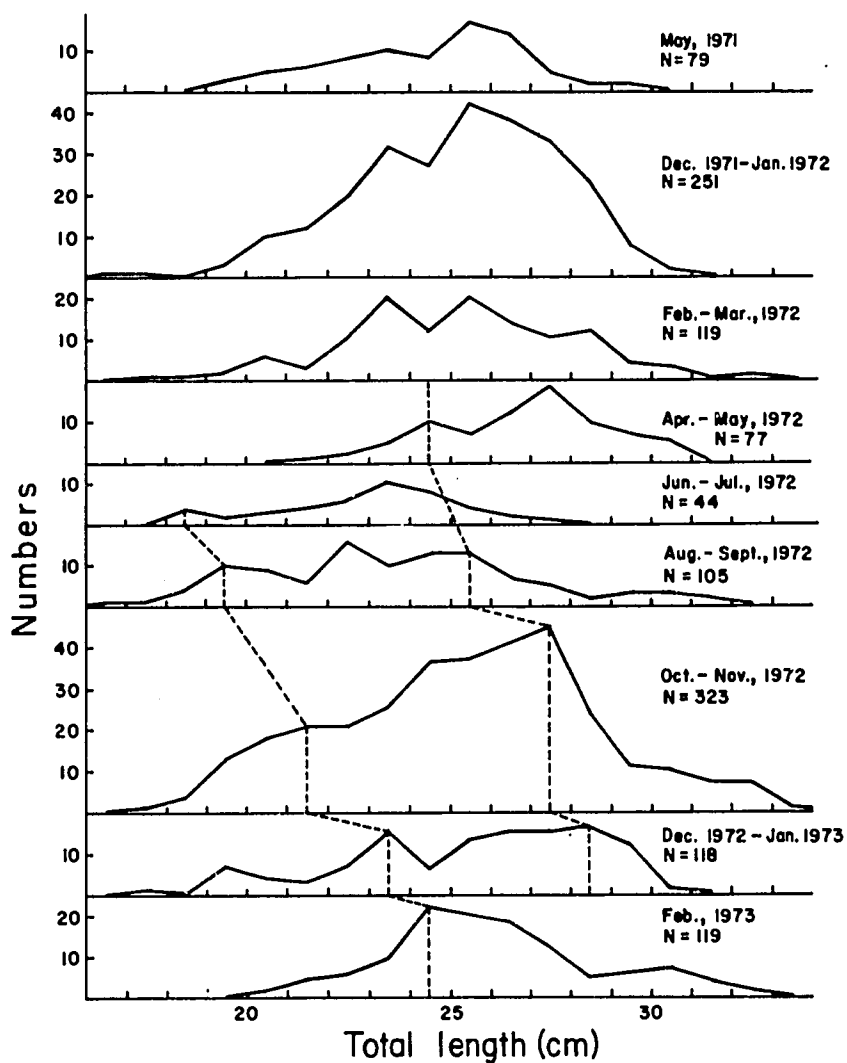


Fig. 7.4. Bimonthly length-frequency distributions of samples of *Cephalopholis fulva* from Pedro Bank, May 1971 and December 1972 to February 1973. Broken lines show the modal progressions utilized in estimating the growth rate.

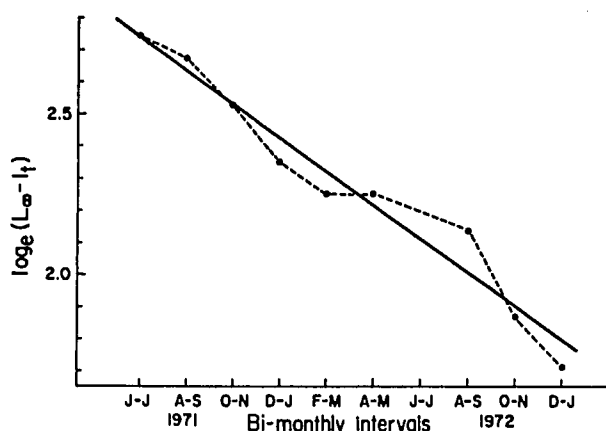


Fig. 7.5. Modal lengths of bimonthly samples of *Cephalopholis fulva* expressed as values of $\log_e(L_\infty - l_t)$. Data from Fig. 7.4. Best fit of the regression is obtained when $L_\infty = 34$ cm TL. Mean slope, $K = 0.63$ per 12 months.

region of 24.5 cm TL in December 1971-January 1972 appeared to attain about 28.5 cm by December 1972-January 1973.

The latter progression is not at all clear owing to the bimodality of the samples taken between December 1971 and May 1972, and it is possible that two year-classes are represented by these modes. However, this would imply an abrupt decrease in the growth rate after about 23.5 cm TL is attained and it thought to be more likely that the bimodality results from the successive January-March and June-July spawnings (Table 7.8).

A regression of values of $\log_e(L_\infty - l_t)$ gives the best fit when L_∞ is set at 34.0 cm TL (Fig. 7.5), and the coefficient of growth, K , is thus about 0.63.

Petrometopon cruentatum: Samples of this species were too small to provide adequate length-frequency distributions, and no indications of age and growth were obtained from scales or otoliths. The series of samples taken at the Port Royal Reefs between November 1969 and January 1972 suggested that recruits enter the fishery at a length of about 19 cm in November and attain about 23.5 cm TL within a year. The asymptotic length is thought to be in the region of 33 to 35 cm TL, and the coefficient of growth, K , might therefore be about 0.33 to 0.35.

Mycteroperca venenosa: The sulcus acusticus of otoliths of *Mycteroperca venenosa* showed regular markings. These were stained red by methyl violet B and were examined by immersing the otoliths in xylene and viewing them under a low-power binocular microscope using transmitted light. The depth of the sulcus acusticus and the number of stained ridges increased with increase in size of the fish. The numbers of stained ridges are plotted against the total lengths of 27 *M. venenosa* in Fig. 7.6.

If the dense ridges observed in the sulcus acusticus of *M. venenosa* are formed annually, then a period of 4 yr is required for fishes to reach a total length of 46 to 57 cm (average 51 cm) and a size of

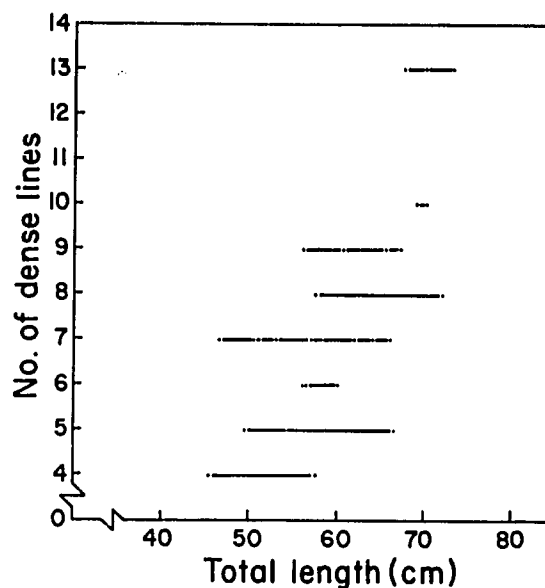


Fig. 7.6. The numbers of dense lines in the sulcus acusticus plotted against total lengths of 27 *Mycteroperca venenosa*.

about 70 cm TL is reached at about age 10 yr (i.e., a growth rate of about 3+ cm/yr). If the asymptotic length is about 86 cm, the coefficient of growth, K , is about 0.1.

Randall (1962, 1963) tagged 80 *M. venenosa*, and 8 of the recoveries had been at liberty for more than 200 days. Using a value of $L_\infty = 86$ cm the calculated growth rate, K , of these eight individuals lies between 0.10 and 0.27, with a mean of 0.17.

Epinephelus striatus: Data obtained during this study did not provide any information on growth rates. Randall (1962, 1963) tagged 124 *E. striatus* at St. John, U.S. Virgin Islands and recaptured 45 after periods exceeding 1 mo. Re-analysis of Randall's data suggests that tagging suppressed growth in many cases. Twelve individuals, each free for more than 200 days, showed appreciable increases in size and, assuming that L_∞ is in the region of 90 cm TL, had a mean rate of growth, K , of 0.09, and a range from 0.05 to 0.13.

Alphistes afer: The scales of *A. afer* appeared to show regular annulus formation. This species is uncommon in Jamaican waters. Scales from six of a total of seven specimens examined over the period extending from November 1971 to January 1972 showed one annulus (Table 7.14). The annuli appeared as narrow continuous rings running roughly parallel to the edges of the scales in the lateral anterior regions. In the lateral fields, the circuli within the band tended to be broken up into irregularly shaped bits. This continued into the anterior field or was replaced there by a significant space between successive circuli. In some instances, the formation of new radii appeared to be associated with the annulus in the anterior region of the scale. The average marginal increment was 0.37 mm. The average length at

Table 7.14. Summary of observations on scales of *Alphistes afer*.

Total length (cm)	Scale radius (mm)	Position of annulus (mm)	Marginal increment (mm)	Date collected	Sex	Gonad stages
22.1	3.26	2.83	0.43	Nov. 1971	?	I
20.8*	3.35*	—	—	Nov. 1971	?	I
24.8	3.01	2.61	0.40	Dec. 1971	?	I
24.9	3.20	3.06	0.14	Dec. 1971	F	R
23.3	3.32	3.02	0.32	Dec. 1971	F	R
26.9	3.90	3.45	0.45	Jan. 1972	F	R
26.1	4.07	3.60	0.47	Jan. 1972	F	R
Averages						
24.6	3.46	3.09	0.37	—	—	—

*Not included in averages.

"annulus" formation calculated by proportionality was 21.9 cm and is probably related to the onset of gonad activity at the beginning of the spawning season.

BEHAVIOR

Migrations

Moe (1972), in his description of the movement and migration of fishes in Florida waters noted that the small reef-dwelling groupers are predominantly non-migratory

POPULATION STRUCTURES

Sex Ratios

In groupers the sex ratio is closely related to the size composition of the population, and since sex could only be determined macroscopically when fishes were in the active to ripe state, the sex ratios obtained represent those of mature fishes during the breeding season. The sex ratios of five species of groupers are summarized in Table 7.15.

Generally, females are more numerous than males. Samples of *Epinephelus striatus* and *Mycteroperca venenosa* included mostly large fishes and this would probably account for males being more numerous than females.

The high proportion of females in the populations of *E. guttatus* and *Petrometopon cruentatum* at Port Royal (Table 7.15) probably results from the high fishing intensity which results in most fishes being caught before they reach the size of sexual transition. The mean size of *E. guttatus* at the Port Royal Reefs was 26 cm TL as compared with about 33 cm TL on oceanic banks.

Age and Length Composition

The average annual length compositions of catches have been calculated by the methods described in Chapter 3.

and seldom venture from the protection of the reef. It has also been shown that *Epinephelus* spp. and *Mycteroperca* spp. maintain residence on a particular reef for extended periods (Bardach 1958; Randall 1962, 1963; Springer and McErlean 1962; Topp 1963; Moe 1966). However, Moe (1966, 1967) and Beaumariage (1969) presented evidence for developmental migration and extensive offshore movement in the red grouper, *Epinephelus morio*.

During this study, length-frequency distributions of *Epinephelus guttatus* and *E. striatus* suggested a similar movement from the Port Royal Reefs to the South Jamaican Shelf, at the size of sexual maturity.

Schooling

Groupers are essentially solitary (Smith 1961) although as described previously, some species of *Epinephelus* and *Mycteroperca* school during the spawning season.

Reproductive Behavior

Manday and Fernandez (1966) described the pre-spawning behavior of captive *E. striatus* as the constant nudging of the females on their sides by the males, apparently with the intention of inducing spawning. This nudging is not continuous and shows no apparent relation to selection of pairs.

Populations

Epinephelus guttatus: The percentage frequency of successive length groups captured in traps and on hook and line are compared in Fig. 7.7. Data are from cruises of the *R.V. Caranx* in which both fishing gears were employed at the same depths and in the same areas at Pedro Bank. Traps captured fishes of slightly larger average size, but the distributions are very similar. It is therefore concluded that traps and lines are reasonably unselective and that samples obtained by hook and line or by trap fishing can be combined for purposes of estimating the size composition of the catches.

Table 7.15. Sex ratios of groupers commonly caught in Jamaican waters.

Species	Number examined	Ratio M:F	Area
<i>Epinephelus guttatus</i>	31	1:5.60	Port Royal Reefs 1970
	244	1:2.81	Oceanic banks
<i>E. striatus</i>	38	1:0.72	Oceanic banks
<i>Mycteroperca venenosa</i>	50	1:0.85	Oceanic banks
<i>Cephalopholis fulva</i>	352	1:2.14	Oceanic banks
<i>Petrometopon cruentatum</i>	49	1:6.00	Port Royal Reefs 1970 and 1971

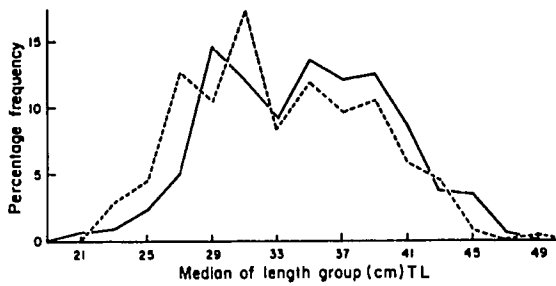


Fig. 7.7. Length-frequency distributions of catches of *Epinephelus guttatus* caught at Pedro Bank in traps (solid line) and on hook-and-line (broken line).

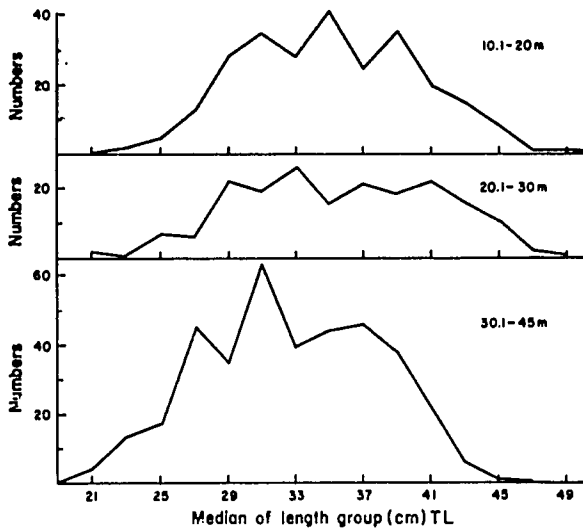


Fig. 7.8. Length-frequency distributions of catches of *Epinephelus guttatus* caught in traps and on hook and line in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones of Pedro Bank.

Figure 7.8 shows the gross length-frequency distributions of catches taken in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones in unexploited parts of Pedro Bank. Relatively fewer of the larger fishes (average 40 cm TL) were taken in the 30.1 to 45 m zone, and the mean size decreased slightly with increasing depth. This probably results from the relatively greater amount of line fishing done in the deepest zone. It is therefore concluded that all size groups are probably equally represented in the 10.1 to 45 m depth range.

Figure 7.9 shows the percentage length-frequency distributions of catches taken at the unexploited parts of Pedro Bank, at the Pedro Cays and at California Bank. It appears that this species is fully recruited to the fishery at 34.0 to 35.9 cm TL. The samples from the unexploited parts of Pedro Bank and from California Bank both had modes at 30.0 to 31.9 cm TL but owing to the uneven temporal distribution of catches or to small sample size, both estimates of catch composition are classed as "poor", whereas that from the Pedro Cays fishery is considered to be "fair" (Chapter 3).

On the basis of the Pedro Cays sample, the sizes at first retention, mean retention and full retention are 18

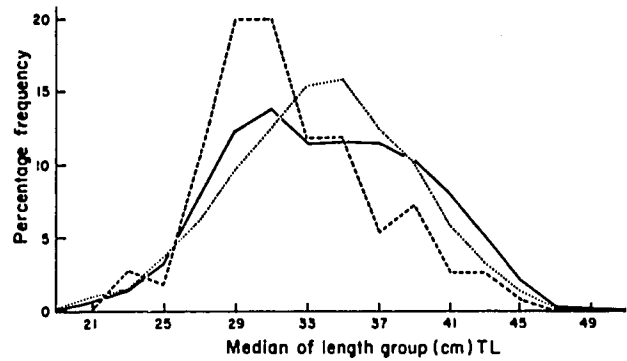


Fig. 7.9. Comparison of the estimated mean annual length-frequency distributions of catches of *Epinephelus guttatus* from California Bank (---), Pedro Cays (....) and unexploited parts of Pedro Bank (—). California Bank—N = 110, time period = 12 months; Pedro Cays—N = 712, time period = 4 months and Pedro Bank—N = 962, time period = 6 months.

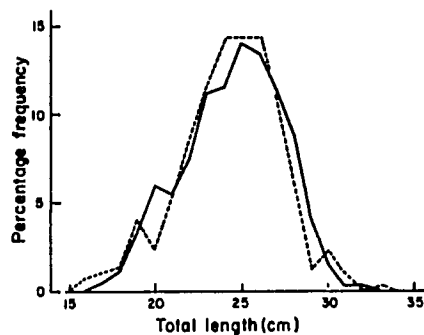


Fig. 7.10. Length-frequency distributions of catches of *Cephalopholis fulva* caught in traps (solid line) and on hook and line (broken line).

cm, 31 cm and 35 cm TL, respectively. The minimum size theoretically retainable by the 4.13 cm wire mesh used by the trap fishermen is 16.7 cm TL (Table 7.11) but no *E. guttatus* of less than 18 cm TL were ever captured during this study.

Cephalopholis fulva: The size compositions of samples taken in traps and by hook and line under comparable circumstances are shown in Fig. 7.10. There is no difference in mode, median and range, and it appears that the size at recruitment is governed by behavioral traits of the species and not by the selective properties of the fishing gears.

Figure 7.11 shows the size compositions of catches taken in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones of Pedro Bank. Fishes in the larger size groups (27 to 37 cm TL) appear to be relatively more abundant in the shallowest zone. However, a closer inspection of the data reveals that most of this bias is attributable to a single large sample. It is therefore likely that, as was the case with *E. guttatus*, the various size groups are more or less evenly distributed through all depth zones or that any differences are rather slight.

The mean length compositions of samples from the unexploited parts of Pedro Bank, from California Bank,

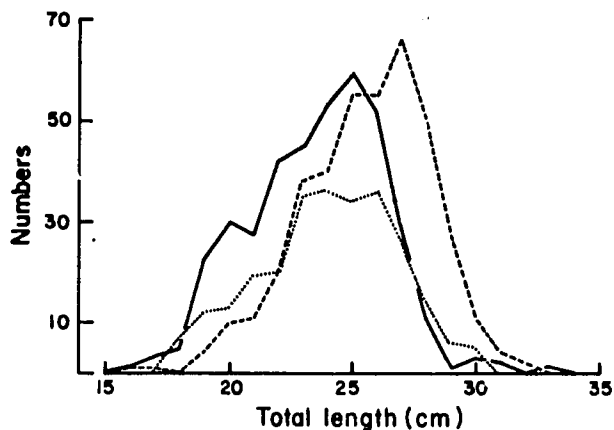


Fig. 7.11. Length-frequency distributions of catches of *Cephalopholis fulva* caught in traps and on hook and line in the 10.1 to 20 m (broken line), 20.1 to 30 m (dotted line) and 30.1 to 45 m (solid line) depth zones of Pedro Bank.

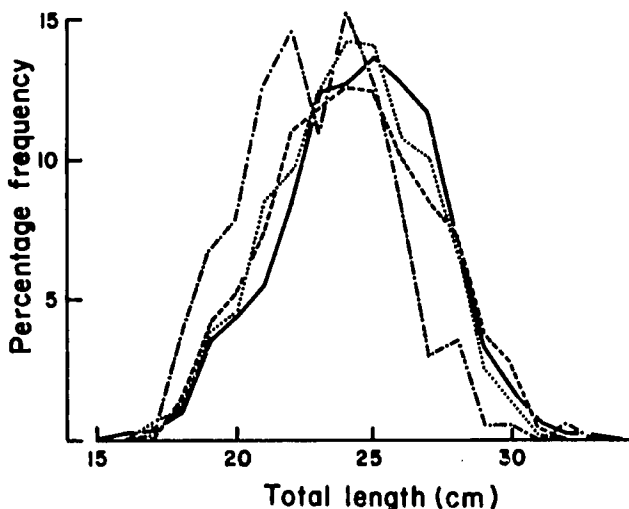


Fig. 7.12. Comparison of the estimated mean annual length-frequency distributions of catches of *Cephalopholis fulva* from California Bank (.....), Serranilla Bank (.....), Pedro Cays (---) and unexploited parts of Pedro Bank (—). California Bank—N = 165, time period = 12 months; Serranilla Bank—N = 381, time period = 4 months; Pedro Cays—N = 1,320, time period = 4 months; Pedro Bank—N = 1,251, time period = 3 months.

and of commercial catches from the Pedro Cays area and from Serranilla Bank are shown in Fig. 7.12. They appear to be fully available to the fishing gears at or before 25.0 to 25.9 cm TL.

The minimum, mean and full retention lengths are 16.5 cm, 23.0 cm and 25.5 cm TL, respectively. The minimum size theoretically retainable by the 4.13 cm mesh used in the trap fishery is 17.0 cm TL.

Petrometopon cruentatum: Samples of this species were generally too small for detailed analyses. The gross length-frequency distributions of a sample of 151 specimens captured at the Port Royal Reefs and 284 specimens measured in commercial catches from the Pedro Cays area are shown in Fig. 7.13.

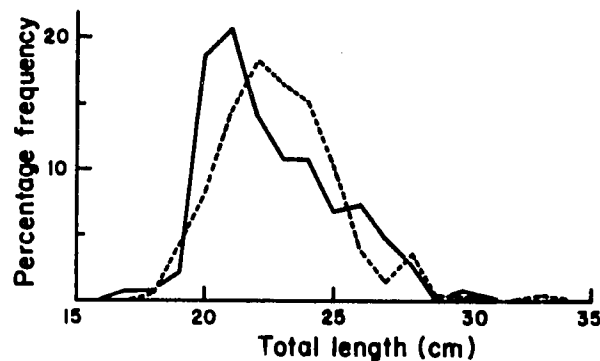


Fig. 7.13. Comparison of the estimated mean annual length-frequency distribution of catches of *Petrometopon cruentatum* from the Port Royal Reefs (—) and from the Pedro Cays area (---). Port Royal Reefs—N = 151, time period = 12 months; Pedro Cays area—N = 284, time period = 12 months.

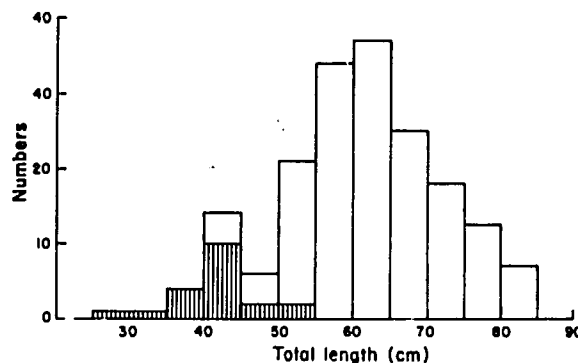


Fig. 7.14. Length-frequency distribution of catches of *Epinephelus striatus* from unexploited oceanic banks (N = 163) and at the Port Royal Reefs (N = 20). Sample from Port Royal Reefs is vertically hatched.

In a sample of 31 specimens taken by fishermen at Discovery Bay in traps with 3.30 cm mesh, only three fishes exceeded 21 cm TL, and the modal length was only 16.5 cm. This is a good example of the changes induced by intensive fishing with small-meshed nets. The mean weight of individuals in the latter catch was only 75 g compared with a mean weight of 157 g in the Port Royal catches.

The theoretical minimum size retainable by 4.13 cm wire mesh is 14.8 cm TL. The smallest specimen actually taken in this mesh was in the 16.0 to 16.9 cm TL group. The mean retention size is about 20 cm TL.

Epinephelus striatus: Samples of this species taken in traps and on hook and line at unexploited oceanic banks totalled 163 specimens, and 20 specimens were taken at the Port Royal Reefs.

Figure 7.14 shows that the size range captured in traps at the Port Royal Reefs (27 to 51 cm TL) falls mostly outside of that at the oceanic banks (40 to 84 cm TL) and that the populations at oceanic banks became fully recruited to the fishery at 60.0 to 64.9 cm TL. There is no satisfactory explanation as to why the smaller-size ranges do not appear in trap and line catches

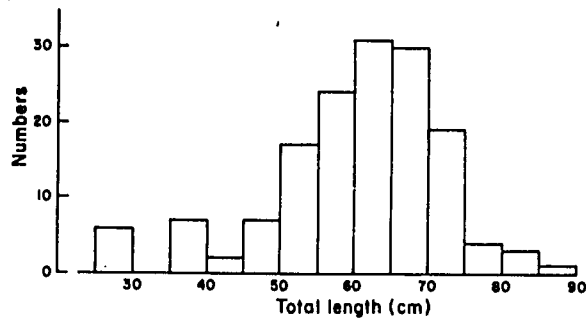


Fig. 7.15. Length-frequency distribution of catches of *Mycteroperca venenosa* from oceanic banks: N = 151.

from oceanic banks. It is possible that the sub-adults prefer shallower waters but many of the oceanic banks have minimum depths of 30 to 40 m, and support relatively large numbers of adults, but still do not yield appreciable numbers of small specimens. The mean size at which they became available in offshore areas is about 57 cm TL.

Mycteroperca venenosa: A sample of 151 specimens was taken on hook and line and in traps at various unexploited oceanic banks. As was the case with *E. striatus*, the smallest-size groups are under-represented in the samples, and the modal size is in the region of 65 cm TL (Fig. 7.15). Six small individuals (26.2 to 29.6 cm TL) were taken at Pedro Bank in March and April 1972. They became available to the fishing gear in offshore areas at a mean size of about 57 cm TL, the same length as was estimated for *E. striatus*.

Other species: The size composition of samples of the rarer species are indicated below. All lengths are total lengths.

Epinephelus adscensionis: One specimen caught outside the Barrier Reef at Port Royal measured 51.0 cm.

E. morio: One 82.0 cm specimen was collected from Pedro Bank and one 79 cm specimen from Serranilla Bank.

E. itajara: Two juveniles from the Port Royal mangroves measured 19.4 cm and 37.8 cm, respectively. Two specimens caught at the Port Royal Reefs measured 85.5 and 124.5 cm. Large specimens (100 to 200 cm) are occasionally seen and caught in Kingston Harbour.

Mycteroperca bonaci: Nine specimens were caught at the Port Royal reefs. Total length range was 36 to 61 cm with a mean length of 47 cm. Two were caught offshore, one of 62 cm and one of 133 cm that weighed 28.15 kg.

M. tigris: Twelve juveniles (length range 28 to 49 cm TL; mean TL 36.6 cm) were examined from Bajo Nuevo and six (length range 24 to 40 cm; mean length 30.2 cm) were examined from Pedro Bank during 1972. Four others (length range 46 to 67 cm, mean 52.7 cm) were caught during 1967-1969 on various oceanic banks.

M. interstitialis: Four specimens of 40 to 62 cm TL (mean 47.0 cm) were caught at 20-m Bank, Pedro Bank during April 1970. One collected during March 1972, from the Pedro Cays area measured 40.5 cm.

M. cidi: Three specimens were caught at the Port Royal Reefs (length range 41 to 57 cm, with a mean of 48.3 cm TL).

M. rubra: One juvenile was caught in April 1970, using a hand-line at the Port Royal Marine Laboratory jetty at a depth of approximately 2 to 3 m. Total length was 20.7 cm.

Alphesthes afer: Ten specimens were collected from the commercial catch from Pedro Bank, from December 1971 to April 1972, and had a length range of 22 to 26 cm with a mean length of 24 cm.

Dermatolepis inermis: Two caught at Pedro Bank—lengths 37.4 and 69.0 cm.

Paranthias furcifer: Six caught on oceanic banks using traps and lines. Length range 16 to 20 cm; mean length 18.5 cm.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

Nothing is known of the causes of natural mortality in groupers. The species appear to have relatively high catchabilities and are readily taken by a wide variety of fishing gear.

Mortality Rates

The absolute ages of the species of groupers dealt with in this report are not known and the following estimates of mortality rates are based entirely upon the length compositions of samples as described in Chapter 3. The limitations inherent in this method must be borne in mind, and the estimates are subject to fairly wide margins of possible error.

Epinephelus guttatus: Estimates of the size distribution of catches of this species at unexploited parts of Pedro Bank and the Pedro Cays area (Fig. 7.9) are based upon fairly large samples. The size distribution at California Bank is less well-defined. The growth parameters previously estimated are $K = 0.24$ and $L_{\infty} = 52$ cm TL. The rates of decline in abundance of successive length groups after full recruitment at 35.0 to 35.9 cm TL are given in Table 7.16.

The calculated value of M/K at the unexploited parts of Pedro Bank is 2.83 and, when $K = 0.24$, $M = 0.68$. The fishing mortality rates, F , calculated for the populations at the Pedro Cays and at California Bank, are 0.19 and 0.22, respectively, equivalent to rates of exploitation, E , of 0.22 and 0.24.

Cephalopholis fulva: Estimates of catch composition are available for stocks at unexploited Pedro Bay, the Pedro Cays, Serranilla Bank and California Bank (Fig. 7.12). The rates of decline of successive length groups beyond full retention at 25.0 to 25.9 cm TL are shown in Table 7.17. The growth parameters are $L_{\infty} = 34$ cm TL and $K = 0.68$.

Table 7.16. Derivation of mortality rates from the relative abundances of successive length groups of *Epinephelus guttatus* beyond full recruitment at 34.0 to 35.9 cm TL at unexploited parts of Pedro Bank, the Pedro Cays area and California Bank. $L_{\infty} = 52$ cm TL and $K = 0.24$.

Length group cm TL	Unexploited Pedro Bank		Pedro Cays		California Bank	
	% Frequency	Relative abundance	% Frequency	Relative abundance	% Frequency	Relative abundance
34.0-35.9	11.6	1.00	15.8	1.00	11.9	1.00
36.0-37.9	11.4	.98	12.6	.80	5.4	.45
38.0-39.9	10.3	.89	10.2	.65	7.2	.61
40.0-41.9	8.0	.69	5.8	.37	2.7	.23
42.0-43.9	5.0	.43	3.3	.21	2.7	.23
44.0-45.9	2.2	.19	1.4	.09	0.9	.08
46.0-47.9	0.3	.03	0.1	.01	0	0
48.0-49.9	0.1	.01	0	0	0	0
Mean TL	38.7 cm		37.9 cm		37.8 cm	
If $L_{\infty} = 52$ cm						
Z/K =	$(\frac{52.0 - 38.7}{38.7 - 34.0})$		$(\frac{52.0 - 37.9}{37.9 - 34.0})$		$(\frac{52.0 - 37.8}{37.8 - 34.0})$	
If $K = 0.24$	2.93 = M/K		3.62		3.74	
Z =	0.68 = M		0.87		0.90	
F =	0		0.19		0.22	
E =	0		0.22		0.24	

Table 7.17. Derivation of mortality rates* from the relative abundances of successive length groups of *Cephalopholis fulva* beyond full recruitment at 25.0 to 25.9 cm TL at unexploited parts of Pedro Bank, the Pedro Cays, Serranilla Bank and California Bank. $L_{\infty} = 34$ cm TL and $K = 0.63$.

Length group cm TL	Unexploited Pedro Bank		Pedro Cays		Serranilla Bank		California Bank	
	% Frequency	Relative abundance	% Frequency	Relative abundance	% Frequency	Relative abundance	% Frequency	Relative abundance
25.0-25.9	13.63	1.00	12.39	1.00	14.03	1.00	12.7	1.00
26.0-26.9	12.68	.93	10.00	.81	10.73	.77	7.3	.58
27.0-27.9	11.63	.85	8.49	.69	9.97	.71	3.0	.24
28.0-28.9	7.10	.52	7.29	.59	6.70	.45	3.6	.28
29.0-29.9	3.30	.24	3.80	.31	2.47	.18	0.6	.05
30.0-30.9	1.86	.14	2.83	.23	1.30	.09	0.6	.05
31.0-31.9	0.53	.04	0.50	.04	0.13	.01	0	0
32.0-32.9	0.13	.01	0	0	0	0	0.6	.05
33.0-33.9	0.05	+	0.07	+	0	0	0	0
Mean TL	27.2 cm		27.3 cm		27.0 cm		26.7 cm	
If $L_{\infty} = 34$ cm								
Z/K	$(\frac{34.0 - 27.2}{27.2 - 25.0})$		$(\frac{34.0 - 27.3}{27.3 - 25.0})$		$(\frac{34.0 - 27.0}{27.0 - 25.0})$		$(\frac{34.0 - 26.7}{26.7 - 25.0})$	
=	3.09 = M/K		2.91		3.50		4.29	
If $K = 0.63$								
Z =	1.95 = M		1.83		2.21		2.70	
F =	0		?		0.26		0.75	
E =	0		?		0.12		0.28	

*Note: In the original edition of this chapter the mean TL at unexploited Pedro Bank was incorrectly calculated, thus producing erroneous estimates of M/K and M. These have been corrected in this edition.

Table 7.18. Derivation of mortality rates from the relative abundances of successive length groups of *Petrometopon cruentatum* beyond full recruitment at 21.0 to 21.9 cm TL at the Pedro Cays and the Port Royal Reefs. L_{∞} = 34 cm TL and $K = 0.34$.

Length group cm TL	Pedro Cays		Port Royal Reefs	
	No. captured	Relative abundance	No. captured	Relative abundance
21.0-21.9	55	1.00	21	1.00
22.0-22.9	50	.91	16	.76
23.0-23.9	43	.78	16	.76
24.0-24.9	29	.53	10	.48
25.0-25.9	11	.20	11	.52
26.0-26.9	4	.07	7	.33
27.0-27.9	10	.18	4	.19
28.0-28.9	1	.02	0	0
29.0-29.9	1	.02	2	.10
30.0-30.9	0	0	0	0
31.0-31.9	0	0	0	0
32.0-32.9	1	.02	0	0
Mean TL If $L_{\infty} = 34$ cm	23.3 cm		23.8 cm	
Z/K =	$(\frac{34.0 - 23.3}{23.3 - 21.0})$		$(\frac{34.0 - 23.8}{23.8 - 21.0})$	
=	4.65		3.64	
If $K = 0.34$				
Z =	1.6		1.2	

The calculated value of M/K is 3.09, and $M = 1.95$. Fishing mortality rates (F) are calculated to be 0.26 and 0.75 at Serranilla Bank and California Bank, respectively, and the rates of exploitation, E , range between 0.12 and 0.28.

Petrometopon cruentatum: This species is relatively uncommon in the unexploited parts of Pedro Bank, and it has not been possible to estimate the size composition of an unexploited population.

Table 7.18 and Fig. 7.13 show that the rates of decline of successive length groups were similar at the Port Royal reefs and at the Pedro Cays, but in neither case are the sample sizes satisfactory, and the estimates of mortality rates are very poorly based. In addition, the growth rate is not known with any precision and the estimates of $L_{\infty} = 34$ cm TL and $K = 0.34$ are speculative. The total mortality rate, Z , is estimated to be 1.6 at the Pedro Cays and 1.4 at the Port Royal Reefs.

Epinephelus striatus: Table 7.19 shows the relative abundances of successive length groups of *E. striatus* beyond the modal size group of 60.0 to 64.9 cm TL. Samples were from unexploited oceanic banks (Fig. 7.14). The asymptotic size is not well known and maximum sizes given in the literature range between 90 cm TL and 120 cm TL if L_{∞} is about 90 cm TL, and $K = 0.05$ to 0.13 the value of M/K is about 2.33 and $M = 0.17$ to 0.30.

Table 7.19. Derivation of mortality rates from relative abundances of successive length groups of *Epinephelus striatus* and *Mycteroperca venenosa* captured at unexploited oceanic banks. Growth parameters are very imprecisely known: *M. venenosa*, L_{∞} = approximately 86 cm TL and $K =$ approximately 0.10 to 0.27; *E. striatus*, L_{∞} = approximately 90 cm TL, $K =$ approximately 0.05 to 0.13.

Length group cm TL	Number captured <i>E. striatus</i>	Number captured <i>M. venenosa</i>
60.0-64.9	37	31
65.0-69.9	25	30
70.0-74.9	18	19
75.0-79.9	15	4
80.0-84.9	7	3
85.0-89.9	0	1
Mean TL	69 cm	69 cm
M/K =	$(\frac{90 - 69}{69 - 69})$	$(\frac{86 - 68}{68 - 60})$
=	2.33	2.25
M =	0.17-0.30	0.23-0.61

Moe (1969) estimated that exploited stocks of *E. morio* in the Gulf of Mexico had an instantaneous mortality rate Z of 0.322.

Mycteroperca venenosa: Fishes captured at unexploited oceanic banks had a modal size of 60.0 to 64.9 cm TL (Fig. 7.15), and declined in abundance with increasing size at a rate similar to *E. striatus* (Table 7.19). Growth estimates are imprecise: if $L_{\infty} = 86$ cm TL and $K = 0.10$ to 0.16, then $M/K = 2.25$ and $M = 0.23$ to 0.61.

ABUNDANCE AND DENSITY

Seasonal Availability

Groupers were relatively infrequently caught at the Port Royal Reefs and no seasonal variations in availability are discernible in the catch data. There was no seasonal trend in the catch rates of any species of groupers at Pedro Bank.

Periods of very high availability related to spawning aggregations, mostly in December and January, have been reported from many areas (Bardach 1958; Smith 1972).

Relative Abundance

Relative abundances are expressed in terms of numbers of fishes captured per 1,000 hexagonal traps each soaked for 1 day (see Chapter 5).

Table 7.20. Relative mean numerical abundance (catch per 1,000 hexagonal trap-nights) of groupers at various parts of Pedro Bank and at California Bank. Effort standardized in terms of catch per 1,000 hexagonal traps soaked for 1 day. Eighty percent confidence limits given in brackets.

	California Bank	Pedro Cays	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank
<i>Cephalopholis fulva</i>	376 (275-477)	423 (195-650)	574 (422-726)	1,101 (636-1,566)	229 (157-301)
<i>Petrometopon cruentatum</i>	47	49	17	11	1
<i>Epinephelus guttatus</i>	149 (65-232)	97 (59-134)	429 (274-584)	599 (262-936)	232 (114-350)
<i>Epinephelus striatus</i>	0	0	3	10	80
<i>Mycteroperca venenosa</i>	3	6	3	3	24
Other groupers and hinds	5	0	3	2	0

The mean catch rates of *Epinephelus guttatus* and *Cephalopholis fulva* at various parts of Pedro Bank and at California Bank are given in Table 7.20, variability was high and confidence limits can only be given at the 80% level. Catch rates on hook and line showed even greater variability, mostly related to the effect of wind and current upon working conditions and not necessarily related to the abundance of groupers at the sampling station, and hook-and-line catch rates are not incorporated into this section.

In the case of *E. guttatus*, the mean catch rate near the exploited Pedro Cays was 97 ± 38 fishes/1,000 trap-days and was significantly less ($p = 0.80$) than the catch rates obtained in the adjacent unexploited Eastern and Southern Pedro Bank (429 ± 155 fishes/1,000 trap-days and 599 ± 337 fishes/1,000 trap-days, respectively). California Bank (exploited) produced 149 ± 84 fishes/1,000 trap-days, but this was not significantly different from the rate obtained at Western Pedro Bank (232 ± 118 fishes/1,000 trap-days) which is ecologically similar, but unexploited.

Cephalopholis fulva was less abundant (229 ± 72 fishes/1,000 trap-days) at Western Pedro Bank than in the shallower Eastern and Southern regions (574 ± 152 and $1,101 \pm 465$ fishes/1,000 trap-days, respectively). Apparent differences in catch rates between other areas were not statistically significant.

Catches of species other than *E. guttatus* and *C. fulva* were too small and/or too variable to warrant statistical treatment. Table 7.21 shows the gross catch rates (total catch divided by total trap-days of fishing effort) in each of the areas and depth zones investigated. It is apparent that variations in abundance are related to the area rather than to the depth. Catch rates of the large groupers, *E. striatus* and *M. venenosa*, were usually greater at Western Pedro Bank than in equivalent depths in the eastern and southern parts of the bank, while the reverse was true in the case of the small species.

It is interesting to note that *Petrometopon cruentatum* was more abundant at the Pedro Cays and at California Bank, than in equivalent depth zones in unexploited areas, whereas all other species yielded

substantially lower catch rates in exploited areas. It appears likely that *P. cruentatum* benefits in some way from reduced competition or predation in the exploited areas.

NATALITY AND RECRUITMENT

Adolescent groupers were not caught at the Port Royal Reefs in large-enough numbers to give estimates of the time and magnitude of recruitment. No large groupers (*Mycteroperca* spp. or *Epinephelus striatus*) were caught on the Port Royal Reefs after May 1971. It is assumed that all of those originally present had been removed from the areas fished by that time. In the 10 mo after May 1971 (i.e., up to February 1972), it appeared that no large individuals had come into the area to fill the habitats. This suggests low recruitment rates into the Port Royal fishery.

Recruitment of juvenile *E. guttatus* and *C. fulva* to the Pedro Bank fishery occurs around August to September. An increase in the percentage of juvenile (20 to 45 cm TL) *E. striatus*, *Mycteroperca venenosa* and *M. tigris* was encountered in commercial catches between September and November.

The available estimates of Z and of mean catch rates are summarized in Table 7.22, together with the estimates of recruitment indices (R' , the theoretical number of recruits at the mean recruitment length, l_r , required to produce the observed catch rate) and the mean recruitment lengths, l_r .

Within each species, there is a wide degree of variation in the estimated recruitment indices in the areas investigated. Apart from the large potential errors which are inherent in estimates of this sort, differences in the mortality rates between settlement of post-larvae and recruitment to the fishable stocks are probably dependent upon the suitability of the habitats for adolescents, abundance of predators (which is decreased in exploited areas) and inter- and intra-specific competition which is affected by community composition and which is in turn affected by the degree of exploitation.

Table 7.21. Relative numerical abundance (number captured per 1,000 trap-days) of species of groupers in various depth zones at Pedro Bank and California Bank.

		California Bank	Pedro Cays	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank
<i>Cephalopholis fulva</i>	10.1-20 m	—	319	—	862	—
	20.1-30 m	—	0	521	335	174
	30.1-45 m	284	—	459	—	122
<i>Petrometopon cruentatum</i>	10.1-20 m	—	62	—	10	—
	20.1-30 m	—	0	4	11	0
	30.1-45 m	38	—	22	—	1
<i>Epinephelus guttatus</i>	10.1-20 m	—	83	—	397	—
	20.1-30 m	—	0	268	173	50
	30.1-45 m	109	—	378	—	188
<i>Epinephelus striatus</i>	10.1-20 m	—	0	—	7	—
	20.1-30 m	—	0	2	16	23
	30.1-45 m	0	—	0	—	45
<i>Mycteroperca venenosa</i>	10.1-20 m	—	2	—	2	—
	20.1-30 m	—	0	0	11	9
	30.1-45 m	4	—	6	—	17
Other groupers and hinds	10.1-20 m	—	0	—	33	—
	20.1-30 m	—	0	4	5	0
	30.1-45 m	4	—	0	—	0

Note: Dashes indicate that the depth zone is not present in the study area.

Table 7.22. Mean catch rates, estimated mortality rates and estimated recruitment indices of groupers in various areas. Catch rates derived from Table 7.14.

		Mean catch rate (No./1,000 trap-days)	Z	Recruitment index (R ^b)	Mean recruitment length (l _r)
<i>Epinephelus guttatus</i>	Eastern Pedro Bank	429 (274- 584)	0.68	292 (186- 397)	31.0 cm
	Southern Pedro Bank	599 (262- 936)		407 (178- 636)	
	Western Pedro Bank	229 (114- 350)		158 (78- 238)	
	Pedro Cays	97 (59- 134)	84 (51- 117)	0.87	
	California Bank	149 (65- 132)	0.90	134 (59- 209)	
<i>Cephalopholis fulva</i>	Eastern Pedro Bank	574 (422- 726)	1.95	1,119 (823-1,416)	23.0 cm
	Southern Pedro Bank	1,101 (636-1,566)		2,147 (1,240-3,054)	
	Western Pedro Bank	229 (157- 301)		447 (306- 587)	
	Pedro Cays	423 (195- 650)	1.83	774 (357-1,190)	
	California Bank	376 (275- 477)	2.15	808 (591-1,026)	
<i>Petrometopon cruentatum</i>	Pedro Cays	49	1.6	78	20 cm
	California Bank	47	?	?	
	Port Royal Reefs	25	1.2	30	
<i>Epinephelus striatus</i>	Pedro Bank (unexploited areas)	3-80	0.17-0.30	0.5-24	57 cm
<i>Mycteroperca venenosa</i>	Pedro Bank (unexploited areas)	3-24	0.23-0.61	0.7-15	57 cm

Table 7.23. Summary of estimated population parameters for various species of groupers exploited by traps with 4.13 cm wire mesh or by hook and line. All lengths are total lengths in cm.

	<i>Epinephelus guttatus</i>	<i>Cephalopholis fulva</i>	<i>Petrometopon cruentatum</i>	<i>Epinephelus striatus</i>	<i>Mycteroperca venenosa</i>
Calculated minimum retainable length in traps l_0	16.7	17.0	14.8	?	?
Minimum length captured l_1	18.0	16.5	16.5	27.5	26.2
Mean retention length l_r	31.0	23.0	20	57*	57*
Full retention length l_c	35.0	25.5	21.5	62.5*	62.5*
Asymptotic length L_∞	52	34	33-35	90	86
Asymptotic weight (g) W_∞	1,880	640	690	12,900	?
Coefficient of growth K	0.24	0.63	0.33-0.35	0.09	0.17
Coefficient of natural mortality M	0.68	1.95	?	0.17-0.30	0.23-0.60
M/K	2.83	3.09	?	2.33	2.25
Mean length at maturity l_m	<25	<16	<16	<48	<51
Mean length at sex change l_s	38	27	?	?	?
l_m/L_∞	<0.48	<0.47	<0.47	<0.53	<0.59
l_c/L_∞	0.67	0.75	0.63	0.69	0.73

*Oceanic banks—hook-and-line and traps

The recruitment indices of the large groupers are only a small fraction of those estimated for *E. guttatus* and *C. fulva*.

DYNAMICS OF THE POPULATIONS

The population parameters estimated for species of groupers are summarized in Table 7.23. The ratio of M/K is similar (2.25 to 3.09) for the four species for which estimates are available.

Reference to Beverton and Holt's (1964) tables of yield functions suggests that the estimated values of $c (= l_c/L_\infty)$ lie above the values required to produce eumetric yields. For example, in the case of *E. guttatus*, the rates of exploitation at California Bank and at the Pedro Cays have been estimated to be 0.24 and 0.22, respectively. A reduction in the value of l_c/L_∞ from 0.67 to about

0.30 would theoretically be required to produce eumetric yields at this present rate of exploitation at the above-mentioned areas.

No estimates of rates of exploitation are available for *E. striatus* and *M. venenosa*, but in both cases the mean lengths at recruitment are well in excess of those required to maximize the yield at any level of fishing effort.

As a general case, it would appear that most of the species of groupers are in an underexploited state at Pedro Bank and California Bank, mostly as a result of the large size at which they become available to the fishing gear.

In the nearshore parts of the Jamaican shelf the situation is more complex, and the high rate of exploitation results in most fishes being captured at lengths within the recruitment ogive and the modal lengths of catches tend towards the minimum retainable size in response to increasing fishing effort. These matters are further considered in Chapter 18.

**CHAPTER 8:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE JACKS, CARANGIDAE**

by
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(March 1974)

Identity

TAXONOMY

Ginsburg (1952) stated that the family Carangidae is notably heterogeneous, including genera which differ widely in structure and appearance, and that species of the genus *Caranx*, although differing in dentition, shape and body color, seem to form a natural series. Among the other genera, *Seriola* is probably closely related to *Elagatis*. *Selar* is closely related to *Decapterus* and *Alectis* probably descended from *Caranx* or a similar genus. *Selene* is closely related to *Vomer* which probably also descended from *Caranx* or a similar species, but independent of *Alectis*.

NOMENCLATURE

Six genera and 12 species (Table 8.1) have been

collected on or over reef habitats during this study. In addition, juvenile *Chloroscombrus chrysurus* (Linnaeus) 1766, from the bell of an unidentified jellyfish, adults of the same species and adult *Oligoplites saurus* (Bloch and Schneider) 1801 have been examined from Kingston Harbour. Other carangids listed by Caldwell (1966) as occurring in Jamaican waters include: *Trachinotus carolinus* (Linnaeus) 1766, *Trachinotus falcatus* (L) 1766, *Trachinotus glaucus* (Bloch) 1793 and *Vomer setapinnis* (Mitchell) 1826. These species do not frequent reef areas.

HYBRIDIZATION

No reports of hybridization among jacks were encountered during this study.

Distribution

GEOGRAPHICAL DISTRIBUTION

Bohlke and Chaplin (1968) and Randall (1968) noted that the genera of the family Carangidae consist of many species that are widely distributed in the tropical oceans of the world. Four of the 12 species listed from Jamaican waters are circumtropical, one occurs in both the Atlantic and Pacific oceans, four are recorded from both sides of the Atlantic, and three are listed as occurring only in the western Atlantic.

During this study, all the species listed in Table 8.1

were taken at oceanic banks (Fig. 2.1) with the exception of *Selene vomer* which was taken only at the Port

*A substantial portion of this report is derived from a thesis submitted to the University of the West Indies by R. Thompson for the degree of Master of Science. The thesis was based upon data collected by the Fisheries Ecology Research Project up to May 1972. The sections on growth, sexuality, population structure, mortality and recruitment have been prepared by J. Munro, and incorporate all data collected by the project between November 1969 and March 1973.

Royal Reefs (Fig. 3.1). *Seriola dumerili*, *S. rivoliana*, *Caranx lugubris* and *Alectis crinitus* were not taken at

the Port Royal Reefs and apparently do not frequent nearshore reefs at any stage in their life histories.

Table 8.1. Scientific and common names of carangids caught on or over reefs during this study (from Randall (1968) and/or Bohlke and Ciaplin (1968)).

Scientific names	Common names
1. <i>Seriola dumerili</i> (Risso) 1810	Greater amberjack
2. <i>Seriola rivoliana</i> Cuvier and Valenciennes 1833	Almaco jack
3. <i>Elagatis bipinnulatus</i> (Quoy and Gaimard) 1824	Rainbow runner
4. <i>Selar crumenophthalmus</i> (Bloch) 1793	Bigeye scad
5. <i>Caranx ruber</i> (Bloch) 1793	Bar jack
6. <i>Caranx bartholomaei</i> Cuvier and Valenciennes 1833	Yellow jack
7. <i>Caranx fusus</i> (Geoffroy-St. Hilaire) 1809	Blue runner
8. <i>Caranx hippos</i> (Linnaeus) 1766	Crevalle jack
9. <i>Caranx latus</i> Agassiz 1829	Horse-eye jack
10. <i>Caranx lugubris</i> Poey 1860	Black jack
11. <i>Alectis crinitus</i> (Mitchell) 1826	African pompano
12. <i>Selene vomer</i> (Linnaeus) 1758	Lookdown

HABITAT AND DEPTH DISTRIBUTION

During this study, juvenile *Caranx bartholomaei* were collected from shallow (2 to 4 m) *Thalassia* flats in Kingston Harbour. Adolescent (15 to 25 cm FL) *C. bartholomaei*, *C. ruber* and *C. fusus* are quite common in the shallow areas (0 to 15 m) of the semi-enclosed Port Royal reef system. Juvenile (4 to 10 cm FL) *C. bartholomaei*, *C. hippos* and *Elagatis bipinnulatus* have been encountered in the Port Royal reef system in association with floating sargassum and other floating objects. Adult *C. ruber*, *C. hippos* and *C. latus* are occasionally caught at the Port Royal Reefs.

Adolescents and adults of most species more commonly frequent the shelf edges, sill reefs and upper slopes of the deep reef (60.1 to 100 m) but were never caught at depths exceeding 100 m during this study (see Chapter 4).

The absence of large *C. ruber*, *C. bartholomaei* and *C. fusus* at the Port Royal Reefs suggests a movement of these individuals to the outer margins of the shelf at or before maturity.

Bionomics and Life History

REPRODUCTION

Sexuality and Gonads

Sexes are separate and distinct and all specimens examined were either male or female. The gross structure of the gonad is typical of a gonochoristic teleost and similar to the description of Moe, Lewis and Ingle (1968) for *Trachinotus carolinus*. Ripe ovaries of the species examined were typically bright yellow and testes were creamy white.

Maturity

Tables 8.2 and 8.3 show the gross length distributions of all samples of male and female *Caranx ruber* and *Caranx latus* obtained during the present study, together with the percentages of mature (ripe or spent) fishes found in each length group.

It appears that male and female *C. ruber* attain maturity at a minimum size of 22.0 to 23.9 cm FL, and most fishes are probably mature by 26 to 27 cm FL. The mean length at maturity is probably about 24 cm TL for both sexes.

In the case of *C. latus*, the smallest mature fishes were a male of 35.5 cm FL and two females in the 34.0 to 34.9 cm FL length group. Most fishes probably are mature by about 42.5 cm FL.

Samples of other species of carangids were not sufficiently large to define the size at maturity and the

fork lengths of the smallest ripe or spent fishes observed during this investigation are listed in Table 8.4.

Fecundity

Moe et al. (1968) estimated 426,400 well-developed eggs in a ripe female (25.5 cm FL) *Trachinotus carolinus*. During this study, ripe ovaries of three *Caranx ruber* (25.0 cm, 28.0 cm and 31.0 cm FL) were estimated to contain 131,917, 67,750 and 230,690 eggs, respectively. Ripe ovaries of large *Seriola dumerili*, *C. latus*, *C. bartholomaei* and *C. hippos* were observed that occupied over one-third of the abdominal cavity. Such ovaries probably contain over one million eggs.

Mating and Fertilization

There appear to be no reports on the mating of jacks. The absence of an intromittent organ suggests that fertilization is probably external.

Spawning Seasons

McKenney et al. (1958) noted that *Caranx crysos* (= *fuscus*) may spawn throughout the year with the main spawning activity occurring from January through August. Berry (1959) estimated that the spawning season which contributes *Caranx* spp. to the Gulf Stream extends from February to September. Munro et

Table 8.2. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Caranx ruber* at unexploited oceanic banks.

Length group cm FL	Males		Females		Indeterminate sex, no. examined	Total number examined
	Number examined	% ripe or spent	Number examined	% ripe or spent		
14.0-15.9					2	2
16.0-17.9					7	7
18.0-19.9	2	(0)			9	11
20.0-21.9	2	(0)	5	(0)	7	14
22.0-23.9	30	23	28	25	10	68
24.0-25.9	47	23	68	43	22	137
26.0-27.9	37	32	34	35	7	74
28.0-29.9	12	(17)	42	33	5	59
30.0-31.9	9	(56)	28	36	4	41
32.0-33.9	7	(43)	15	27	0	22
34.0-35.9	5	(20)	12	(17)	1	18
36.0-37.9	5	(0)	7	(43)	1	13
38.0-39.9	6	(33)	3	(33)		10
40.0-41.9	1	(100)	2	(0)		3
42.0-43.9	0	-	0	-		0
44.0-45.9	0	-	0	-		0
46.0-47.9	0	-	3	(67)		3
48.0-49.9	0	-	0	-		0
50.0-51.9	0	-	0	-		0
52.0-53.9	0	-	3	(100)		3
Totals	163		250		75	485

Table 8.3. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Caranx latus* at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	% ripe	No. examined	% ripe
25.0-29.9	0	-	3	(0)
30.0-34.9	7	(0)	7	(29)
35.0-39.9	29	10	21	24
40.0-44.9	48	19	30	37
45.0-49.9	33	15	21	43
50.0-54.9	17	(12)	23	57
55.0-59.9	18	28	23	65
60.0-64.9	4	(0)	3	(33)
65.0-69.9	0	-	3	(100)
70.0-74.9	0	-	1	(100)
Totals	156		135	

al. (1973) reported on the spawning season of jacks in the Caribbean, and that paper is summarized below for individual species, supplemented with additional information collected subsequently.

Seriola dumerili: Two ripe fishes were collected at Pedro Bank, one in August 1969, the other in November 1970.

S. rivoliana: One ripe female was collected at Pedro Bank in November 1970.

Table 8.4. Size at sexual maturity of nine species of carangids from Jamaican waters.

Species	Sex	Number of ripe fish	Smallest ripe fish FL (cm)
<i>Seriola dumerili</i>	M	1	93.0
	F	2	79.7
<i>S. rivoliana</i>	M	1	53.0
<i>Selar crumenophthalmus</i>	F	2	19.6
<i>C. bartholomaei</i>	M	11	23.0
	F	2	45.4
<i>C. fusus</i>	M	46	26.0
	F	20	28.0
<i>C. hippos</i>	M	4	55.0
	F	3	66.2
<i>C. lugubris</i>	M	10	34.6
	F	13	38.2

Elagatis bipinnulatus: This species was observed in spawning condition at the Morant Cays in July 1970.

Selar crumenophthalmus: Two ripe females were caught at Pedro Bank in May 1970.

Caranx ruber: Table 8.5 shows that ripe fishes were found in all months of the year, but as the total number of mature fishes captured was not large (N=328), it is not possible to define the spawning season/s. The high proportions of ripe fishes seen in April and October

Table 8.5. Monthly percentages of inactive, active and ripe fishes in samples of *Caranx ruber* from oceanic banks. No spent fishes were ever encountered.

Month	No. examined	Inactive	Percentage Active	Ripe
January	7	(42)*	(29)	(29)
February	30	63	20	17
March	34	38	50	12
April	42	19	26	55
May	12	(25)	(8)	(67)
June	0		No data	
July	9	(22)	(22)	(56)
August	12	(25)	(33)	(42)
September	80	13	61	26
October	41	17	22	61
November	51	67	16	17
December	10	(80)	(0)	(20)
328				

*Percentages given in brackets are based on samples of only 7 to 12 fishes.

suggest that, in common with other reef fishes, these might be the main spawning months.

C. latus: Table 8.6 shows that ripe fishes were found in all months and spawning is therefore continuous. However, as was the case with *C. ruber*, the number of mature fishes encountered was rather small (N=321) and it appears that most spawning might occur in or around February-April and September-October.

C. bartholomaei: All individuals (21) captured at the Port Royal Reefs were immature. Five ripe fishes were collected on Pedro Bank in May 1971, three in February 1972, and two in November 1972.

C. fusus: Three active and one ripe fish were collected from the Port Royal Reefs during April to May 1971 and two active and one ripe fish during January 1970. Sixty-three ripe fish were collected in May 1971, and three in June 1972, on Pedro Bank.

C. hippos: One active fish was caught on the Port Royal Reefs in May 1971. Seven ripe fishes were collected on Navidad Bank during November 1967. In July 1970, ripe fishes were taken at the Morant Cays.

C. lugubris: Ripe fishes were captured at oceanic banks during February, April, May and July to September.

Alectis crinitus: One active female was collected at Pedro Bank in February 1970.

Selene vomer: One ripe-running male was taken at the Port Royal Reefs in April 1971.

Spawning Grounds

Razniewski (1970) reported the occurrence of prespawning and/or spawning concentrations of four species of jacks over the northwest African shelf during the summer of 1967. The presence of a concentration of

Table 8.6. Monthly percentages of inactive, active, ripe and spent fishes in samples of *C. latus* from oceanic banks.

Month	No. examined	Percentage			
		Inactive	Active	Ripe	Spent
January	7	(43)	(14)	(43)	(0)
February	29	14	31	55	0
March	0	Active fishes seen in commercial catch			
April	0	Ripe fishes seen in commercial catch			
May	76	8	63	29	0
June	4	(0)	(0)	(100)	(0)
July	23	57	26	17	0
August	42	31	57	10	2
September	31	39	29	32	0
October	54	22	41	28	9
November	11	(9)	(55)	(36)	(0)
December	44	71	25	2	2
321					

spawning *Caranx fusus* on northwestern Pedro Bank during May 1971 suggests that this species aggregates in certain areas to spawn. Bohlke and Chaplin (1968) suggested that most carangid species, if not all, spawn "offshore."

Spawn

Chacko (quoted by Berry 1959) noted that eggs of *Caranx hippos* had a diameter of 0.7 to 0.9 mm, and possessed a pigmented yolk and one yellowish oil globule (0.18 mm diameter) with dark pigments. No carangid eggs in the final stages of maturation were collected during this study, but 20 ripe eggs of *Caranx ruber* measured 0.75 mm to 0.85 mm in diameter with an average diameter of 0.79 mm.

PRE-ADULT PHASE

Work on the larval and juvenile history of members of the genus *Caranx* has been done by Berry (1959) and McKenney et al. (1958) and for a description of developmental stages these works should be consulted. The size at transformation from larva to juvenile in *Caranx* spp. was estimated by Berry to be about 8.0 mm SL.

During this study, juvenile *C. bartholomaei* (length range 3.5 to 8.0 cm FL) were seen and collected in the Port Royal reef area and also in Kingston Harbour. Small schools of *C. latus* consisting of 5 to 15 individuals were observed regularly around the jetty of the Port Royal Marine Laboratory during March and April of 1970-1972. A school consisting of hundreds of juvenile *C. hippos* and a few *Elagatis bipinnulatus* were found concentrated around the floating remains of a dugout canoe at Nassau reef, Port Royal, during November 1970. One *C. hippos* captured from this school measured 6.7 cm FL and one *E. bipinnulatus* measured 5.0 cm FL.

ADULT PHASE

There is very little published information on aspects of the adult life history of species of *W. Atlantic carangids*.

Barroso (1965) reported on the possible competition for food between *Caranx lugubris* and *Lutjanus aya* from northeast Brazil. Many carangids frequent reefs to obtain food (Randall 1967) and would therefore be expected to compete with other carnivores living on the reefs.

Berry (1959) noted the occurrence of juvenile *Caranx* spp. in the stomach of larger pelagic fishes, especially dolphin (Coryphaenidae), barracuda (Sphyraenidae), scombrids and *Seriola* spp. Groupers (*Mycteroperca* spp.) are also capable of capturing fast-swimming carangids (Randall 1967).

Trematodes were regularly found in the body cavity of adult *C. latus* and the flesh of large amberjacks, *S. dumerili*, is usually infested with a larval tapeworm (pers. comm., fishermen and vendors at Port Royal). A specimen of *S. dumerili* (121 cm FL) collected from Banner Reef, Pedro Bank, during February 1972 was infested with this tapeworm.

NUTRITION AND GROWTH

Food and Feeding

Randall (1967) and McKenney et al. (1958) reported on the food habits of jacks. Randall divides the family (by diet) into fish-feeders (*Caranx* spp. and *Seriola* spp.), plankton-feeders (*Decapterus* spp. and *Selar* spp.) and mollusc-feeders such as *Trachinotus* spp. McKenney et al. (1958) reported that *C. crysos* (= *fuscus*) is mainly a zooplankton-feeder throughout its larval and early juvenile life and subsists mainly upon cyclopoid and calanoid copepods. Austin and Austin (1971) reported the diet of juvenile *C. latus* and *C. hippos* from Puerto Rican mangroves to be made up entirely of harpacticoid copepods. Barroso (1965) listed fishes, crustaceans and molluscs from the stomach of *C. lugubris* from northeast Brazil.

Hand-line fishing at Pedro Bank suggested that the greatest catches of *C. latus* are made at full moon during the first few hours after sunset. After about 10 hr catch rates are significantly reduced. Species of the genera *Seriola* and *Elagatis* will take a line trolled near the surface and *E. bipinnulatus* and *Selar crumenophthalmus* were caught using surface lines at night. The species of the genus *Caranx* are usually caught near to the bottom, although *C. latus* and *C. lugubris* will rise from depths of over 40 m to take a line near the surface.

Growth Rates

Relative growth patterns

The relationships of fork lengths to total lengths are given in Table 8.7. Many of the larger fishes observed

had the tips of the caudal fin missing and these were not used in determining the relationship. The results show a similarity in relative caudal length for all of the species, e.g., fork lengths of 20 cm for *Caranx ruber*, *C. bartholomaei*, *C. fuscus* and *C. latus* correspond to total lengths of 24.0 cm, 24.0 cm, 24.2 cm and 24.3 cm, respectively.

Ginsburg (1952) stated that the carangids are noted for body forms differing with the genus from slender (e.g., *Seriola*, *Elagatis*, *Selar*) to excessively deep (*Trachinotus*, *Alectis*, *Vomer* and *Selene*). Species of the genus *Caranx* are intermediate in body form. The fork length-body depth relationships of *C. ruber*, *C. bartholomaei* and *C. fuscus* are summarized in Table 8.8. The relationships show that for fishes of the same fork length, *C. bartholomaei* has a deeper body than *C. ruber* which in turn has a deeper body than *C. fuscus*.

The maximum aperture of the wire mesh used in the Jamaican trap fishery is 4.13 cm. Fork lengths of *C. ruber*, *C. bartholomaei* and *C. fuscus* at this body depth are 13.1, 11.3 cm and 16.6 cm, respectively. Fork lengths of the smallest fishes caught at the Port Royal reefs were 13 cm for *C. ruber*, 14 cm for *C. bartholomaei* and 15 cm for *C. fuscus*. This indicates that these species are probably present on the Port Royal Reefs at sizes smaller than those retainable by the mesh used.

Equations describing the relationship between fork length and total body weight of *C. ruber*, *C. bartholomaei* and *C. fuscus* are given in Table 8.9.

Table 8.7. Relationships between total lengths (TL) and fork lengths (FL) of four species of jacks from Jamaican waters.

Species and formula	Number of measurements	Length range cm FL
<i>Caranx ruber</i>		
TL = 1.3 + 1.13 FL	23	16-52
<i>C. bartholomaei</i>		
TL = 0.8 + 1.16 FL	37	15-69
<i>C. fuscus</i>		
TL = -0.1 + 1.21 FL	31	20-32
<i>C. latus</i>		
TL = 1.1 + 1.16 FL	17	18-65

Table 8.8. Relationships between fork length (FL) and maximum body depth (D) of three species of jacks from Jamaican waters.

Species and formula	Number of measurements	Length range cm FL
<i>Caranx ruber</i>		
D = 0.5 + 0.277 FL	37	15-52
<i>C. bartholomaei</i>		
D = 1.0 + 0.278 FL	25	14-59
<i>C. fuscus</i>		
D = 0.4 + 0.273 FL	21	23-32

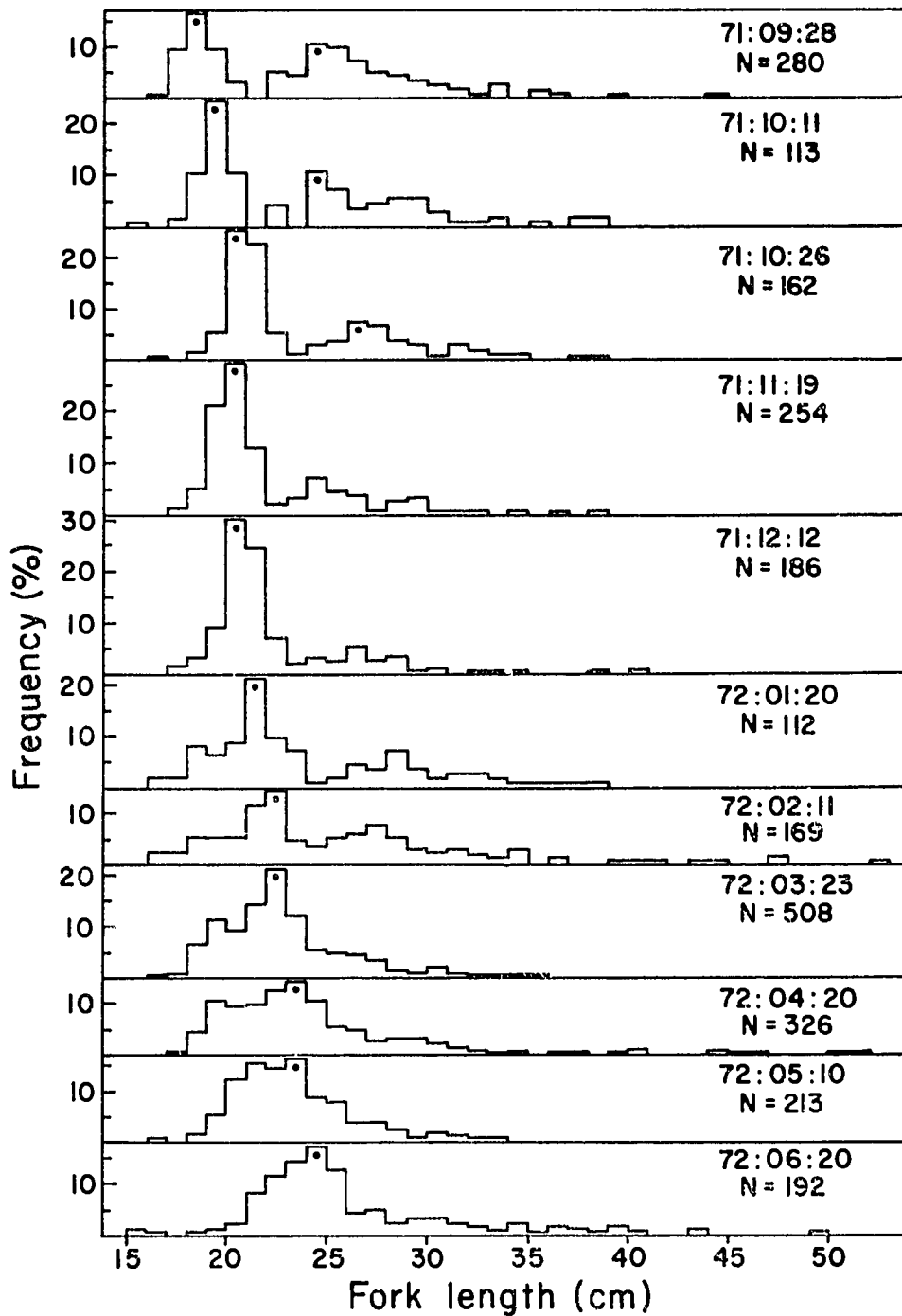


Fig. 8.1. Length-frequency histograms of *Caranx ruber* taken from the commercial catch, Pedro Bank, during 1971 and 1972. Dots indicate the major modal progressions.

Lengths

Maximum sizes of 12 species of jacks captured during this study are listed in Table 8.10. The largest total lengths recorded by Bohlke and Chaplin (1968) or by Randall (1968) are also given, together with calculated conversions of TL to FL where the relationship is known. With the exception of *C. latus* the largest fishes captured during this study are all within the known size range.

Figure 8.1 shows the length distributions of 11 samples of the commercial catch of *C. ruber* from the Pedro Cays area, taken between September 1971 and June 1972. The modal progressions are clearly discernible and a regression of $\log_e (L_\infty - l_t)$ against time (calendar months) is shown in Fig. 8.2. The best fit of points is obtained when L_∞ is estimated to be 52 cm FL, and the slope, K , of the regression is 0.02/mo or 0.24/yr.

Table 8.9. Relationships between fork lengths (FL) and weights (W) of three species of jacks from Jamaican waters. All lengths are in centimeters and weights in grams.

Species and formula	Number of measurements	Length range cm FL
<i>Caranx ruber</i> $\log W = -2.079 + 3.191 \log L$ $W = 0.00834 L^{3.191}$	242	13-33
<i>C. bartholomaei</i> $\log W = -2.199 + 3.368 \log L$ $W = 0.00632 L^{3.368}$	71	14-29
<i>C. fusus</i> $\log W = -2.183 + 3.302 \log L$ $W = 0.0065 L^{3.302}$	104	22-47

Table 8.10. Observed maximum fork lengths of carangids from Jamaican waters compared with measurements given in the literature.

Species	Observed maximum fork length (cm)	Maximum reported total length* (cm)
<i>Seriola dumerili</i>	124	154.9
<i>S. rivoliana</i>	53	81.3
<i>Elagatis bipinnulatus</i>	65	106.7
<i>Selar crumenophthalmus</i>	22	—
<i>Caranx ruber</i>	52 (60)**	60.9
<i>C. bartholomaei</i>	69 (81)	99.0
<i>C. fusus</i>	48 (58)	76.2
<i>C. hippos</i>	79	101.6
<i>C. latus</i>	73 (85)	76.2
<i>C. lugubris</i>	69	99.0
<i>Alectis crinitus</i>	76	91.4
<i>Selene vomer</i>	21	30.5

*Bohlke and Chaplin (1968) or Randall (1968).

**Calculated total lengths in brackets.

Age and growth

Growth estimates for the pompano, *Trachinotus carolinus*, from Florida and Louisiana were made by Bellinger and Avault (1970), Berry and Iversen (1967), Finucane (1969) and Moe et al. (1968). During this study, no information on age or growth was obtained from the examination of scales or otoliths. Scales of *Caranx ruber*, *C. bartholomaei*, *C. fusus* and *Seriola dumerili* were small, cycloid, with a few well-spaced circuli and showed no markings that could be used for age determinations. Otoliths are small and fragile and difficult to extract. Otoliths of *C. ruber* were examined but showed no markings indicative of age. With the exception of *C. ruber*, catches of species of carangids were too small or too sporadic for estimates of growth

to be based upon modal progressions in length-frequency distributions.

BEHAVIOR

Migrations

Moe (1972) noted that although movement and migration are important facets in the life history of carangids, little is known of their migratory patterns. Jordan and Evermann (1898) noted that some carangid species move northward in summer. During July and August in the Bahamas, schools of *Caranx ruber* are seen

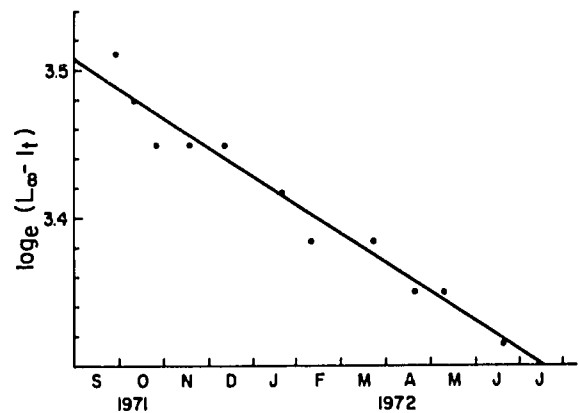


Fig. 8.2. Modal lengths of samples of *Caranx ruber* expressed as values of $\log_e(L_\infty - l_t)$. Data from Fig. 2. Best fit of regression is obtained when $L_\infty = 52$ cm FL. The slope, K , is 0.24 per 12 months.

swimming near the surface (Bohlke and Chaplin 1968, and personal observations) although the general movement and destination of these schools are unknown. Tagging studies have yielded little information on the movement of jacks, as recovery rates are low, undoubtedly due to their greater mobility as compared to other reef fishes (Randall 1962).

Length distributions obtained during the present study indicate a movement of *C. ruber*, *C. bartholomaei* and to a lesser degree *C. fusus* away from the Port Royal Reefs at the onset of sexual maturity.

Schooling

Jacks are typically schooling fishes and schools of *Caranx ruber* and *Elagatis bipinnulatus* were seen swimming near the surface over reefs during this study. Large numbers of *C. fusus* and *C. latus* caught over a short period of time indicate schooling of these species. Catches of *C. bartholomaei* and *Seriola dumerili* suggest that large individuals of these species move over the reef singly or in small groups.

Populations

POPULATION STRUCTURES

Sex Ratios

Catches of most species of jacks were too small and/or too sporadic to give adequate estimates of sex ratios. The sex ratio (males:females) of mature *Caranx ruber* was 1:1.53 (total number examined, N = 413). For *C. latus* the sex ratio was M:F = 1:0.87 (N = 291); for *C. lugubris*, M:F = 1:0.55 (N = 65); and for *C. fusus* M:F = 1:0.27 (N = 181).

Age and Length Composition

Caranx ruber: Figure 8.3 shows the estimated mean annual size compositions of trap catches of this species from the Port Royal Reefs, unexploited parts of Pedro Bank, the Pedro Cays area and Serranilla Bank. Samples from the latter two areas are derived from the commercial landings. Analytical techniques follow the methods outlined in Chapter 3.

The minimum retainable size (l_1) is in the region of 13.5 cm FL, but the modal size retained (l_c) varies according to area and, presumably, depth being 16.5 cm FL at the Port Royal Reefs, 20.5 cm FL at the Pedro Cays and 25.5 cm FL at unexploited parts of Pedro Bank and in the commercial catch from Serranilla Bank. The Serranilla Bank sample is, however, based on samples taken between October and March and the smallest recruits did not appear in the catches (Fig. 8.1).

The body depth of a fish of 25.5 cm FL is about 7.6 cm (Table 8.8) and at this size is fully retainable by rigid 4.13 cm wire mesh. The differences in modal sizes of the catches, therefore, must result from differences in

the availability of the smaller-sized groups and it is believed that juvenile *C. ruber* normally inhabit shallow reef areas and move towards deeper water with the onset of maturity. In this context, it is of interest to note that only 17 *C. ruber* were captured at California Bank (total effort 382 trap-days) and it appears likely that shallow habitats are essential to the settlement and/or survival of this species.

The mean recruitment length to the Pedro Cays fishery is 19.5 cm TL at depths to 30 m and 22.7 cm FL on the unexploited deeper portions of Pedro Bank at depths of 10 to 45 m.

Caranx latus: Figure 8.4 shows the length-frequency composition of the total line catch (3/0-6/0 hooks) of *C. latus* at unexploited parts of Pedro Bank, in depths of 10 to 100 m. There are no data for exploited stocks. The mean recruitment length is 39.5 cm FL and they are fully recruited to the gear within the 42.0 to 43.9 cm length group.

Table 8.11 summarizes data on the size distributions of nine other carangid species from oceanic banks. Average lengths of males and females of *C. latus* and *C. lugubris* showed differences of less than 1 cm and 2.5 cm, respectively. Borges (1966) examined a large number of *C. lugubris* from northeast Brazil and found average lengths of 50.0 cm and 48.0 cm, respectively, for males and females. During this study, 37 male *C. lugubris* had a length range of 32 to 67 cm FL with an average length of 52.0 cm. Sixteen females had a length range of 35 to 69 cm FL and an average length of 49.5 cm.

Samples of 45 *C. bartholomaei* and 12 *C. fusus* taken in traps at the Port Royal Reefs had size ranges of 14 to 23 cm FL and 15 to 31 cm FL, respectively, suggesting

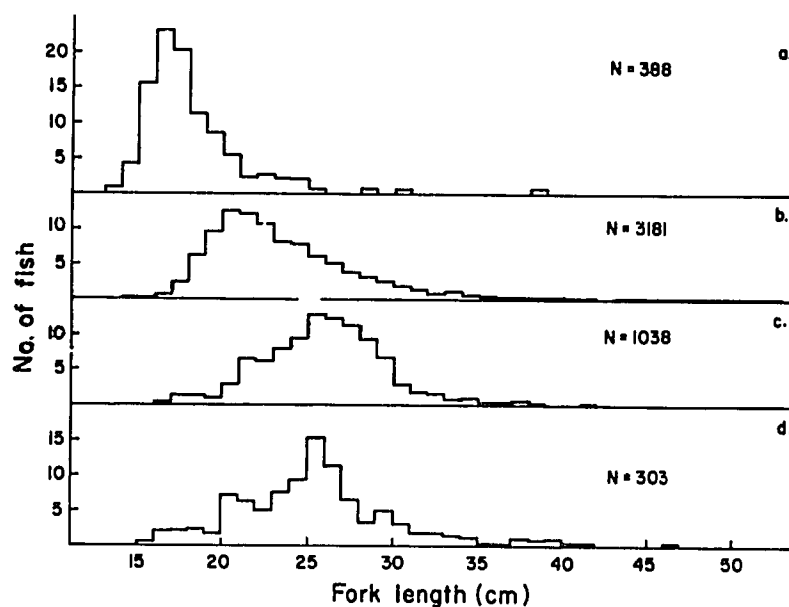


Fig. 8.3. Estimated mean annual length-frequency distributions of trap catches of *Caranx ruber* at (a) the Port Royal Reefs, (b) the Pedro Cays area, (c) Serranilla Bank and (d) unexploited parts of Pedro Bank.

Table 8.11. Size composition (FL, cm) of nine species of carangids from oceanic banks.

Species	Number of measurements	Smallest	Largest	Average length
<i>Seriola dumerlii</i>	21	38	124	80
<i>S. rivollana</i>	8	25	53	36
<i>Elagatis bipinnulatus</i>	15	50	65	57
<i>Selar crumenophthalmus</i>	2	19	22	—
<i>Caranx hippos</i>	38	37	79	52
<i>C. bartholomaei</i>	35	15	61	37
<i>C. fusus</i>	181	26	48	42
<i>C. lugubris</i>	114	32	69	50
<i>Alectis crinitus</i>	6	58	76	67

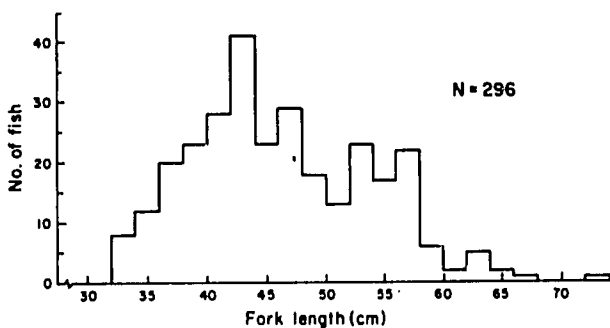


Fig. 8.4. Gross length-frequency distribution of total line catch (3/0-6/0 hooks) of *Caranx latus* at unexploited parts of Pedro Bank.

that like *C. ruber* these species tend to move away from shallow reefs as they increase in size.

MORTALITY AND MORBIDITY

There is no evidence concerning factors responsible for mortality and morbidity of carangids. The main predators upon these species are unknown.

The age compositions of populations of carangids are unknown and mortality rates cannot be directly calculated. Table 8.12 shows the relative abundances of successive length groups of *Caranx ruber* in various areas and calculations of mortality rates based upon the length composition of the populations as described in Chapter 3.

The estimates of Z/K for *C. ruber* are high in all areas and $Z/K (= M/K) = 6.3$ at unexploited parts of Pedro Bank. If the rate of growth, K , is 0.24, then the natural mortality rate, M , is about 1.5 at sizes exceeding 25 cm FL. However, the estimated mortality rate at the Pedro Cays (exploited) is 1.3 and suggests that the impact of the fishery upon the stock is minimal, and also that the margins of error of estimates based upon length compositions are probably fairly wide. It is likely that *C. ruber* are highly mobile and that the stocks move freely over most parts of Pedro Bank and that the effects of the fishery upon the overall mortality rate of the stock are

consequently minimized. It is therefore concluded that the natural mortality rate, M , is within the range 1.3-1.5 at lengths exceeding 25 cm FL.

The estimated mortality rate, Z , at the Serranilla Bank is 1.9.

At the Port Royal Reefs, the estimated mortality rate, $Z = 2.0$, includes a component of migration away from the reefs into deeper water in addition to natural and fishing mortalities.

The size composition of the catches of *C. latus* at unexploited parts of Pedro Bank (Fig. 8.4) indicates that the value of M/K is in the region of 2.5 if L_{∞} is assumed to be 70 cm FL. However, the catch length-frequency distribution is based on a relatively small sample ($N = 296$) and is somewhat irregular, and the estimate should be regarded as a first approximation.

ABUNDANCE AND DENSITY

Seasonal Availability

No consistent trends were observed in the seasonal availability of any species of carangid. Rather more large catches appeared to be taken during the spawning seasons (February-April) and September-October but the data are too sparse to substantiate this observation.

Relative Abundance

Relative abundances of species of jacks, expressed as numbers captured per 1,000 trap-days or 100 line-hours, are summarized in Tables 8.13-8.15. It is of interest to note that *Caranx ruber* and *C. bartholomaei*, the most important carangids in the trap fishery, are never taken on baited hooks (large adults will occasionally take a trolled feather lure or spoon) and that *C. latus*, the most important carangid in the line fishery, is uncommonly captured in traps.

C. ruber was most abundant in the shallower eastern and southern portions of Pedro Bank and at the Pedro Cays, but was uncommon at Western Pedro Bank (30 to 45 m) and at California Bank, of similar depth. It is the only carangid of any importance in the trap fishery at the Port Royal Reefs.

There appear to be no consistent trends in the distributions and relative abundances of other species of carangids.

NATALITY AND RECRUITMENT

Juvenile *Caranx* spp. ranging in size from 3 to 12 cm FL were observed at the Port Royal Reefs and in Kingston Harbour area during February to June, after which their numbers decreased, except for November 1970, when a large school of *Caranx hippos* and *Elagatis bipinnulatus* was observed on the Port Royal reefs.

The main influx of recruits of *C. ruber* to the Pedro

Table 8.12. Relative abundances of successive length groups of *Caranx ruber* beyond full recruitment in various areas and computations of mortality rates. $L_{\infty} = 52$ cm FL and $K = 0.24$.

Median of length group FL cm	Port Royal Reefs		Pedro Cays area			Unexploited Pedro Bank		Serranilla Bank	
	Mean % frequency in catch	Relative abundance (over 16.0 cm FL)	Mean % frequency in catch	Relative abundance (over 20.0 cm FL)	Relative abundance (over 25.0 cm FL)	Mean % frequency in catch	Relative abundance (over 25.0 cm FL)	Mean % frequency in catch	Relative abundance (over 25.0 cm FL)
16.5	22.9	1.00	0.63			2.2		0.4	
17.5	20.1	.88	2.37			2.1		1.3	
18.5	11.1	.48	6.22			2.2		1.2	
19.5	8.6	.38	9.58			1.7		1.1	
20.5	5.4	.24	12.58	1.00		7.2		3.0	
21.5	2.3	.10	12.33	.98		6.3		6.7	
22.5	2.7	.12	10.82	.86		5.0		6.2	
23.5	2.1	.09	8.12	.65		7.6		8.1	
24.5	2.1	.09	7.88	.63		9.5		9.6	
25.5	0.7	.03	6.12	.49	1.00	15.5	1.00	12.8	1.00
26.5	0	0	5.15	.41	.84	11.4	.73	12.4	.97
27.5	0	0	3.82	.30	.62	6.6	.43	11.5	.90
28.5	0.7	.03	3.18	.25	.52	3.4	.22	9.4	.74
29.5	0	0	2.55	.20	.42	5.0	.32	6.9	.54
30.5	0.7	.03	1.80	.14	.29	3.2	.20	3.1	.24
31.5			1.38	.11	.23	1.7	.11	1.8	.14
32.5			0.83	.07	.14	1.7	.11	1.7	.13
33.5			1.15	.09	.19	1.5	.10	0.8	.06
34.5			0.62	.05	.10	1.2	.08	1.0	.08
35.5			0.48	.04	.08	0.3	.02	0.4	.03
36.5			0.32	.03	.05	0.3	.02	0.3	.02
37.5			0.27	.02	.04	1.1	.07	0.6	.05
38.5			0.27	.02	.04	0.9	.05	0.1	.01
39.5			0.27	.02	.04	0.9	.05	0	0
40.5			0.18	.01	.03	0.4	.03	0	0
41.5			0.01	+	+	0.4	.03	0.1	.01
42.5			0	0	0	0	0		
43.5			0.10	.01	.02	0	0		
44.5			0.13	.01	.02	0	0		
45.5			0.10	.01	.02	0	0		
46.5			0.07	.01	.01	0.3	0.2		
47.5			0.07	.01	.01				
48.5			0	0	0				
49.5			0.03	+	.01				
50.5			0.03	+	.01				
51.5			0.05	+	.01				
52.5			0.07	.01	.01				
Mean fork length of fully recruited stock			18.9		24.6	29.1	28.7		28.1
If $L_{\infty} = 52$ cm									
Z/K =		$\frac{52.0 - 18.9}{18.9 - 16.0}$		$\frac{52.0 - 24.6}{24.6 - 20.0}$	$\frac{52.0 - 29.1}{29.1 - 25.0}$		$\frac{52.0 - 28.7}{28.7 - 25.0}$		$\frac{52.0 - 28.1}{28.1 - 25.0}$
=		8.45		5.94	5.52		6.30		7.77
If $K = 0.24$									
Z =		2.03		1.43	1.32		1.51 = M		1.86

Table 8.13. Catch rates of jacks in baited traps at Pedro Bank and California Bank expressed as numbers per 1,000 hexagonal trap-days.

	No. per 1,000 trap-days				
	<i>Caranx ruber</i>	<i>Caranx latus</i>	<i>Caranx bartholomaei</i>	<i>Caranx fusus</i>	<i>Seriola dumerilli</i>
Pedro Cays	112	3	25	0	0
Pedro Bank					
Eastern	187	4	4	4	0
Southern	257	1	7	0	14
Western	85	7	26	21	4
California Bank	45	0	5	0	0

Cays fishery at about 19.5 cm FL appears to occur around September or October (Fig. 8.1).

Recruitment indices ($R' = Z(C/f)$ = the theoretical number of recruits required to produce the observed mean catch per 1,000 trap-days) for *C. ruber*, are summarized in Table 8.16. The relative abundance of recruits is greatest in the southern and eastern parts of Pedro Bank and lowest in the deep waters of western Pedro Bank, and California Bank and at the shallow Port Royal Reefs.

DYNAMICS OF THE POPULATIONS

The biological and population parameters estimated

Table 8.14. Catch rates of jacks in various depth zones at Pedro Bank, expressed as numbers per 100 line-hours of fishing effort.

Area Depth zone (m)	Sill reef and shelf edge			"Drop-off"	Deep reef	
	10.1-20	20.1-30	30.1-40	40.1-60	60.1-100	100-250
Effort (line-hours)	310	300	482	158	120	80
<i>Caranx latus</i>	23	10	21	6	46	0
<i>C. lugubris</i>	+	+	1	0	5	0
<i>C. fusus</i>	+	0	38	0	0	0
<i>Alectis crinitus</i>	0	1	0	+	0	0
<i>Seriola dumerilli</i>	+	0	+	0	2	0
<i>S. rivoliana</i>	0	0	0	+	+	0

Table 8.15. Mean catch rates of jacks in unbaited traps at the Port Royal Reefs (November 1969 to February, 1972) expressed as corrected numerical catch from 1,000 Z- or S- traps soaked for 1 day each.

Species	Mean no. per 1,000 trap-days
<i>Caranx ruber</i>	37
<i>C. bartholomaei</i>	3
<i>C. hippos</i>	+
<i>C. fusus</i>	+
<i>Selene vomer</i>	+

for *Caranx ruber* and *C. latus* are summarized in Table 8.17.

The value of M/K is estimated to lie between 5.5 and 6.3 in the case of *C. ruber* and reference to Beverton and Holt's (1964) tables of yield functions for fishery assessment indicates that maximum yields will be attained when $c (= I_r/L_\infty) = 0.30-0.38$ at rates of exploitation, E , exceeding 0.50; equivalent to mean lengths at recruitment of 15.5 to 20.0 cm FL. These are close to the values which actually prevail in the Port Royal Reefs and Pedro Cays fisheries.

In the case of *C. latus*, the value of M/K is about 2.5 (but the estimate is based on a rather small sample). The

Table 8.16. Estimated recruitment indices for *Caranx ruber* in various areas.

	\bar{I}_r cm FL	Number per 1,000 trap-days C/f	Mortality rate Z	Recruitment index R'
Pedro Cays area	19.5	112	1.43	160
Eastern Pedro Bank	22.5	187	1.51	282
Southern Pedro Bank	22.5	257	1.51	388
Western Pedro Bank	22.5	85	1.51	128
California Bank	?16	45	1.43-2.03	64-91
Port Royal Reefs	16.0	37	2.03	75

yield function tabulations indicate that eumetric yields would be attained at rates of exploitation, E , exceeding 0.5 when $c = l_T/L_\infty = 0.44$ to 0.54, equivalent to mean

recruitment lengths of about 31 to 38 cm FL. Figure 8.4 shows that the mean recruitment length in catches from unexploited stocks is about 39 cm FL.

Table 8.17. Summary of estimated population parameters for various species of carangids. All lengths are fork lengths in cm. Values given in brackets are approximations.

	<i>Caranx ruber</i>	<i>Caranx latus</i>	<i>Caranx bartholomaei</i>	<i>Caranx fusus</i>
Mean length at maturity, l_m	24.0	35-40		
Minimum length at maturity	22.5	34.5	23.0	26.0
l_m/L_∞	0.46	(0.50-0.57)		
Asymptotic length, L_∞	52	(70)		
Coefficient of growth, K	0.24			
Minimum retainable size in traps (4.13 cm mesh)	13.1	-	11.3	16.6
Coefficient of natural mortality, M	1.3-1.5			
M/K	5.5-6.3	(2.46)		

**CHAPTER 9:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE SNAPPERS, LUTJANIDAE**

by

R. Thompson* and J.L. Munro

(March 1974)

Identity

The taxonomic features of the Lutjanidae have been described by Jordan and Evermann (1898), Anderson (1967), Bohlke and Chaplin (1968) and Randall (1968).

They are mostly unspecialized carnivores, distinguished from the Pomadasyidae, Sparidae and "anthiid" Serranidae mostly by features of their dentition and cranial anatomy (Anderson 1967).

Caldwell (1966) listed 6 genera and 13 species of snappers from Jamaican waters, all of which have been caught during the present study. Scientific and common names of these species are given in Table 9.1. Scientific names are after Anderson (1967) and common names are after Randall (1968) and Bohlke and Chaplin (1968).

Pristipomoides andersoni (= *P. aquilonaris* Goode and Bean) has also been recorded from Jamaica (Anderson 1967) but was not collected during this study.

The morphological features of the species listed in Table 9.1 are described by Anderson (1967), Bohlke and Chaplin (1968), Randall (1968) and Jordan and Evermann (1896).

Starck (1971) described the color patterns exhibited by the shallow-water species of the genera *Lutjanus* and

Ocyurus and considered their adaptive significance. Slope-dwelling individuals of the genera *Lutjanus*, *Pristipomoides*, *Rhomboplites* and *Etelis* are all reddish pink.

Table 9.1. Scientific and common names of snappers caught in Jamaican waters.

Scientific name	Standard common names
1. <i>Etelis oculatus</i> (Valenciennes) 1828	Queen snapper
2. <i>Pristipomoides macrophthalmus</i> (Muller and Troschel) 1848	Voraz ¹
3. <i>Apsilus dentatus</i> (Guichenot) 1853	Black snapper
4. <i>Rhomboplites aurorubens</i> (Cuvier and Valenciennes) 1829	Vermilion snapper
5. <i>Ocyurus chrysurus</i> (Bloch) 1791	Yellowtail snapper
6. <i>Lutjanus mahogoni</i> (Cuvier and Valenciennes) 1828	Mahogany snapper
7. <i>Lutjanus synagris</i> (Linnaeus) 1758	Lane snapper
8. <i>Lutjanus buccanella</i> (Cuvier and Valenciennes) 1828	Blackfin snapper
9. <i>Lutjanus griseus</i> (L.) 1758	Grey snapper
10. <i>Lutjanus apodus</i> (Walbaum) 1792	Schoolmaster snapper
11. <i>Lutjanus jocu</i> (Bloch and Schneider) 1801	Dog snapper
12. <i>Lutjanus analis</i> (Cuvier and Valenciennes) 1828	Mutton snapper
13. <i>Lutjanus vivanus</i> (Cuvier and Valenciennes) 1828	Silk snapper

¹ After Anderson (1967) but commonly called the Deep Wenchman in Jamaica.

*A substantial portion of this report is derived from a thesis submitted to the University of the West Indies by R. Thompson for the degree of Master of Science. The thesis was based upon data collected by the Fisheries Ecology Research Project up to May 1972. The sections on growth, sexuality, population structure, mortality and recruitment have been prepared by J. Munro, and incorporate all data collected by the project between November 1969 and March 1973.

HYBRIDIZATION

Investigations by Anderson (1967) and Rodriguez Pino (1961) indicate that *Lutjanus ambiguus* (Poey) 1860 is possibly a hybrid of *L. synagris* and *Ocyurus*

chrysurus. Another case of probable hybridization was reported by Jordan and Evermann (1898) who stated that *Lutjanus lutjanoides* (Poey) 1860 is possibly a hybrid of *O. chrysurus* and *Neomanis* (= *Lutjanus*) *jocu*.

Distribution

GEOGRAPHICAL DISTRIBUTION

The Lutjanidae can be regarded as a typically tropical family of the Perciformes, their world-wide range largely coinciding with the range of reef-building corals (Druzhinin 1970). In the western Atlantic, the geographical range of snappers extends as far north as Massachusetts and south to Brazil. Included in the range are Bermuda, the Bahamas and the Caribbean Islands (Bohlke and Chaplin 1968; Randall 1968; Rivas 1970).

Druzhinin (1970) noted that of the species listed in Table 9.1, only four (*Etelis oculatus*, *Ocyurus chrysurus*, *Lutjanus apodus* and *L. griseus*) have been recorded from the eastern Atlantic. The rest are confined to the western Atlantic.

These investigations involved examination of catches from Pedro, Morant, Albatross, Serranilla and Salmon Banks, Bajo Nuevo and Alice Shoal; small oceanic banks near Jamaica (California and Mackerel Banks); from the northern and southern shelves of Jamaica and from the Mosquito Cays area of the Nicaraguan Shelf (Figs. 2.1 and 2.2). Most of the species listed in Table 9.1 were taken in all of the abovementioned areas, and it appears that there are few barriers to dispersal. The exceptions are *L. synagris* and *L. mahogoni* of which specimens were recorded from the Jamaican shelf and the Nicaraguan shelf, but were never captured at any of the oceanic banks.

HABITAT AND DEPTH DISTRIBUTION

The habitats of snappers range from inshore grass

beds, mangrove areas, estuaries and lagoons to offshore reefs (Starck 1971). Rivas (1949) noted that *Lutjanus jocu* and *L. apodus* frequently occur in fresh water and Breder (quoted by Rivas 1949) reported *L. griseus* from Lake Forsyth, a body of fresh water on Andros Island, Bahamas.

During this study, line and trap catches indicated that the distribution of most species of snappers is limited to the coralline shelf and deep-reef zones of the island and oceanic shelves.

Ocyurus chrysurus is most abundant at depths of 20 to 40 m near the edges of shelves and banks. *L. buccanella* is distributed over the range of depth from 40 to 160 m. *Apsilus dentatus* is most abundant at depths of 60 to 100 m, whereas *L. vivanus* is caught in greatest numbers from depths of 100 to 250 m. During this study, *Pristipomoides macrophthalmus* was caught over the depth range 60 to 400 m (see also Chapter 4).

Several species have been caught on mud slopes. These include *L. synagris*, *L. analis* and *L. buccanella* at Cow Bay, southeast coast of Jamaica at depths of 100 to 120 m; *P. macrophthalmus* at a depth of 300 m and *Etelis oculatus* at a depth of 460 m, on the slopes of the south Jamaica shelf.

The depth distributions reported here agree generally with those reported by Rivas (1970) and Brownell and Rainey (1971) for snappers in the western Atlantic. Rivas (1970) stated that in some *Lutjanus* species, if not all, the juveniles occur in depths shallower than the mean and the larger adults deeper than the mean depth. Our observations generally tended to confirm this but indicated that there is no rigid relationship between size and the depth at which individuals are captured.

Bionomics and Life History

REPRODUCTION

Gonads

The ripe gonads of all snapper species examined were similar in gross morphology. The ovaries are granular in texture, flesh pink in color and round in cross section. The testes are generally light grey, creamy in texture, and the lobes are usually flattened and triangular in cross section.

Sexuality

The snappers are apparently all gonochoristic species in which the sexes are distinct, each fish being either a male or a female. No indications of hermaphroditism

have been observed during this study and none were encountered in the literature. Length distributions of catches suggest that most species exhibit sexually dimorphic growth rates and sizes at maturity but the data are only conclusive in the cases of *Lutjanus buccanella*, *L. vivanus* and *Apsilus dentatus* (Tables 9.2, 9.3 and 9.4).

Maturity

Length-frequency distributions of catches of male and female snappers examined during this study are shown in Tables 9.2 to 9.6, together with the percentages of mature fishes in each length group. The mean sizes at sexual maturity of male *Lutjanus buccanella*, *L. vivanus* and *Apsilus dentatus* are larger than those for the

Table 9.2. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Lutjanus buccanella* at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
19.0-20.9	1	0	0	—
21.0-22.9	0	—	6	17
23.0-24.9	9	0	13	23
25.0-26.9	12	25	54	48
27.0-28.9	22	45	86	33
29.0-30.9	36	47	130	37
31.0-32.9	28	32	96	30
33.0-34.9	34	38	25	36
35.0-36.9	40	48	16	25
37.0-38.9	40	75	13	46
39.0-40.9	38	58	6	33
41.0-42.9	21	43	2	0
43.0-44.9	9	56	0	—
45.0-46.9	9	44	0	—
47.0-48.9	4	100	2	100
49.0-50.9	2	100	0	—
Total	305		449	

females. This suggests a faster growth rate for males, or that males are maturing later than females. In the case of *Ocyurus chrysurus*, fewer ripe or spent females were found in the smaller length groups (Table 9.5), although the modal sizes of the samples were similar. The data for *L. apodus* are inconclusive (Table 9.6).

The estimated mean sizes of maturity are as follows:

<i>Lutjanus buccanella</i>	: males, 25 to 27 cm FL; females, 23 to 25 cm FL.
<i>L. vivanus</i>	: males, 55 to 60 cm FL; females 50 to 55 cm FL.
<i>Apsilus dentatus</i>	: males, 43 to 45 cm FL; females 39 to 41 cm FL.
<i>Ocyurus chrysurus</i>	: males, about 26 cm FL; females 29 to 31 cm FL.
<i>L. apodus</i>	: about 25 cm FL both sexes.

Data on other species of snappers are too few to estimate the mean size at maturity. Sizes of the smallest ripe or spent individuals in the samples were as follows:

<i>L. jocu</i>	: female, 32.3 cm FL.
<i>L. synagris</i>	: male, 18.3 cm FL; female 17.6 cm FL.
<i>Rhomboplites aurorubens</i>	: female, 30.8 cm FL.
<i>Pristipomoides macrophthalmus</i>	: female, 18.0 cm FL.

Fecundity

No fecundity estimates were made during the present

Table 9.3. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Lutjanus vivanus* at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
20.0-24.9	1	0	5	0
25.0-29.9	22	0	36	0
30.0-34.9	45	0	41	0
35.0-39.9	38	0	20	0
40.0-44.9	47	0	27	4
45.0-49.9	27	0	13	0
50.0-54.9	18	0	20	30
55.0-59.9	37	35	16	57
60.0-64.9	25	52	9	89
65.0-69.9	1	0	3	67
70.0-74.9	1	0	0	—
Totals	262		190	

Table 9.4. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Apsilus dentatus* at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
28.0-29.9	1	0	1	0
30.0-31.9	1	0	3	0
32.0-33.9	6	0	8	0
34.0-35.9	3	0	6	0
36.0-37.9	8	0	13	8
38.0-39.9	12	0	25	12
40.0-41.9	16	0	29	38
42.0-43.9	18	17	39	54
44.0-45.9	22	23	43	56
46.0-47.9	33	36	36	50
48.0-49.9	67	40	23	57
50.0-51.9	79	33	11	64
52.0-53.9	36	19	3	33
54.0-55.9	16	6	2	100
56.0-57.9	4	0	0	—
Totals	322		242	

study, but previous works show that snappers produce large numbers of eggs. Rojas (1960) estimated 1,355,000 eggs from the ovary of a specimen of *L. analis*. Rodriguez Pino (1962) estimated a range of 347,000 to 995,000 eggs from six *L. synagris* from the Cuban coast, and Piedra (quoted by Druzhinin 1970) estimated a range of 100,000 to 1,473,000 eggs in four *O. chrysurus*, also from Cuba.

Mating and Fertilization

Observations made by Wicklund (1969) and Starck

Table 9.5. Percentages of mature fishes and comparison of length-frequency distributions of catches of male and female *Ocyurus chrysurus* at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
20.0-21.9	1	0	1	0
22.0-23.9	6	0	3	0
24.0-25.9	1	(100)	1	0
26.0-27.9	16	56	2	0
28.0-29.9	10	40	6	17
30.0-31.9	26	58	28	36
32.0-33.9	36	72	22	45
34.0-35.9	49	53	35	49
36.0-37.9	53	45	25	56
38.0-39.9	30	40	33	52
40.0-41.9	25	52	26	46
42.0-43.9	21	57	29	59
44.0-45.9	30	50	22	45
46.0-47.9	29	55	24	58
48.0-49.9	23	70	15	80
50.0-51.9	21	57	18	67
52.0-53.9	8	50	10	60
54.0-55.9	4	25	5	60
56.0-57.9	0	-	1	(100)
Totals	389		306	

(1971) indicate that snappers spawn in groups. A pre-spawning milling behavior occurs and then eggs and sperm are released in the water where fertilization takes place.

Spawning Seasons

Druzhinin (1970) reported that both *L. synagris* and *O. chrysurus* spawned in Cuban waters from March to September with peaks in June to August and April to May, respectively. Erdman (1956) reported that *O. chrysurus* spawned in Puerto Rican waters in March. Starck (1971) found that *L. griseus* spawned at the Florida Cays in July and August.

Data gathered by the present investigation up to June 1971 were reported on by Munro et al. (1973). Additional data gathered up to February 1973 are included in the following analysis. The total number of fishes examined (N) is indicated for each species.

Lutjanus buccanella (N = 1,961): Table 9.7 shows the monthly percentages of sexually inactive, active, ripe and spent fishes. Ripe fishes were taken in February-May and August-November, with maxima in April and September.

Lutjanus vivanus (N = 494): Few additional data are available and the conclusions of Munro et al. (1973) remain unchanged. Ripe fishes were found in March-May and August, September and November.

Table 9.6. Numbers of mature male and female *Lutjanus apodus* in catches taken at unexploited oceanic banks.

Length group cm FL	Males		Females	
	No. examined	No. ripe or spent	No. examined	No. ripe or spent
20.0-24.9	2	0	3	1
25.0-29.9	7	2	14	3
30.0-34.9	10	7	5	1
35.0-39.9	4	2	12	6
40.0-44.9	8	3	4	4
45.0-49.9	6	3	0	--
Totals	37		38	

Table 9.7. Monthly percentages of inactive, active, ripe and spent fishes in samples of *Lutjanus buccanella*.

	No. examined	Inactive	Percentage		
			Active	Ripe	Spent
January	21	100	0	0	0
February	125	60	26	6	8
March	136	79	1	5	15
April	358	16	40	42	2
May	720	76	12	12	0
June	0		No data		
July	67	36	64	0	0
August	129	82	15	3	0
September	153	42	22	34	1
October	50	42	12	42	4
November	184	70	18	12	0
December	18	78	22	0	0
Total	1,961				

Apsilus dentatus (N = 1,229): Munro et al. (1973) reported the greatest proportions of ripe fishes were found in January-April and September-November. The few additional samples obtained subsequent to June 1971 do not alter this conclusion. No data are available for the months of June and December.

Ocyurus chrysurus (N = 986): Table 9.8 shows that ripe or spent fishes were found in all months of the year, but in the lowest proportions in the summer months and in November-December. It appears from the data that the main spawnings are in February-April and, secondarily, in September-October. This is at variance with Druzhinin's (1970) observation that this species spawned in Cuban waters in March-September, with a maximum in April-May. No ripe fishes were ever taken at the shallow, nearshore Port Royal reefs where a total of 126 fishes were examined.

Lutjanus apodus (N = 205): Ripe and/or recently spent fishes were collected in February-June and August-November. Ripe fishes were taken both at oceanic banks and at the nearshore Port Royal Reefs.

Table 9.8. Monthly percentages of inactive, active, ripe and spent fishes in samples of *Ocyurus chrysurus*.

	No. examined	Inactive	Percentage		Spent
			Active	Ripe	
January	29	10	28	62	0
February	29	0	17	34	48
March	6	(0)	(0)	(100)	(0)
April	39	0	8	74	18
May	51	4	29	51	16
June	10	(10)	(0)	(50)	(40)
July	139	32	40	10	17
August	15	(7)	(27)	(53)	(13)
September	119	15	11	34	40
October	82	13	7	65	15
November	271	39	14	22	25
December	70	69	16	2	13
Total	860				

Lutjanus jocu (N = 30): Ripe females were collected in February-March and one ripe female and one spent male were collected in November.

Pristipomoides macrophthalmus (N = 40): Two ripe females were collected in October.

Rhomboplites aurorubens (N = 5): One active male was caught during May and one ripe and three active females during November.

No ripe *L. griseus*, *L. analis*, *L. mahogoni* or *Etelis oculatus* were examined during this study.

Spawning Grounds

No spawning aggregations of snappers were encountered.

Eggs (Structure and Size)

Specimens of *P. macrophthalmus* with transparent, fully developed eggs, were taken off the South Jamaica Shelf at a depth of 200 m during October 1971. Egg diameters ranged from 0.75 mm to 1.0 mm and the mean diameter was 0.81 mm (20 measurements). This was the only instance in which fully developed eggs were obtained, and it is possible that the final stages of egg maturation takes place just prior to spawning.

PRE-ADULT PHASES

No accounts of embryonic and early juvenile life of snappers were found in the literature. Munro et al. (1973) noted that no long-lived oceanic larval or post-larval phases have been reported for snappers, as have been reported for many other reef fish families and

suggested that they probably have a relatively short planktonic larval or post-larval life.

Very early juvenile stages of snappers are not often seen but appear to not be as secretive as hinds and groupers. Juveniles of *Lutjanus griseus*, *L. apodus*, *L. synagris* and *Ocyurus chrysurus* are fairly commonly seen in Kingston Harbour in shallow *Thalassia* beds, around mangrove roots and among jetties and pilings.

Juvenile *L. buccanella* ranging in size from about 10 to 22 cm FL were observed by V. Gaut (pers. comm.) swimming above coral reefs in 20 to 30 m at Runaway Bay and Peartree Bottom (North Jamaica coast) during September 1970. Eighty-nine juvenile *L. vivanus* were caught aboard the UNDP/FAO Research Vessel, *Alcyon*, on a cruise off Luguillo, Puerto Rico at a depth of 40 m (G. Chislett, pers. comm.). The size range was 14 to 35 cm (average 19.4 cm FL) and the average weight was 135 g. Also, 10 *L. vivanus* juveniles (15.9 to 24.3 cm FL) were taken in traps in a depth of 30 m at the northern edge of Pedro Banks.

These observations suggest that the juvenile deep water snappers usually frequent shallower water than the adults.

ADULT PHASE

There are singularly few sources of information on aspects of the adult phase of the life histories of Caribbean species of snappers. Published data are referred to, where relevant, in the following pages.

Competitors and Predators

Barroso (1965) mentions the possible competition for food between *Caranx lugubris* and *Lutjanus aya* in northeast Brazil. These two species are found in the same habitat and have similar diets. On reefs, snappers must certainly compete among themselves for food and space. Competition with groupers (Serranidae) jacks (Carangidae) moray eels (Muraenidae) and grunts (Pomadasysidae) probably also occurs, although the extent of competition is not known.

There is no information concerning predation upon snappers, but species of the major reef predators such as sharks, groupers and barracuda are probably the most important causes of mortality.

Parasites

Schroeder (1971) described nine species of trematodes from the intestine and pyloric caeca of *Lutjanus griseus* taken from Lower Matecumbe Key, Florida. He concluded that the habitat of the snapper is the most important factor in determining the nature of their trematode populations. Brownell and Rainey (1971) found a tapeworm pleuroceroid larva in the viscera of *L. vivanus* and *L. buccanella* and noted that the degree of infection in snappers appeared to be much less than in groupers.

Longevity

Alegria and de Menezes (1970) and Rodriguez Pino (1962) used otoliths to estimate ages of *Lutjanus synagris* up to 6 yr, from northeast Brazil and Cuba, respectively. Starck (1971) used scales to estimate ages of *L. griseus* up to 9 yr from the Florida Keys. Fonteles Filho (1970) estimated ages up to 18 yr for *L. purpureus* from northeast Brazil.

NUTRITION AND GROWTH

Feeding and Food

Longley and Hildebrand (1941) reported that schools of *Lutjanus griseus* and *L. apodus* which were present on reefs at Tortugas, Florida, during the day, dispersed at dusk and went in search of food. Starck and Davis (1966) observed that after dark at Alligator Reef, Florida, *L. apodus* foraged individually in rocky areas on the reef top whereas *L. griseus* fed in the more open areas of the reef top and back reef and also frequented mixed rubble, grass and sand bottoms. *Ocyurus chrysurus* is semipelagic and ranges throughout the reef habitat and feeds actively both by day and by night.

Randall (1967) reported that Lutjanids in the Virgin Islands feed primarily on crabs and fishes, with shrimps, lobsters, gastropods, stomatopods and octopus completing the diet. Within a species, the larger individuals consumed proportionately more fishes. Juvenile *O. chrysurus* feed primarily on zooplankton and the adults upon benthic and pelagic animals.

Brownell and Rainey (1971) found that the main items in the stomachs of *L. buccanella* taken at the Virgin Islands, were isopods (37.5%) and fish (33.3%), with shrimps, spiny lobsters, crabs, octopus and squid making up the rest of the diet. The stomach contents of *L. vivanus* consisted of fish (50.1%), shrimp (17.8%) and crabs (11.0%), with isopods and other invertebrate groups completing the diet.

The stomachs of 18 juvenile *L. griseus* collected by P. Reeson (pers. comm.) from the Great Salt Pond on the south coast of Jamaica, contained 60% by volume of larval fish and 40% crabs and shrimp. A black snapper, *Apsilus dentatus* collected at the Morant Cays contained a small scyllarid lobster in its stomach. In July 1970, adult *L. vivanus*, *L. buccanella* and *A. dentatus* caught at the Morant Cays all had stomachs distended with an orange-brown pelagic tunicate.

Growth Rates

Relative growth patterns

The relationships between fork lengths, standard lengths and total lengths of six species are summarized in Table 9.9.

Table 9.9. Relationships between fork lengths (FL), standard lengths (SL) and total lengths (TL) of six species of snappers.

Species and formulae	Number of measurements	Length range FL cm
<i>Lutjanus buccanella</i> SL = $-1.1 + 0.96 \text{ FL}$ TL = $0.2 + 1.08 \text{ FL}$	17	20-42
<i>Lutjanus vivanus</i> SL = $0.7 + 0.86 \text{ FL}$ TL = $0.3 + 1.09 \text{ FL}$	47	23-52
<i>Lutjanus analis</i> SL = $-0.2 + 0.85 \text{ FL}$ TL = $C + 1.09 \text{ FL}$	13	22-45
<i>Lutjanus synagris</i> SL = $-0.2 + 0.86 \text{ FL}$ TL = 1.087 FL	23	10-41
<i>Lutjanus apodus</i> SL = $-1.7 + 0.898 \text{ FL}$ TL = $0.9 + 1.04 \text{ FL}$	19	24-48
<i>Ocyurus chrysurus</i> SL = $0.3 + 0.828 \text{ FL}$ TL = $-0.8 + 1.266 \text{ FL}$	23	8-52

The relationships between fork lengths and body depths of *Lutjanus apodus*, *L. synagris* and *Ocyurus chrysurus* are given in Table 9.10. The average maximum aperture of the wire mesh used on Jamaican fish traps is 4.13 cm. Fork lengths of *O. chrysurus*, *L. apodus* and *L. synagris* at a body depth of 4.13 cm are 14.0, 14.3 and 13.4 cm, respectively. About 50% of the fishes of these sizes which enter traps should be retained.

The relationships between fork lengths and weights of *O. chrysurus*, *L. apodus* and *L. synagris* are given in Table 9.11.

Maximum size

The maximum sizes (TL) reported by Bohlke and Chaplin (1968) and the lengths (FL) of the largest snappers measured during these investigations are given in Table 9.12. Where conversion factors are known, the calculated total lengths are also given. Of the lengths reported here, those of *Lutjanus synagris*, *L. apodus*, *L. buccanella*, *L. vivanus*, and *Apsilus dentatus* all exceed the maximum sizes previously reported.

Age and growth

Crocker (1962) and Starck (1971) used scales to age grey snappers, *Lutjanus griseus*, from south Florida. Rodriguez Pino (1962) aged *L. synagris* from Cuba by examining otoliths. Fonteles Filho (1970) and Alegria and de Menezes (1970), respectively, estimated the

Table 9.10. Relationships between fork lengths (FL) and body depths (D) of three species of snappers.

Species and formulae	Number of measurements	Length range FL cm
<i>Ocyurus chrysurus</i> FL = -1.2 + 3.686 D	18	8-23
<i>Lutjanus apodus</i> FL = 2.7 + 2.811 D	6	15-27
<i>Lutjanus synagris</i> FL = -0.7 + 3.416 D	13	9-25

Table 9.11. Relationships between fork lengths (FL) and weights (W) of three species of snappers. All lengths are expressed in centimeters and weights in grams.

Species and formula	Number of fish	Length range FL cm
<i>Ocyurus chrysurus</i> Log W = -1.838 + 3.032 Log L W = 0.0145 L ^{3.032}	393	15-49
<i>Lutjanus apodus</i> Log W = -2.049 + 3.204 Log L W = 0.00891 L ^{3.204}	106	17-35
<i>Lutjanus synagris</i> * Log W = -1.722 + 2.943 Log L W = 0.0189 L ^{2.943}	224	17-35

*Gutted weights

ages of specimens of *L. purpureus* and *L. synagris* from northeast Brazil.

During this study, estimates of growth of reef fishes have been based mostly on analyses of length-frequency distributions and examination of scales and otoliths. However, the snappers have proven to be a difficult group to deal with. In most cases, the success of sampling or the availability of commercial catches was highly erratic and no temporal progression of length-frequency modes could be observed. Very large samples were occasionally obtained and some samples showed polymodal length-frequency distributions in which the modes probably represented individual cohorts.

Scales from young fishes showed the best potential for age determinations. The centers of the scales of larger fish often are opaque, obscuring the circuli. This opaqueness is apparently caused by the deposition of additional scale-building material around the center of the scales, especially along the radii. The percentage of regenerated scales is very high in most species and approaches 100% even in moderate-sized specimens of *L. buccanella*, *L. synagris*, *L. apodus* and *L. jocu*. The

Table 9.12. Observed maximum fork lengths of snappers from Jamaican waters compared with measurements in the literature.

Species	Sex	Observed maximum fork length (cm)	Maximum reported total length* (cm)
<i>Lutjanus mahogoni</i>	M	26	37.5
<i>L. synagris</i>	M	41 (44.6)**	37.5
<i>L. analis</i>	M	60 (64.2)	75.0
<i>L. jocu</i>	M	72	77.5
<i>L. apodus</i>	F	57 (60.1)	60.0
<i>L. griseus</i>	M	45	90.0***
<i>L. buccanella</i>	M	49 (53.2)	50.0
	F	49 (53.2)	
<i>L. vivanus</i>	M	72 (78.7)	75.0
	F	68 (74.4)	
<i>Ocyurus chrysurus</i>	M	55 (68.8)	75.0
	F	56 (70.1)	
<i>Apsilus dentatus</i>	M	56	45.0
	F	54	
<i>Rhomboplites aurorubens</i>	F	39	50.0
<i>Pristipomoides macrophthalmus</i>	M	35	

*Bohlke and Chaplin (1968).

**Calculated total lengths in brackets.

***Rarely exceeds 8 lb (3.6 kg), Randall (1968).

numbers of regenerated scales present on *Ocyurus chrysurus*, *L. vivanus* and *Apsilus dentatus* are much lower. Occasionally well-developed rings are seen on some scales of a fish but are absent from others.

Otoliths of *L. buccanella*, *L. vivanus*, *L. mahogoni*, *O. chrysurus* and *A. dentatus* revealed no regular clear and dark alternating bands suitable for age determination. Snapper otoliths show the same general characteristics as those of groupers (Chapter 7). The otoliths of *L. buccanella* and *L. vivanus* are similar in size and shape although the sulcus acousticus is more deeply grooved in *L. buccanella*. The otoliths of *A. dentatus* and *O. chrysurus* of similar size are less than one-half the size of those of *L. buccanella* and *L. vivanus*.

In all cases, the estimates of growth of snappers presented in the following pages are based upon very poor evidence and should be regarded only as first approximations.

Lutjanus buccanella: The only evidence of growth of this species is derived from a large sample obtained by G. Chislett (UNDP/FAO Caribbean Fishery Development Project) at Navidad Bank, during May 1970. The length-frequency distributions of both males and females are polymodal (more clearly so in the case of the males), (Fig. 9.1), and it is likely that the right-hand modes represent the combined frequencies of several cohorts. The histograms suggest that males increase in size from about 31.5 cm FL to at least about 42.5 cm FL within either 1 yr or 6 mo, depending upon whether the cohorts

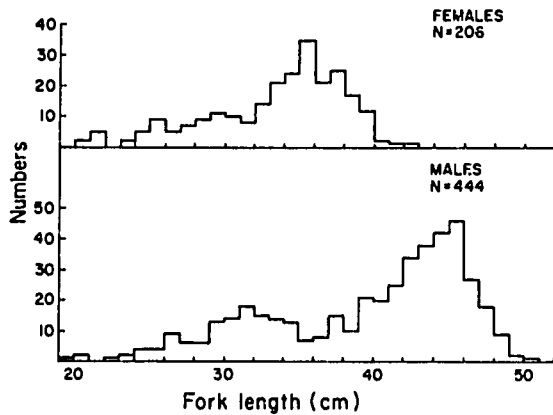


Fig. 9.1. Frequency histograms of *Lutjanus buccanella* from Navidad Bank showing bimodal distributions. Collected by G. Chislett-Alcyon, cruise 70-5, May, 1970.

are derived from the biannual spawnings or represent year classes.

The females might grow from a length of 29.5 cm to about 34.5 cm in the same time. These are very speculative interpretations. If the asymptotic lengths of males and of females are about 54 cm FL and 46 cm FL, respectively, the corresponding coefficients of growth, K , would be 0.70 and 0.35. These are relatively large values, and the modes therefore presumably represent year classes.

Moseley (1966) showed that *L. aya* from the Gulf of Mexico grew 20 to 25 cm SL during their first year and those between 25 cm and 40 cm SL grew about 8 cm/yr. Allowing for the larger maximum size of *L. aya* the estimates for *L. buccanella* do not seem unreasonable in comparison. The estimated growth rate of *L. purpureus* from N.E. Brazil (Fonteles Filho 1970) is less than that suggested here.

Apsilus dentatus: Figure 9.2a shows polymodal length-frequency distributions of male and female *A. dentatus* collected at Pedro Bank and Alice Shoal (Fig. 2.1) in August 1969, and Fig. 9.2b shows the length distribution of a sample of 550 fishes (sexes not determined) taken by the *M.V. Alcyon* at Navidad and Silver Banks in March 1968.

It appears that males might grow from a modal size of 40.5 cm FL to at least 48.5 cm FL in a year. If the asymptotic length is about 58 cm FL successive modes would be expected at 53, 55 and 56.5 cm FL, which is in reasonable agreement with the modes shown in Fig. 9.2a and 9.2b. The major mode at 50.5 cm FL in both Fig. 9.2a (males) and Fig. 9.2b is thought to result from a combination of overlapping modes, and hook selection factors.

In the case of females, the succession of modes (Fig. 9.2a) at 40.5, 44.5, 47 and 49.5 cm FL is a reasonable approximation of an asymptotic progression when the asymptotic length is 56 cm FL. The slopes (k) of Walford plots are about 0.51 and 0.74 for males and females, respectively, and the coefficients of growth, K are 0.65 and 0.30.

The scales of 52 *A. dentatus* (39 to 51 cm FL, sex not determined) were examined, and 37 showed one or more "annuli." The "annuli" were very distinct, where formed, and resulted from resorption of the circuli, particularly in the lateral field. The modal scale radius at formation of the first annulus was 7.0 to 7.4 mm, equivalent to about 41 to 42 cm FL. This is close to the size of maturity previously estimated. It appears that a more detailed study of scales of this species might produce improved estimates of age and growth.

Ocyurus chrysurus: There is no evidence of sexual dimorphism in the growth rates of this species (Table 9.5), and it is therefore not necessary to treat the length distributions of the sexes separately.

Piedra (quoted by Druzhinin 1970) found that *O. chrysurus* from the Cuban coast grew to 12.4 cm FL during their first year and then grew an average of approximately 4 cm/yr for the next 6 yr to reach 36.3 cm FL at 7 yr.

Figure 9.3 shows the length-frequency distribution of *O. chrysurus* caught in traps at the Port Royal Reefs. The arrows indicate possible modal progression of a cohort recruited at a length of about 17.5 cm FL in August-September 1970 (Lunar Months 10-11) and which reached about 23 cm in the ensuing year.

Figure 9.4 shows the length-frequency distribution of a sample of 684 fishes taken by the *M.V. Alcyon* in June 1967. There are modes at 33.5 cm, and 39.5 cm and possibly a third mode in the region of 42.5 to 44.5 cm FL. If the asymptotic length is about 60 cm FL, the coefficient of growth, K , is about 0.25. This is a faster rate than is indicated by the samples from the Port Royal Reefs, and both rates are much more rapid than that estimated by Piedra (quoted by Druzhinin 1970).

Lutjanus apodus: The data collected during the present study did not yield any estimates of the growth rate of this species. Randall (1962, 1963) recovered eight tagged specimens. Most specimens showed negligible growth rates, and the highest estimate of K which can be derived from any of the returns is only 0.18 (when L_{∞} is set at 57 cm TL). It is clear that the tags affected this species most adversely.

Lutjanus synagris: Scales of 5 fishes out of a total of 6 examined from the Port Royal Reefs showed one "annulus." This was seen as a cutting-over of circuli in the posterior lateral field which was continuous with an increased spacing between two successive circuli in the anterior field. The length range was 17.6 to 26.8 cm FL (mean length 21.7 cm FL) and the scale radius was 3.9 mm. The mean radius of the "annulus" was 3.4 mm and the calculated average length at annulus formation assuming proportional growth in scales and fish is 18.9 mm FL.

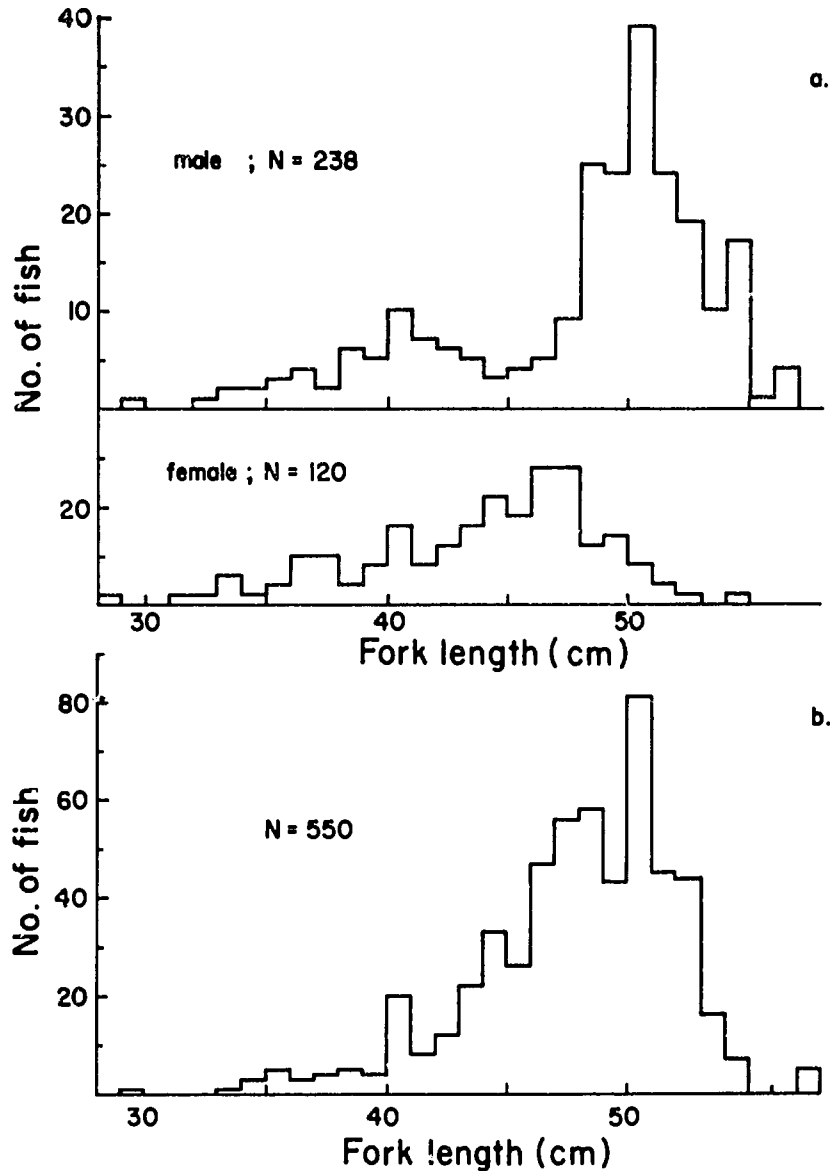


Fig. 9.2. (a) Length-frequency distributions of samples of male and female *Apsilus dentatus* caught at Pedro Bank and Alice Shoal in August 1969. (b) Length-frequency distribution of a sample of 550 *Apsilus dentatus* taken at Silver and Navidad Banks in March 1968. Sexes not determined.

Almost all scales of *L. synagris* collected from catches taken at the Mosquito Cays, Nicaraguan shelf, were regenerated (size range of 20 to 35 cm FL).

Lutjanus mahogoni: Three fishes of six examined had one "annulus" on each scale, similar in appearance to those of *L. synagris*. The length range was 21.9 to 23.6 cm FL (mean length 23.0 cm) and the mean scale radius was 5.2 mm. The mean radius of the "annulus" was 4.8 mm and the calculated length at annulus formation was 21.2 cm FL.

BEHAVIOR

Migrations

Beaumariage (1969) obtained returns of tagged

Lutjanus analis, *L. campechanus*, *L. griseus* and *Ocyurus chrysurus* off the Florida coast of the Gulf of Mexico. Although in most instances long-term returns of marked fishes were few, the data indicated little movement of adult snappers. The exception to this was the red snapper *L. campechanus* which showed appreciable movement (Beaumariage and Wittich 1966) when released in depths greater than 15 fathoms (27 m). Moe, Beaumariage and Topp (1970) also reported on a red snapper which moved about 80 nautical miles after 6 yr of freedom.

Data from this study indicate that juvenile *Ocyurus chrysurus* commonly occur over shallow grass flats; the later juveniles inhabit shallow reef areas; and the adults are found on deeper reefs. Starck and Davis (1966) consider this species to be a semi-pelagic wanderer over the reef habitat.

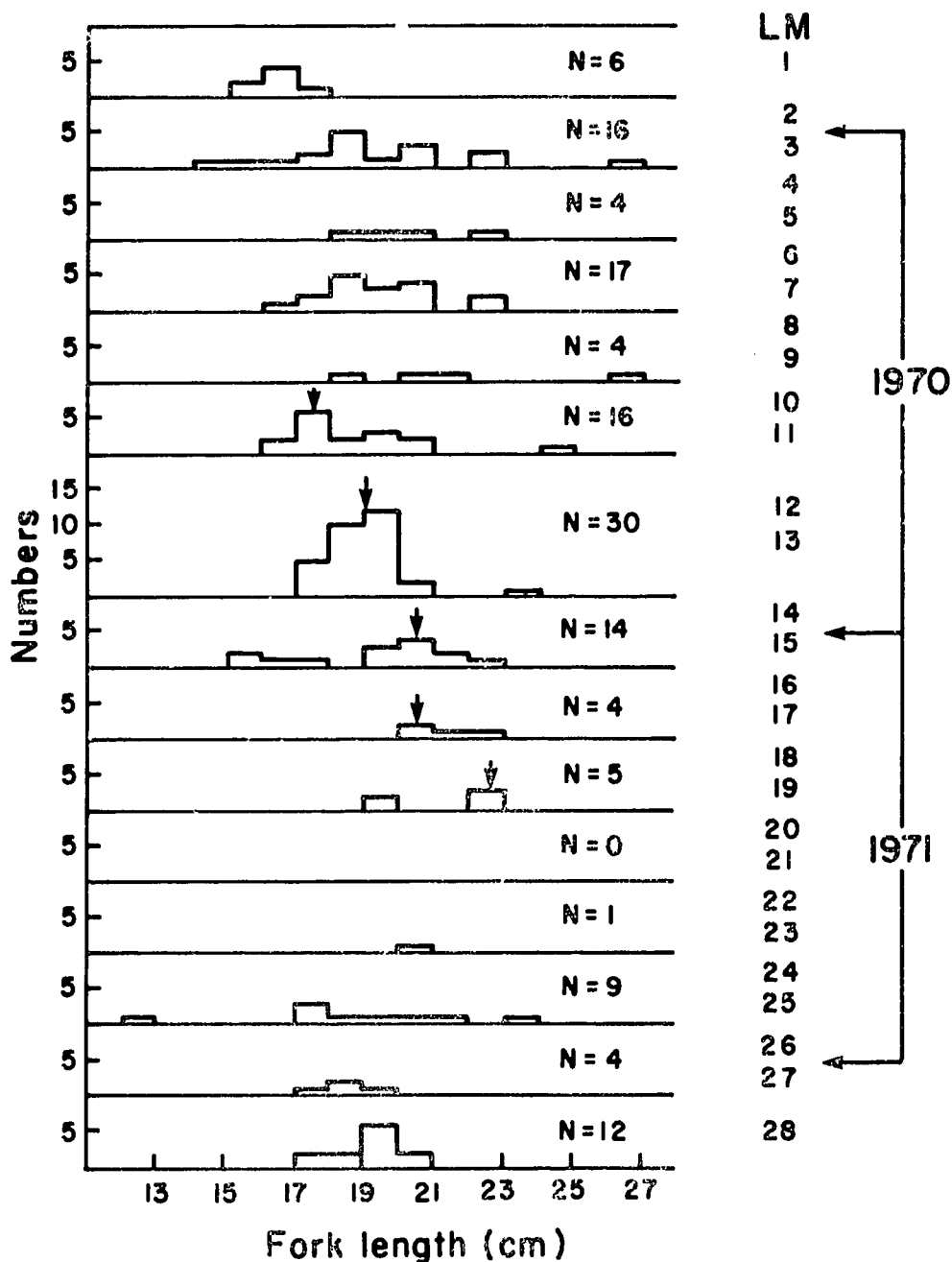


Fig. 9.3. Length-frequency distributions of *Ocyurus chrysurus* captured at the Port Royal Reefs over a period of 28 lunar months (1969-1972). Arrows indicate modal progression of a cohort. LM = lunar month.

Schooling

Longley and Hildebrand (1941) and Starck and Davis (1966) have reported schools of *Lutjanus apodus* and *L. griseus* over reefs in Florida during the day. Small schools of juvenile *L. buccanella* were observed on the north Jamaica coast by V. Gaut (pers. comm.), who also reported schools of *L. mahogoni* in association with *Haemulon plumieri* at Grand Cayman. *Ocyurus chrysurus* was observed in schools in varying sizes on the Port Royal Reefs. Large catches of the black snapper, *Apsilus dentatus* were occasionally obtained from Pedro Bank over a short period of time, suggesting a schooling habit for this species.

Potts (1970) showed that schools of *L. monostigma* from Aldabra, Indian Ocean, did not exhibit any obvious response to temperature but found that current was the main factor that determined the orientation and position of the school. Potts described three types of response to predators, namely, a low-intensity fright response, a mild fright response and a strong fright response. During this study, when attempts were made to remove juvenile *O. chrysurus* from an aquarium tank, they would react by lying motionless on their sides at the bottom of the tank. It is not known if this type of behavior is utilized to escape predators in the usual habitat of these fishes.

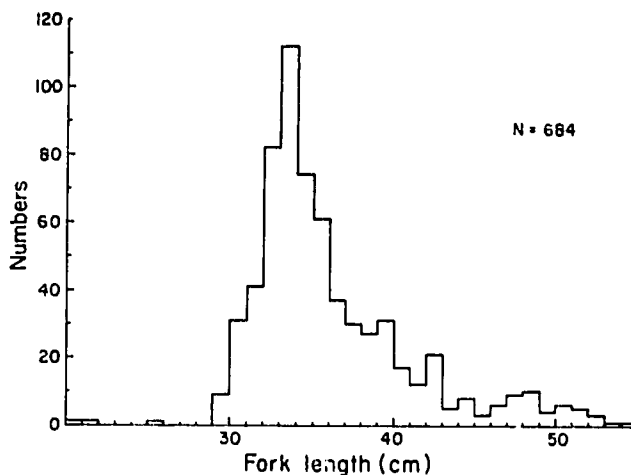


Fig. 9.4. Length-frequency distribution of a sample 684 *Ocyurus chrysurus* caught at Pedro Bank in June 1967.

Populations

POPULATION STRUCTURES

Sex Ratios

The sex ratios of the species of snappers commonly caught on oceanic banks are close to unity in most cases, and variations observed appear to be related to depth and type of fishing gear.

Table 9.13 shows variations of sex ratio according to gear and depth for *Lutjanus buccanella*, *L. vivanus* and *Apsilus dentatus* from Pedro Bank. The variation is very marked for *L. buccanella* which had a ratio of M:F = 1:2.1 in trap catches and a ratio of M:F = 1:0.7 in line-caught fishes. Similarly, *L. vivanus* and *A. dentatus* showed a predominance of females in trap catches while males were relatively more numerous in line catches.

Table 9.13. Variations of sex ratios of three species of snappers caught on Pedro Bank, relative to gear and depth.

Species	Gear	Depth range (m)	Total number	Sex ratio M:F
<i>Lutjanus buccanella</i>	Traps	40-100	515	1:2.1
	Lines	40-280	142	1:0.7
<i>Lutjanus vivanus</i>	Traps	100-200	67	1:1.0
	Lines	80-280	386	1:0.7
<i>Apsilus dentatus</i>	Traps	50-100	30	1:1.0
	Lines	50-120	564	1:0.7

Age and Length Composition

It has not been possible to determine the ages of any species of snapper; consequently, there is no information on the age compositions of catches or of the populations.

Figures 9.5 to 9.7 show comparisons of the gross length-frequency compositions of trap- and line-caught

samples of *Lutjanus buccanella*, *L. vivanus* and *Apsilus dentatus*. Relatively greater numbers of small *L. buccanella* were taken in traps, usually fished in shallower depths, but there are no major differences in the modes or the length range (Fig. 9.5). In contrast, trap catches of *L. vivanus* were comprised almost entirely of small fishes and the largest individuals were never taken in traps (Fig. 9.6). There appears to be no difference in the size compositions of trap and line catches of *A. dentatus* (Fig. 9.7).

Figure 9.8 shows the size compositions of trap catches of *Ocyurus chrysurus* at the Port Royal Reefs and of line catches at Pedro Bank. The differences are probably more indicative of the migration towards deeper water (which appears to occur at a size of about 20 cm FL) than an indication of the effect of intensive exploitation. Trap and line catches of this species from comparable depths showed no evidence of gear selectivity, but the small size of the trap catches at oceanic banks precludes any definite conclusion. Similarly, Fig. 9.9 shows that large specimens of *L. apodus* were never taken at the Port Royal Reefs, and there is probably a general tendency to move into deeper water at or before sexual maturity.

The estimated mean annual length-frequency compositions of catches of *L. buccanella*, *A. dentatus* and *O. chrysurus* are shown in Figs. 9.10 to 9.12 (see Chapter 3 for methodology). The catches are all from unexploited parts of Pedro Bank and thus representative of the virgin stocks.

Female *L. buccanella* are fully recruited at 28.0 to 29.9 cm FL. The size-frequency distribution of males is somewhat irregular and is bimodal, at 30.0 to 31.9 and 34.0 to 35.9 cm FL (Fig. 9.10). The males are probably fully recruited at about 31 cm FL. The mean recruitment length is about 28 cm FL (both sexes).

Figure 9.11 shows that male *A. dentatus* are fully recruited at 48.0 to 49.9 cm FL while females are fully recruited at 44.0 to 45.9 cm FL. The mean recruitment lengths are about 45.5 cm FL and 41.5 cm FL, respectively.

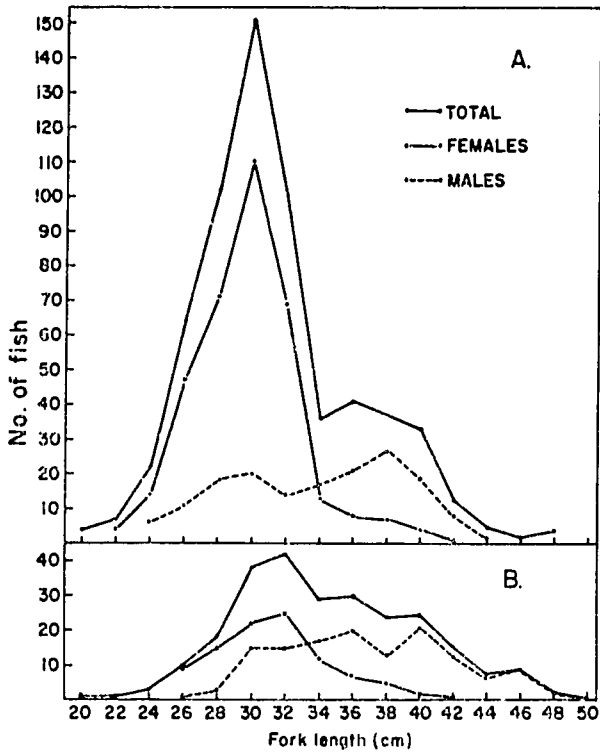


Fig. 9.5. Frequency polygons of *Lutjanus buccanella* caught on Pedro Bank. (A) Traps fished at 40 to 100 m. Males: N = 165; Females: N = 350; Total: N = 620. (B) Lines fished at depths of 40 to 280 m. Males: N = 143; Females: N = 99; Total: N = 259.

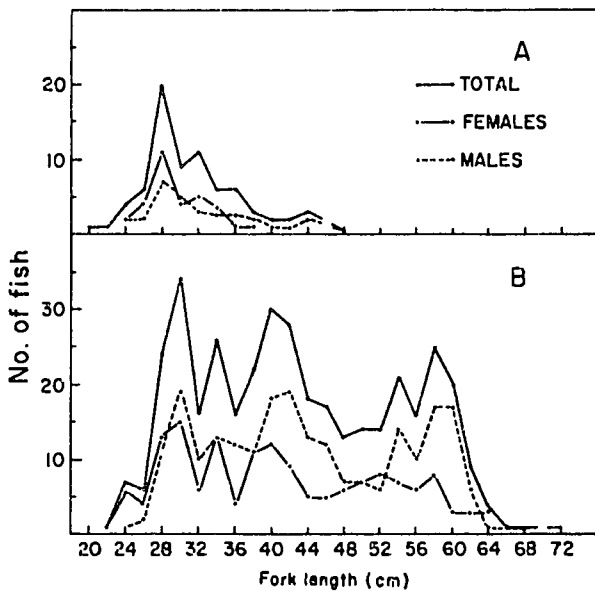


Fig. 9.6. Frequency polygons of *Lutjanus vivanus* caught at oceanic banks. (A) Traps fished at 100 to 160 m. Males: N = 34; Females: N = 33; Total: N = 77. (B) Lines fished at 80 to 200 m. Males: N = 230; Females: N = 156; Total: N = 386.

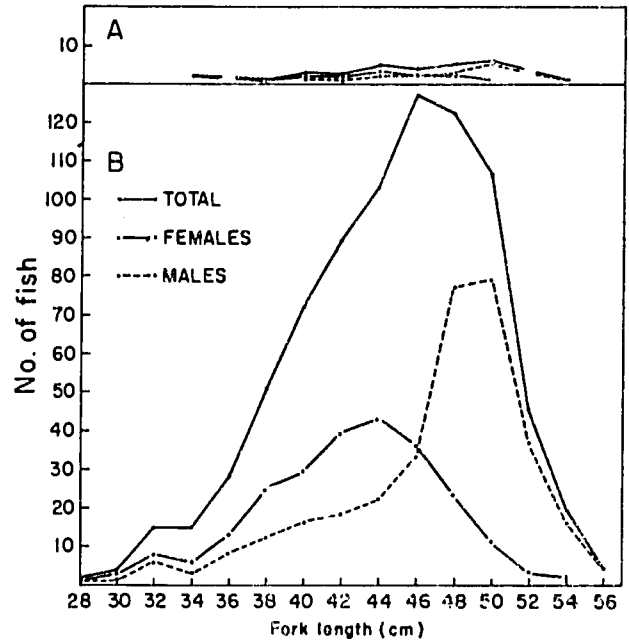


Fig. 9.7. Frequency polygons of *Apsilus dentatus* caught at oceanic banks. (A) Traps fished at 40 to 100 m. Males: N = 15; Females: N = 15; Total: N = 30. (B) Lines fished at 60 to 100 m. Males: N = 322; Females: N = 242; Total: N = 802.

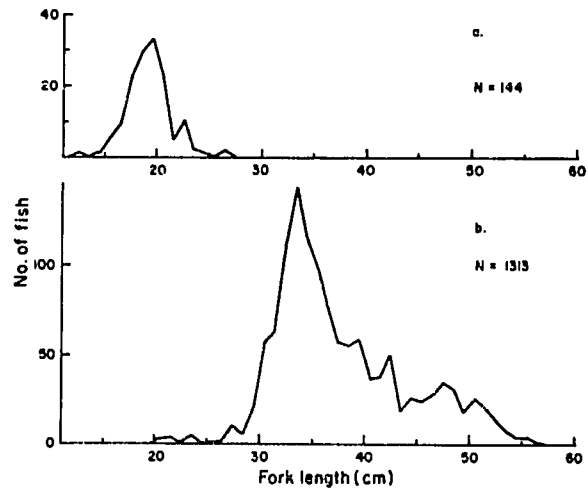


Fig. 9.8. Length-frequency distributions of *Ocyurus chrysurus* captured (a) in traps at the Port Royal Reefs and (b) on lines at Pedro Bank.

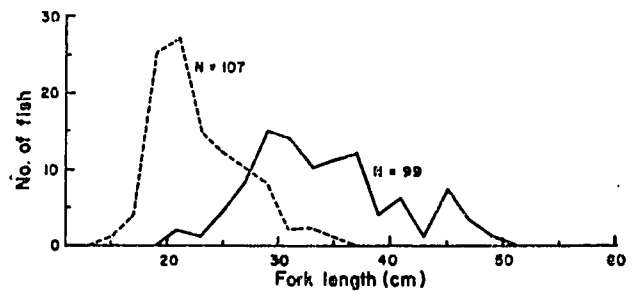


Fig. 9.9. Comparison of length-frequency distribution of trap catches of *Lutjanus apodus* at the Port Royal Reefs (broken line) and trap and line catches at Pedro Bank (solid line).

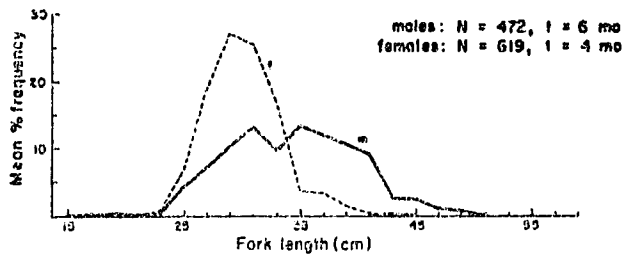


Fig. 9.10. Estimated mean annual length-frequency distributions of line catches of male (m) and female (f) *Lutjanus buccanella* at unexploited parts of Pedro Bank.

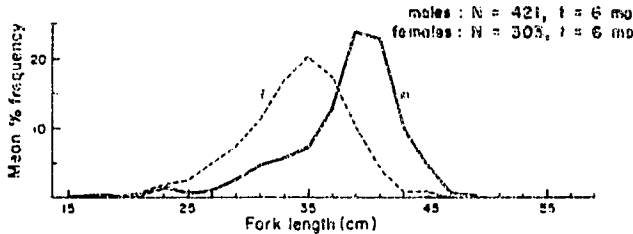


Fig. 9.11. Estimated mean annual length-frequency distributions of line catches of male (m) and female (f) *Apsilus deniatus* at unexploited parts of Pedro Bank.

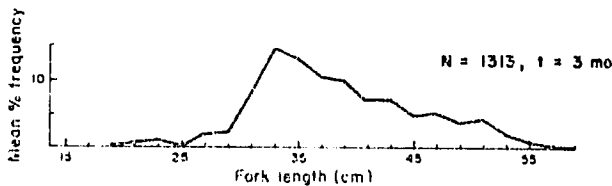


Fig. 9.12. Estimated mean annual length-frequency distributions of line catches of *Ocyurus chrysurus* at unexploited parts of Pedro Bank.

Figure 9.12 shows that *O. chrysurus* (males and females) are fully recruited at 32.0 to 33.9 cm FL. The mean recruitment length is 31.0 cm FL.

The samples of 288 male and 191 female *L. vivanus* taken on lines at Pedro Bank showed rather irregular, polymodal, gross length frequency distributions (Fig. 9.13). The distributions appear to have been strongly influenced by hook selection factors, but the species appears to be fully recruited to the smallest hook size (Mustad 5/0 straight and circle hooks) used in the deep-reef zone at 28.0 to 31.9 cm FL.

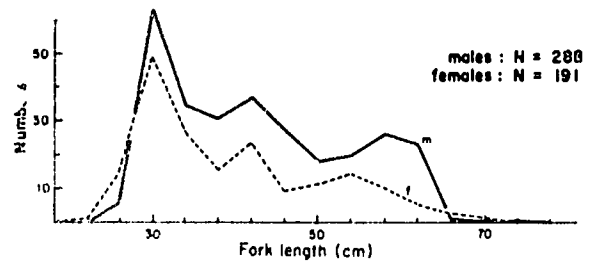


Fig. 9.13. Gross length-frequency distributions of samples of male and female *Lutjanus vivanus* taken on lines at unexploited parts of Pedro Bank.

Table 9.14 summarizes the data on the size composition of the less commonly caught species. Three *L. jocu* collected from Pedro Bank had fork lengths of 72.3, 65.5 and 32.5 cm. The average length of this species at the Port Royal Reefs was 30 cm. Three *Etelis oculatus* measured 24.3, 30.7 and 50.0 cm FL.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

There is no direct evidence concerning the causes of mortality in adolescent or adult snappers. They presumably fall prey to sharks, groupers and barracuda. No very heavy infestations of parasites have been noted. In nearshore Jamaican waters, line and trap fishing and beach seines take a heavy toll of adolescents and small adults. A fairly intensive hand-line fishery is conducted along the margins of the island shelf.

Mortality Rates

Catch rates of snappers in areas presently subjected to exploitation were usually negligible and consequently did not provide samples of sufficient size to enable mortality estimates to be made.

There are no data on the age composition of catches from Pedro Bank or elsewhere, and mortality rates of the commonest species have been derived from length-frequency distributions (see Chapter 3 for details).

Table 9.14. Size composition of the less abundant snapper species caught in Jamaican waters. All lengths are FL in cm and C indicates that data for the sexes are combined.

Species	Area	Gear	Sex	No. of measurements	Smallest	Largest	Average
<i>Lutjanus mahogoni</i>	Port Royal Reefs	Traps	C	22	18	25	21.8
<i>L. griseus</i>	Port Royal Reefs	Traps	C	8	20	45	26.5
<i>L. jocu</i>	Port Royal Reefs	Traps	C	26	16	70	30.0
<i>L. analis</i>	Port Royal Reefs	Traps	C	7	23	60	38.6
<i>L. synagris</i>	Port Royal Reefs	Traps	C	39	16	31	20.4
<i>Pristipomoides macrophthalmus</i>	Pedro Bank	Lines	M	13	15	35	25.4
			F	20	17	34	27.0

Table 9.15. Relative abundances of successive length groups of fully recruited male and female *Lutjanus buccanella* in 60 to 250 m at unexploited parts of Pedro Bank and computations of mortality rates.

Length group (FL, cm)	Males		Females	
	% frequency in catch	Relative abundance	% frequency in catch	Relative abundance
28.0-29.9	10.5	-	27.1	1.00
30.0-31.9	13.2	-	25.4	.94
32.0-33.9	9.9	-	11.4	.42
34.0-35.9	13.6	1.00	3.6	.13
36.0-37.9	12.0	.88	3.5	.13
38.0-39.9	10.7	.79	1.7	.06
40.0-41.9	9.2	.68	.2	.01
42.0-43.9	2.8	.21	.6	.02
44.0-45.9	2.6	.19	0	0
46.0-47.9	1.2	.09		
48.0-49.9	.8	.06		
50.0-51.9	0	0		
52.0-53.9	.2	.01		
54.0-55.9	0	0		
Mean length of recruited stock	38.76 cm		30.89 cm	
	If $L_{\infty} = 54$ cm		If $L_{\infty} = 46$ cm	
	$Z/K = \frac{54.0 - 38.76}{38.76 - 34.0}$		$Z/K = \frac{46.0 - 30.89}{30.89 - 28.0}$	
	= 3.20		= 5.23	
	If $K = 0.70$		If $K = 0.35$	
	$Z = 2.24 = M$		$M = 1.83 = M$	

Table 9.16. Relative abundances of successive length groups of fully recruited male and female *Apsilus dentatus* in 45 to 100 m at unexploited parts of Pedro Bank and computations of mortality rates.

Length group (FL, cm)	Males		Females	
	% frequency in catch	Relative abundance	% frequency in catch	Relative abundance
44.0-44.9	3.80	-	10.40	1.00
45.0-45.9	3.35	-	10.10	.97
46.0-46.9	4.45	-	7.20	.69
47.0-47.9	8.30	-	10.35	.99
48.0-48.9	12.55	-	5.70	.55
49.0-49.9	11.45	-	3.95	.38
50.0-50.9	12.55	1.00	1.75	.17
51.0-51.9	10.50	.84	2.70	.26
52.0-52.9	5.25	.42	.75	.07
53.0-53.9	4.75	.38	.25	.02
54.0-54.9	4.25	.34	1.00	.10
55.0-55.9	.65	.05	0	0
56.0-56.9	.65	.05		
57.0-57.9	0	0		
Mean length of recruited stock	52.04 cm		47.19 cm	
	If $L_{\infty} = 58$ cm		If $L_{\infty} = 56$ cm	
	$Z/K = \frac{58.0 - 52.04}{52.04 - 50.0}$		$Z/K = \frac{56.0 - 47.19}{47.19 - 44.0}$	
	= 2.92		= 2.76	
	If $K = 0.65$		If $K = 0.30$	
	$Z = 1.90 = M$		$Z = 0.83 = M$	

Tables 9.15 to 9.17 show the relative rates of decline in abundance of successive length groups in catches of *Lutjanus buccanella*, *Apsilus dentatus* and *Ocyurus chrysurus* from unexploited parts of Pedro Bank, together with calculations of values of M/K and M . The estimated values of M/K are high in all cases and the estimates of M correspondingly high.

ABUNDANCE AND DENSITY

Catches of lutjanids in all the areas investigated were too sparse or too sporadic to show any consistent seasonal variations in availability to the fishing gears; but as a general case, it appears that availability might be reduced in the mid-summer months.

Relative Abundance

There is no information on the absolute abundance or

population density of any of the species of snappers. Relative abundance can be expressed in terms of catch rates on lines or in traps, and the available data are summarized in Tables 9.18 to 9.20.

The trap-catch rates are very low and represent insignificant proportions of the total catch in all areas. However, the relative catchability of snappers on lines appear to be much greater and lutjanids predominate in line catches in most depth zones (see also Chapter 4).

On the sill reefs and shelf areas, including the Port Royal Reefs, the trap-catch rates of *Ocyurus chrysurus* and *Lutjanus apodus* far exceed those of all other lutjanids (Tables 9.19 and 9.20). Catches of *L. buccanella* in traps on the sill reefs and shelf-edges are sometimes numerically fairly large (Table 9.18), but comprised entirely small, immature fishes.

Catch rates of *L. vivanus*, *L. buccanella* and *A. dentatus* on hook and line in the deep-reef zones (61 to 250 m) are relatively great (Table 9.19), but the actual extent of the deep-reef habitat is very small compared to the shelf areas.

Table 9.17. Relative abundances of successive length groups of fully recruited *Ocyurus chrysurus* in 10 to 60 m at unexploited parts of Pedro Bank and computation of the mortality rate.

Length group (FL, cm)	% frequency in catch	Relative abundance
32.0-33.9	14.75	1.000
34.0-35.9	13.16	.892
36.0-37.9	10.53	.714
38.0-39.9	9.83	.666
40.0-41.9	7.18	.487
42.0-43.9	7.10	.481
44.0-45.9	4.73	.321
46.0-47.9	5.23	.355
48.0-49.9	3.80	.258
50.0-51.9	4.23	.287
52.0-53.9	2.03	.138
54.0-55.9	.93	.063
56.0-57.9	.08	.005
58.0-59.9	0	0
Mean length of recruited stock	40.01 cm	
	If $L_{\infty} = 60$ cm	
	$Z/K = \frac{60.0 - 40.01}{40.01 - 32.0}$	
	= 2.495	
	If $K = 0.25$	
	$Z = 0.62 = M$	

NATALITY AND RECRUITMENT

Some species (*Ocyurus chrysurus*, *Lutjanus griseus*, *L. apodus* and *L. synagris*) are known to spend most of their juvenile lives in shallow mangrove and grass flat areas (Starck 1971 and personal observations) and are not recruited to the reef fisheries until a size of 12 to 20

Table 9.18. Catch rates of snappers in baited traps at Pedro Bank and California Bank, expressed as numbers per 1,000 hexagonal trap-days.

	Numbers per 1,000 trap-days			
	<i>Ocyurus chrysurus</i>	<i>Lutjanus buccanella</i>	<i>Lutjanus apodus</i>	<i>Lutjanus jocu</i>
Pedro Cays area	10	0	0	0
Pedro Bank				
Eastern	0	24	16	0
Southern	14	0	7	0
Western	20	10	45	3
California Bank	0	0	3	0

cm FL is reached. Minimum sizes of *O. chrysurus*, *L. synagris*, *L. apodus*, *L. jocu* and *L. mahogoni* caught on the Port Royal Reefs were 12, 16, 13, 16 and 18 cm FL, respectively. *O. chrysurus* and *L. apodus* were fully recruited to the Port Royal trap fishery at fork lengths of 19 and 21 cm, respectively.

Juveniles of slope-dwelling species (*L. buccanella*, *L. vivanus* and *Apsilus dentatus*) are recruited to the Jamaican trap fishery at sizes of 20, 20 and 28 cm FL, respectively. However, as they move down the slope with increasing size to depths at which traps are not normally set, their recruitment is temporary. Nevertheless, it is likely that the trap fishery conducted along the sill reefs and edges of the Jamaican shelf takes a heavy toll of potential recruits to the line fishery for the mature stocks.

These data are unsuitable for estimation of recruitment indices to the fishery or of relative rates of recruitment to different areas.

DYNAMICS OF THE POPULATIONS

The biological and population parameters estimated for the species of lutjanids are summarized in Tables

Table 9.19. Catch rates of snappers in various depth zones at Pedro Bank expressed as numbers per 100 line-hours of fishing effort.

Area Depth zone Effort (line-hours)	Sill reef and shelf edge			"Drop-off"	Deep reef	
	10.1-20 m 310	20.1-30 m 300	30.1-40 m 482	40.1-60 m 158	61-100 m 120	101-250 m 80
<i>Lutjanus buccanella</i>	6	10	15	6	42	16
<i>L. vivanus</i>	+	0	0	20	16	58
<i>L. apodus</i>	1	1	4	9	0	0
<i>L. analis</i>	+	0	0	0	0	0
<i>L. griseus</i>	0	0	0	+	0	0
<i>Apsilus dentatus</i>	0	+	0	4	69	0
<i>Ocyurus chrysurus</i>	36	27	27	13	8	1
<i>Rhomboplites aurorubens</i>	0	0	0	0	1	0
<i>Pristipomoides macropthalmus</i>	0	0	0	0	1	4
<i>Etelis oculatus</i>	0	0	0	0	0	1

Table 9.20. Mean catch rates of snappers in unbaited traps at the Port Royal Reefs (November 1969 to February 1972) expressed as corrected numerical catch from 1,000 traps soaked for 1 day each.

	Mean no. per 1,000 trap-days
<i>Lutjanus mahogoni</i>	3.5
<i>L. synagris</i>	7.1
<i>L. analis</i>	+
<i>L. jocu</i>	3.5
<i>L. apodus</i>	17.7
<i>L. griseus</i>	0.9
<i>Ocyurus chrysurus</i>	20.3

9.21 and 9.22. The estimated values of M/K lie between 2.5 and 3.2, except in the case of female *Lutjanus buccanella* where M/K is estimated to be 5.2. Reference to Beverton and Holt's (1964) tables of yield functions

show that for most species the value of \underline{c} ($= l_r/L_\infty$) which gives the greatest yield per recruit lies between $\underline{c} = 0.38$ and $\underline{c} = 0.52$ when the rate of exploitation is in the range 0.50 to 0.90.

It appears that ecological or behavioral factors (e.g., intra-specific aggression and competition for baited hooks) largely determine the mean recruitment length in the presently unexploited Pedro Bank stocks and that if these stocks were exploited, the "full retention size" (\underline{l}_c) would decrease with increasing rates of exploitation to a point where real gear-selection factors (mesh size relative to body depth and hook size relative to the size of the mouth) determined the lower limit of the size at recruitment.

The stocks of *O. chrysurus* at the nearshore Port Royal Reefs are probably heavily exploited, as the ratio l_r/L_∞ is only 0.30; a value which would only approximate to that giving the eumetric yield if the rate of exploitation was 0.20. The actual rate of exploitation is unknown, but undoubtedly exceeds 0.20. It is very likely that the same situation prevails among all other species of snappers inhabiting the nearshore reefs.

Table 9.21. Summary of estimated biological parameters of species of lutjanids in Jamaican waters. Values given in brackets are approximations.

		L_∞ cm, FL	W_∞ g	K	M	M/K	lm cm, FL	lm/L
<i>Lutjanus buccanella</i>	males	54	?	.70	2.2	3.2	25-27	0.46-0.50
	females	46	?	.35	1.8	5.2	23-25	0.50-0.54
<i>L. vivanus</i>	males	(70)	?	?	?	?	55-60	(0.78-0.86)
	females	(70)	?	?	?	?	50-55	(0.71-0.78)
<i>Apsilus dentatus</i>	males	58	?	.65	1.9	2.9	43-45	0.74-0.78
	females	56	?	.30	0.8	2.8	39-41	0.70-0.73
<i>Ocyurus chrysurus</i>	males	60	3,600	0.25	0.6	2.5	(26)	0.43
	females	60	3,600	0.25	0.6	2.5	29-31	0.48-0.52
<i>Lutjanus apodus</i>	males & females	(57)	3,800	(0.18)	?	?	(25)	(0.44)

Table 9.22. Sizes of snappers at first, mean and full recruitment to various fishing gears at Pedro Bank and the Port Royal Reefs. Values marked with an asterisk are calculated values, all others are observed. Asymptotic lengths of *Lutjanus vivanus* and *L. apodus* are approximations based on known maximum sizes.

		Depth	Gear	Sex	Fork lengths (cm)				
					l_1	l_r	l_c	L_∞	l_r/L_∞
<i>Lutjanus buccanella</i>	Pedro Bank	60-250 m	5/0-6/0 hooks	M	20.5	28	31	54	.52
				F	22.5	28	29	46	.61
<i>L. vivanus</i>	Pedro Bank	60-250 m	5/0-6/0 hooks	M & F	22	26	30	(70)	(.37)
<i>Apsilus dentatus</i>	Pedro Bank	60-100	5/0-6/0 hooks	M	29	45.5	49	58	.78
				F	29	41.5	45	56	.74
<i>Ocyurus chrysurus</i>	Pedro Bank	10-45 m	3/0-4/0 hooks	M & F	20	31	33	60	.52
	Port Royal Reefs	7-15 m	traps-4.13 cm mesh	M & F	14*	18	19.5	60	.30
<i>Lutjanus apodus</i>	Pedro Bank	10-45 m	3/0 and 4/0 hooks	M & F	20	27	29	(57)	(.47)
	Port Royal Reefs	7-15 m	traps-4.13 cm mesh	M & F	14*	19.5	21	(57)	(.34)

**CHAPTER 10:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE GRUNTS, POMADASYIDAE**

by
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(July 1974)

Identity

The Pomadasyidae are unspecialized perciform fishes. The general characteristics are similar to those of the snappers (Lutjanidae) from which they differ primarily in dentition (Randall 1968). They have a world-wide tropical and sub-tropical distribution.

Morphological details of the western Atlantic species are given by Bohlke and Chaplin (1968), Randall (1968) and Jordan and Evermann (1898). There are no reports of hybridization between any species of grunts although many species are morphologically very similar and almost indistinguishable in the pre-adult stages.

Six genera occur in the western Atlantic: *Haemulon* Cuvier, and *Anisotremus* Gill, all species of which are associated with coral reefs; and *Orthopristis* Girard, *Conodon* Cuvier and Valenciennes, *Pomadasy* Lacepede and *Genyatremus* Gill which are more characteristic of mud and sandy areas. This report is concerned only with Atlantic species of the genera *Haemulon* and *Anisotremus*.

The 16 species of *Haemulon* and *Anisotremus* that occur in the western Atlantic, as classified by Courtenay (1961, 1965) and Randall (1968), are listed in Table 10.1.

*A substantial portion of this report is derived from a thesis submitted to the University of the West Indies by V.C. Gaut for the degree of Master of Science. The thesis was based upon data collected by the Fisheries Ecology Research Project up to May 1972. The sections on sexuality, population structure, mortality and recruitment have been prepared by J. Munro, and incorporate all data collected by the project between November 1969 and March 1973.

Arnov (1952) studied the systematics of the genus *Haemulon* and Courtenay (1961) revised the systematics and described juvenile pigmentation. Courtenay described 13 species of *Haemulon* in the western Atlantic and he included in this genus two species which had previously been ascribed to *Bathystoma* Scudder (*H. aurolineatum*

Table 10.1. Scientific and common names of grunts caught in Jamaican waters.

Scientific names	Common names
1. <i>Haemulon plumieri</i> (Lacepede) 1802	White grunt
2. <i>H. album</i> Cuvier and Valenciennes 1830	Margate
3. <i>H. sciurus</i> (Shaw) 1830	Blue striped grunt
4. <i>H. flavolineatum</i> (Desmarest) 1823	French grunt
5. <i>H. aurolineatum</i> Cuvier and Valenciennes 1830	Tomtate
6. <i>H. bonariense</i> Cuvier and Valenciennes 1830	Black grunt
7. <i>H. macrostomum</i> (Gunther) 1859	Spanish grunt
8. <i>H. melanurum</i> (Linnaeus) 1758	Cottonwick
9. <i>H. carbonarium</i> (Poey) 1860	Caesar grunt
10. <i>H. chrysargyreum</i> Gunther 1859	Small mouth grunt
11. <i>H. striatum</i> (Linnaeus) 1758	Striped grunt
12. <i>H. parrai</i> (Desmarest) 1823	Sailor's choice
13. <i>H. steindachneri</i> (Jordan and Gülbart) 1882	'tin grunt
14. <i>H. boschmae</i> (Metzelaar) 1919	Bronze-striped grunt
15. <i>Anisotremus virginicus</i> (Linnaeus) 1758	Porkfish
16. <i>A. surinamensis</i> (Bloch) 1791	Black margate

and *H. striatum*), and one previously ascribed to *Brachygenys* Scudder (*H. chrysargyreum*). Courtenay (1965) re-described *H. boschmae*, a species from the north coast of South America, previously known as *Pristipoma boschmae* Metzelaar, or *Isaciops facis* Miles. Ginsburg (1948) described three sub-species of *Bathystoma*

aurolineatum.

The genus *Anisotremus* has not been as well documented. Two species occur in the Caribbean and these have been classified and described by Jordan and Evermann (1898).

Distribution

DISTRIBUTION OF THE GENERA *HAEMULON* AND *ANISOTREMUS*

The genera *Haemulon* and *Anisotremus* both have a tropical and sub-tropical distribution in the western Atlantic and the eastern Pacific. The genus *Haemulon* is represented by 16 species, 13 of which occur exclusively in the Caribbean and adjacent regions. In addition, two species occur on the Pacific coast of Central America, and one species, *H. steindachneri*, occurs both in the Pacific and in the Caribbean (Courtenay 1961).

The genus *Anisotremus* is represented by six species in the Pacific and two in the western Atlantic (Jordan and Evermann 1898); however, the Caribbean species, *A. surinamensis*, may also occur in the Pacific. *A. virginicus*, which occurs in the Caribbean, may have a "twin" species in the Pacific species, *A. taeniatus*, (Jordan and Evermann 1898), and the Caribbean species *H. parrai* may also have a "twin" in the Pacific species, *H. schudderi*, (Ekman 1967). According to Ekman (1967), this phenomenon is seen in many marine animals, resulting from the appearance of the Central American isthmus during the late Pliocene. Isolation of the two identical faunas allowed divergent evolution of the species on either side, and this has given rise to twin species.

Distribution of western Atlantic Species of *Haemulon* and *Anisotremus*

The majority of species range from Bermuda, the Bahamas, the Florida Cays and the southern Gulf of Mexico, through the West Indies, Central America and the north coast of South America to the northern coast of Brazil. According to Courtenay (1961), the most northerly record is of *H. aurolineatum* from Cape Cod (41°N), and *H. plumieri* and *H. sciurus* are reported to move northwards in the summer months. The southernmost record is of *H. bonariense* from Buenos Aires (Courtenay 1961).

Pomadasyids have a wide distribution range but the relative abundance of the species varies from region to region. *H. boschmae* has only been recorded from the north coast of South America (Courtenay 1965). It is apparently the species with the most restricted distribution. *H. steindachneri* is most common in the continental waters of Central America, northern South America and Brazil (Courtenay 1961). *H. bonariense* has not been recorded from the Florida Cays or the Bahamas (Bohlke and Chaplin 1968), although it has been recorded in Bermuda (Beebe and Tee-Van 1933). It is common in the West Indies and along the north coast of South

America. *H. parrai*, though common on the Florida Cays and in the Bahamas (Bohlke and Chaplin 1968), has rarely been seen in Jamaica. Of the species recorded in Bermuda, *A. virginicus*, *H. plumieri* and *H. macrostomum* have been introduced (Beebe and Tee-Van 1933), but there are no recent records to indicate the results of these introductions.

Distribution in Jamaican Waters

Thirteen species of *Haemulon* and two of *Anisotremus* have been recorded from Jamaican waters (Caldwell 1966). *H. boschmae* has not been recorded, and *H. steindachneri*, which is more common in continental waters, was recorded once by Caldwell (1966), but was not found during these investigations. *H. parrai* does occur in Jamaican waters, but it was found to be uncommon on the Port Royal Reefs.

Despite the proximity of Pedro Bank and the Jamaican south coast shelf, our data show differences in the pomadasyid species present at the Port Royal Reefs and those at Pedro Bank (Table 10.2). This may be partly explained by differences in hydrographic conditions since *H. album*, *H. melanurum* and *H. striatum* all show a preference for clear, open water (Courtenay 1961).

Table 10.2. Pomadasyid species taken at the Port Royal Reefs and at Pedro Bank.

Species	Port Royal Reefs	Pedro Bank
<i>H. sciurus</i>	X	
<i>H. bonariense</i>	X	
<i>H. macrostomum</i>	X	
<i>A. virginicus</i>	X	
<i>A. surinamensis</i>	X	
<i>H. parrai</i>	(uncommon)	
<i>H. plumieri</i>	X	X
<i>H. aurolineatum</i>	X	X
<i>H. flavolineatum</i>	X	X
<i>H. carbonarium</i>	X	X
<i>H. chrysargyreum</i>	X	X
<i>H. album</i>	(uncommon)	X
<i>H. melanurum</i>		X
<i>H. striatum</i>		X

Natural Characteristics of Regions of Distribution

The geographical range of *Haemulon* and *Anisotremus* species corresponds largely with the range of coral reefs which extend from Florida, the Bahamas and Bermuda to Brazil. Few species have been recorded outside these limits.

Distribution of Life Stages

Pomadasyid eggs and larvae are probably pelagic, their dispersal being dependent upon the direction and speed of flow of currents in the area. Settlement takes place in shallow water, and the young of many species school on nursery grounds, such as shallow back-reef areas or grass beds, until reaching maturity when they

join the adult schools. The adults of most species of *Haemulon* and *Anisotremus* are typically found schooling on coral reefs by day and feeding in adjacent areas by night. Table 10.3 gives the characteristic diurnal and nocturnal habitats (Starck and Davis 1966; Randall 1968) of the adults of the 16 western Atlantic pomadasyid species.

Table 10.3. Characteristic diurnal and nocturnal habitats of the adults of pomadasyid species that occur on Caribbean coral reefs (from Starck and Davis 1966; Randall 1968; and underwater observations made during this study).

Species	Diurnal habitat	Nocturnal habitat
<i>H. sciurus</i>	Schooling shallow among <i>Acropora palmata</i> , commonly about 7 m on sea-ward side of reef crest; round coral stacks and patch reefs; sill reef.	Sand and rubble, grass or rocky substrate; among alcyonarians and sponges; found deeper on reef than by day.
<i>H. melanurum</i>	Schooling near coral outcrops.	Probably feeding over reef flats.
<i>H. steindachneri</i>	Coral, sand or rocky substrate, also sometimes over mud, extending from shallow inshore waters down to 60 m or more.	
<i>H. parrai</i>	Schooling in open areas of rubble and rock near coral stacks, extending from shore to edge of deep water.	Sandy bottom near schooling areas.
<i>H. flavolineatum</i>	Schooling close to coral, especially <i>A. palmata</i> and <i>A. cervicornis</i> , from reef crest to sill reef; schools commonly shallow, from 1 to 10 m.	Sandy back-reef areas.
<i>H. carbonarium</i>	Schooling shallow under <i>A. palmata</i> , and other corals with strong relief; observed near to beds of brown algae close to shore. Reported to enter tidal creeks.	Feeding over areas of rock and rubble or coral.
<i>H. album</i>	Young adults school in rocky areas near alcyonarian and sponges. Large adults do not school, but swim over sandy and mixed bottoms.	Feeding over sand flats and mixed bottoms (corals, alcyonarians, sponges).
<i>H. bonariense</i>	Silty bottom near reef base and mixed coral zone, also rocky areas; sometimes enter mangroves.	Probably feeding on adjacent grass or mud flats.
<i>H. macrostomum</i>	Schooling on reef tops; or solitary in caves and under ledges.	Dispersed over areas adjacent to reef, including mud flats.
<i>H. plumieri</i>	From reef crest to sill reef and top of drop off, often solitary or in small groups. Schools near gorgonians and sponges, also over flat rocky bottom.	Grass flats and rubble.
<i>H. aurolineatum</i>	Reef crest to sill reef, schooling near coral, or in small groups among, e.g., <i>A. cervicornis</i> .	Sandy back reef areas, also down to 45 m on muddy bottom.
<i>H. chrysargyreum</i>	Reef crest, particularly seaward side, schooling among <i>A. palmata</i> and <i>A. cervicornis</i> ; also inshore rocky areas.	Back-reef zone, also shallow rocky bottom with gorgonians and scattered <i>A. palmata</i> .
<i>H. striatum</i>	Schooling on drop-off slope in 20 to 30 m, active schools above <i>Agaricia</i> and <i>Monastrea</i> sp.	Probably similar to daytime habitat.
<i>H. boschmae</i>	Deep water down to 100 m, but common shallow near rocks and coral, often close to shore.	
<i>A. virginicus</i>	Coral stacks and rocky areas, also <i>A. cervicornis</i> ; reported near mangroves.	Rubble with alcyonarians.
<i>A. surinamensis</i>	Schooling on sloping rocky shores, near coral stacks, in caves, or frequently solitary; from 10 m to sill reef and drop-off slope.	Feeding in rocky areas.

Bionomics and Life History

REPRODUCTION

Gonads

The gonads of pomadasyids are paired elongate organs lying against the dorsal wall of the body cavity adjacent to the swim bladder. From an early age, testis and ovary are readily distinguishable macroscopically, the testis being angular in cross-section and opaque, while the ovary is rounded and more translucent. As they mature, the testis turns white and the ovary pink-brown. Before ovulation, the ripe eggs are spherical, with a diameter of about 0.5 mm (measured for *H. plumieri*, *H. aurolineatum* and *H. bonariense*), opaque, colored white, yellow or pink, and negatively buoyant in water.

Ripe ovaries of most species were frequently found to contain eggs of two distinct size ranges: large ripe ova ready for ovulation and minute resting stages, which would probably develop into ova in a subsequent breeding season. This suggests that two or more spawning seasons may occur each year for some species, while others may spawn more or less continuously throughout the year. Ripe ovaries were collected from several species, and Table 10.9 gives the ovary weights of five species together with ovary weight as a percentage of the total body weight.

Sexuality

Body shape and coloration are identical in the males and females of all the pomadasyid species studied, but there is evidence of sexual dimorphism in the growth rates of some species in which the males have been found to be larger than the females.

There is no evidence to suggest either hermaphroditism or sex reversal in any of the species studied.

Maturity

Tables 10.4 to 10.7 show the proportions of ripe male and female *Haemulon plumieri*, *H. flavolineatum*, *H. sciurus* and *H. album* found in successive length groups.

H. plumieri males appear to be fully mature at 24.0 to 25.9 cm FL and the mean size at maturity, l_m , is about 20 cm FL. Females appear to become mature at a slightly larger size (26.0 to 27.9 cm FL) and the mean size at maturity is about 22 cm FL (Table 10.4).

A substantial proportion of the smallest length groups of *H. flavolineatum* captured were mature and it is likely that individuals might often mature at lengths of 12 cm FL or less (Table 10.5). The proportion of mature fishes reached a maximum within the 17 to 19 cm FL range and it is likely that the mean size at maturity is around 15.5 cm FL.

The sample of *H. sciurus* was rather small (Table 10.6), but it appears that few fishes mature before 18

cm FL and that full maturity is probably at about 22 cm FL.

H. album (Table 10.7) becomes fully mature at 26.0 to 27.9 cm FL. The mean size at maturity is about 24 cm FL.

The lengths and weights of the smallest ripe males and females of 13 species recorded during the investigations are given in Table 10.8. With the exception of *H. aurolineatum* and *H. flavolineatum*, the lengths at first maturity of all species are much greater than the length at first recruitment to traps with 4.13 cm mesh (see Table 10.30). At high rates of exploitation, most pomadasyids will be captured by the fishery before attaining maturity.

Table 10.4. Percentages of mature fishes and comparison of length-frequency distributions of male and female *Haemulon plumieri* in Jamaican waters. Percentages in brackets are based on samples of fewer than 20 fishes.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
12.0-13.9	12	(0)	27	0
14.0-15.9	85	4	171	4
16.0-17.9	153	8	161	4
18.0-19.9	124	22	136	17
20.0-21.9	100	27	137	34
22.0-23.9	66	28	123	41
24.0-25.9	67	55	140	56
26.0-27.9	50	38	180	82
28.0-29.9	82	32	188	77
30.0-31.9	114	45	61	67
32.0-33.9	30	47	12	(75)
34.0-35.9	3	(33)	1	(100)
36.0-37.9	2	(50)	2	(100)
38.0-39.9	0	—	0	—
Totals	888		1,339	

Fecundity

Fecundity, defined as the number of eggs spawned by a female in a single breeding season, can be estimated by counting the number of eggs in a ripe ovary prior to spawning. Estimation of annual fecundity is difficult for tropical fish species since many have more than one breeding season and some breed continuously throughout the year (Bagenal, in Ricker 1968). Fecundity is proportional to the size of the fish, and from a series of egg counts, the fecundity coefficient for a species can be calculated.

The relationship of fecundity (e) to weight (w) is linear (Bagenal, in Ricker 1968) and is represented by the equation

$$e = b w + a$$

where b is the fecundity coefficient and a is a constant.

Table 10.5. Percentages of mature fishes and comparison of length-frequency distributions of male and female *Haemulon flavolineatum* in Jamaican waters. Percentages in brackets are based on samples of fewer than 20 fishes.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
12.0-12.9	2	(0)	2	(50)
13.0-13.9	9	(22)	9	(11)
14.0-14.9	36	14	46	24
15.0-15.9	54	9	76	28
16.0-16.9	58	10	72	32
17.0-17.9	69	14	75	56
18.0-18.9	56	21	34	50
19.0-19.9	25	32	14	(50)
20.0-20.9	10	(10)	5	(20)
Totals	319		333	

Table 10.6. Percentages of mature fishes and comparison of length-frequency distributions of male and female *Haemulon sciurus* in Jamaican waters. Percentages in brackets are based on samples of fewer than 20 fishes.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
14.0-15.9	7	(0)	8	(13)
16.0-17.9	28	7	17	(0)
18.0-19.9	39	5	26	15
20.0-21.9	56	13	38	13
22.0-23.9	23	26	32	16
24.0-25.9	15	(53)	24	29
26.0-27.9	7	(86)	9	(33)
28.0-29.9	0	—	1	(100)
Total	175		155	

Fecundity estimates were made for seven pomadasiid species but calculation of the fecundity coefficient was only possible for *H. plumieri* and *H. album*. Fig. 10.1 shows fecundity estimates plotted against weight for *H. plumieri* and the slope of the line represents the fecundity coefficient, or the increase in number of eggs per gram of body weight. The fecundity coefficient was calculated to be $b = 607$ and the y axis intercept $a = -93,000$ therefore, for *H. plumieri*, $e = 607w - 93,000$.

From Fig. 10.1 it can be seen that fishes of a similar size showed wide variations in fecundity, and this may partly be explained by the suggestion that ripe ova are spawned in batches.

Although only six fecundity estimates were made for *H. album*, when fecundity was plotted against weight, the distribution of points was such that a straight line could be approximated; and a rough estimate of the

Table 10.7. Percentages of mature fishes and comparison of length-frequency distributions of male and female *Haemulon album* in Jamaican waters. Percentages in brackets are based on samples of fewer than 20 fishes.

Length group cm FL	Males		Females	
	No. examined	% ripe or spent	No. examined	% ripe or spent
20.0-21.9	2	(0)	0	—
22.0-23.9	3	(0)	4	(25)
24.0-25.9	11	(9)	9	(0)
26.0-27.9	18	(17)	15	(27)
28.0-29.9	16	(19)	21	19
30.0-31.9	26	19	24	42
32.0-33.9	38	34	32	38
34.0-35.9	24	29	28	50
36.0-37.9	13	(54)	19	(58)
38.0-39.9	17	(59)	15	(67)
40.0-41.9	8	(50)	4	(100)
42.0-43.9	4	(0)	2	(100)
44.0-45.9	7	(57)	1	(0)
46.0-47.9	1	(0)	4	(75)
48.0-49.9	1	(0)	1	(100)
50.0-51.9	6	(50)	8	(75)
Total	195		187	

Table 10.8. Length and weight of smallest ripe males and females of 13 pomadasiid species caught by the Project in traps (4.13 cm mesh width) and on lines.

Species	Male		Female	
	Length (cm)	Weight (g)	Length (cm)	Weight (g)
<i>H. plumieri</i>	14.5	60	14.3	59
<i>H. sciurus</i>	17.0	96	15.8	78
<i>H. flavolineatum</i>	13.5	50	12.7	39
<i>H. aurolineatum</i>	14.7	55	13.0	34
<i>H. bonariense</i>	17.3	89	17.1	87
<i>H. macrostomum</i>	22.7	252	28.0	477
<i>H. carbonarium</i>	18.2	131	19.0	145
<i>H. album</i>	24.5	263	23.0	217
<i>H. melanurum</i>	20.4	147	19.0	129
<i>H. chrysargyreum</i>	15.3	63	17.2	75
<i>H. striatum</i>			15.0	
<i>A. virginicus</i>			18.0	167
<i>A. surinamensis</i>	22.9	276	23.7	356

fecundity coefficient was $b = 220$ and the y-axis intercept was zero: therefore, for *H. album*, $e = 220w$.

For the samples of the other species studied (with the exception of *H. chrysargyreum* of which only one individual was studied), the mean fecundity values were calculated and are given in Table 10.10. For all seven species, the highest fecundity values observed in the samples are listed in Table 10.11.

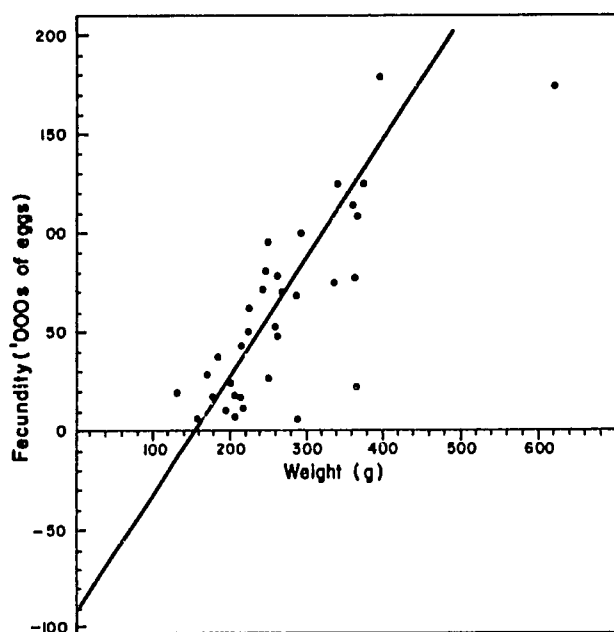


Fig. 10.1. *H. plumieri*: relationship of fecundity (e) to weight (w) in g. Slope of the line = 607; Y axis intercept = -93,000; therefore, $e = 607 w - 93,000$.

Table 10.9. Mean ripe ovary weight as a percentage of mean body weight of five pomadasyd species.

Species	Sample size (n)	Mean body weight (g)	Mean ovary weight (g)	Mean % body weight
<i>H. plumieri</i>				
158-250 g	12	209	3.96	1.82
251-388 g	13	326	10.20	2.88
<i>H. album</i>	8	1,764	44.40	2.57
<i>H. flavolineatum</i>	4	114	3.15	2.72
<i>H. aurolineatum</i>	7	91	3.73	4.07
<i>H. sciurus</i>	6	283	4.29	1.27

Mating and Fertilization

There are no records of mating behavior having been observed in any pomadasyids. However, Moe (1966) observed aggregations of *H. plumieri* in spawning condition in a shallow area of patch reefs off Florida, and it seems likely that several species collect in large numbers on spawning grounds in the breeding season. Probably, pairing of males and females does not take place and fertilization occurs externally when eggs and sperms are liberated into the water simultaneously.

Spawning Seasons

Observations on the spawning seasons of Caribbean reef fishes collected up to June 1972 were reported by Munro et al. (1973) and additional data collected up to March 1973 are included here. Tables 10.12 to 10.16 show monthly variations in the proportions of inactive,

Table 10.10. Mean fecundity of samples of four pomadasyd species.

Species	Sample size (n)	Mean length of sample (cm)	Mean weight of sample (g)	Fecundity of sample
<i>H. flavolineatum</i>	9	16.9	109	31,000
<i>H. aurolineatum</i>	13	15.4	69	30,000
<i>H. sciurus</i>	3	24.2	283	32,000
<i>H. bonariense</i>	4	19.2	116	22,000

Table 10.11. Greatest fecundities observed in specimens of seven pomadasyd species; also length, weight and ovary weight of the individuals.

Species	Length (cm)	Weight (g)	Ovary weight (g)	Number of eggs
<i>H. flavolineatum</i>	18.0	127	4.4	48,000
<i>H. aurolineatum</i>	18.1	135	7.5	83,000
<i>H. sciurus</i>	23.2	268	4.1	42,000
<i>H. bonariense</i>	18.0	102	—	31,000
<i>H. chrysargyreum</i>	15.7	81	—	35,000
<i>H. plumieri</i>	27.3	388	19.2	179,000
<i>H. album</i>	54.4	3,045	75.0	602,000

Table 10.12. Monthly percentages of inactive (I), active (A), ripe (R) and spent (S) gonads in samples of mature *Haemulon plumieri* in Jamaican waters.

Month	Number examined	Percentage			
		I	A	R	S
January	157	38	18	38	6
February	176	31	29	34	8
March	120	28	38	25	9
April	275	7	8	47	38
May	222	33	35	21	11
June	163	55	34	4	7
July	155	52	32	11	5
August	147	51	27	19	3
September	174	72	13	5	10
October	199	56	11	22	11
November	262	39	22	22	17
December	217	58	26	9	4
Total	2,267				

active, ripe and spent fishes recorded for five species, and Table 10.17 gives data for a further seven species. For all species, data collected from all localities between September 1967 and March 1973 have been combined on a monthly or bimonthly basis.

Table 10.13. Bimonthly percentages of inactive (I), active (A), ripe (R) and spent (S) gonads in samples of mature *Haemulon sciurus* in Jamaican waters.

Months	Number examined	Percentage			
		I	A	R	S
January-February	67	8	58	30	5
March-April	45	31	44	20	4
May-June	38	74	21	3	3
July-August	56	55	30	0	14
September-October	61	77	15	2	7
November-December	67	36	51	10	3
Total	334				

Table 10.14. Monthly percentages of inactive (I), active (A), ripe (R) and spent (S) gonads in samples of mature *Haemulon flavolineatum* in Jamaican waters.

Month	Number examined	Percentage			
		I	A	R	S
January	24	54	21	25	0
February	193	49	31	21	0
March	72	28	38	35	0
April	87	46	41	13	0
May	54	11	78	11	0
June	43	23	54	23	0
July	39	54	33	13	0
August	48	10	69	21	0
September	47	30	38	32	0
October	127	37	10	53	0
November	144	96	4	1	0
December	229	37	16	48	0
Total	1,107				

Table 10.15. Bimonthly percentages of inactive (I), active (A), ripe (R) and spent (S) gonads in samples of mature *Haemulon album* in Jamaican waters.

Months	Number examined	Percentage			
		I	A	R	S
January-February	157	5	33	59	3
March-April	38	3	40	42	16
May-June	110	57	29	11	3
July-August	29	31	59	10	0
September-October	59	32	12	46	10
November-December	43	61	26	12	2
Total	436				

Haemulon plumieri (Table 10.12) n = 2,267: The greatest proportions of ripe fishes were found in January through April, with a possible subsidiary peak in October-November, and a minimum of activity in June-July

Table 10.16. Bimonthly percentages of inactive (I), active (A), ripe (R) and spent (S) gonads in samples of mature *Haemulon aurolineatum* in Jamaican waters.

Months	Number examined	Percentage			
		I	A	R	S
January-February	74	50	15	35	0
March-April	31	19	48	29	3
May-June	72	56	11	32	1
July-August	29	21	55	21	3
September-October	63	91	6	3	0
November-December	78	74	10	15	0
Total	347				

and December. The lowest proportions of inactive gonads were observed in April, and over 71% of the gonads observed in September were inactive.

Moe (1966) reported dense aggregations of *H. plumieri* in reef areas off the west coast of Florida in May 1963, and the females were distended with roe. In June, he reported some ripe females and many that were spent, and by July no ripe females were present. In Puerto Rico, Erdman (1956) reported ripe *H. plumieri* in March. However, Cervigon (1966) found no ripe *H. plumieri* in Venezuelan waters between February and May 1961, which is contrary to all other observations, and the difference may be due to location.

Haemulon sciurus (Table 10.13) n = 334: This species showed most breeding activity from November through April, with the lowest proportions of inactive fishes in January and February.

Haemulon flavolineatum (Table 10.14) n = 1,107: High proportions of ripe and active gonads were observed in all months except November, and it appears that breeding of this species probably is continuous at a low level throughout the year. No spent fishes were ever observed. Juveniles and young have been seen at most times of year in Jamaican waters.

Haemulon album (Table 10.15) n = 436: The main breeding season of this species is probably from January through April, with another minor peak in September-October.

In February 1970, catches of *H. album* from S.E. Pedro Bank and Albatross Bank were comprised almost entirely of ripe fishes, whereas catches from Salmon Bank were 70% active and only 30% ripe, indicating that spawning is not necessarily synchronous in different localities.

Haemulon aurolineatum (Table 10.16) n = 347: Most ripe fishes were observed between January and June and the greatest proportions of inactive fishes were observed in September-December. In Puerto Rico, Erdman (1956)

Table 10.17. Monthly summary of gonad data for seven pomacentrid species collected between September 1967 and March 1973, combined for all localities. Gonad stages represented by: I—Inactive; A—Active; R—Ripe; S—Spent.

Species		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>H. bonariense</i> n = 136	I		2			6	3	8	12	4	21	3	2
	A	1	3	2	2	6	1	7	6	1	12		2
	R	1	9	3	2			10	1	1	4		
	S			1									
<i>H. melanurum</i> n = 260	I	1				1			1	5	15		15
	A	1	4		32	9				5	3		
	R	3	48		73	3			1	11	19	1	
	S		6		2					1			
<i>H. macrostomum</i> n = 73	I	1	2	5	3		3	2	6	6	5	5	7
	A	3	1	1	1		5	2	5	2			
	R				3		1	1	1				
	S									1		1	
<i>H. carbonarium</i> n = 19	I						1	2	2				
	A	2				2	1		2	1			
	R		1			1							
	S					2		1					
<i>H. striatum</i> n = 15	I			9									
	A			1								2	1
	R			2									
<i>A. virginicus</i> n = 108	I	6	14		2	22	9	3	6	8	3	13	15
	A					1	1				1		
	R					2							
	S							1				1	
<i>A. surinamensis</i> n = 29	I					2		7	1			2	
	A			2	1	1		3	2				
	R				2	1			1			2	
	S				1						1		

reported ripe specimens in March and Cervigon (1966) stated that this species reproduced throughout most of the year in Venezuelan waters, with a peak in July. In Jamaican waters, juveniles and young were observed at most times of the year.

Haemulon bonariense (Table 10.17) n = 136: Ripe fishes were recorded from January through April and from July through October, with peaks in February and July.

Haemulon melanurum (Table 10.17) n = 260: This species showed a high proportion of ripe fishes in February and April, and 50% were ripe in September and October. The data are fragmentary but suggest a pattern similar to that shown by *H. plumieri*.

Haemulon macrostomum (Table 10.17) n = 73: At the Port Royal reefs, ripe fishes were taken in April, June, July and August. Erdman (1956) observed this species in breeding condition during June and July in Puerto Rican waters.

Haemulon carbonarium (Table 10.17) n = 19: Data were sparse, but two ripe fishes were recorded, one in February the other in May.

Haemulon striatum (Table 10.17) n = 15: Two ripe fishes were taken in March, off the north coast of Jamaica.

Haemulon chrysargyreum n = 4: Four individuals were taken and all were ripe. Three were caught in March and one in December.

Haemulon parrai n = 4: Three individuals taken in July, November and December were all inactive, and one taken in July was a spent male. In Venezuela, Cervigon (1966) observed this species to be inactive in May. He recorded one ripe female in March.

Haemulon steindachneri: This species was not found by the project in Jamaican waters, but in Venezuela, Cervigon (1966) recorded inactive and ripe fishes in June 1961, and active fishes in December 1962.

Anisotremus virginicus (Table 10.17) n = 108: A high proportion of inactive fishes was found at all times of year. Two ripe females were found in May, but no ripe males were found at any time. It seems probably that this species moves away from the Port Royal Reefs to spawn.

Anisotremus surinamensis (Table 10.17) $n = 29$: Ripe fishes were found in April, May, August and November. Cervigon (1966) reported many active and ripe individuals during December 1960, in Venezuelan waters.

With the exception of *H. flavolineatum*, the peak breeding season for most pomadasid species appears to be between January and April, though some species (e.g., *H. plumieri*, *H. album* and *H. sciurus*) may also show a minor peak in September-November. A few ripe individuals of most species were found throughout the year. Samples taken at the Port Royal Reefs and offshore banks all followed this basic pattern.

For several species, a higher proportion of ripe fishes was recorded in 1970 than in 1971, and in 1972 higher than in 1971. This suggests that varying proportions of the population may breed each year, or that movements of the spawning population might vary from year to year.

It is not known how many times the females of any pomadasid species spawn in one year. However, the fact that there is a definite peak spawning season for several species suggests that the majority of the females of these species spawn once a year. Some species show a minor secondary spawning peak. Several show a low level of spawning activity throughout the year, and for these species it seems likely that spawning occurs more than once a year. Gonad studies showed that ripe ovaries of some species frequently contained minute resting eggs as well as the ripe ova. This suggests that a second spawning might be a common occurrence.

Factors Affecting Spawning

The surface water temperature off the Jamaican south coast varies from about 26.5°C in March to 29.5°C in September, October and November (Beers, Stevens and Lewis 1968), and Munro et al. (1973) suggested that spawning was initiated when the water temperature dropped to 28°C. The peak of spawning activity was attained when temperature was at a minimum, and from June to December when water temperature exceeded 28°C, few fishes were found in breeding condition.

Beers et al. (1968) found that peaks in primary production occurred in May or June with a minor bloom in October or November. Therefore, reef-fish spawning peaks apparently precede blooms in plankton productivity.

Spawn

Ovaries in spawning condition (stage VI) were rarely observed for the pomadasids, and it is probable that ovulation takes place shortly before spawning. At ovulation, the eggs increase in size and become transparent. Ovaries of *H. plumieri* and *H. sciurus* in spawning condition were studied, and in each case, only a portion of the ripe eggs had been ovulated which indicated that

not all the eggs were spawning simultaneously, but in batches over a period of time.

The spawn of *H. sciurus* measured 0.92 to 0.93 mm or nearly twice the diameter of the pre-ovulatory eggs. The spawn was spherical, transparent, non-adhesive, with a slight negative buoyancy in sea water. Each egg contained one oil droplet floating uppermost measuring about 0.18 mm in diameter.

The spawn of *H. plumieri* was approximately 1.0 mm in diameter. Many of the eggs were distorted and flaccid; possibly, these had remained in the ovary lumen after a recent spawning.

PRE-ADULT PHASE

Planktonic Phase

The transparency of pomadasid spawn suggests that the eggs are pelagic (Breder 1962), but there are no records of pomadasid eggs being identified from the plankton, and there is no information about the period of embryonic development before hatching.

Pomadasid larvae, measuring 5.0 to 7.0 mm (total length) were recorded in plankton hauls off Cuba (Guitart Manday 1971). The larvae were collected by night between the surface and a depth of 50 m, but daytime sampling at the same depths yielded none.

The duration of the planktonic phase is not known, but eggs and larvae must be carried by currents, and in the Caribbean with scattered islands and banks, losses may be high as a result of failure to reach a settlement area. The presence of pomadasids in Bermuda indicates either a long larval life, or the ability to extend planktonic existence if no settlement area is encountered. Original recruitment of the Bermuda fish populations must have been from the Caribbean, the Bahamas, or Florida, and since few species have diverged significantly (Courtenay 1961) from the Caribbean stock, recruitment from these areas probably occurs at frequent intervals if not annually. A southern eddy of the Gulf Stream reaches Bermuda from the Bahamas having traversed about 1,600 km of ocean, and at a speed of 0.5 knots (U.S. Naval Oceanographic office, 1968), this would take about 80 days. Caldwell (1959) suggested that sargassum weed and floating debris may play an important part in the protection of planktonic larvae and the prolongment of their pelagic existence.

Juvenile Phase

Courtenay (1961) described the juveniles of 13 *Haemulon* species and compiled an identification key. The juveniles of most *Haemulon* and *Anisotremus* species show a basic pattern of two dark stripes and a caudal spot. Body shape as well as coloration, are distinct from that of adults.

Small schools of unidentified juvenile pomadasids have been observed throughout the year in Jamaican

waters, but particularly in April, May and August. They have been found at depths varying from 2 to 25 m in various habitats including reef areas, particularly above blocks of *Montastrea* sp. and *Madracis* sp., on sand flats among the spines of the sea urchin *Diadema antillarum*, over *Thalassia testudinum* beds, among mangrove roots, and beneath the Port Royal Marine Laboratory jetty at the entrance to Kingston harbour. The smallest juveniles observed were approximately 1 to 2 cm in length.

Juvenile pomadasysids are diurnal plankton-feeders (Randall 1968) and they have been observed by day feeding actively in the water column beneath the Port Royal Marine Laboratory jetty. Juveniles from beneath the jetty, identified as *H. flavolineatum* (Courtenay 1961) and measuring 2 cm (FL), were caught in a hand-net by day and their stomachs were found to be filled with planktonic copepods identified by Dr. J. Graham of the Zoology Department, U.W.I., as

- Calanoida — *Acartia tonsa* Dana
Eucalanus sp.
Paracalanus parvus Caus
P. crassirostris Dahl
- Cyclopoida — *Corycaeus subulatus* Henrick
- Harpacticoida — unidentified

Juvenile *A. virginicus* are reported by Longley and Hildebrand (1941) and Randall (1968) to be fish cleaners, taking external parasites from barracuda, Bermuda chub, grey snapper and barjack.

Transformation from juvenile to adult form involves changes in color pattern and body shape, and also a change from diurnal plankton-feeding to nocturnal benthic-feeding in most species. Table 10.18 gives approximate lengths at which this transformation occurs for 13 *Haemulon* species (Courtenay 1961) and two *Anisotremus* species (Bohlke and Chaplin 1968). The juvenile pattern is lost completely in the adults of some

Table 10.18. Approximate standard lengths at transformation from juvenile to adult color pattern and body form (from Courtenay 1961; Randall 1968; Bohlke and Chaplin 1968).

Species	Approx. length (SL, cm) at transformation
<i>H. plumieri</i>	4.0
<i>H. sciurus</i>	3.5-6.5
<i>H. album</i>	> 9.2
<i>H. flavolineatum</i>	> 4.9
<i>H. aurolineatum</i>	> 5.4
<i>H. bonariense</i>	5.5
<i>H. macrostomum</i>	> 6.0
<i>H. carbonarium</i>	> 5.1
<i>H. melanurum</i>	6.5
<i>H. chrysargyreum</i>	> 4.2
<i>H. striatum</i>	< 4.6
<i>H. parrai</i>	> 5.9
<i>H. steindachneri</i>	< 8.1
<i>A. virginicus</i>	8.0
<i>A. surinamensis</i>	> 6.4

species (*H. plumieri* and *H. sciurus*), is retained within the adult pattern of some species (*H. aurolineatum*, *H. macrostomum* and *H. carbonarium*), and can be displayed at will by the adults of other species (*H. flavolineatum* and *H. bonariense*).

Adolescent Phase (From Transformation into Adult Form to Sexual Maturity)

The young of most species may be found schooling on nursery grounds, probably joining the adult schools on the reefs at maturity. However young *H. flavolineatum*, *H. aurolineatum*, *H. carbonarium* and *H. chrysargyreum* have also been observed schooling on the reefs close to the adult schools.

Common nursery grounds for many species are shallow (1 to 5 m) back-reef areas with sand, turtle grass, scattered coral heads and gorgonians. Young *H. plumieri* and *H. sciurus* have been observed in such areas and *H. flavolineatum* are often found in dense schools round the coral heads. Young *H. plumieri* and *H. aurolineatum* have been observed over turtle grass beds where they tend to congregate at the edge of sand patches, and small schools of *H. album* have been seen round isolated coral heads at the western tip of Jamaica.

The young of several species (*H. flavolineatum*, *H. aurolineatum*, *H. plumieri*, *H. chrysargyreum*, *H. macrostomum* and *A. virginicus*) have been observed under the Port Royal Marine Laboratory jetty throughout most of the year, but few fishes over 10 cm in length were caught there, indicating a movement away from the area before that size is attained.

Young pomadasysids are largely nocturnal benthic feeders, as are the adults of most species. Young *H. flavolineatum* were observed moving away from a reef area in small schools at dusk and feeding over nearby sand flats where adult schools were also feeding.

ADULT PHASE

Competitors

Competition for food

Table 10.19, extracted from Randall (1967) shows analyses of the stomach contents of adult pomadasysids. It can be seen that most species feed on a wide variety of invertebrate animals, and the composition of the diet is similar for many species. However, interspecific competition for food is probably not very great because of the wide variety of food items taken and because each species apparently favors a certain type of food. For instance, *H. album* showed a preference for sipunculids which were of small importance to other species, and the echinoids in its diet were mainly spatangoid species whereas other pomadasysids fed more commonly on regular echinoids. *H. flavolineatum* showed a preference for polychaetes which it shared with *H. aurolineatum*

Table 10.19. Analysis of stomach contents of 11 pomadasyid species, given as percentage of total volume for each species (from Randall 1967). Items comprising over 20% of the stomach contents of a species are italicized.

No. examined	Crabs	Shrimps	Polychaetes	Pelecypods	Gastropods	Ophiuroids	Echinoids	Sipunculids	Crustaceans (unidentified)	Stomatopods	Fish	Holothurians	Chitons	Hemichordates	Octopods	Tunicates	Anthozoans	Crab Larvac	Copepods	Fish eggs	Isopods	Amphipods	
<i>H. flavolineatum</i>	47	16	3	40	3	3	2	10	2		5	6		3								4	
<i>H. aurolineatum</i>	28		34	31	2	2			9									8	3	6		3	
<i>A. virginicus</i>	16	16	15	14	6	4	17		5							2			2		8	3	
<i>H. chrysargyreum</i>	30	21	16	19	15	2		1	6											4	5	6	
<i>H. sciurus</i>	60	27	10	5	15	5	6	9	3	2	4	3			2	1					1	2	
<i>H. parrai</i>	33	33	38	3	3	5	2					3					3						7
<i>H. plumieri</i>	22	26	6	15	1	7	6	12	8	5	3	3		3									
<i>H. carbonarium</i>	30	38	4	8		15	6	11	5				10										
<i>H. album</i>	57	8	4	14	5	3	5	20	25	1	2			4									
<i>A. surinamensis</i>	62	13	2		1	16	5	54	1	2	2												
<i>H. macrostomum</i>	28	8						87	5														

but the latter species also fed heavily on shrimp which were of less importance to *H. flavolineatum*. *H. macrostomum* fed largely on echinoids, which were also the major food item of *A. surinamensis*, but the latter species supplemented its diet with a wide variety of other invertebrates.

Many other reef fishes compete with pomadasyids for various invertebrate groups as food, and according to Randall (1967), the most important competitors are porgies (Sparidae), goatfishes (Mullidae), wrasses and hogfishes (Labridae) and mojarras (Gerreidae).

Competition for space

The number of fishes on a reef is related not only to the extent of the reef itself but also to the extent and richness of nearby feeding grounds, since many fish species, including the pomadasyids, leave the reef at night to feed in adjacent regions. Thus, by day, a small patch-reef surrounded by sand flats may seem to accommodate more fishes than the reef itself could possibly support (Randall 1963b). In such a situation there may well be competition for schooling space, and pomadasyids may even compete with one another. Several species, for instance *H. sciurus*, *H. chrysargyreum*, *H. flavolineatum* and *H. carbonarium*, have often been observed schooling together. *H. sciurus* has also been seen schooling with the snapper *Lutjanus mahogoni*, and *H. flavolineatum* with the yellow goatfish *Mulloidichthys martinicus*.

Shelter within a reef is far more restricted than the peripheral schooling space. Small groups of *A. surinamensis* have been observed congregating in caves by day, competing for space with other diurnal cave dwellers,

such as the soldierfish, *Myripristis jacobus*, the bigeye, *Priacanthus cruentatus*, and the copper sweeper, *Pempheris schombbergki*, and though these fishes are small, they are often present in large numbers.

Predators

Pomadasyids are preyed upon by reef predators including groupers (Serranidae), snappers (Lutjanidae), and jacks (Carangidae). Randall (1967) recorded reef fish species which he found in the stomachs of predators. Information concerning pomadasyids is given in Table 10.20. Cummings et al. (1966) observed barracuda preying upon *H. album* by day, and also by night when the margates were feeding on plankton attracted to

Table 10.20. Fish species known to prey upon pomadasyids from analyses of stomach contents (from Randall 1967).

Prey	Predators
<i>H. aurolineatum</i>	<i>Gymnothorax moringa</i> , <i>Aulostomus maculatus</i> , <i>Lutjanus analis</i> , <i>L. cyanopterus</i> , <i>L. jocu</i> , <i>Ophichthus ophis</i> , <i>Epinephelus striatus</i> , <i>Seriola dumerili</i> .
<i>H. flavolineatum</i>	<i>Aulostomus maculatus</i> , <i>Epinephelus striatus</i> , <i>Mycteroperca bonaci</i> , <i>M. tigris</i> , <i>M. venenosa</i> .
<i>H. carbonarium</i>	<i>Antennarius multiocellatus</i> .
<i>H. sciurus</i>	<i>Lutjanus cyanopterus</i> .
<i>H. plumieri</i>	<i>Lutjanus jocu</i> .
<i>Haemulon</i> sp.	<i>Synodus intermedius</i> , <i>Sphyræna barracuda</i> , <i>Petrometopon cruentatum</i> , <i>Lutjanus apodus</i> .

underwater lights. The amberjack, *Seriola dumerili*, was also seen preying upon schooling margates and swallowing whole fishes up to 20 cm in length. Starck and Davis (1966) stated that *Lutjanus griseus*, a nocturnal feeder, often preyed upon fishes, such as pomadasysids feeding in the same area. The species of parasite found in *H. plumieri* and *H. sciurus* indicate that sharks may also prey upon these pomadasysids.

Parasites, Diseases and Injuries

External parasites

Some species, particularly *H. flavolineatum*, were often seen with a large isopod on the cheek, but there is no information on other external or gill parasites of pomadasysids. The apparent lack of external parasites implies that grunts are "cleaned" by other reef dwellers, and *H. sciurus* has been observed being cleaned by young Spanish hogfish, *Bodianus rufus*.

Internal parasites

Nahhas and Cable (1964) found *H. sciurus* to be the most heavily parasitized pomadasysid species. In 16 specimens examined in Jamaica, most of which were infected, they found 56 parasites of four different species. Manter (1930) reported one individual *H. sciurus* to contain eight different species of trematode, as well as Acanthocephala and nematodes.

Adult trematodes are commonly found in pomadasysids, infesting the stomach, intestine or caeca (Nahhas and Cable 1964). The invertebrate intermediate host may be a lamellibranch, amphipod or gastropod, and the parasite probably reaches its final host by way of the food chain. Nahhas and Cable (1964) investigated nine species of pomadasysid in Jamaica and Curacao and they identified 20 trematode species.

Cestode bladder larvae were frequently found in the body cavities of *H. sciurus* and *H. plumieri* during project investigations. These were identified by Dr. D.I. Gibson of the British Museum of Natural History as otobothriid cestodes, possibly *Otobothrium (Pseudobothrium) dipsacum* Linton 1897, for which species sharks are the final hosts.

Nematodes are common parasites of pomadasysids in Jamaican waters. In the course of these studies, nematodes were frequently found in the body cavity associated with gut mesenteries, and sometimes in the ovaries. Nematodes from the ovary of *H. plumieri* were broadly grouped by Dr. D.I. Gibson as filarial nematodes similar to *Philometra*. An ovary weighing 29.5 g taken from *H. album* was found to contain a knot of nematodes which amounted to 8.5% of the ovary weight. The fecundity of the fish would probably be curtailed by a similar proportion, and in a heavily infested population the reproductive potential could be severely reduced by these ovarian parasites.

Acanthocephala also parasitize pomadasysids, but there is no information concerning the manner of infestation.

Diseases and injuries

There is no information on diseases of pomadasysids, and most injuries probably result from predatory attack. Several pomadasysids which had sections of the tail or dorsal fin missing were caught by the project and occasional *H. plumieri* individuals were found to be blind in one eye. Cummings et al. (1966) noted the presence of several maimed and scarred fishes in the school of *H. album* under study. These were mainly injuries which had been inflicted by predators, but some resulted from the loss of tags. It appeared that wounds healed readily, but missing parts of the body were not regenerated.

Hardiness

According to Courtenay (1961), *H. plumieri* and *H. aurolineatum* have been recorded further north on the east coast of North America than any other pomadasysid species. He also mentioned that these were the only species which remained in shallow water off Florida during the cold winter of 1957. Storey (1937) mentioned that numbers of *H. plumieri* were killed by cold weather at Sanibel Island, Florida and suggested (also Caldwell 1959) that many fishes which are found further north in the summer may not survive the low winter temperatures. This is probably true for *H. aurolineatum* at Cape Cod and also for *H. bonariense* at Buenos Aires.

It is possible that juveniles and young pomadasysids have a greater tolerance than adults of salinity and temperature ranges. Young *H. plumieri* and *H. aurolineatum* have been found at Cedar Cay, Florida (Reid 1954) where there are extensive areas of shallow water, and the salinity and temperature are very variable. Young *H. plumieri* have also been recorded from the Everglades National Park, Florida (Roessler 1970) at salinities from 21.8 to 42.8‰ and temperatures from 20.6 to 30.6°C. Tabb and Manning (1961) recorded juveniles of *A. virginicus*, *H. aurolineatum*, *H. plumieri* and *H. sciurus* from Northern Florida Bay which is an area having wide variations in salinity.

Dispersal of pomadasysids across the Orinoco and Amazon estuaries is probably effected by juveniles which must have a tolerance for low salinity and high turbidity in order to cross the extensive estuarine waters.

Smith (1967 and 1969) used *H. plumieri* as an experimental fish for digestion studies, and several specimens were starved for as long as 30 days prior to experimentation. During these investigations, regular underwater observation of undisturbed fish traps indicated that over 4% of the *H. plumieri* individuals known to have entered traps over 2-wk periods had died in the traps within that time.

NUTRITION AND GROWTH

Feeding

The adults of most pomadasid species are nocturnal benthic-feeders, and any daytime feeding is incidental (Longley and Hildebrand 1941; Randall 1964). At dusk, the diurnal schools disperse and individuals or small groups forage over sand or grass flats, until the approach of dawn when they return to the reefs and form schools again.

Adult *H. striatum* and *H. boschmae* are exceptional in retaining the diurnal plankton-feeding habits characteristic of juvenile pomadasids (Randall 1968). In Jamaican waters, *H. striatum* were observed schooling above coral at a depth of 20 to 30 m and feeding actively on plankton. Starck and Davis (1966) reported that schools of *H. striatum* dispersed by night, but no feeding activity was observed. Other species which feed partly on plankton as adults include *H. aurolineatum*, *H. chrysargyreum* and small *H. album*.

Cummings et al. (1966) used video-acoustic techniques at Bimini, Bahamas to make continuous observations on a school of *H. album* which comprised fishes from 20 to 40 cm in standard length. They were observed feeding occasionally when schooling by day, and dispersing to feed over adjacent areas by night. At dawn, they returned to the same schooling area where they formed a diffuse school and fed in the water column. As the light intensity increased, feeding activity decreased and the school became more compact.

By day, Cummings et al. (1966) observed large *H. album* individuals (50 cm SL) actively moving about and feeding singly or in small groups and apparently not associated with the school mentioned above. On Pedro Bank, a large individual (58 cm FL) caught by the project at 1730 hr on a hand-line had a full stomach with partially digested contents, indicating that it had been feeding during the afternoon. Measurements of average volume of stomach contents of *H. album* made by Cummings et al. (1966) indicated a preference for night feeding in fishes of the size range 16 to 48 cm (SL), but with increasing size, the proportion of daytime feeding apparently increased.

Cummings et al. (1966) stated that sounds associated with *H. album* feeding increased at night. They described two types of sound: "bursts" consisting of 3 to 10 rapid pulses associated with bottom feeding, and "pops" which were single, short pulses associated with plankton-feeding, recorded mainly in the early morning. Both sounds are produced by stridulation of the pharyngeal teeth, resonated through the swim bladder (Burkenroad 1930). When feeding on benthic organisms, they observed *H. album* individuals staying motionless with head down for as long as a minute before plunging after the prey in the sand. A level position was then resumed, and "bursts" were recorded as sand was expelled from the mouth and gill openings.

Food

All species of pomadasids are carnivores feeding largely on invertebrates, although some species supplement their diet with small fishes. Table 10.19 shows data for 11 pomadasid species, extracted from a survey carried out by Randall (1967). The figures given are percentages of the total volume of stomach contents collected from all individuals of each species caught. Randall (1967) found fragments of seagrass in the stomachs of many pomadasids, but he assumed that any plant material was ingested incidentally during feeding.

At Tortugas, Florida, Longley and Hildebrand (1941) made notes on food items taken by fishes including several pomadasid species. In addition to the items listed in Table 10.19 they observed *H. chrysargyreum* taking copepods, ostracods and crab zoeae from the plankton. *A. virginicus* sometimes took small fishes and *H. macrostomum* fed on small fishes, gastropods, starfishes, amphipods and isopods, which indicates a more varied diet than that shown in Table 10.19. Starck and Davis (1966) reported that the decapods ingested by *A. surinamensis* included majid and porcelainid crabs.

Cummings et al. (1966) studied stomach contents of *H. album* individuals caught by day and by night. They presented results as the percentage of fishes found with a particular food item in the stomach, and gave no quantitative data. Crabs were found in the highest percentage of fishes caught by day and by night, but according to Randall (1967) crabs comprise only a small proportion of the diet of *H. album*. Sipunculids were found in only a small number of fishes caught by night, whereas Randall (1967) found that sipunculids had been eaten by all of the 57 individuals examined.

On Pedro Bank, a large *H. album* individual (58 cm) was found with two small surgeonfishes in the stomach, and Randall (1967) recorded a monocanthid fish from the stomach of this species.

Randall et al. (1964) investigated the predators of the sea urchin *Diadema antillarum*, and several pomadasids were listed. They found *D. antillarum* to be the main dietary item for *A. surinamensis*, while *H. macrostomum* also fed heavily on this species, and the snout bones of both pomadasids were often stained purple by penetration of sea urchin spines. Other pomadasids occasionally found feeding on *D. antillarum* included *H. plumieri*, *H. sciurus* and *H. carbonarium*.

Growth

Relative growth

Fork length/weight relationships for 12 pomadasid species are given in Table 10.21. Data for all species, except *H. album* and *H. melanurum* were derived from the Port Royal reefs. Ideally, a year's data collected from continuous sampling should be used since condition may vary with time of year, availability of food and

Table 10.21. Relationship of fork length (cm) to weight (g) for 12 species of pomadasyids.

Species	No. of fishes	Size range Length in cm	$w = al^b$	
			a	b
<i>H. flavolineatum</i>	204	6.4-12.5	0.0114	3.22
	136	12.7-17.5	0.0107	3.25
<i>H. plumieri</i>	939	13.6-26.4	0.0238	2.93
<i>H. sciurus</i>	183	16.3-27.4	0.0314	2.84
<i>H. album</i>	112	27.6-58.6	0.0144	3.07
<i>H. aurolineatum</i>	101	7.2-11.6	0.0694	3.25
	69	12.1-18.0	0.0298	2.79
<i>H. bonariense</i>	86	14.0-22.0	0.0485	2.64
<i>H. melanurum</i>	83	17.7-23.5	0.0557	2.63
<i>H. macrostomum</i>	58	15.6-30.9	0.0176	3.06
<i>H. chrysargyreum</i>	17	8.3-17.4	0.0141	3.08
<i>H. carbonarium</i>	17	15.7-23.4	0.0404	2.74
<i>A. virginicus</i>	13	5.0- 9.4	0.0154	3.15
	64	12.0-23.0	0.0102	3.33
<i>A. surinamensis</i>	29	17.9-33.2	0.0233	3.01

spawning activity. This was attained for *H. plumieri*, *H. sciurus* and *H. flavolineatum*, but for other Port Royal species data were collected over periods greater than one year and data for the two offshore species, *H. album* and *H. melanurum*, were derived from single large catches.

For *H. aurolineatum*, *H. flavolineatum* and *A. virginicus*, fork length/weight relationships have been calculated for young as well as adult fishes. Table 10.21 shows that for *H. flavolineatum* and *A. virginicus* the relationship is similar for young and adults, but for *H. aurolineatum* weight increases rapidly in young fishes and more slowly in adults as shown in Fig. 10.2. The point at which the two lines intersect is equivalent to a length of 12.2 cm and a weight of 31.6 g, indicating that this is the size at which the growth pattern of the species changes.

Cummings et al. (1966) calculated a length/weight relationship for *H. album* and expressed it in terms of standard length in cm and weight in oz. When converted to fork length in cm and weight in g, the relationship is $W = 0.0148 L^{3.03}$ which is similar to that given in Table 10.21 calculated from the present data.

Table 10.22 gives the relationship of fork length (FL) to standard length (SL) for seven pomadasyid species, and fork length to total length (TL) for three species.

Table 10.23 shows the relationship of scale radius to fork length for three species from Jamaican waters and for *H. sciurus* from Bermuda waters also. The two equations for *H. sciurus* show that, although the rate of increase of scale radius relative to length was similar in the two areas, the radii of scales collected in Bermuda were 0.4 mm smaller than the radii of scales collected in Jamaican waters.

Table 10.22. Relationship of fork length (FL) to standard length (SL) and total length (TL) in cm, where x, x' and y, y' are constants.

Species	SL = xFL + y		TL = x'FL + y'	
	x	y	x'	y'
<i>H. plumieri</i>	0.92	-0.5	1.15	0
<i>H. album</i>	0.91	-0.7	1.15	0
<i>H. flavolineatum</i>	0.83	0.5	1.09	1.1
<i>H. sciurus</i>	0.90	-0.5		
<i>H. bonariense</i>	0.91	-0.5		
<i>H. aurolineatum</i>	0.88	0.3		
<i>A. virginicus</i>	0.94	-0.8		

Table 10.23. Relationship of scale radius (r) in mm to fork length (l) in cm of three pomadasyid species, where $r = x/l + y$ and x and y are constants.

Species	x	y
<i>H. plumieri</i>	0.16	1.35
<i>H. album</i>	0.19	0.77
<i>H. sciurus</i> - Port Royal	0.20	0.80
- Bermuda	0.19	0.40

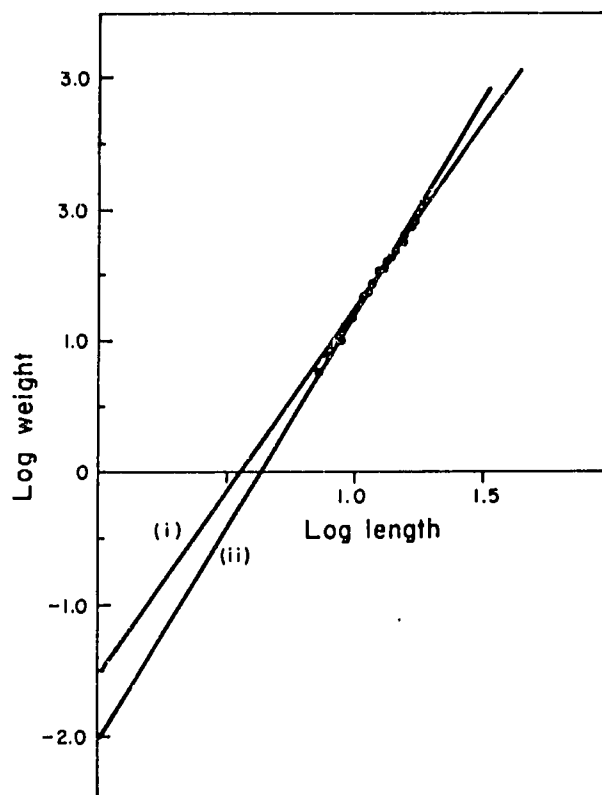


Fig. 10.2. *Haemulon aurolineatum*: relationship of fork length to body weight of (i) adult fishes and (ii) immature fishes. The point of intersection indicates the length at which the juvenile growth pattern changes to that of the adult.

Table 10.24 shows the relationship of body depth measured at the deepest point of the body to fork length for 10 species.

Maximum size

Records of maximum lengths of 16 species and the largest specimens of 14 species recorded by the project are given in Table 10.26. With the exception of *H. plumieri*, the largest specimens recorded by the project were smaller than the maximum length records in the literature, allowing for discrepancies between fork length and total length measurements. Asymptotic fork lengths have been calculated for *H. plumieri*, *H. album* and *H. sciurus* and estimated for another five species. These lengths are listed in Table 10.27.

Table 10.24. Relationship of length, *l* (cm) to body depth, *d* (cm), of ten pomadasid species, where $d = xl + y$ and *x* and *y* are constants.

Species	<i>x</i>	<i>y</i>
<i>H. plumieri</i>	0.366	-0.50
<i>H. flavolineatum</i>	0.354	-0.42
<i>H. sciurus</i>	0.323	-0.09
<i>H. album</i>	0.353	0
<i>H. bonariense</i>	0.380	-1.00
<i>H. macrostomum</i>	0.370	-0.50
<i>H. aurolineatum</i>	0.300	-0.20
<i>H. chrysargyreum</i>	0.275	0
<i>A. virginicus</i>	0.470	-0.50
<i>A. surinamensis</i>	0.405	0

Table 10.25. Maximum length records for pomadasyids. References: B and C. Bohlke and Chaplin (1968); R—Randall (1968); C—Cervigon (1966).

Species	Largest recorded during project investigations		Maximum length records	
	Fork length (cm)	Locality	Total length (cm)	Reference
<i>H. plumieri</i>	40.6	Navidad Bank	45.7 (40.0 FL)	B and C
<i>H. album</i>	58.6	Pedro Cays	65.0 (62.0 FL)	R
<i>H. flavolineatum</i>	20.9	E. Pedro Bank	30.5 (27.0 FL)	R
<i>H. sciurus</i>	28.0	Kingston Harbour entrance	45.7	R
<i>H. aurolineatum</i>	19.5	Pedro Cays	25.0	R
<i>H. melanurum</i>	28.2	Navidad Bank	33.0	R
<i>H. bonariense</i>	22.1	Port Royal Reefs	40.0	C
<i>H. macrostomum</i>	31.8	Port Royal Reefs	43.0	C
<i>H. carbonarium</i>	23.4	Port Royal Reefs	35.8	R
<i>H. chrysargyreum</i>	17.4	Port Royal Reefs	23.4	R
<i>H. striatum</i>	16.9	Discovery Bay	27.8	R
<i>H. parrai</i>	24.4	Port Royal Reefs	40.4	R
<i>H. steindachneri</i>	—		26.5	R
<i>H. boschmae</i>	—		19.2	R
<i>A. surinamensis</i>	33.2	Port Royal Reefs	61.0	B and C
<i>A. virginicus</i>	23.7	Port Royal Reefs	34.0	B and C

Table 10.26. Asymptotic fork lengths calculated for *H. plumieri*, *H. album*, *H. sciurus* and estimated for another five species.

Species	Asymptotic fork length (cm)
<i>H. plumieri</i>	42.0
<i>H. album</i>	65.0
<i>H. sciurus</i>	40.00
<i>H. flavolineatum</i>	25.0
<i>H. aurolineatum</i>	23.0
<i>H. bonariense</i>	30.0
<i>H. melanurum</i>	30.0
<i>A. virginicus</i>	30.0

Absolute growth

Previous estimates of growth rates of *H. plumieri*, based on tagging programs have been made by Randall (1961) and Moc (1966, 1967), but the growth rates measured were slow, as discussed later in this section. In the course of this study, three methods were employed for the measurement of growth rates:

1. Continuous data from the Port Royal Reefs provided a series of length-frequency histograms over the 2-yr sampling period for some species, and modal progression gave a measure of the population growth rate.

2. Offshore data were not continuous from any one area, but large catches of a species often showed a bimodal or trimodal length-frequency distribution. If it is assumed that these modes represent year-classes, then the distance between two peaks indicates the increase in modal length of a year-class over one year.

3. Marks or rings were observed on the scales of several pomadasyid species collected in Jamaican waters; however, although they were found on some scales of all the species studied, only those of *H. album* were analyzed with any success. Scales of *H. sciurus* collected in Bermuda were also studied and all showed clear rings. Menon (1950) stated that a water temperature change of at least 5°C was necessary for ring formation, and the annual water temperature at Bermuda varies by about 10°C but in Jamaican waters variation is only 3 to 4°C, and it is possible that ring formation is related to spawning activity rather than to temperature change. Tesch (in Ricker 1968) and Lux (undated) described methods of age determination from scale rings.

Haemulon plumieri: Length-frequency distributions of catches from offshore localities often had distinct modes, as shown in the four histograms in Fig. 10.3 which represent catches taken in different localities at various times of year during the period 1969 to 1971. If it is assumed that the modes in these histograms represent year-classes, and that the growth rate is the same in all four populations, then the distance between successive modes can be taken to represent one year's growth, and the data can be used in the estimation of growth rate.

Taking the modal lengths marked with arrows in Fig. 10.3 and plotting l_t against l_{t+1} , a Walford plot (Ricker 1958, after Walford 1946) was drawn (Fig. 10.4). The straight line approximating most closely to these four points cuts the diagonal at 42 cm, giving an estimate of the asymptotic length, L_∞ , for *H. plumieri*. The slope of this line $k_{12} = 0.69$, and since $k = e^{-K}$ then, the instantaneous annual growth rate $K_{12} = 0.37$.

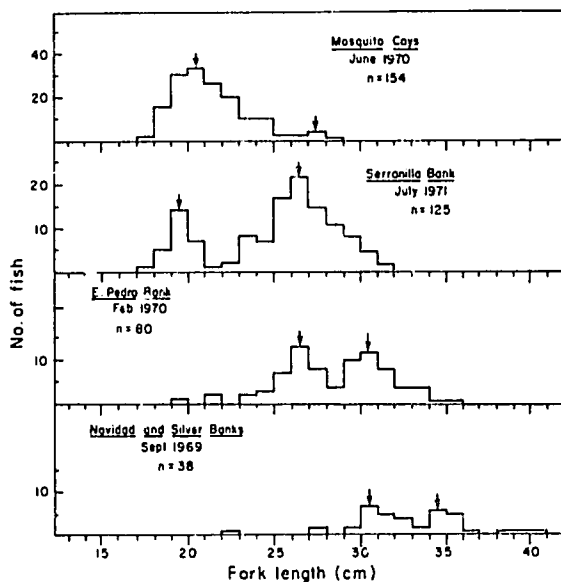


Fig. 10.3. *Haemulon plumieri*: length-frequency distributions of trap catches (probable mesh size 4.13 cm maximum dimension) from four areas. Arrows mark peaks which probably represent year-classes and which have been used to construct the Walford plot in Fig. 10.4.

Samples from the Port Royal Reefs were analyzed over periods of two lunar months, and 13 consecutive bimonthly length-frequency histograms (smoothed by moving mean of three) are shown in Fig. 10.5. Initially, male and female data were analyzed separately in order to investigate differential growth rates, but the data were sparse, and there appeared to be no significant difference in rate, in spite of the fact that offshore data (relating to fishes of a greater size range) showed that male *H. plumieri* were larger than the females of the species.

Each histogram in Fig. 10.5 shows one or two modes and modal progression is evident. In some adjacent histograms, a mode is seen to remain stationary at 16 to 17 cm, probably representing recruitment extending over several months, and only when recruitment is complete does the mode begin to progress to the right. Taking the modes marked with arrows in Fig. 10.5, an exponential form of the Walford plot (Ricker 1968) was used to measure the growth rate. This method is preferable in this case because it gives a better spread of the points than the method described above. For each of the modal lengths, $\log_e (L_\infty - l_t)$ was calculated (taking $L_\infty = 42$ cm, as calculated above) and the resultant values were plotted against time as shown in Fig. 10.6. Two series of points were obtained and a straight line was drawn through each. The slopes of these lines give estimates of the instantaneous annual growth rate and these values were found to be

$$(i) K_{12} = 0.31$$

$$(ii) K_{12} = 0.33$$

and the mean value $K_{12} = 0.32$.

The two figures obtained for K_{12} indicate a slightly faster rate of growth in offshore populations of *H. plumieri* than in those of the Port Royal Reefs. The difference may be due to Lee's phenomenon (Tesch, in Ricker 1968) taking effect at Port Royal because, if the larger, fast-growing fishes are being fished out first or migrating offshore, then the modal progression is effectively retarded since the residue of smaller, slower-growing fishes is being sampled and measured.

The mean of the estimated growth rates offshore and at Port Royal is $K_{12} = 0.345$ and therefore $k_{12} = 0.71$.

Applying the formula derived from the von Bertalanffy growth equation (Ricker 1955) in which

$$l_{(t+1)} = L_\infty (1 - k) + k l_t$$

a growth curve was constructed for *H. plumieri* (Fig. 10.7). As estimated above, $L_\infty = 42$ cm, and the mean value for $k_{12} = 0.71$. The absolute age of a fish at a given size is unknown and the growth curve was therefore drawn commencing from a length of 15 cm, attained at t years of age.

The growth rate measurements resulting from tagging programs, presented by Randall (1962) and Moe (1966, 1967) were slow compared with those given above. In

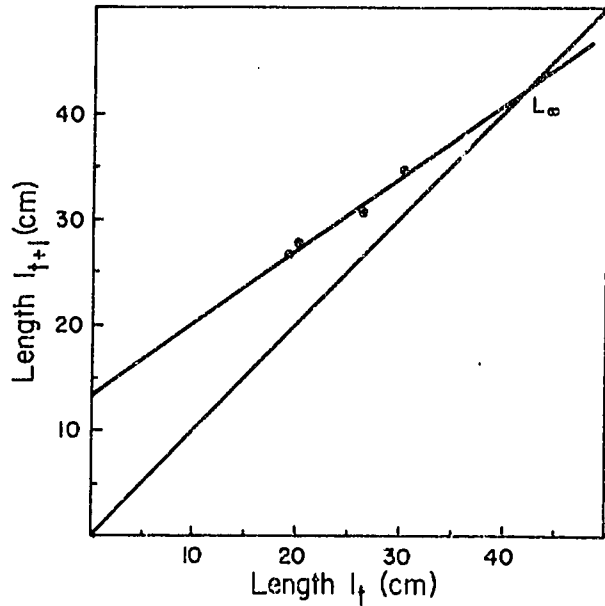


Fig. 10.4. *Haemulon plumieri*: Walford plot for estimation of growth rate, K and asymptotic length, L_{∞} from trap catch data shown in Fig. 10.3. The time interval, t , is assumed to be one year. From this figure, $L_{\infty} = 42$ cm, slope of the line, $k = 0.69$, therefore the instantaneous annual growth rate $K = 0.57$.

the Virgin Islands, Randall measured rates of increase in length between 0.78 to 0.90 mm/mo for fishes between 15.0 to 22.4 cm (TL). In Florida, Moe (1966) measured an increase in length of 1.4 mm and 3.6 mm/mo for individuals measuring, respectively, 28.7 cm and 23.4 cm (TL). For comparison, in Jamaican waters, an *H. plumieri* individual measuring 20.3 cm (FL) (equivalent to 23.4 cm TL) is expected to grow to 26.6 cm in 1 yr. Therefore, the mean monthly increase in length for that year would be 5.3 mm (an arbitrary figure, since, in fact, the monthly increase in length decreases exponentially), which is greater than that measured by Moe for a fish of similar size and much greater than rates measured by Randall for smaller fishes. It seems likely that tags significantly retard the rate of growth. Moe (1967) stated that tagging results indicated a reduced rate of

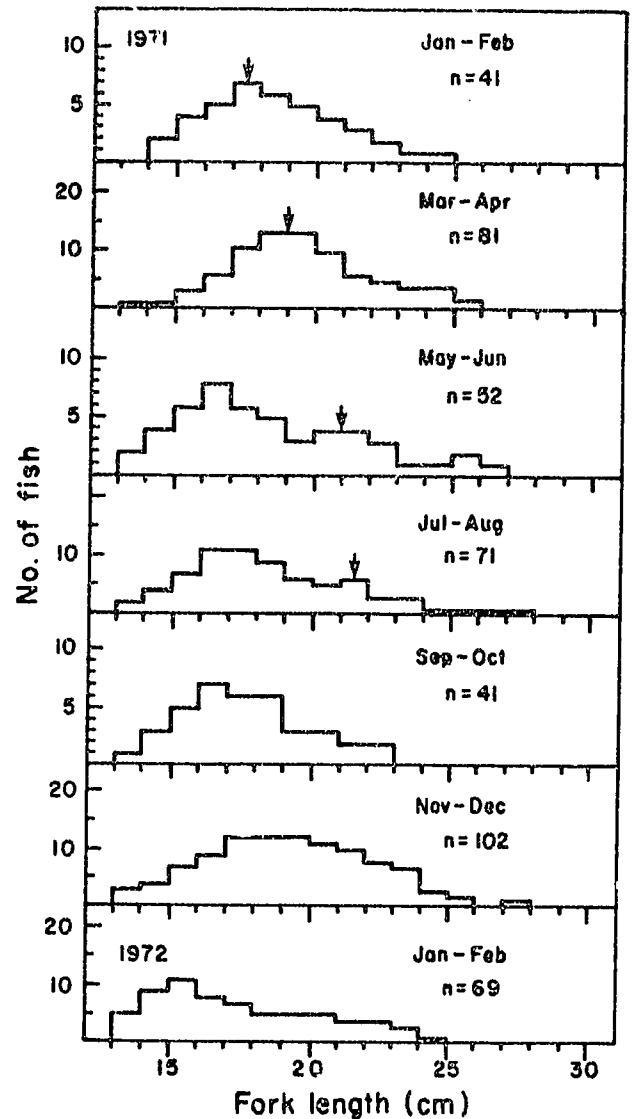
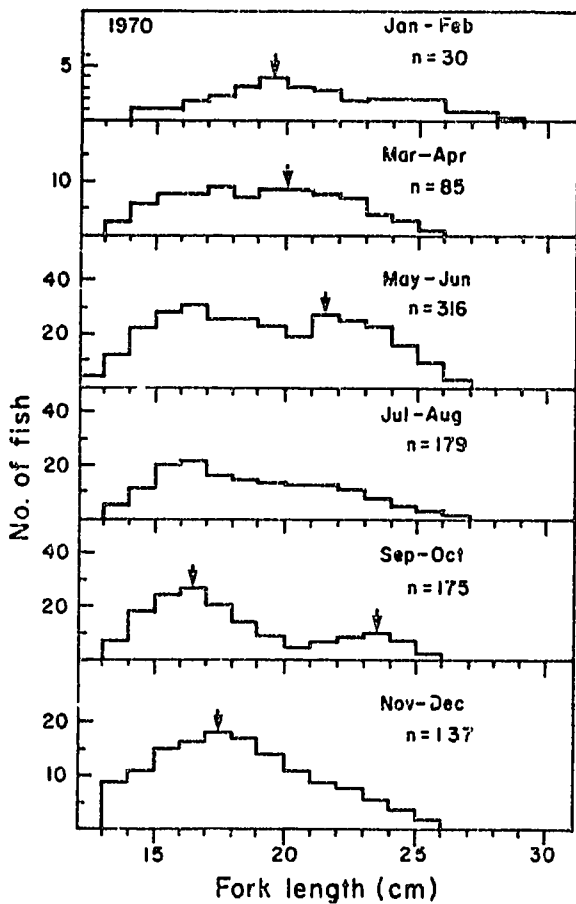


Fig. 10.5. *Haemulon plumieri*: bimonthly length-frequency distributions (smoothed by moving mean of three) of Port Royal trap catches (maximum mesh dimension of traps 4.13 cm). Arrows mark modal progressions used for growth rate estimations in Fig. 10.6.

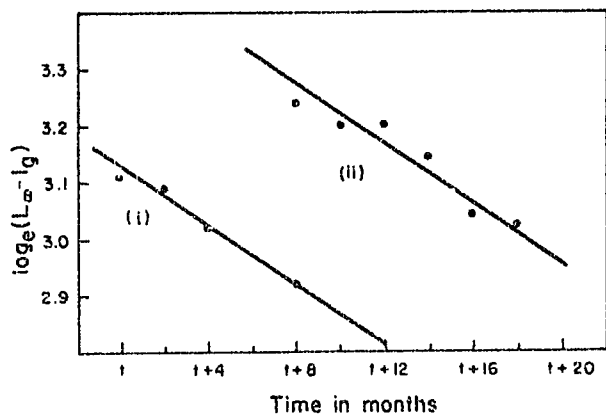


Fig. 10.6. *Haemulon plumieri*: estimation of growth rate from Port Royal Reefs data. The points plotted here were calculated by taking $\log_e (L_\infty - l_t)$ of each mode marked in Fig. 10.5, where $L_\infty = 42$ cm as calculated in Fig. 10.4. The time interval t , is measured in months. The slopes of these lines are (i) $K = 0.31/12$ and (ii) $K = 0.33/12$. Therefore, taking the mean of these values on a yearly basis $K_{12} = 0.32$, which is an estimate of the instantaneous annual growth rate.

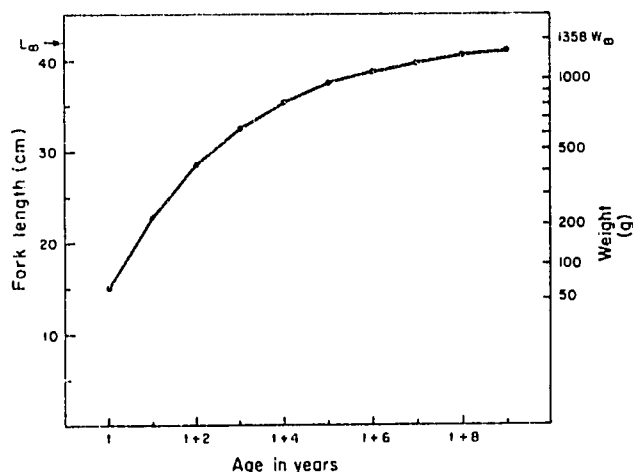


Fig. 10.7. *Haemulon plumieri*: calculated growth curve where $L_\infty = 42$ cm, $k = 0.71$ and $t = 1$ year.

growth at lengths greater than 20.0 cm (FL). He estimated one fish recaptured at a length of 33.8 cm (FL), to be 5 yr of age from otolith studies.

Rings were found on scales from more than 50% of one hundred *H. plumieri* individuals caught on the Port Royal Reefs and Pedro Bank over a period of about 1 yr. However, the rings did not seem to conform to an overall pattern, and approximately equal proportions of males and females showed rings. Ring formation may be connected with breeding, but there was no apparent correlation between marginal increment and the gonad stage in individual fishes.

Haemulon album: There were no continuous length-frequency data that might show modal progressions

collected for this species from any locality. However, the length-frequency distributions of catches taken from Salmon and Albatross Banks in February 1970 (Fig. 10.8) showed three distinct modes comprised of both male and female fishes. Assuming that the modes represent year-classes and that the distance between modes represents one year's growth, these data can be used for growth rate estimation.

Taking the three modal lengths indicated in Fig. 10.8, for each value $\log_e (L_\infty - l_t)$ was calculated and the resultant values were plotted against time as shown in Fig. 10.9. Using this method, L_∞ must be estimated, and if, taking a certain value, the points do not lie on a straight line, adjustment of the L_∞ value may give a more linear location of points. For *H. album* the points lay on a straight line when $L_\infty = 65$ cm. The slope of this line represents the instantaneous annual growth rate and it was found to be $K_{12} = 0.2$ and since $k = e^{-K}$ then $k_{12} = 0.82$.

A growth curve was constructed for *H. album* using the formula

$$l_{t+1} = L_\infty (1 - k) + k l_t$$

as described for *H. plumieri*. As estimated above, $L_\infty = 65$ and $k = 0.82$ and since the absolute age of a fish of any size was unknown, the curve (shown in Fig. 10.10) commences from a length of 20 cm, attained at t years of age.

Scales were collected from 32 individuals (20 to 62 cm FL) from offshore localities. Of these, scales from 24 individuals showed one or more clear rings, but scales from the other eight individuals were large, heavily thickened and could not be read. The radii of all the measurable rings were grouped into 0.2 mm classes and a frequency histogram was plotted (Fig. 10.11). Three fairly distinct peaks were evident, and the corresponding radius measurements were back-calculated (Fig. 10.12), using the fish length-scale radius relationship (Table 10.23), to give estimates of length at the formation of each ring as shown in Table 10.27. Of the length measurements obtained, 25.9 cm (FL) and 33.0 cm (FL) correspond well with the modal lengths in Fig. 10.8, which infers that the two respective rings were probably annuli. The length measurement 20.3 cm (FL) is higher than expected, indicating that the interval between the formation of the first and second ring was probably less than a year.

Table 10.27. *Haemulon album*: estimation of fork length at scale ring formation, as back-calculated in Fig. 10.12 from modes indicated in Fig. 10.11.

Ring radius (mm)	Back-calculated fork length (cm)
4.6	20.3
5.7	25.9
7.1	33.0

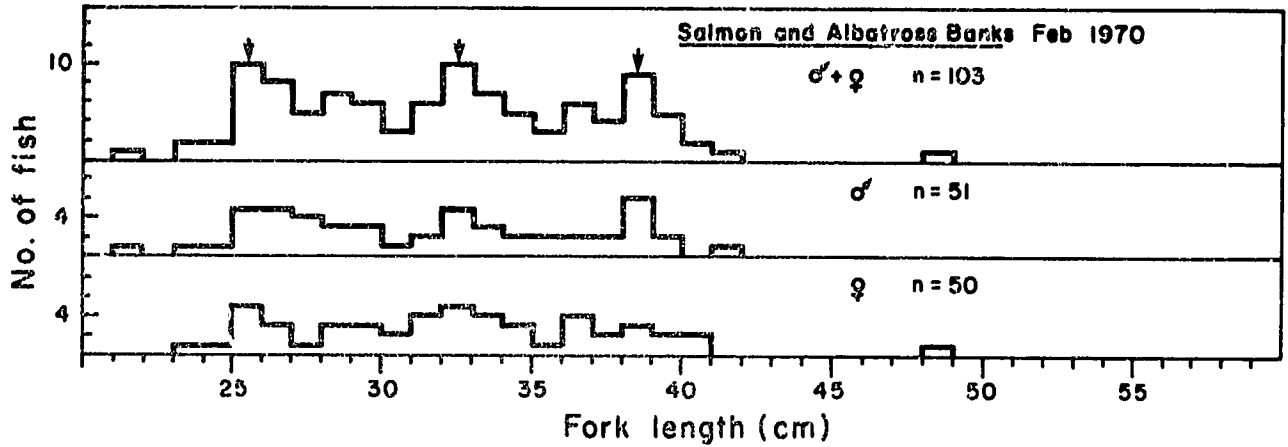


Fig. 10.8. *Haemulon album*: length-frequency distribution of trap catch (maximum mesh dimension: 4.13 cm) from Salmon and Albatross Banks in February 1970. (i) total catch ($n = 103$); (ii) catch of males ($n = 51$); (iii) catch of females ($n = 50$). Arrows mark peaks which probably represent year classes and which have been used for growth rate estimation in Fig. 10.9.

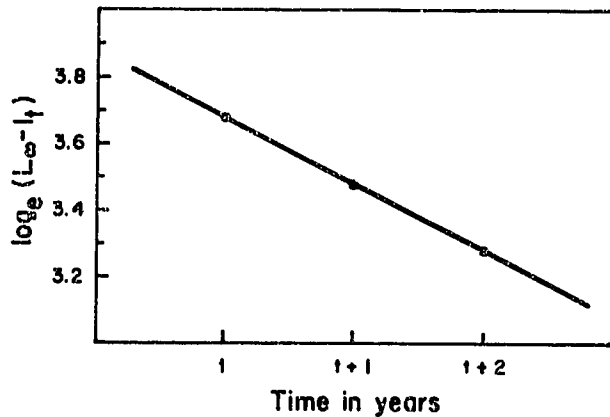


Fig. 10.9. Estimation of growth rate for *Haemulon album*. The points in this diagram were plotted by calculating $\log_e (L_\infty - l_t)$ for each of the three modes indicated in Fig. 10.8. L_∞ was estimated to be 65 cm. The slope of this line, $K = 0.2$ is the instantaneous annual growth rate.

Haemulon sciurus: On the Port Royal Reefs, catches of *H. sciurus* were small, and data were analyzed over periods of 3 mo to give the length-frequency histograms (smoothed by moving mean of three) shown in Fig. 10.13. Modal progression is evident, and modes marked with arrows were used in the estimation of growth rate. Taking each of the modal lengths, $\log_e (L_\infty - l_t)$ was calculated and the resultant values were plotted against time as shown in Fig. 10.14. With the value of $L_\infty = 40$ cm, the points approximated to straight lines, and the slopes of these lines, which represent the instantaneous annual growth rate, were found to be

(i) $K_{12} = 0.28$

(ii) $K_{12} = 0.24$

and taking the mean value, $K_{12} = 0.26$.

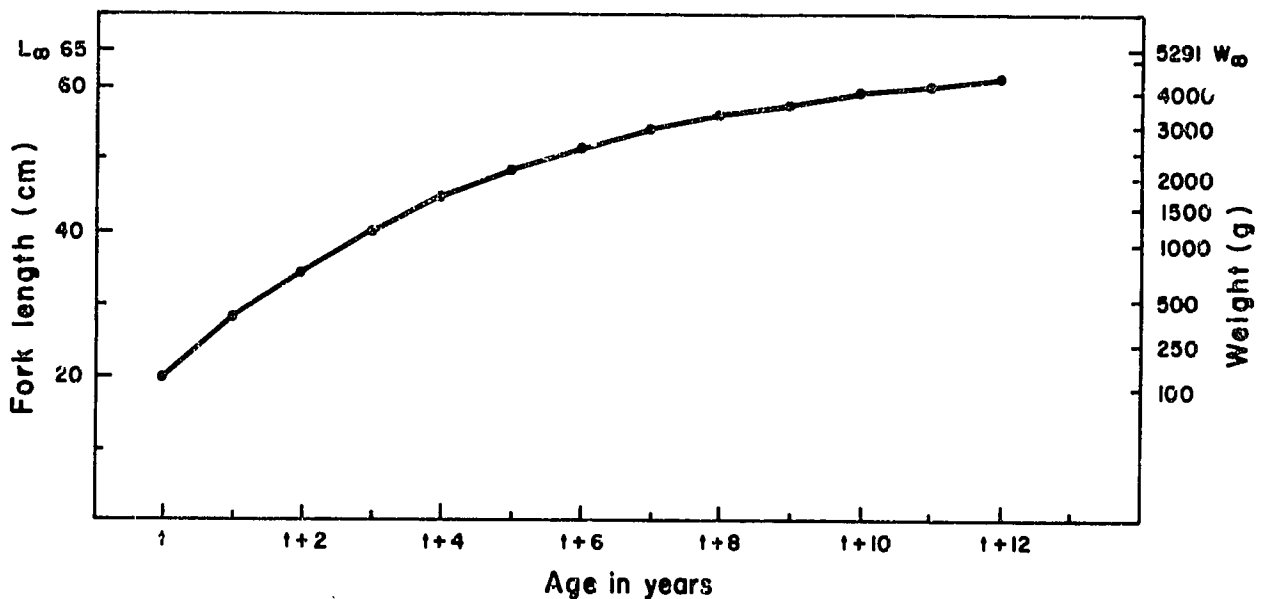


Fig. 10.10. *Haemulon album*: calculated growth curve, where $L_\infty = 65$ cm, $k = 0.82$ and $t = 1$ year.

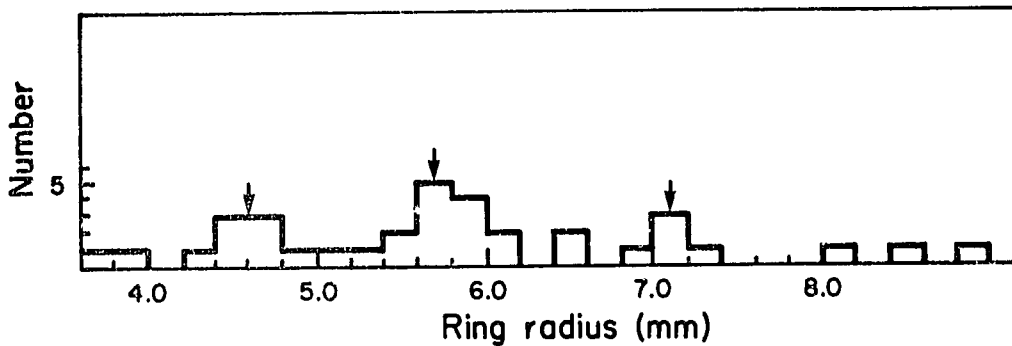


Fig. 10.11. *Haemulon album*: frequency distribution of ring radii read from the scales of twenty four individuals (length range 20 to 63 cm).

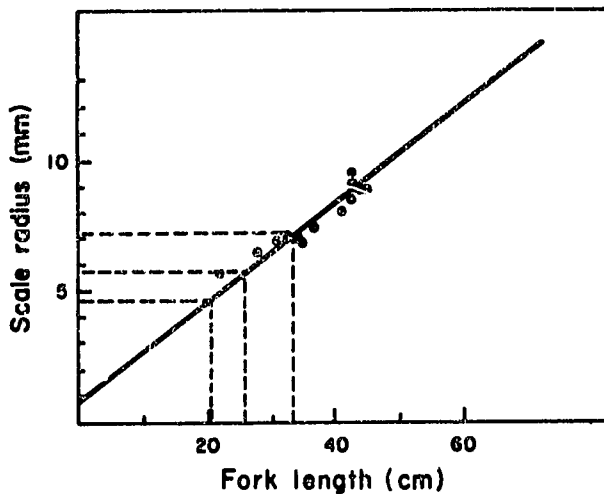


Fig. 10.12. *Haemulon album*: relationship of scale radius to fork length (Table 10.27) showing back-calculation of lengths corresponding to the modal ring radii in Fig. 10.11.

A growth curve (shown in Fig. 10.15) was constructed for *H. sciurus* using the formula described for *H. plumieri*, and the values $k_{12} = 0.77$, $L_{\infty} = 40$ cm, and $l = 14$ cm at t years of age.

Scales from 58 *H. sciurus* individuals caught on the Port Royal Reefs were examined and 32 (20 male, 12 female) showed rings, but they did not appear to conform to a pattern.

In Bermuda, scales were collected from 21 *H. sciurus* individuals during December 1971, and all the scales showed two or three distinct rings (Fig. 10.16), the number of rings varying with the size of scale. The frequency distribution of ring radii in Fig. 10.17 shows three fairly distinct peaks which indicates that most of the rings were laid down within specific times, probably during consecutive winters. From the Bermuda scale radius/fork length relationship given in Table 10.23, approximate lengths at ring formation were estimated as for *H. album* and these are given in Table 10.28. The first ring may be formed at the time of transformation to the adult form, and the second and third rings are probably annuli, indicating growth from 10.5 to 16.7 cm

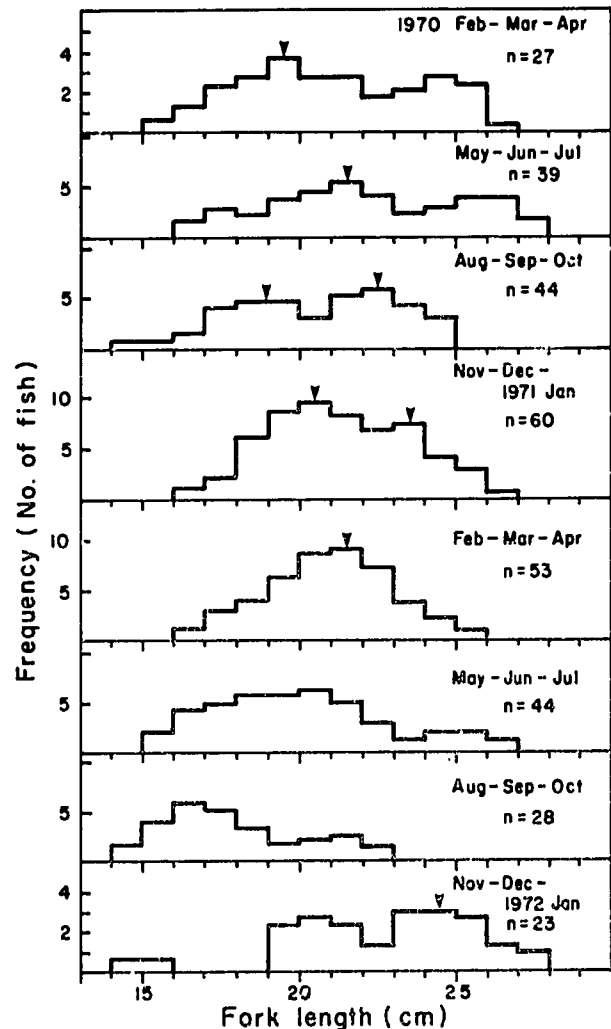


Fig. 10.13. *Haemulon sciurus*: length-frequency distributions of quarterly trap catches (maximum mesh dimension 4.13 cm) from the Port Royal Reefs (smoothed by moving mean of three). Modal progressions used in growth rate estimation (Fig. 10.14) are marked with arrows.

(FL) in 1 yr which is slightly slower than the rate expected in Jamaican waters: Using the growth rates estimated from Port Royal data, a fish of 10.5 cm (FL) is expected to grow to 17.3 cm in 1 yr.

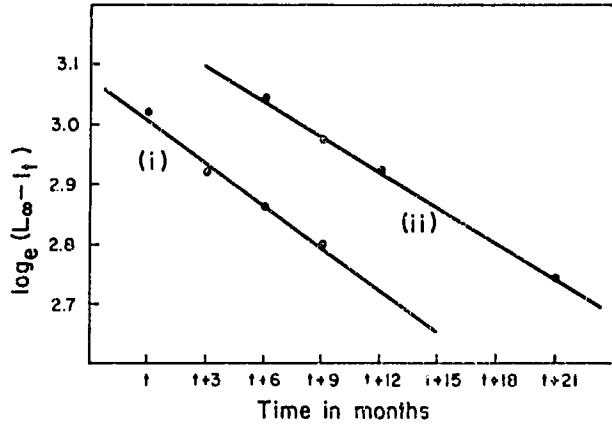


Fig. 10.14. Estimation of growth rate for *Haemulon sciurus*. The points in this diagram were plotted by calculating $\log_e(L_\infty - l_t)$ for each of the modes indicated in Fig. 3.14. L_∞ was estimated to be 40 cm. The slopes of these lines are (i) $K = 0.28/12$; (ii) $K = 0.24/12$ and taking the mean of these values on a yearly basis $K_{12} = 0.26$ which is the instantaneous annual growth rate.

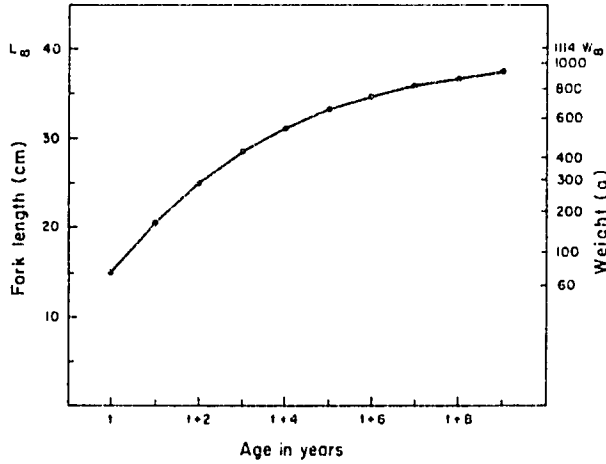


Fig. 10.15. *Haemulon sciurus*: calculated growth curve where $L_\infty = 40$ cm, $k = 0.77$ and $t = 1$ year.

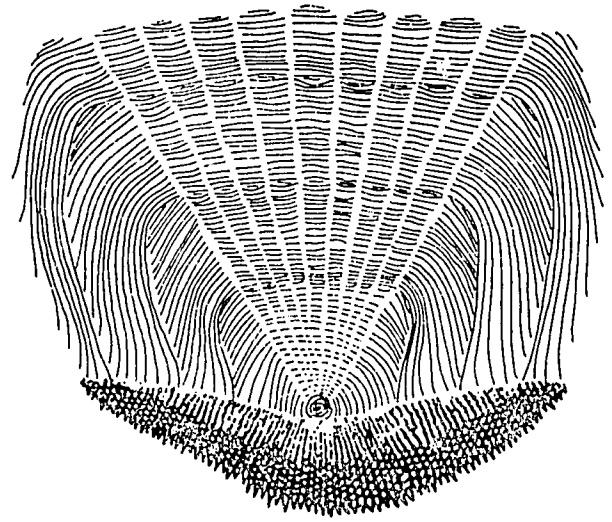


Fig. 10.16. Diagram to show a ctenoid scale of *Haemulon sciurus*. Three annuli can be seen: in the anterior field they appear as broken circuli, and in the lateral field as one complete circulus outside many shortened circuli. The fish was an inactive female of fork length 20.7 cm and the radius of the scale was 4.3 mm. Magnification $\times 19.5$. This diagram was traced from a photograph of a scale collected at Bermuda in December 1971. Approximately one in four of the circuli are shown.

Table 10.28. *Haemulon sciurus*, Bermuda: back-calculated fork length at formation of scale rings, taking modes indicated in Fig. 10.18 and using the formula for fork length/scale radius relationship given in Table 10.23.

Ring radius (mm)	Back-calculated fork length (cm)
1.4	5.3
2.4	10.5
3.6	16.8

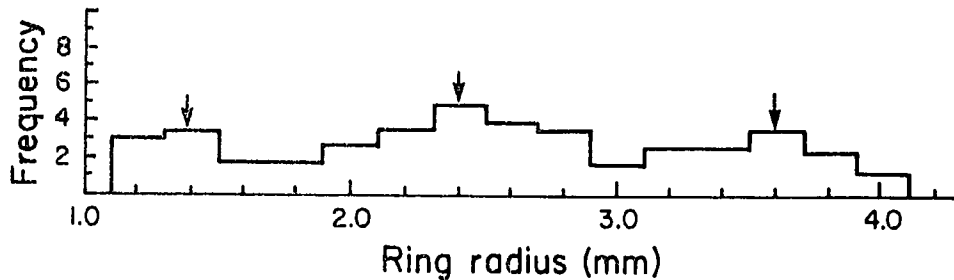


Fig. 10.17. *Haemulon sciurus*: frequency distribution of scale rings read from twenty one scales collected in Bermuda. Modes used for back-calculation of lengths are marked by arrows. (Histogram smoothed by moving mean of three.)

Other species: There are no adequate data for the estimation of growth rates for any other pomadaspid species. *H. flavolineatum* and *H. aurolineatum*, though occasionally caught in large numbers, are both recruited

to the trap fishery at relatively large sizes, and Port Royal data showed no modal progressions, while offshore catches usually gave unimodal length-frequency distributions.

BEHAVIOR

Migrations and Local Movements

By day, most pomadasid species congregate in reef areas and movements are minimal, but nocturnal wanderings in search of food may be quite extensive. At night, Starck and Davis (1966) observed *H. flavolineatum* at distances of a 0.8-1.6 km away, and *H. sciurus* 0.4 km away and deeper than by day.

Some species may undertake seasonal migrations, particularly during the breeding season when large numbers of individuals may congregate to spawn, as described by Moe (1966) for *H. plumieri*. In addition to this, a summer movement of *H. plumieri* and *H. sciurus* northwards along the east coast of North America was reported by Courtenay (1961).

Migrations may take place at certain times in the life cycle; for instance, on approaching maturity young pomadasids must migrate from their nursery grounds to the adult schooling areas. Length distributions of *H. plumieri* on the Port Royal reefs indicated that at a length of about 25 cm this species may migrate away from that area, since few fish larger than this were caught there. However, where they migrate to is not known. On Pedro Bank, few *H. plumieri* individuals smaller than 25 cm were caught, indicating a migration of fishes of that size into the area, but it seems most unlikely that adults migrate across the expanse of deep water that separates the bank from the south Jamaican shelf.

Off Bimini, Bahamas, McLean and Herrnkind (1971) observed two dense schools of grunts, comprised mainly of *H. plumieri*, after a prolonged storm during October 1969. The schools were apparently moving southwards, away from murky water to the north, at a speed of about 1.5 m/sec.

Adult pomadasids of several species may remain in the same schooling area for long periods. Cummins et al. (1966) noted that tagged *H. album* returned to the same school every morning, and Bardach (1958) observed eight tagged *H. sciurus* schooling in the same place for a period of 200 days. Results from tagging programs indicate that *H. plumieri* individuals show local movements but they may not move over great distances. In the Virgin Islands, Randall (1963a) recovered one *H. plumieri* 1,000 m from the release site after 2 yr. In Florida, Beaumariage (1969) recovered three *H. plumieri* from the release site after about 4 yr at large. However, Moe (1966) reported that 12 out of 39 tagged *H. plumieri* recovered off Florida had moved 5 km or more from the release site. He also noted that tagged adults were returned from the area throughout the year, indicating that seasonal migrations were unlikely.

Schooling

All pomadasids, except large *H. album* (Cummings et al. 1966) are diurnally schooling species. Most species

school in shallow reef areas and the size of a school varies from a few fishes to several hundred. The size composition of adult schools was observed to be quite uniform, though occasionally small schools of mixed sizes of *H. plumieri* were seen with the young of that species. Individuals in a school were observed to be inactive, hanging motionless in the water, with heads pointing slightly downwards. The fishes were generally orientated in the same direction, facing up-current if there was any water movement.

Various species of pomadasids were frequently seen schooling together. Schools of mixed species, such as *H. flavolineatum*, *H. sciurus* and *H. chrysargyreum*, were common, though each species tended to form a discrete group within the school, which may be more accurately viewed as an aggregation of schools.

Schools of mixed genera were often seen, and *H. flavolineatum* was observed schooling with *Mulloidichthys martinicus*, *H. striatum* with *Lutjanus buccanella*, and *H. sciurus* with *L. mahogoni*. Starck and Davis (1966) reported mixed schools of *H. parrai* and *L. griseus*, and also *H. sciurus* together with *L. griseus* and *M. martinicus*.

No detailed studies were carried out on the density of schools, but observations indicated that the distance between fishes was inversely proportional to the light intensity. Observing a school of *H. flavolineatum* at dusk, the fishes were seen gradually moving apart until they finally dispersed just before dark. During the day, it was observed that the shadow cast by a heavy cloud was sufficient to cause a loosening of the school.

Off Bimini, Bahamas, McLean and Herrnkind (1971) reported two very dense schoolings during a mass movement of grunts, mainly *H. plumieri*. The two schools were ellipsoid, measuring 4 x 3 m and 5 x 4 m. The distance between fishes was taken as 10 cm and the number in each school was estimated to be 4,510 and 10,021, respectively. The density of fishes in these schools was far greater than that of stationary schools normally observed in reef areas.

According to Hobson (1965) and Starck and Davis (1966), when a school of pomadasids is under predatory attack, the immediate reaction is a tightening of the school, the fishes move close to the reef and swim among one another; and they suggested that this reaction has the effect of merging the stripes and making individual fishes difficult to discern. Starck and Davis (1966) observed a specimen of *Caranx bartholomaei* swimming into a school of grunts and scattering the individuals. The grunts swam rapidly for cover in the reef and the predator then pursued a single fish. Cummings et al. (1966) recorded sounds termed "blasts" produced by *H. album* under predatory attack. These were low-frequency pulses lasting up to 1.4 sec, possibly produced as a result of rapid swimming movements.

Behavior in Relation to Fish Traps

The schooling habit of pomadasids appears to be an

important factor in trap fishing. Data from underwater observations indicated that when a few *H. plumieri* individuals had entered a trap, conspecific attraction tended to draw in more individuals (Munro et al. 1970). Other pomadasyd species that were sometimes found in large numbers in a single trap included *H. sciurus*, *H. bonariense*, *H. flavolineatum* and *A. virginicus*.

Data collected by regular underwater observation of undisturbed fish traps showed that fishes are able to escape from traps. The rate of escapement from traps shown by *H. plumieri* is low compared with overall rates measured by Munro (1974) for all species entering the traps.

Populations

POPULATION STRUCTURE

Sex Ratios

The sex ratios of catches of nine pomadasyd species are given in Table 10.29. Catches of *H. plumieri*, *H. bonariense* and *A. virginicus* all show significantly higher proportions of females than males, whereas the other species show approximately one to one ratios. The ratios of these three species may reflect a greater abundance of females in the population, possibly explained by a higher female survival rate, but there are no data concerning the relative catchabilities of males and females and it is possible that the females have a greater tendency to enter traps.

The total trap catch of *H. plumieri* from the Port Royal reefs contained a high proportion of females, but Fig. 10.18 shows that the sex ratios varied around the 50% level over a 2-yr period with no apparent seasonal pattern.

sizes were selective for the larger specimens in the population. Relatively few *H. album* were captured in traps and it was not possible to determine whether the size compositions of the trap- and line-caught samples were significantly different.

The estimated mean annual length frequency compositions of catches of species of grunts are shown in Figs. 10.20 to 10.23. With the exception of *H. album*, all data refer to trap catches (analytical methods are described in Chapter 3). Male *H. plumieri*, *H. flavolineatum*, *H. macrostomum* and *H. melanurum* were of slightly greater average size than the females, but the differences were not sufficient to warrant separate analyses of the sexes. Likewise, there was some evidence that the average size of grunts at Pedro Bank increased slightly with increases in depth, but the differences were not sufficient to warrant separate analyses by depth zones.

Age and Length Composition

There is no information concerning the age composition of pomadasyd populations since no estimates of absolute age have been made for any species.

Only *H. plumieri* and *H. album* were captured on hook and line in substantial numbers. In the case of *H. plumieri*, the sample captured on lines was of greater mean and modal length than that taken in traps (Fig. 10.19) and it is evident that the relatively large hook

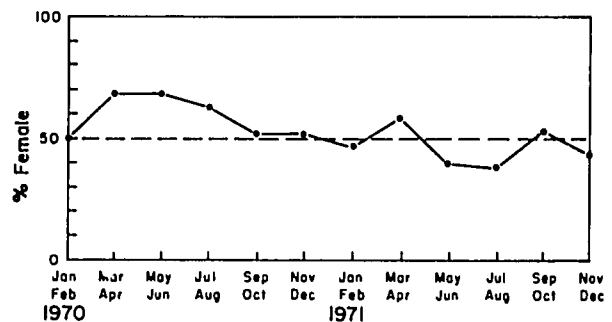


Fig. 10.18. Variations of sex ratio in bimonthly trap catches of *Haemulon plumieri* from the Port Royal Reefs over a 2-yr period.

Table 10.29. Sex ratios of catches of nine pomadasyd species taken at the Port Royal Reefs, at unexploited areas of Pedro Bank and at the Pedro Cays. All data are from trap catches apart from those of *H. album* which are from line catches. (Where application of the chi-square test showed that proportions are significantly different from 50% at the 0.01 level of significance, the figures are italicized.)

Species	Port Royal Reefs			Pedro Cays			Pedro Bank (unexploited)		
	Male	Female	% Female	Male	Female	% Female	Male	Female	% Female
<i>H. plumieri</i>	582	770	57	16	23	59	194	422	69
<i>H. flavolineatum</i>	102	91	47	110	102	48	71	94	57
<i>H. sciurus</i>	176	154	47						
<i>H. bonariense</i>	39	96	71						
<i>H. macrostomum</i>	35	39	53						
<i>H. aurolineatum</i>	26	29	53						
<i>H. melanurum</i>							104	111	52
<i>H. album</i>							72	71	50
<i>A. virginicus</i>	20	76	79						

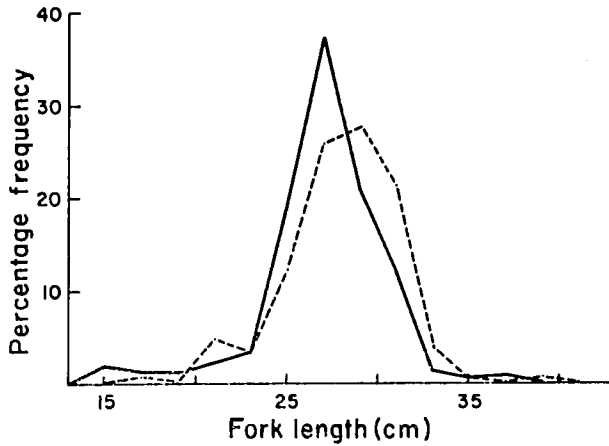


Fig. 10.19. Comparison of length distributions of line catches (broken line) and trap catches (solid line) of *Haemulon plumieri* from stations where both gears were used.

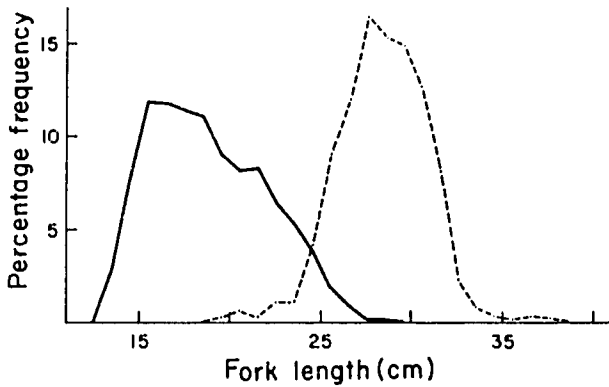


Fig. 10.20. Estimated annual percentage length-frequency distributions of trap catches of *Haemulon plumieri* at the Port Royal Reefs (solid line; $n = 1376$, $t = 2$ months) and at unexploited parts of Pedro Bank (broken line; $n = 910$, $t = 4$ months).

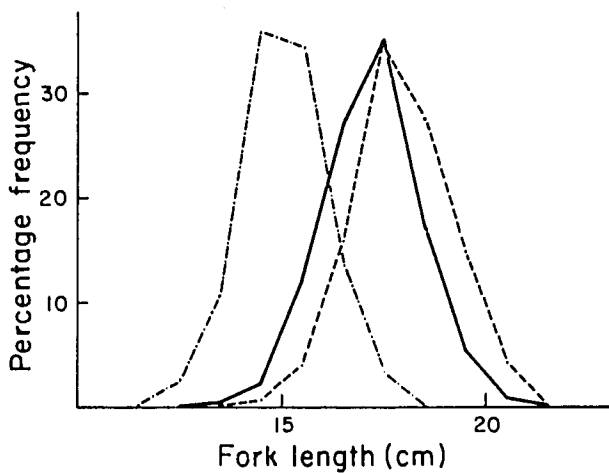


Fig. 10.21. Estimated mean annual percentage length-frequency distribution of trap catches of *Haemulon flavolineatum* at the Port Royal Reefs (---; $n = 207$, $t = 12$ months), at the Pedro Cays (—; $n = 328$, $t = 6$ months) and at unexploited parts of Pedro Bank (----; $n = 734$, $t = 6$ months).

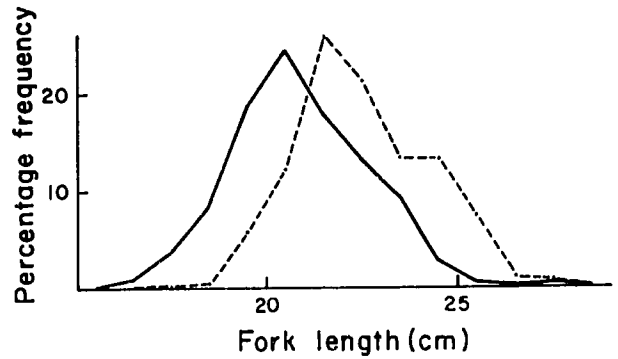


Fig. 10.22. Estimated mean annual percentage length-frequency distributions of trap catches of *Haemulon melanurum* at Serranilla Bank (—; $n = 214$, $t = 12$ months) and at unexploited parts of Pedro Bank (----; $n = 399$, $t = 6$ months).

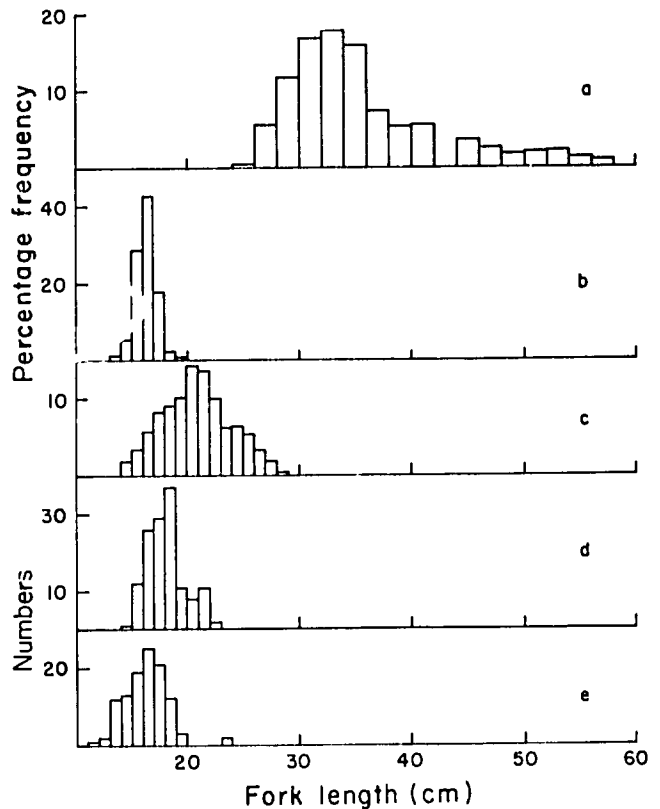


Fig. 10.23. Size compositions of catches of species of grunts: (a) *Haemulon album*: estimated mean annual percentage length-frequency distribution of line catches at unexploited parts of Pedro Bank ($n = 217$, $t = 6$ months). (b) *Haemulon aurolineatum*: estimated mean annual percentage length-frequency distribution of trap catches at unexploited parts of Pedro Bank ($n = 235$, $t = 6$ months). (c) *Haemulon sciurus*: estimated mean annual percentage length-frequency distribution of trap catches at the Port Royal Reefs ($n = 335$, $t = 6$ months). (d) *Haemulon bonariense*: gross length-frequency distribution of trap catches at the Port Royal Reefs ($n = 137$, $t = 12$ months). (e) *Anisotremus virginicus*: gross length-frequency distribution of trap catch at the Port Royal Reefs ($n = 111$, $t = 12$ months).

Table 10.30. Observed minimum, mean and full fork lengths of (i) eleven pomadasyd species at recruitment to the trap fishery and calculated minimum length retainable by traps with a maximum mesh dimension of 4.13 cm; (ii) two pomadasyd species at recruitment to the line fishery.

Fishing gear	Species	Locality	Observed minimum recruitment length (cm) l_1	Mean recruitment length (cm) l_T	Full recruitment length (cm) l_C	Calculated minimum length retainable by 4.13 cm mesh
(i) Traps	<i>H. plumieri</i>	Port Royal	12.8	14.9	15.5	12.6
		Pedro Bank (unexploited)	19.5	26.2	27.5	
	<i>H. sciurus</i>	Port Royal	14.5	18.5	20.5	13.1
		<i>H. flavolineatum</i>	Port Royal	12.5	14.2	
	Pedro Cays		13.5	16.7	17.5	12.9
	Pedro Bank (unexploited)		14.5	17.1	17.5	
	<i>H. macrostomum</i>	Port Royal	14.3	19.5	20.5	12.5
	<i>H. album</i>	Pedro Bank (unexploited)	21.3			11.7
	<i>H. melanurum</i>	Pedro Bank (unexploited)	17.2	20.9	21.5	–
		Serranilla Bank	16.5	19.6	20.5	
	<i>H. bonariense</i>	Port Royal	14.8	17.3	18.5	13.5
	<i>H. aurolineatum</i>	Pedro Bank (unexploited)	13.5	15.9	16.5	14.4
	<i>H. chrysargyreum</i>	Port Royal	15.3	–	–	15.0
	<i>A. virginicus</i>	Port Royal	11.8	15.2	16.5	9.9
<i>A. surinamensis</i>	Port Royal	22.9	–	–	10.2	
(ii) Lines	<i>H. plumieri</i>	Pedro Bank (unexploited)	17.5	26.8	29.0	–
	<i>H. album</i>	Pedro Bank (unexploited)	24.5	30.8	33.0	–

Figure 10.20 shows the overlap of length ranges of the catches of *H. plumieri* from the Port Royal Reefs and Pedro Bank is very small, the larger fishes taken at the Port Royal Reefs being of similar size to the smaller fishes taken at Pedro Bank. *H. plumieri* were fully recruited to the Port Royal fishery at 15.5 cm FL, and the mean length at recruitment, l_T , was 14.9 cm. At unexploited parts of Pedro Bank, the modal length of trap catches was 27.5 cm FL and the mean recruitment length was 26.2 cm FL. The sample taken at the Pedro Cays totalled only 95 fishes and cannot be used to assess the effect of the fishery upon the size composition of the populations.

Figure 10.21 shows the estimated mean size compositions of catches of *H. flavolineatum* at the Port Royal Reefs, Pedro Cays and at unexploited parts of Pedro Bank. The pattern is similar to that described for *H. plumieri*, with full recruitment at 17.5 cm FL at the Pedro Cays and at Pedro Bank and at only 14.5 cm FL at the Port Royal reefs. The mean recruitment length is 17.1 cm FL at unexploited parts of Pedro Bank, 16.7 cm FL at the Pedro Cays and 14.2 cm FL at the Port Royal Reefs.

Samples of *H. melanurum* were obtained at unexploited parts of Pedro Bank and by measuring commercial catches from Serranilla Bank. Figure 10.22 shows that the trap catches of unexploited stocks had a modal length of 21.5 cm FL whereas the exploited stocks start to decline in abundance after 20.5 cm FL is attained. The mean lengths at recruitment are 20.9 cm FL and 19.6 cm FL, respectively.

The estimated mean annual size compositions of line catches of *H. album* and of trap catches of *H. aurolineatum* at unexploited parts of Pedro Bank and of trap catches of *H. sciurus*, *H. bonariense* and *Anisotremus virginicus* at the Port Royal Reefs are shown in Fig. 10.23.

Samples of other species of grunts were insufficient for estimation of mean length composition of catches. Data on the observed minimum, mean and full-retention lengths of 12 species of pomadasyids are summarized in Table 10.30. The calculated minimum size retainable by a rigid 4.13 cm wire mesh is also given and is indicative of whether mesh size is the factor determining size at recruitment or whether other factors delay recruitment until a larger size is attained. It appears that the size at recruitment to the Port Royal Reefs fishery is generally determined by the mesh size, but *H. plumieri*, *H. flavolineatum*, *H. album* and probably also *H. melanurum* are not available to the fishery at the Pedro Cays until a size is attained which is substantially larger than that retainable by the 4.13 cm mesh.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

Natural mortality of pomadasyids is caused by predation, disease and senility. However, if fishes above a certain size migrate away from the sampling area this would affect the length composition of the population, thus increasing the apparent natural mortality rate.

Mortality Rates

The mortality rate, Z , can be calculated from length-composition data using the equation developed by Beverton and Holt (1956) and later discussed by Gulland (1965) and Kipling and Frost (1970) (see Chapter 3 for details).

The reliability of mortality rates estimated from length-frequency distributions depends greatly upon the adequacy of population length composition data. Trap fishing at the Port Royal Reefs and at unexploited parts of Pedro Bank provided data giving a good representation of population structure for *H. plumieri*, but catches of other species were comparatively small.

Growth rates and asymptotic lengths have been calculated for *H. plumieri*, *H. sciurus* and *H. album* and

the total mortality rate, Z , (M in unexploited areas) has been estimated for these species (Tables 10.31, 10.34, 10.35). Z/K has been estimated for another five species for which the growth rates are not known, but for which the asymptotic lengths have been approximated (Tables 10.26, 10.32, 10.33, 10.35).

The length-frequency distributions of catches of *H. plumieri* and *H. flavolineatum* at the Port Royal Reefs have been adjusted in the manner described in Chapter 3, because the stocks at the Port Royal Reefs become virtually extinct while still within the length range covered by the recruitment ogive (Figs. 10.20 and 10.21). The adjusted length distribution of catches of *H. plumieri* and *H. flavolineatum* at the Port Royal Reefs and the observed length-frequency distributions at unexploited parts of Pedro Bank and/or at the Pedro

Table 10.31. Derivation of mortality rates from the relative abundances of successive length groups of *Haemulon plumieri* beyond full recruitment to traps (4.13 cm mesh) at the Port Royal Reefs, and at unexploited parts of Pedro Bank. $L_{\infty} = 42$ cm, $K = 0.345$.

Length group cm, FL	Unexploited Pedro Bank		Port Royal Reefs		Adjusted frequency
	% frequency	Relative frequency	% frequency	Relative frequency	
12.0-12.9			0.08	.01	
13.0-13.9			2.83	.24	
14.0-14.9			7.82	.66	
15.0-15.9			11.78	1.00	
16.0-16.9			11.65	.99	
17.0-17.9			11.27	.96	
18.0-18.9			11.02	.94	
19.0-19.9	0.27	.02	8.97	.76	
20.0-20.9	0.57	.03	8.08	.69	
21.0-21.9	0.33	.02	8.18	.69	34.5
22.0-22.9	1.07	.07	6.42	.54	7.7
23.0-23.9	1.13	.07	5.17	.44	6.3
24.0-24.9	4.20	.26	3.80	.32	1.2
25.0-25.9	9.00	.55	1.92	.16	0.3
26.0-26.9	11.80	.72	0.85	.07	0.1
27.0-27.9	16.43	1.00	0.07	.01	+
28.0-28.9	15.30	.93	0.07	.01	+
29.0-29.9	14.83	.90	0	0	0
30.0-30.9	12.60	.77	0	0	0
31.0-31.9	8.03	.49	0	0	0
32.0-32.9	2.40	.15	0	0	0
33.0-33.9	0.83	.05	0	0	0
34.0-34.9	0.37	.02	0	0	0
35.0-35.9	0.07	+	0	0	0
36.0-36.9	0.27	.02	0	0	0
37.0-37.9	0.20	.01	0	0	0
\bar{L}_c		27.0 cm		21.0 cm	
Mean FL		29.45 cm		22.0 cm	
If $L_{\infty} = 42$ cm					
Z/K		$= \frac{42.0 - 29.45}{29.45 - 27.0}$		$= \frac{42.0 - 22.0}{22.0 - 21.0}$	
If $K = 0.345$		$= 5.12 (= M/K)$		$= 20.0$	
Z		$= 1.77 (= M)$		$= 6.90$	
F		$= 0$		$= 5.13$	
E		$= 0$		$= 0.74$	

Table 10.32. Derivation of mortality rates from the relative abundances of successive length groups of *Haemulon flavolineatum* captured in traps (4.13 cm mesh) in various areas. L_{∞} = 25 cm FL, K is unknown.

Length group cm, FL	Unexploited Pedro Bank		Pedro Cays area		Port Royal Reefs		Adjusted frequency
	% Frequency	Relative frequency	% Frequency	Relative frequency	% Frequency	Relative frequency	
12.0-12.9							
13.0-13.9			.3	.01	2.4	.01	
14.0-14.9	.30	.01	2.4	.07	10.6	.30	100.0
15.0-15.9	3.85	.11	11.9	.34	34.3	.96	8.7
16.0-16.9	15.67	.46	26.9	.77	13.5	.38	0.8
17.0-17.9	34.19	1.00	34.8	1.00	3.4	.10	0.1
18.0-18.9	27.44	.80	17.4	.50	0	0	0
19.0-19.9	18.42	.43	5.5	.16	0	0	0
20.0-20.9	4.17	.12	.9	.03	0	0	0
\bar{L}_c	17.0 cm		17.0 cm		14.0 cm		
Mean length	18.36 cm		18.04 cm		14.6 cm		
If L_{∞} = 25 cm	$= \frac{25.0 - 18.36}{18.36 - 17.0}$		$= \frac{25.0 - 18.04}{18.04 - 17.0}$		$= \frac{25.0 - 14.6}{14.6 - 14.0}$		
Z/K	= 4.88 (= M/K)		= 6.69		= 17.33		
F/K	= 0		= 1.81		= 12.45		
E	= 0		= 0.27		= 0.72		

Table 10.33. Derivation of mortality rates from the relative abundances of successive length groups of *Haemulon melanurum* captured in traps (4.13 cm mesh) at Pedro and Serranilla Banks. L_{∞} = 30 cm, K is unknown.

Length group cm, FL	Unexploited Pedro Bank		Serranilla Bank	
	% frequency	Relative frequency	% frequency	Relative frequency
16.0-16.9			.9	.04
17.0-17.9	.2	.01	3.7	.15
18.0-18.9	.4	.02	8.4	.35
19.0-19.9	5.7	.22	18.7	.77
20.0-20.9	12.2	.47	24.3	1.00
21.0-21.9	25.9	1.00	17.8	.73
22.0-22.9	21.2	.82	13.1	.54
23.0-23.9	13.3	.51	9.3	.38
24.0-24.9	13.2	.51	2.8	.12
25.0-25.9	7.3	.28	.5	.02
26.0-26.9	.9	.03	0	0
27.0-27.9	.6	.02	.5	.02
\bar{L}_c	21.0 cm		21.0 cm	
Mean length	23.00 cm		22.53 cm	
If L_{∞} = 30 cm	$= \frac{30.0 - 23.0}{23.0 - 21.0}$		$= \frac{30.0 - 22.53}{22.53 - 21.0}$	
Z/K	= 3.50 (= M/K)		= 4.88	
F/K	= 0		= 1.38	
E	= 0		= 0.28	

Table 10.34. Derivation of mortality rates of *Haemulon album* from the relative abundances of successive length groups captured on hook and line at unexploited parts of Pedro Bank. L_{∞} = 65 cm, K = 0.20.

Length group cm, FL	Unexploited Pedro Bank	
	% frequency	Relative abundance
24.0-25.9	.4	.02
26.0-27.9	5.5	.31
28.0-29.9	11.5	.66
30.0-31.9	16.8	.95
32.0-33.9	17.7	1.00
34.0-35.9	15.8	.89
36.0-37.9	7.1	.40
38.0-39.9	5.3	.30
40.0-41.9	5.4	.31
42.0-43.9	1.4	.08
44.0-45.9	3.5	.20
46.0-47.9	2.4	.14
48.0-49.9	1.6	.09
50.0-51.9	1.9	.11
52.0-53.9	2.1	.12
54.0-55.9	1.3	.07
56.0-57.9	.9	.05
58.0-59.9	0	0
\bar{L}_c	= 32.0 cm	
Mean length	= 38.69 cm	
If L_{∞} = 65 cm	$= \frac{65.0 - 38.69}{38.69 - 32.0}$	
Z/K	= 3.93	
Z	= 0.79 = M	

Table 10.35. Derivation of mortality rates of species of grunts from the relative abundances of successive length groups captured in traps (4.13 cm mesh).

Length group cm, FL	<i>Haemulon aurolineatum</i> Pedro Bank		<i>Haemulon sciurus</i> Port Royal Reefs		<i>Haemulon bonariense</i> Port Royal Reefs		<i>Anisotremus virginicus</i> Port Royal Reefs	
	% frequency	Relative frequency	% frequency	Relative frequency	Number	Relative frequency	Number	Relative frequency
11.0-11.9							1	—
12.0-12.9							2	—
13.0-13.9	1.7	.04					12	—
14.0-14.9	5.5	.13	1.8		1	—	13	—
15.0-15.9	28.9	.67	3.4		12	—	19	—
16.0-16.9	43.0	1.00	5.8		26	—	25	1.00
17.0-17.9	17.9	.42	8.4		29	—	21	.84
18.0-18.9	2.6	.06	9.1		37	1.00	12	.48
19.0-19.9	.4	.01	10.2		11	.30	3	.12
20.0-20.9			14.3	1.00	8	.22	0	0
21.0-21.9			13.7	.96	11	.30	0	0
22.0-22.9			10.0	.70	2	.05	0	0
23.0-23.9			6.3	.44			2	.08
24.0-24.9			6.4	.45				
25.0-25.9			5.3	.37				
26.0-26.9			3.3	.23				
27.0-27.9			1.8	.13				
28.0-28.9			.3	.02				
L_{∞}	= 23 cm		= 40 cm		= 30 cm		= 30 cm	
K	= ?		= 0.26		= ?		= ?	
\bar{I}_c	= 16.0 cm		= 20.0 cm		= 18.0 cm		= 16.0 cm	
Z/K	= $\frac{23.0 - 16.9}{16.9 - 16.0}$		= $\frac{40.0 - 22.8}{22.8 - 20.0}$		= $\frac{30.0 - 19.5}{19.5 - 18.0}$		= $\frac{30.0 - 17.6}{17.6 - 16.0}$	
Z	= 6.78 (= M/K)		= 6.14		= 7.00		= 7.75	
	= ?		= 1.60		= ?		= ?	

Cays are shown in Tables 10.31 and 10.32. As it is possible that errors might arise in making such adjustments, the estimates of mortality rates at the Port Royal reefs should be regarded only as first approximations.

For similar reasons, the estimated values of the ratio Z/K for *H. sciurus*, *H. bonariense* and *A. virginicus* at the Port Royal reefs (Table 10.35) are most probably highly conservative, as the recruitment ogives of unexploited stocks have not been determined.

There is a reasonable degree of uniformity in the calculated values of M/K , Z/K and E which are given in Tables 10.31 to 10.35.

ABUNDANCE AND DENSITY

Density and Biomass

Standing crops of coral reef fishes have been measured by Bardach (1959) in Bermuda, by Randall (1963) in the Virgin Islands, and by Nagelkerken (1971) in Curacao.

Bardach (1959) estimated the summer standing crop of fishes on an isolated reef in Bermuda from underwater fish counts and approximate weights of the species observed. The total weight of fishes on the reef, which

had an area of 1 ha, was estimated to be 490 kg, or 0.049 kg/m². The reef accommodated a large school of *H. sciurus* comprised of an average of 276 individuals with a total weight of about 110 kg. Bardach also made counts on a small area of fringing reef where the standing crop of pomadasysids was found to be much lower. These estimates resulted from counts made in three consecutive years, which all gave very similar figures, indicating small annual changes in density during that period.

In the Virgin Islands, Randall (1963) measured the standing crop of fishes on an isolated artificial reef, with an area of about 50 m², which had been in existence for 2 yr 4 mo. The fishes were collected by encircling the reef with nets, and then applying poison to the area. The estimate of standing crop that he obtained was 1.74 kg/m² or 55.08 fishes/m² which is considerably greater than that obtained by Bardach (1959). Young pomadasysids were the most abundant fishes, comprising 0.74 kg/m² or 37.4 fishes/m², and young *H. plumieri* alone comprised 25.3 fishes/m². Randall also carried out two poison stations at an extensive fringing reef, where he found the standing crop to be very much lower, 0.160 kg/m² or 2.25 fishes/m² and 0.158 kg/m² or 4.90

Table 10.36. Mean catch rates of grunts in baited traps (4.13 cm mesh) at Pedro Bank and California Bank, expressed as numbers per 1,000 hexagonal trap-days.

Species	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank	Pedro Cays area	California Bank
<i>Haemulon aurolineatum</i>	7	335	78	28	0
<i>H. striatum</i>	0	1	0	0	3
<i>H. flavolineatum</i>	3,095	375	1	1,290	173
<i>H. melanurum</i>	326	1	7	23	0
<i>H. album</i>	26	6	11	8	44
<i>H. chrysargyreum</i>	2	0	0	10	0
<i>H. plumieri</i>	262	481	83	97	3
<i>H. carbonarium</i>	5	0	0	25	0
<i>H. sciurus</i>	0	0	0	0	0
<i>H. parra</i>	0	0	0	0	0
<i>H. bonariense</i>	0	0	0	0	0
<i>H. macrostomum</i>	0	0	0	0	0
<i>Anisotremus virginicus</i>	0	0	0	0	0
<i>A. surinamensis</i>	0	0	0	0	0
Total pomadasysids	3,723	1,199	180	1,481	223

fishes/m² respectively and pomadasysids, mainly *A. surinamensis*, *H. flavolineatum* and *H. carbonarium*, comprised only a small proportion.

In Curaçao, Nagelkerken (1971) estimated the standing crop of fishes in zones of *Millepora alcicornis* and *Acropora palmata*. He collected all the fishes from several quadrats of 16 m² in each zone, and he estimated the standing crop of the *M. alcicornis* zone to be 0.167 kg/m² and that of the *A. palmata* zone to be 0.157 kg/m², but no pomadasysids were collected from the quadrats.

Bardach (1959) and Randall (1963) both measured the daytime density of fishes. In both cases, the isolated reefs accommodated large schools of pomadasysids. However, these fishes are merely sheltering on the reef by day, and at night when they move away to feed in adjacent areas, the density of fishes remaining on the reef would be very much less. Thus by day, fishes such as pomadasysids are highly concentrated around small reefs, and an estimate taking into account the extent of adjacent feeding grounds would give a more accurate measure of density.

No direct information on density or biomass of pomadasysids per unit area was obtained during these investigations.

Seasonal Availability

Figure 10.24 shows details of the monthly variations in "availability" (see Munro 1974 and Chapter 3) of pomadasysids at the Port Royal Reefs between January 1970 and January 1972. For most species, availability is at a minimum between September and November, and there is some degree of regularity in the seasonal availability of the four predominant species.

Relative Abundance

The relative abundances of species of grunts at the Port Royal Reefs and at various parts of Pedro Bank and California Bank are given in Tables 10.36 and 10.37. Catch rates are expressed in terms of numbers of fishes theoretically captured in 1,000 hexagonal traps each set for one day.

For most species at Pedro Bank, the greatest relative abundance occurred in the eastern portion of the bank and fewest grunts were found in the deeper western areas where coral cover appears to be less extensive. *Haemulon plumieri* and *H. flavolineatum* are numerically predominant in most areas. *H. sciurus* is abundant at the Port Royal Reefs but absent from Pedro Bank, whereas the situation is reversed in the case of *H. melanurum* and neither species was captured at California Bank.

Within the comparatively small area of the Port Royal

Table 10.37. Mean catch rates of grunts in unbaited traps (4.13 cm mesh) at the Port Royal Reefs in 1970 and 1971, expressed as corrected numerical catch from 1,000 traps each soaked for 1 day.

Species	1970	1971
<i>Haemulon plumieri</i>	265	278
<i>H. sciurus</i>	74	100
<i>H. flavolineatum</i>	91	60
<i>H. bonariense</i>	21	11
<i>H. macrostomum</i>	14	6
<i>H. aurolineatum</i>	3	3
<i>Anisotremus virginicus</i>	4	20
<i>A. surinamensis</i>	4	4
Total pomadasysids	476	482

Reefs, relative abundance of species seems to vary from reef to reef. *H. plumieri* and *A. virginicus* were more abundant at Yahoo Reef than at Nassau Reef, whereas the reverse was true for *H. sciurus*, *H. flavolineatum* and *H. bonariense*.

Haemulon album was taken mainly on lines and the data confirm that this species was more abundant at the

deeper western and eastern extremities of Pedro Bank and at California Bank than in the shallow southern portions of the Pedro Bank. It was never taken at the Port Royal Reef.

In general, the data indicate that pomadasyids are most abundant at unexploited parts of Pedro Bank, and though the Pedro Bank and Port Royal figures cannot be

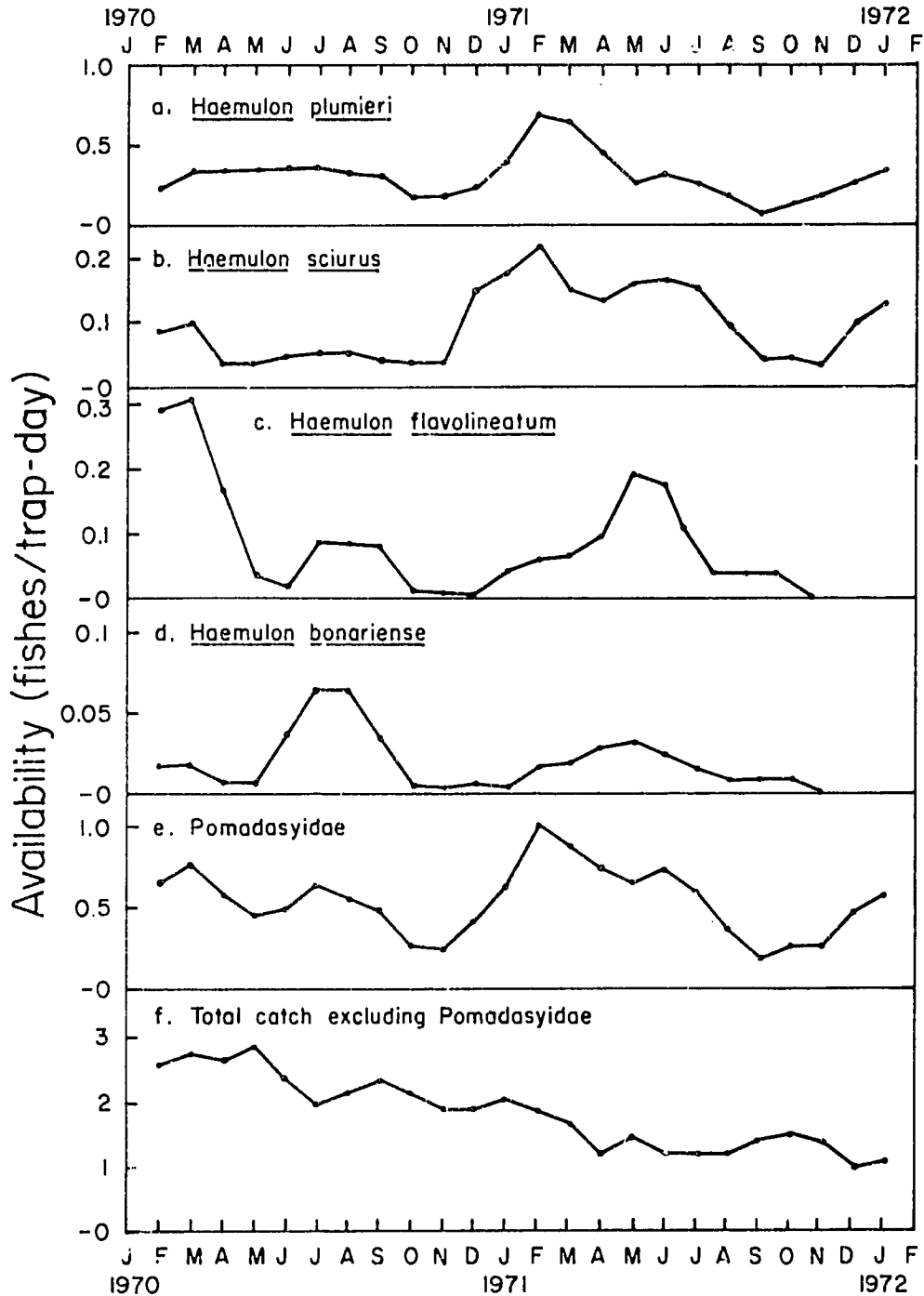


Fig. 10.24. Variations in monthly mean availability of the four commonest pomadasyid species that comprise the trap catch at the Port Royal Reefs. Graphs are smoothed by a moving mean of three.

directly compared because of the use of baited traps offshore, it is probable that the pomadasyids are in fact more abundant at Pedro Bank than at the Port Royal Reefs.

NATALITY AND RECRUITMENT

Reproduction Rates

There are no direct data on reproduction rates because the number of spawning seasons in a year is not known for any species.

The rate of egg production of *H. plumieri* is expected to be much higher on Pedro Bank where the average size of the catch was much greater than on the Port Royal Reefs. Taking the fecundity coefficient and mean weight of mature *H. plumieri* taken on the Port Royal Reefs (about 220 g), the mean fecundity was calculated to be about 42,000 eggs per female per spawning season. However the mean weight of *H. plumieri* in the trap catch on unexploited parts of Pedro Bank was about 400 g and the mean fecundity was calculated to be about 150,000 eggs per female per spawning season.

progress to the right. This indicates that the main months of recruitment extended from May to October. However, fishes in the 14 to 15-cm length group were present in all months showing that some recruitment occurred throughout 1970 and 1971.

Quarterly histograms of trap catches of *H. sciurus* at the Port Royal Reefs (Fig. 10.13) indicate that recruitment took place in the months of August to October in 1970 and 1971.

Data from offshore areas were too scattered to give information on recruitment. However, a catch of *H. album* taken in traps at Morant Bank in July 1970 showed a distinct peak of small fishes which suggests that recruitment might occur at that time.

Indices of recruitment, R' , can be calculated as $R' = (\overline{C/f})Z$, in which $\overline{C/f}$ is the mean catch rate and Z is the total mortality rate. The index, R' , is the theoretical annual number of recruits at the mean retention length, l_r , required to produce the observed catch per unit effort. Mortality rates, Z , are known only for three species; *H. plumieri*, *H. album* and *H. sciurus*. The estimated recruitment indices are summarized in Table 10.38.

Table 10.38. Estimated recruitment indices for species of grunts in various areas.

Species	l_r cm, FL	No. per 1,000 trap-days $\overline{C/f}$	Mortality rate Z	Recruitment index R'
<i>Haemulon plumieri</i>				
E. Pedro Bank	26.2	262	1.77	463
S. Pedro Bank	26.2	481	1.77	851
W. Pedro Bank	26.2	83	1.77	147
Port Royal Reefs	14.9	265-278	6.9	1,828-1,918
<i>H. album</i>				
E. Pedro Bank	28	26	0.79	21
S. Pedro Bank	28	6	0.79	5
W. Pedro Bank	28	11	0.79	9
<i>H. sciurus</i>				
Port Royal Reefs	18.5	74-100	>1.6	>118-160

Recruitment

Continuous trap fishing on the Port Royal Reefs over a 2-yr period provided information about months of recruitment of *H. plumieri* and *H. sciurus*, but data were insufficient for any other species. Lengths of eleven species at minimum, mean and full recruitment to traps (mesh size 4.13 cm) are listed in Table 10.30.

Bimonthly histograms of trap catches of *H. plumieri* at the Port Royal Reefs (Fig. 10.5) show a stationary mode at 16.5 cm from May to October in 1970 and 1971, and in subsequent months the mode begins to

DYNAMICS OF THE POPULATIONS

No detailed yield assessments for any pomadasyid species are possible using the present data. However, certain generalizations can be made from the yield function tables prepared by Beverton and Holt (1964). Values of L_∞ , l_r , M/K and E for eight species are given in Tables 10.30-10.35. Reference to the yield function tables indicates that all values of c ($= l_r/L_\infty$) are above the eumetric level at all rates of exploitation.

There is no direct information on rates of recruitment to pomadasyid populations. However, estimates of M/K

and Z/K are high and therefore estimates of yield per recruit (Beverton and Holt 1964) would be correspondingly low. No evidence was found to suggest a decline in any of the pomadasiid populations studied, and in order to maintain the population against a high mortality rate,

the rate of recruitment must also be high.

Availability data (Table 10.37 and Fig. 10.24) pertaining to species on the Port Royal Reefs show that the abundance of pomadasyids remained fairly constant in 1970 and 1971.

CHAPTER 11:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE GOATFISHES, MULLIDAE

by
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Identity

The distinguishing characteristics of the Atlantic Mullidae are the presence of a pair of long barbels on the chin, two well-separated dorsal fins, two spines on the anal fin and a forked tail (Bohlke and Chaplin 1968).

The Atlantic species have been adequately described by Randall (1968), Bohlke and Chaplin (1968) and Jordan and Evermann (1896), who give full details of coloration and distinguishing characteristics.

Four species in four genera are known from the western Atlantic:

Pseudupeneus maculatus (Bloch) 1793—Spotted goatfish

Mulloidichthys martinicus (Cuvier and Valenciennes) 1829—Yellow goatfish

Mullus auratus (Jordan and Gilbert) 1882

Upeneus parvus (Poey) 1851

Their synonymy and morphological details are given by Jordan and Evermann (1896) and by Caldwell (1962). There are no reports of any geographic variations or of the existence of any sub-populations.

Distribution

Mullus auratus is a northern species distributed from Nova Scotia as far south as the Campeche Bank off Yucatan, but apparently is uncommon in the Caribbean Sea (Caldwell 1962). *Upeneus parvus* is found in the Gulf of Mexico, off eastern Florida and the north-eastern coast of South America. Lachner (1954, quoted by Caldwell 1962) stated that this species has also been recorded from Cuba and Puerto Rico, and Caldwell (1966) recorded *U. parvus* from a fish trap at Port Antonio, Jamaica and from a trawl catch taken on the southwest coast of Jamaica. Randall (1968) states that the abovementioned species are characteristic of mud or

silty bottoms in deeper water.

Reef areas between Brazil and the southeastern coast of the United States, and including the Bahamas and the Greater and Lesser Antilles are inhabited by *Mulloidichthys martinicus* and *Pseudupeneus maculatus* and both of these species were captured during these investigations. Randall (1968) states that the adults inhabit reef-sand areas while the young are commonly seen over seagrass beds. The larvae and post-larvae are pelagic (although this has not been confirmed for *M. martinicus*) and metamorphose and transfer to the demersal habitat at sizes of around 4 to 8 cm (Caldwell 1962).

Bionomics and Life History

REPRODUCTION

Gonads

The gonads of *P. maculatus* and *M. martinicus* are unexceptional in appearance. Ripe ovaries are bright yellow.

Sexuality

There is no evidence of any hermaphroditism or intersexuality in the Mullidae.

Figures 11.1a and b show the size distributions of male and female *P. maculatus* captured in fish traps (4.13 cm mesh) on the oceanic Pedro and California Banks and at the Port Royal Reefs. In each case, the males are significantly larger and relatively more abundant than the females, suggesting sexual dimorphism in either relative or absolute growth rates or mortality rates. Caldwell (1962) states that "the males tend

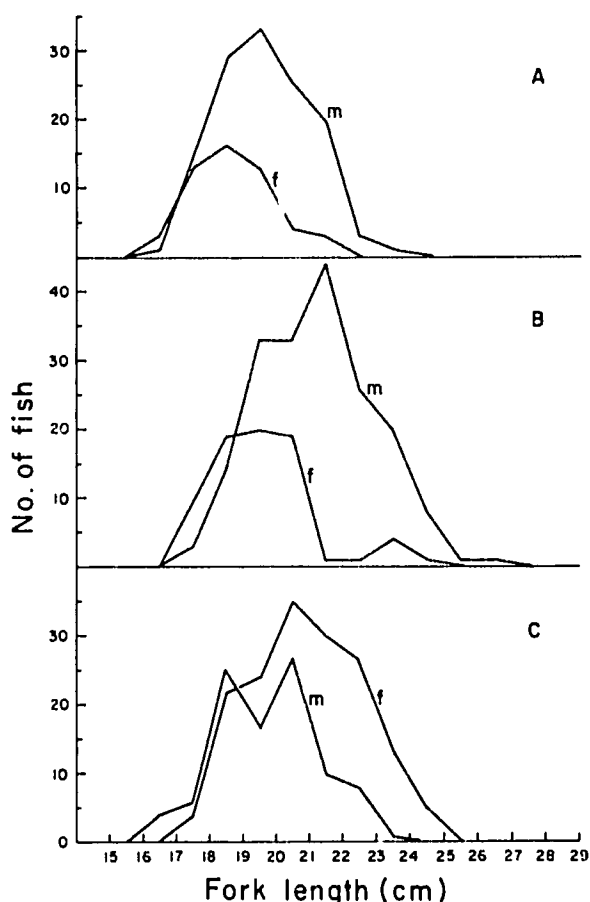


Fig. 11.1. Length-frequency distributions of trap catches of male (m) and female (f) mullids: (a) *Pseudupeneus maculatus* from the Port Royal Reefs. (b) *P. maculatus* from Pedro Bank and California Bank. (c) *Mulloidichthys martinicus* from all sampling areas.

to have higher arched backs and more angular facial profiles whereas the females tend to be more fusiform and have a sloping facial profile," and states that these differences become more pronounced with increasing size.

In contrast to *P. maculatus*, the samples of *M. martinicus* (Fig. 11.1c) showed a predominance of females and the mean size of males was about 1 cm smaller than that of the females. The maximum and minimum sizes captured were also about 1 cm less. This is probably a result of sexually dimorphic growth patterns; below 21 cm FL the males are slightly deeper-bodied and heavier than females of the same length.

Maturity

Table 11.1 shows that the smallest ripe male *P. maculatus* measured about 17.5 cm FL (97 g) and that full maturity is reached at about 18.5 to 19.5 cm FL (116 to 137 g). In the case of the females several of the smallest individuals retained by the 4.13 cm mesh were ripe and the size at maturity is probably less than 16 cm FL (80 g).

Male *M. martinicus* appear to first mature at approximately 18.5 cm FL (118 g) and females at or before 17.5 cm FL (90 g) and full maturity is attained within 1 cm of the abovementioned lengths (Table 11.1).

Fecundity

Estimates of the fecundity of *P. maculatus* and *M. martinicus* are not given in the literature, and no estimates were made during this study.

Mating and Fertilization

Randall and Randall (1963) reported that *P. maculatus* aggregated in large groups to spawn and that eggs and milt were released by groups of fishes after a rapid vertical ascent from the aggregation. Fertilization is thus external. This behavior is also found in parrotfishes, surgeonfishes and wrasses.

Spawning Seasons

Gonads of 456 mature *P. maculatus* were examined between January 1970 and February 1973. The results are shown in Fig. 11.2a. No ripe-running or spent fishes were captured. The main spawning period was from January to April with a subsidiary peak in October. No specimens were obtained in June of any year, and no ripe fishes were found in July and August. From the occurrence of 40-mm juveniles, Caldwell (1962) suggested that the spawning season of *P. maculatus* was protracted. This is confirmed here.

In the case of *M. martinicus*, the gonads of 279 mature fishes were examined. Owing to the relatively

Table 11.1. Proportions of mature male and female *Pseudupeneus maculatus* and *Mulloidichthys martinicus* in successive length groups. All specimens captured in traps at Port Royal Reefs or at oceanic banks.

Median fork length (cm)	<i>P. maculatus</i>				<i>M. martinicus</i>			
	Females		Males		Females		Males	
	No. examined	% ripe	No. examined	% ripe	No. examined	% ripe	No. examined	% ripe
16.5	1	0	3	67	4	0	--	--
17.5	18	6	22	56	6	0	4	25
18.5	43	26	35	34	25	20	22	45
19.5	66	27	33	42	17	41	24	33
20.5	58	17	23	35	27	33	35	34
21.5	63	17	4	0	10	30	30	20
22.5	29	17	1	100	8	13	26	35
23.5	21	9	4	0	1	100	13	38
24.5	8	25	1	0	--	--	5	40
25.5	1	0	--	--	--	--	--	--
26.5	1	0	--	--	--	--	--	--

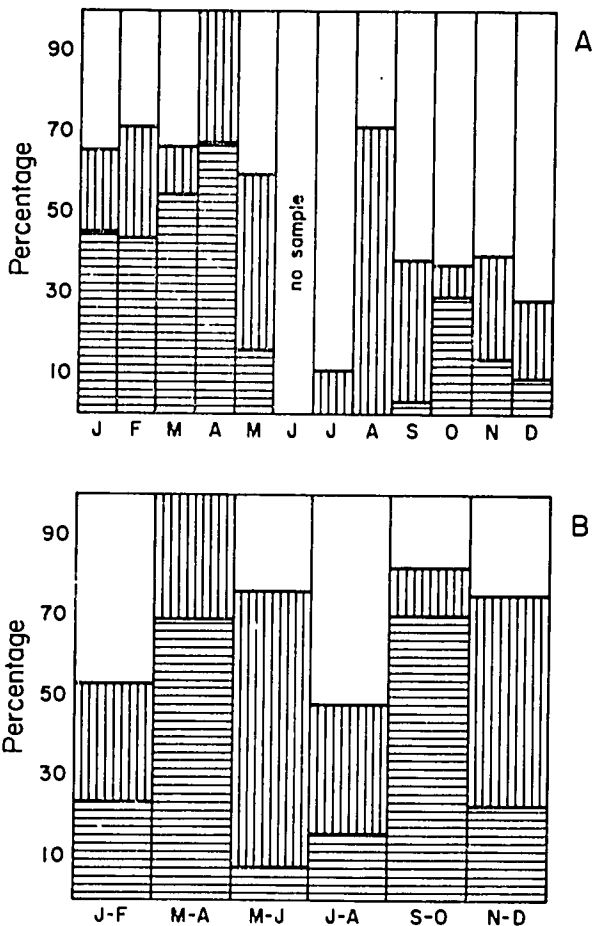


Fig. 11.2. Seasonal variations in the percentage of ripe (cross-hatched), active (vertically hatched) and inactive (unshaded) mullids in Jamaican waters. Data for 1968-1973 combined on a monthly or bimonthly basis. (a) *Pseudupeneus maculatus*; (b) *Mulloidichthys martinicus*.

small size of the sample, the results have been combined on a two-monthly basis (Fig. 11.2b). Spawning occurs mostly in March-April and September-October and few fishes with ripe gonads were found at other times, particularly in the summer months.

It is not known whether individual fishes spawn twice each year or whether only a part of the population spawns in each of the main spawning periods.

Spawn

The unfertilized and fertilized spawn of *P. maculatus* and *M. martinicus* have not been described.

LARVAL AND JUVENILE PHASE

Details of the eggs, larvae and juveniles of Mediterranean species of Mullidae are given by Montalenti (1937). Similar details are not available for western Atlantic mullids.

Embryonic Phase

The embryonic stages of the western Atlantic species of goatfish have not been described.

Larval Phase

The smallest individuals of *P. maculatus* so far described (Caldwell 1962) are of 18.5 mm and 21.5 mm SL, taken in the Gulf Stream and the northern Gulf of Mexico, respectively. The pelagic post-larval stage of *P. maculatus* is illustrated by Caldwell and metamorphosis to benthonic adolescents occurs from lengths of 41 mm SL upwards, but might be delayed until 61 mm SL is attained. Presumably, the metamorphosis can be delayed until shallow water is encountered.

The post-larvae of *M. martinicus* are not described,

the smallest benthonic specimen recorded by Caldwell being of 82.5 mm SL.

Larval and post-larval mullids have been reported as commonly occurring in the food of tunas (Dragovitch 1970), but no description of the larvae has been found in the literature.

Juvenile Phase

During these investigations, the juvenile stages of *P. maculatus* and *M. martinicus* have commonly been seen in shallow, sheltered areas around reefs, *Thalassia* beds and in embayments, and are often mixed with schools of juvenile grunts. Very large schools of juvenile *M. martinicus* were observed by day sheltering in dark, wave-formed caves at Negril, Jamaica, in December 1973. Presumably, they emerge from these sheltered areas at night and feed in the surrounding area.

No details of their ecology are known, but the juveniles presumably have similar feeding habits to those of the adults.

ADULT PHASE

Competitors

According to the analyses of Randall (1967), *P. maculatus* and *M. martinicus* might be, to some extent, competitive for the same foods. Other obvious competitors for food include a wide assemblage of species of grunts, wrasses and small jacks, particularly *Caranx ruber* (Wicklund 1972).

Predators

Randall (1967) recorded specimens of *P. maculatus* from the stomachs of *Fistularia tabacaria*, *Aulostomus maculatus*, *Epinephelus striatus*, *Lutjanus analis*, *L. jocus*, *Caranx fuscus* and *C. ruber*. *M. martinicus* was found in the stomachs of specimens of *Epinephelus guttatus* and *Euthynnus alletteratus*.

It thus seem likely that they commonly fall prey to most of the larger reef predators including sharks, groupers, snappers and jacks. It is possible that the specimen of *M. martinicus* in the stomach of one little tuna, *E. alletteratus* was a pelagic juvenile.

The pelagic larval and post-larval stages of mullids are heavily preyed upon by tunas and in the Caribbean region comprise nearly 11% (by volume) of the diet of skipjack (*Katsuwonus pelamis*), but were not identified from the stomachs of yellowfin tuna (*Thunnus albacares*) (Dragovitch 1970). Bane (1965, cited by Dragovitch 1969) reported goatfishes from the stomachs of blackfin tuna (*T. atlanticus*) taken near Puerto Rico and suggested that the tuna might be feeding close to the bottom. However, the size ranges cited by Bane (5 to 7 cm) are close to the sizes at which mullids are reported

to metamorphose, and it is possible that they were taken in the pelagic zone.

Parasites, Diseases, Injuries and Abnormalities

No parasitized, diseased, injured or abnormal goatfish have been recorded.

Longevity

There is no direct evidence concerning the longevity of western Atlantic goatfishes. From the evidence on age and growth and population structure it would appear that attainment of an age exceeding 5 yr would be most exceptional.

Hardiness

Goatfishes appear to be rather delicate creatures and do not readily survive handling or even brief periods of removal from water. Salinity and temperature tolerances are unknown.

NUTRITION AND GROWTH

Feeding

The mullids feed primarily over muddy or sandy bottoms upon surface or sub-surface-dwelling invertebrates. The long barbels are swept over or through the sediments and are presumably receptive to contacts with prey animals (Randall 1967). Bohlke and Chaplin (1968) suggest that *M. martinicus* feeds mostly at night, whereas *P. maculatus* may feed mostly by day. However, both species have been observed feeding by day during these investigations.

Food

Randall (1967) reported on the stomach contents of 23 specimens of *M. martinicus* and 27 specimens of *P. maculatus*. The samples suggested that both species have similar food preferences, but that *M. martinicus* consumes a greater variety of foods. In the case of *P. maculatus*, crabs (30.2%), shrimps (21.8%) and polychaetes (13.3%) collectively comprised over 65% by volume of the diet, whereas polychaetes (18.6%), crabs and crab larvae (15.9%), pelecypods (13.1%), shrimps and shrimp larvae (11.9%) and ophiuroids (8.9%) comprised the dominant elements in the food of *M. martinicus*. Thus, while there are differences in the proportions of the items observed in the samples, it appears that the species, to a considerable extent, are competitive in their food requirements. There is some evidence of a degree of separation of the species by depth zones, and *P. maculatus* is relatively more abundant in deeper shelf areas having a relatively sparse cover of coral.

Growth Rates

Relative growth patterns

Pseudupeneus maculatus: The length-weight relationships of male and female *P. maculatus* within the range of 16 to 23 cm FL are described by the following equations:

$$\text{for males, } W = 0.0099 L^{3.210}$$

$$\text{for females, } W = 0.0552 L^{2.626}$$

where *W* is the weight in grams and *L* is the fork length in centimeters. There is thus marked allometric growth in both sexes, and this confirms Caldwell's (1962) observation that the differences in the shapes of males and females were more pronounced with increase in size.

The relationship between fork length (FL) and standard length (SL) is

$$FL = 1.08 SL$$

$$\text{or } SL = 0.93 FL$$

The maximum body depth (MD) of *P. maculatus* is about 0.254 FL or FL = 3.93 MD.

Mulloidichthys martinicus: The length-weight relationships within the range 18 to 23 cm FL are described by the following equations:

$$\text{for males, } W = 0.0820 L^{2.493}$$

$$\text{for females, } W = 0.0089 L^{3.223}$$

where *W* is the weight in grams and *L* is the fork length in centimeters.

The markedly allometric growth is the reverse of the case with *P. maculatus*, and the males tend towards a more fusiform shape but are relatively heavier below 21 cm FL.

The relationship between fork length (FL) and standard length (SL) is

$$FL = 1.05 SL$$

$$\text{or } SL = 0.96 FL$$

and the maximum body depth

$$MD = 0.249 FL$$

$$\text{or } FL = 44.01 MD.$$

The maximum size

Pseudupeneus maculatus: Randall (1968) reports that *P. maculatus* reaches a maximum size of about 11 in (27.9 cm) TL, and Bohlke and Chaplin (1968) state that this species grows to about 10 in (25.4 cm) SL. The largest male captured during these investigations measured 26.4 cm FL and the largest female measured 24.9 cm FL.

Apparently, the asymptotic lengths of males and females are in the region of 27.0 cm FL and 25.0 cm FL, respectively. Using the length-weight conversions, the calculated equivalent weights are 362 g and 256 g, respectively.

Mulloidichthys martinicus: This species is reported by Bohlke and Chaplin (1968) to reach a maximum size of

"about one foot" (30.5 cm SL), and Randall (1968) illustrates a specimen of 12.9 in (32.8 cm) TL and states that they have been recorded to about 15.5 in (39.4 cm) TL in Venezuela. The largest specimen recorded during these investigations was of 28.3 cm FL (430 g). The sex was not determined.

It appears that the asymptotic size of females might be in the vicinity of 30 cm FL and 513 g. The largest male was 1 cm smaller than the largest female (Fig. 11.1c) and the asymptotic size of males might be in the region of 29 cm FL and 363 g.

Age and growth

The monthly length-frequency distributions of *P. maculatus* and *M. martinicus* did not show clear modal progressions. This is probably a result of the relatively small samples, the extended or biannual spawning season and, possibly, the apparent ability of the pelagic post-larvae to delay metamorphosis (Caldwell 1962). However, the mullids are among the few species in the region which show well-defined periodic marks on the scales (R. Thompson, unpublished report). The results of scale analyses (done by R. Thompson) used in conjunction with the limited length-frequency data have been sufficient to provide preliminary growth estimates.

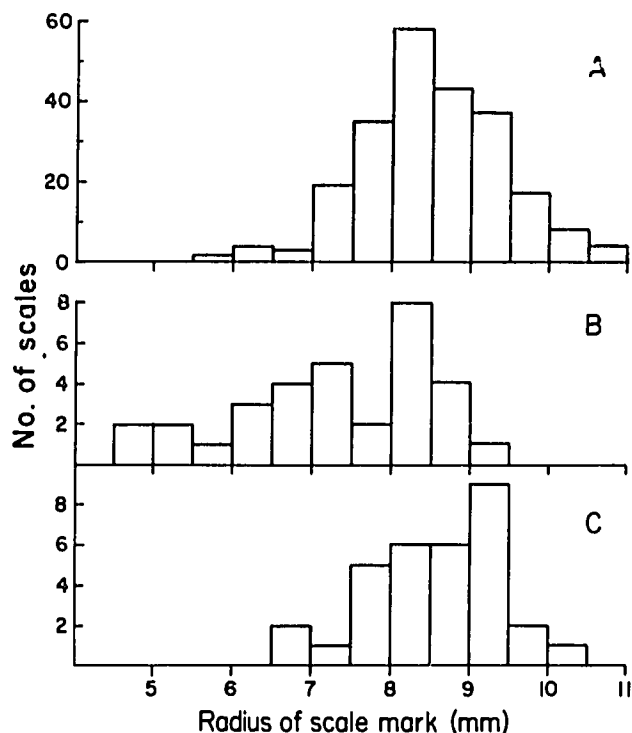


Fig. 11.3. Frequency distributions showing radii at which marks were observed on the scales of a sample of 619 *Pseudupeneus maculatus* from the Serranilla Bank and Pedro Bank. (a) Position of mark on scales having one mark only; (b) Position of first mark on scales having two or more marks; (c) Position of second mark on scales having two or more marks.

Pseudupeneus maculatus: Samples of scales of *P. maculatus* were taken from commercial catches from the Serranilla Bank between June and October 1971, and smaller samples were obtained from Pedro Bank and Port Royal. Except for samples from the Port Royal Reefs, it was not possible to determine the sex of each fish nor to measure all fishes and the data are therefore mostly for males and females combined, and lengths of fishes have been back-calculated from the scale radius-fork length relationship.

The relationship between scale radius and fork length was found to be linear over the range from 17 to 26 cm FL (regression techniques follow Ricker 1973) and can be described as Fork Length = $24.12 \times$ Scale Radius.

Of the 619 sample scales, 300 showed one or more marks. Scales which bore one ring ranged from 7.3 mm to 10.8 mm radius (mean 9.1 mm), whereas scales which showed no marks had radii of 6.4 to 10.2 mm and a mean radius of 8.4 mm.

The scales of 27 males and 11 females from the Port Royal Reefs showed that the first annuli developed at mean sizes of 18.6 cm FL and 16.8 cm FL, respectively.

Figure 11.3 shows that in the case of samples from the Serranilla Bank, the first ring is formed at radii between 4.5 and 11.0 mm, with a pronounced mode at a scale radius of 8.0 mm to 8.5 mm, equivalent to a fork length of 19.3 to 21.5 cm. The mean position of this ring was 8.4 mm from the focus, equivalent to a fork length of 20.2 cm. In the case of scales with two rings, the position of the first ring was bimodally distributed at 7.0 to 7.5 mm and 8.0 to 8.5 mm, while the position of the second ring had a skewed unimodal distribution with the mode at 9.0 to 9.5 mm and relatively large number of rings within the 7.6 to 9.0 mm size range. This suggests that the females might attain maturity at scale radii of 7.0 to 7.5 mm (17 to 18.1 cm FL) while males mature at scale radii of 8.0 to 8.5 mm (19.5 to 20.5 cm FL). The position of the second ring suggests that a length of 21.9 to 22.9 cm FL, equivalent to a scale radius of 9.0 to 9.5 mm, is attained by the males at the next spawning season. The females might attain their second ring at a scale radius of about 7.5 to 8.0 mm (equivalent to about 18.7 cm FL) or less. This is highly conjectural and is supported only by the fact that several length-frequency samples were bimodal with the modes 2 cm apart, which would conform with the rate of increase suggested above.

The abovementioned lengths at ring formation are close to the sizes at sexual maturity which were previously estimated and it is concluded that it is likely, but unproven, that the scale marks are formed as a result of gonad maturation. It is therefore also likely that scale marks are formed in April and October of each year, but it is possible that only a part of the population spawns in autumn (Fig. 11.2a).

For the sample from the Serranilla Bank, the extent of the mean marginal increment was 0.21 mm in June 1971 and increased to 0.31 mm in July and to 0.67 mm by September 1971 (Fig. 11.4), suggesting an increase in

size of about 1.6 cm FL from 20.2 cm FL to about 21.8 cm FL, between April and September. This increase conforms with the increases in size of males which were deduced from the interval between marks on two-ringed scales. [It is important to bear in mind that the females are never fully recruited to the fishery and are under-represented in the samples (Fig. 11.1).]

In summary, it is estimated that males usually attain maturity at a length of about 20.2 cm FL and reach about 22.2 cm FL at the subsequent spawning. In contrast, the females appear to attain maturity at a length of only 17.5 cm and reach 18.7 cm FL by the following spawning season (Fig. 11.5).

From the foregoing it is deduced that the rate of growth, K , is about 0.70 in the case of males when L_{∞} is 27.0 cm FL. For females, K is about 0.35 when L_{∞} is 25 cm FL.

Mulloidichthys martinicus: The samples of this species were too infrequent and small for an analysis of modal progression in length frequency distributions. However, the data suggest that recruits enter the fishery at a size of about 18.5 cm between August and October and reach a modal size of 20.5 cm FL by December, and a length of 23.5 cm FL is attained by the following December.

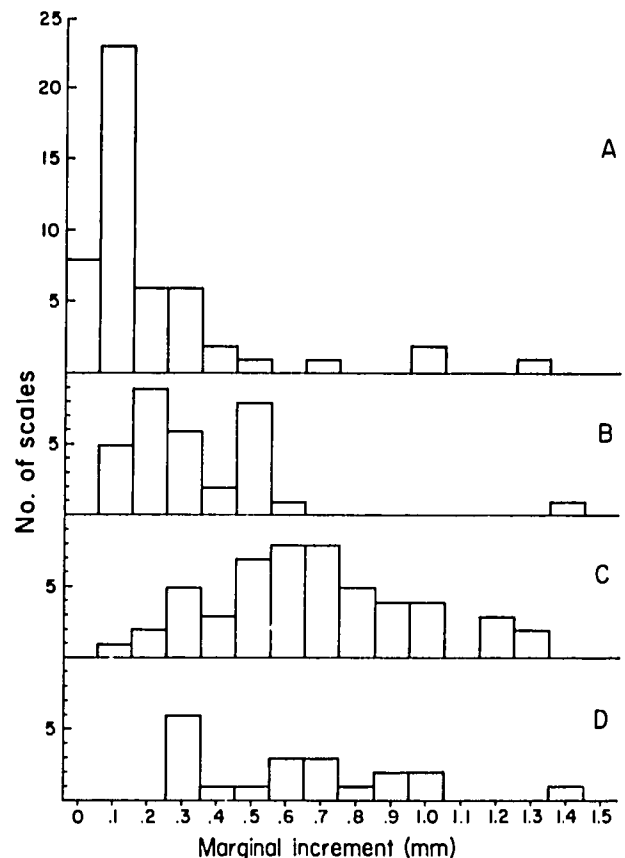


Fig. 11.4. Marginal increments (distance from scale mark to margin of scale) in samples of scales of *Pseudupeneus maculatus* from the Serranilla Bank (a) June 1971, N = 50; (b) July 1971, N = 31; (c) September 1971, N = 52; (d) October 1971, N = 20.

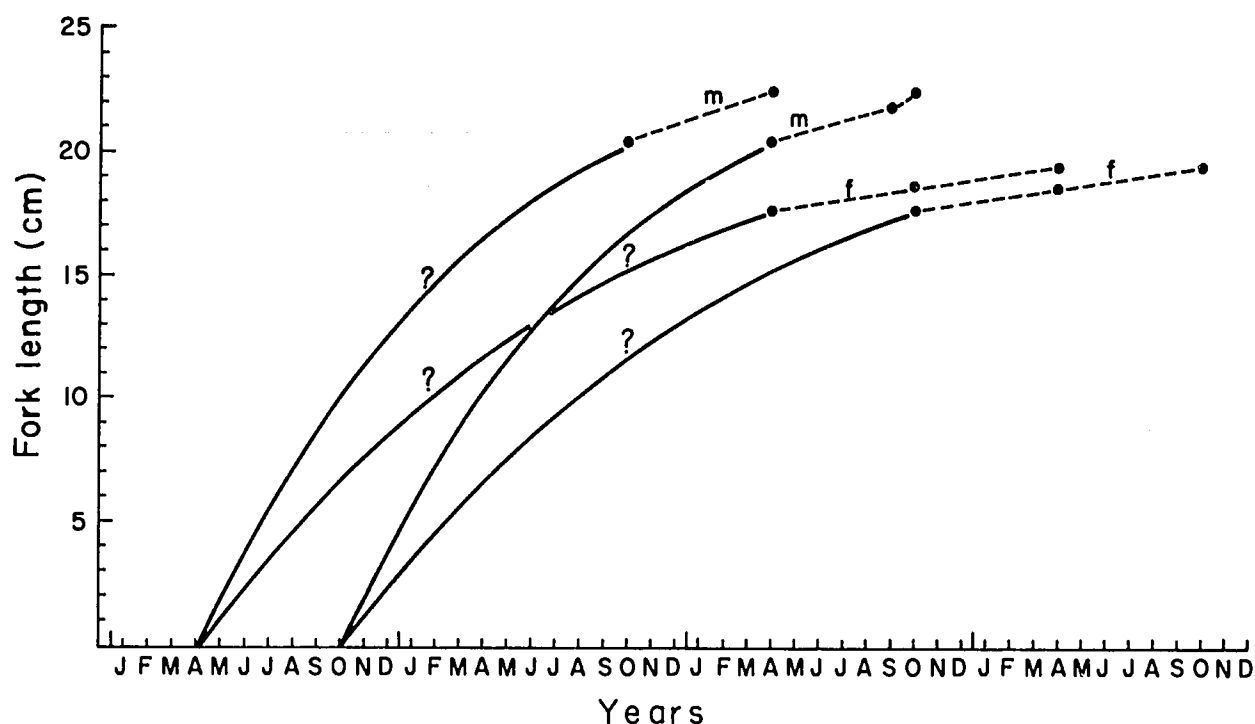


Fig. 11.5. Estimated growth in length of male (m) and female (f) *Pseudupeneus maculatus*. See text for details. The points of origin of the curves might be ± 6 months in error.

A small sample of 42 scales was obtained in September 1971, from commercial catches from Bajo Nuevo and the Pedro Cays. Nineteen of these scales had at least one mark, and 3 scales had two marks. The first mark was at a mean radius of 8.74 mm and the second at 8.93 mm. The sex of the fishes was not determined. The scale radius-fork length relationship is linear over the range from 17 to 28 cm FL and the relationship is: Fork Length = 23.82 Scale Radius.

The first mark is thus formed at a mean fork length of about 20.8 cm, and the second mark is formed at 21.3 cm FL. The marginal increment of the samples varied between 0.2 and 1.4 mm, with a mean of 0.58 mm, implying an average increase of 1.4 cm FL between the spawning season in March-April and September when the samples were obtained. This is approximately the same rate of increase as suggested by the length-frequency distributions.

If the asymptotic lengths of males and females are about 29 cm and 30 cm FL, respectively, the rate of

growth is in the region of $K = 0.4$. It is emphasized that these conclusions are based upon the minimum of evidence. The males are incompletely recruited to the fishery, and it is therefore likely that the data refer mostly to females and that the males have a lower rate of growth.

BEHAVIOR

Adult *M. martinicus* and *P. maculatus* both commonly occur in mixed feeding aggregations together with grunts, wrasses, surgeonfish and other common reef species.

There is no indication that local or regional migrations occur and it appears likely that both species never move significant distances away from the point of settlement of the oceanic pelagic phase.

There is no information on the responses of goatfishes to any environmental or other stimuli.

Populations

POPULATION STRUCTURES

Sex Ratios

The sex ratios of the populations of goatfishes are unknown. The sex ratio of samples of *P. maculatus* captured in traps (4.13 cm mesh) is M:F = 1:0.41 at the

Port Royal Reefs and M:F = 1:0.40 at Pedro Bank. This deviation from the usual is undoubtedly the result of the differential growth rates of the sexes which results in the females reaching a retainable size at a greater age than the males.

In the case of *M. martinicus*, the sex ratio of samples taken in traps was M:F = 1:1.52 in offshore areas, and

1:1.86 at the Port Royal Reefs. As shown in Fig. 11.1c, the females are of substantially larger average size than the males and it is therefore likely that, in contrast to *P. maculatus*, the males grow more slowly than the females and are recruited to the fishery at a greater age.

Age and Length Compositions

As the absolute age-size relationships of *P. maculatus* and *M. martinicus* are unknown, there is no information on the age composition of the population or of the catch. However, the evidence on size composition and growth rates suggests that the majority of individuals do not survive the third year of life.

Pseudupeneus maculatus: The size composition of samples of *P. maculatus* captured at Pedro Bank in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones were compared (Fig. 11.6a). The ranges, modes and

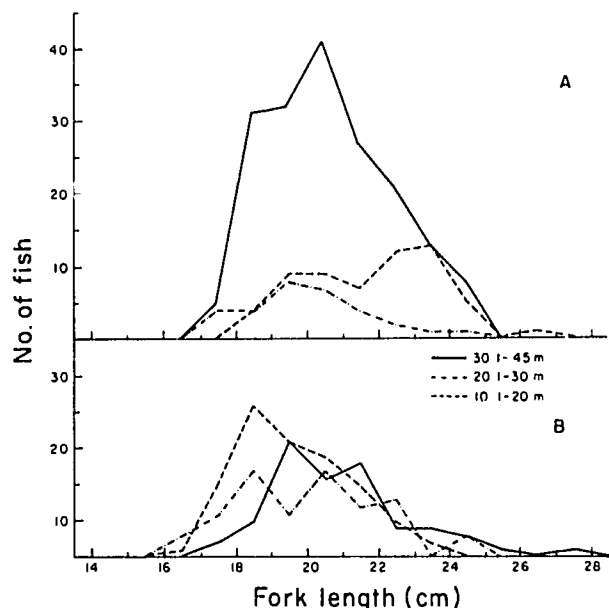


Fig. 11.6. Length-frequency distributions of trap catches of (a) *Pseudupeneus maculatus* and (b) *Mulloidichthys martinicus* from the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones of Pedro Bank.

means of the samples did not vary according to depth and it is concluded that mature fishes occur in all depths on the shelf. It is possible that immature adolescent stages might prefer shallow waters if they are available, but as substantial catches have been obtained on California Bank which has a minimum depth of about 30 m, and at northwestern Pedro Bank, at least 130 km from the nearest shallows, this is unlikely to be a major factor affecting any relationship between size and depth.

The overall size compositions of the populations are unknown. The size compositions of the catches of male *P. maculatus* at Port Royal Cays, and at the unexploited parts of Pedro Bank are shown in Fig. 11.7. There is no reason to suppose that traps are selective above the size

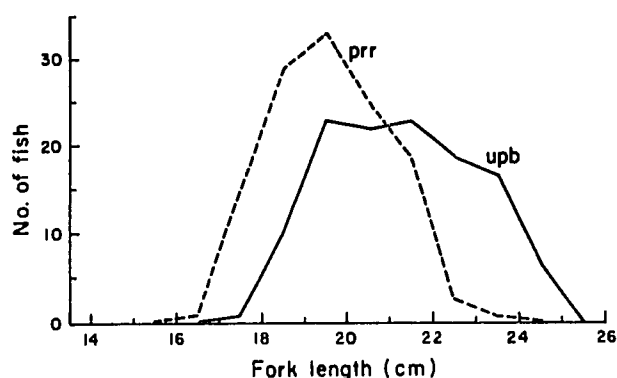


Fig. 11.7. Comparison of estimated mean annual length-frequency distributions of catches of male *Pseudupeneus maculatus* from the exploited Port Royal Reefs (prr) and from the unexploited portions of Pedro Bank (upb). Both estimates are classified as "poor" (see Chapter 3 for details) owing to the relatively small sample size.

which is fully retainable by the mesh, and the trap catch length composition above 21.0 cm is, therefore, probably representative of the population size composition in the case of the males. In the case of the females, only ten specimens measuring more than 21.0 cm FL were obtained (of a total catch of 126 females), and the catch size composition is clearly the result of the interaction of the selective characteristics of the mesh and the population length composition.

Based on the maximum body depth-fork length relationship, the minimum size theoretically retainable by a mesh of 4.13 cm maximum aperture is 16.2 cm FL. The smallest individual taken in our traps was a female of 16.5 cm FL. However, it is clear from the size distribution of the catch that the species is not fully retainable by the mesh until the 21.0 to 21.9 cm length group is attained, and that below this size an increasing proportion of individuals are able to force an exit through the mesh. The mean size at first capture is about 19.0 cm FL.

Mulloidichthys martinicus: The size compositions of catches of *M. martinicus* from the 10.1 to 20-m, 20.1 to 30-m and 30.1 to 45-m depth zones of Pedro Bank did not differ significantly in terms of range, mean or mode (Fig. 11.6b), and it is concluded that with respect to size this species is homogeneously distributed over the depth zones fished.

The overall average size composition of the trap catches from unexploited parts of Pedro Bank is shown in Fig. 11.8. The frequency distributions of those parts of the catch which were sexed are also included. It is apparent that the broad mode of the catch length frequency distribution results from the substantially smaller modal size of the males. A similar, smaller sample from the Pedro Cays has the mode at 20.5 cm, and it is concluded that the populations are not fully recruited to the fishery until a size of over 20 cm FL is attained.

The theoretical minimum size retainable by mesh of

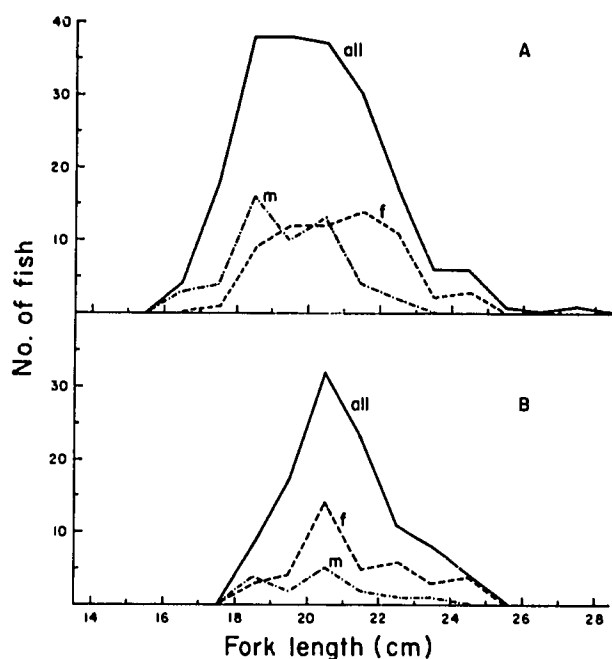


Fig. 11.8. Comparisons of estimated mean annual length-frequency distributions of male (m) and female (f) and of male, female and unsexed (all) *Mulloidichthys martinicus* captured in traps (4.13 cm mesh) at (a) unexploited parts of Pedro Bank and (b) the exploited Pedro Cays area.

4.13 cm maximum aperture is 16.6 cm FL, and the smallest individual actually retained in the traps was 16.2 cm FL. The fishes are not fully retainable until a length of over 20.0 cm is attained (Fig. 11.8a, b) and the mean size at recruitment is 19.3 cm FL.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

There is no direct evidence concerning natural factors responsible for mortality of adolescent or adult goatfishes. However, it would appear likely that the major source of mortality might be predation by groupers, jacks and snappers, and eels and sharks might also be involved. No heavy infestations of parasites were observed.

In the nearshore areas of the Jamaican shelf, at California Bank and at the Pedro Cays, trap fishing is undoubtedly a major cause of mortality. Mullids are also captured in beach seines in back reef areas.

Mortality Rates

As the age compositions of samples of *P. maculatus* or *M. martinicus* are not known, the mortality rates cannot be directly calculated, and recourse must be made to estimates based on assumptions that growth and mortality rates conform with theoretical patterns.

Pseudupeneus maculatus: From the data on size composition (Fig. 11.7), the relative mortality rates can be approximately estimated for male *P. maculatus* at Port Royal and the unexploited parts of Pedro Bank. Other areas did not yield samples of sufficient size upon which such estimates could be based.

Table 11.2 shows the relative rates of decline in abundance of successive length groups of male *P. maculatus* beyond full recruitment at a length, l_c , of 21.0 cm. If the asymptotic fork length can be reasonably be set at 27.0 cm the ratio Z/K can be calculated as

$$Z/K = (L_{\infty} - \bar{l}) / (\bar{l} - l_c) \quad (\text{Beverton and Holt 1956})$$

At the Port Royal reefs,

$$Z/K = 7.45$$

and at unexploited Pedro Bank,

$$Z/K = M/K = 2.70$$

If, owing to the relative absence of predators, the value of M/K at Port Royal is not greater than 2.70, then the value of F/K is not less than $7.45 - 2.70 = 4.75$. If the growth estimates are reasonably accurate (in fact, they are rather speculative) and the growth coefficient $K = 0.70$, then

$$M = 2.70 K = 2.70 \times 0.70 = 1.89$$

and at Port Royal

$$F = 4.75 K = 4.75 \times 0.70 = 3.33$$

Table 11.2. Comparison of the relative abundance of successive length groups of male *Pseudupeneus maculatus* beyond full recruitment at 21.0 cm FL at the Port Royal Reefs and the unexploited parts of Pedro Bank. Only a very small fraction of the female populations is ever recruited to the fishery.

Length group cm, FL	Pedro Bank (unexploited)		Port Royal Reefs (exploited)	
	No. captured	Relative abundance	No. captured	Relative abundance
21.0-21.9	23	1.00	19	1.00
22.0-22.9	19	.83	3	.16
23.0-23.9	17	.74	1	.05
24.0-24.9	7	.30	0	0
25.0-25.9	0	0	0	0
Mean FL	= 22.62 cm		= 21.71 cm	
If $L_{\infty} = 27$ cm	= $\frac{27.0 - 22.62}{22.62 - 21.0}$		= $\frac{27.0 - 21.71}{21.71 - 21.0}$	
Z/K	= 2.70 (= M/K)		= 7.45	

thus

$$Z = F + M = 3.33 + 1.89 = 5.22$$

Mulloidichthys martinicus: Table 11.3 shows the relative decline in abundance of successive length groups beyond the full-retention size, l_c , of 20.0 cm FL. There are insufficient data to treat the sexes separately (Fig. 11.8). The mean length of the fully retainable fishes is 21.59 cm FL at the Pedro Cays, while that of the unexploited Pedro Bank catch is 21.70 cm FL.

Neither the growth rates nor the asymptotic lengths are known with any degree of accuracy. Using a conservative estimate of L_∞ of 29 cm FL (applied to both sexes), the value of Z/K would be in the region of 4.7 for the exploited population and 4.3 (= M/K) for the unexploited population. If the growth rate, K , is about 0.4, the mortality rates would be about 1.9 and 1.7, respectively. These estimates are based upon very inadequate data.

ABUNDANCE AND DENSITY

There is no information on the absolute size of the populations which were studied, nor of the effects of ecological factors upon population density and abundance.

Seasonal Availability

Figure 11.9 shows that at the Port Royal Reefs "availability" (Munro 1974) of *P. maculatus* was greatest

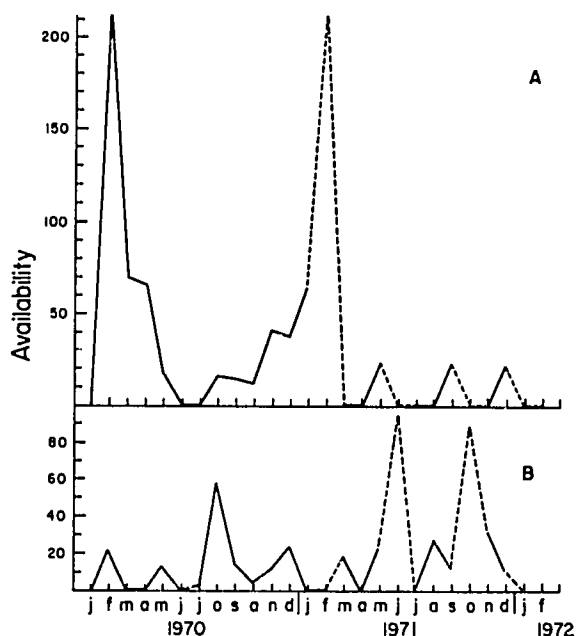


Fig. 11.9. Seasonal availability of (a) *Pseudupeneus maculatus* and (b) *Mulloidichthys martinicus* at the Port Royal Reefs. Availability is the theoretical number of fishes which would enter 1,000 traps set for 24 hours (Munro 1974). Broken lines represent small samples.

Table 11.3. Comparison of the relative abundance of successive length-groups of *Mulloidichthys martinicus* beyond full recruitment at 20.0 cm FL at the Pedro Cays and at unexploited parts of Pedro Bank. Data for males and females combined.

Length group cm, FL	Pedro Bank (unexploited)		Pedro Cays (exploited)	
	No. captured	Relative abundance	No. captured	Relative abundance
20.0-20.9	37	1.00	32	1.00
21.0-21.9	30	.81	23	.72
22.0-22.9	17	.46	11	.34
23.0-23.9	6	.16	8	.25
24.0-24.9	6	.16	4	.13
25.0-25.9	1	.03	0	0
26.0-26.9	0	0		
27.0-27.9	1	.03		
Mean FL If $L_\infty = 29$ cm	= 21.70 cm		= 21.59 cm	
Z/K	= $\frac{29.0 - 21.70}{21.70 - 20.0}$		= $\frac{29.0 - 21.59}{21.59 - 20.0}$	
	= 4.29 (= M/K)		= 4.66	

in January 1970 and January 1971, and that for 1970, the period from May to September produced very low catches. There was no marked seasonal trend in the availability of *M. martinicus* apart from a suggestion that availability might be relatively greater in the latter part of the year.

Relative Abundance

Figure 11.10a shows the trap-catch rates (standardized in terms of numbers of fishes captured per 1,000 hexagonal traps soaked for one day: see Chapter 3) of *P. maculatus* in the areas studied and in the various depth zones of Pedro Bank. Owing to the very great variability in the catch rates, the confidence limits ($p=0.20$) for the means are very wide and in many cases the apparent differences are not statistically significant even at the 80% level of confidence. Nevertheless, the mean catch rate of only 32 fishes/1,000 trap-days at Port Royal and zero catch at Discovery Bay are very much less than the rates encountered elsewhere. The catch rate at Eastern Pedro Bank (602 ± 19 fishes/1,000 trap-days) predominantly from the Southeastern Spur, is greater than that at Banner Reef, 20 m Bank, California Bank and from within the unexploited 10.1 to 20 m depth zone of Pedro Bank.

In contrast to *P. maculatus*, the catch rate of *M. martinicus* was significantly less in the deeper regions of Western Pedro Bank than in both the shallower southern and eastern portions and in areas of equivalent depth at

Eastern Pedro Bank (Fig. 11.10b). There is no significant difference between the catch rates at Pedro Cays and at Banner Reef. The catch rate at the Port Royal reefs and at California Bank was similar to that at Western Pedro Bank.

NATALITY AND RECRUITMENT

There appears to be no information on any aspect of the natality of species of Mullidae.

It has previously been established that *P. maculatus* are recruited to the trap fishery at a minimum size of 16.2 cm FL and are fully recruited at 20.9 cm FL (mean 19.0 cm FL). There is no measure of the absolute abundance or density of the stocks. Consequently, recruitment can only be expressed in terms of the potential catch of recruits per trap soaked per day.

If a fish stock, whether exploited or not, is in a steady state with recruitment and mortality balancing each other continuously, then recruitment, R , is equal to the average stock abundance N , multiplied by the

instantaneous mortality rate, Z (Ricker 1958, p. 30);

$$R = \bar{N}Z$$

The only measure of mean stock abundance available in the present case is the mean relative abundance expressed as the mean numerical catch per 1,000 trap-days of fishing effort.

$$\text{Thus, } R' = (\bar{C}/f)Z$$

in which the value R' is a theoretical index of the relative abundance of recruits required to produce the observed mean catch per unit of effort.

At the Port Royal Reefs the mean availability of *P. maculatus* was 26 fishes/1,000 trap-days. The mortality rate, Z , was 5.22 in the case of males, and assuming the mortality of recruited females to be similar.

$R' = 26 \times 5.22 = 135.7$ fishes/1,000 trap-days at a mean length, l_r , of 19.0 cm.

On unexploited Pedro Bank, $M = Z = 1.89$ and the mean catch rate of *P. maculatus* was 132 fishes/1,000 trap-days in the shallow Banner Reef, 20 m Bank areas, 602 fishes/1,000 trap-days at the Eastern Pedro Bank and 512 fishes/1,000 trap-days at Western Pedro Bank. The estimated recruitment indices are summarized in Table 11.4. No estimates of mortality rates are available for the exploited Pedro Cays area or for California Bank, which yielded mean catch rates of 203 fishes/1,000 trap-days and 161 fishes/1,000 trap-days, respectively. However, the mortality rate probably lies within the range 1.89 to 5.33. The apparently low recruitment rate to the Port Royal Reefs might be the result of the use of fine-meshed beach seines or small-meshed traps in nursery areas, but this cannot be substantiated. Alternatively, ecological conditions might be unsuitable or the flow of currents might be unfavorable to the settlement of oceanic-pelagic post-larval stages at the Port Royal Reefs.

In the case of *M. martinicus*, the mean catch rates ranged from 358 fishes/1,000 trap-days at the Southern Spur, to only 9 fishes/1,000 trap-days in the deeper water of Western Pedro Bank. California Bank yielded 13 fishes/1,000 trap-days and the Port Royal Reefs yielded 14 fishes/1,000 trap-days. The estimated recruitment indices are summarized in Table 11.5, but it must be remembered that the estimates of Z are very speculative.

It appears likely that settlement of oceanic pelagic post-larvae does not occur to any extent in water exceeding about 30 m depth and settlement or survival is perhaps maximized by the presence of heavy coral growth such as occurs at the Southern Spur of Pedro Bank.

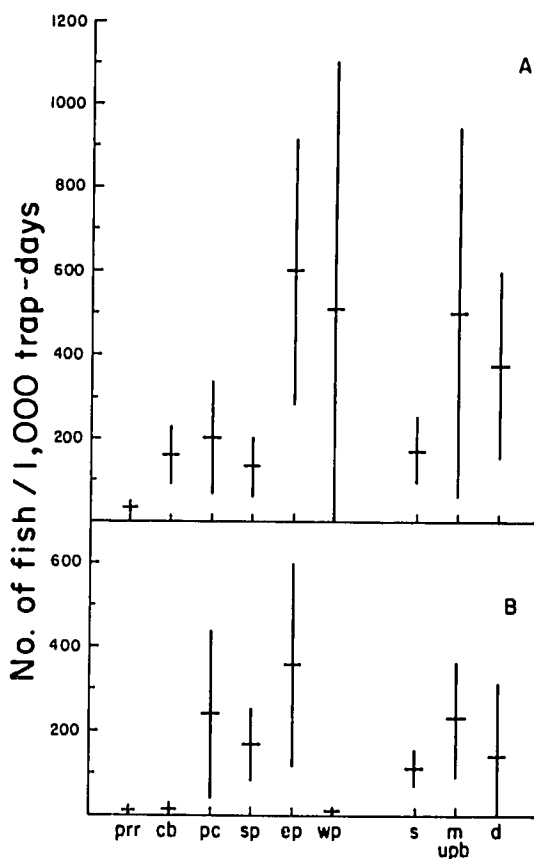


Fig. 11.10. Mean catch per unit effort (numbers of fishes per 1,000 trap-days) and 80% confidence limits for (a) *Pseudupeneus maculatus* and (b) *Mulloidichthys martinicus* at the Port Royal Reefs (prr), California Bank (cb), the Pedro Cays area (pc), Southern Pedro Bank (sp), Eastern Pedro Bank (ep) and Western Pedro Bank (wp) and in the (s) shallow 10.1 to 20 m, (m) medium 20.1 to 30 m and (d) deep zones of unexploited parts of Pedro Bank (upb).

DYNAMICS OF THE POPULATIONS

The biological and population parameters estimated for male and female *P. maculatus* and *M. martinicus* are summarized in Table 11.6.

Table 11.4. Mean catch rates, estimated mortality rates and estimated recruitment indices of *Pseudupeneus maculatus* in various areas.

Area	Fishes/1,000 trap-days	Z	Recruitment index (R') fishes/1,000 trap-days
Pedro Bank			
Eastern Pedro	602	1.89	1,138
Southern Pedro	132	1.89	249
Western Pedro	512	1.89	968
Pedro Cays area	203	> 1.89 & < 5.22	384-1,060
California Bank	161	> 1.89 & < 5.22	304-840
Port Royal Reefs	32	5.22	167

Table 11.5. Mean catch rates, estimated mortality rates and estimated recruitment indices of *Mulloidichthys martinicus* in various areas.

Area	Fishes/1,000 trap-days	Z	Recruitment index (R') fishes/1,000 trap-days
Pedro Bank			
Eastern Pedro	356	1.7	609
Southern Pedro	165	1.7	281
Western Pedro	9	1.7	15
Pedro Cays area	241	1.9	458
California Bank	13	?	?
Port Royal Reefs	14	?	?

Table 11.6. Summary of estimated population parameters for *Pseudupeneus maculatus* and *Mulloidichthys martinicus* exploited by traps with 4.13 cm wire mesh. All lengths are fork lengths in cm.

	<i>P. maculatus</i>		<i>M. martinicus</i>	
	Males	Females	Males	Females
Minimum retainable length, l_1	16.2	16.2	16.6	16.6
Mean retention length, l_T	19.0	19.0	19.3	19.3
Full retention length, l_C	21.0	21.0	20.0	20.0
Asymptotic length, L_∞	27.0	25.0	29.0	30.0
Asymptotic weight (g), W_∞	362	256	363	516
Coefficient of growth, K	0.70	0.35	0.4	0.4
Coefficient of natural mortality, M	1.89	?	1.7	1.7
M/K	2.70	?	4.3	4.3
Length at maturity, l_m	17.5-19.5	≤ 16 cm	18.5-19.5	17.5-18.5
l_m/L_∞	0.65-0.72	≤ 0.64	0.64-0.87	0.58-0.62

The value of M/K is high in all cases, as is to be expected in view of the steep rate of decline of the right-hand side of the catch length-frequency distributions. When traps covered with 4.13 cm hexagonal wire mesh are used, the value $c = l_T/L_\infty$ is 0.70 for male *P. maculatus*, 0.76 for female *P. maculatus*, and 0.64 for *M.*

martinicus (both sexes), and all of the populations are therefore, in a technical sense, underexploited. For example, in the case of male *P. maculatus* recruited to the Port Royal fishery and subjected to a rate of exploitation of $E = F/Z = 0.64$, the yield function (Beverton and Holt 1964) lies between 0.007 and 0.013, whereas

the corresponding maxima at the same rate of exploitation lie between 0.015 and 0.021. Theoretically, these maxima would be attained if the mesh size were reduced to produce a mean selection length of 11.3 to 12.4 cm FL, corresponding to a mesh size of 3.1 to 3.3 cm maximum aperture. For females, which appear to grow much more slowly, the optimum mesh size would probably be even smaller.

In the case of *M. martinicus*, the estimated M/K ratio is 4.90, and the eumetric yields are theoretically attained when c is less than 0.38, in contrast to the prevailing

value of $c = 0.64$. The rate of exploitation of $E = 0.08$ estimated for the Pedro Cays area, is believed to be very conservative, but even if the rate was 0.5, a reduction of the mean selection length to only 8.4 cm FL, to give a value of $c = 0.28$, would be required in order to maximize the yield.

As will be shown in Chapter 18, the reduction of mesh size necessary to achieve eumetric yields of goatfishes is incompatible with the *increase* in mesh size required to attain eumetric yields of other species, which are more important to the Jamaican trap fishery.

CHAPTER 12:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE BUTTERFLY AND ANGELFISHES,
CHAETODONTIDAE

by
K. Aiken
(October 1975)

Identity

TAXONOMY

The taxonomy of the Chaetodontidae according to Smith (1965) is as follows:

- Order : Percoidea
- Suborder : Percoididea
- Family : Chaetodontidae
- Subfamily : Chaetodontinae
Pomacanthinae
Holacanthinae
- Genera : *Chaetodon*
Prognathodes
Pomacanthus
Holacanthus
Centropyge

Fedder (1968) states that there is some debate as to the taxonomic positions of four species of two of the above genera: *Holacanthus ciliaris*, *H. isabelita*, *Pomacanthus arcuatus* and *P. paru*. The main problem according to Fedder (1968) is that "*P. arcuatus* and *P. paru*, and *H. isabelita* and *H. ciliaris* form pairs of very similarly colored juveniles whereas adults of each species are completely different from the juveniles and from each other".

The presently accepted valid scientific names of the western Atlantic species of the Chaetodontidae are given in Table 12.1, together with their common names.

Holacanthus isabelita and *Centropyge argi* were not captured during this study.

Information on the synonyms of the genera and species of Atlantic Chaetodontidae is included in the works of Jordan and Evermann (1898), Meek and Hildebrand (1941), Duarte-Bello (1959), Randall (1968) and Bohlke and Chaplin (1968).

There are several descriptions of the external morphology as well as keys to the chaetodontids in the literature. Meek and Hildebrand (1928) gave keys to genera and species in Panamanian waters and Bohlke and Chaplin (1968) for those in Bahamian waters.

A specimen of the species *Holacanthus tricolor*, 15.2 cm TL (12.7 cm SL), caught at northwest Pedro Bank at a depth of 35 m during 1972 showed a partial color variation distinct from that described as normal in the literature. In this specimen the entire frontal region except for the mouth area was black in color. The coloration of the fish was otherwise as described in the literature.

At present, hybridization is known to occur only between *Holacanthus ciliaris* and *H. isabelita* (Fedder 1968). This phenomenon was investigated in Florida by Fedder (1968) who found angelfishes that possessed intermediate coloration that were hybrids. Fedder's analysis was primarily accomplished by using portions of the general color patterns of adults, but gonads, behavior and relative populations were also studied. He suggested that there was no effective back-crossing and that there was no reason to suspect introgression as accounting for some variation in the parental species. The available

Table 12.1. Scientific and common names of Caribbean Chaetodontidae.

Scientific names	Common names
1. <i>Chaetodon capistratus</i> Linnaeus 1758	Foureye butterflyfish, Mademoiselle, Isabelita, Mariposa
2. <i>Chaetodon striatus</i> Linnaeus 1758	Banded butterflyfish, Striped butterflyfish
3. <i>Chaetodon ocellatus</i> Bloch 1787	Spotfin butterflyfish, Isabelita de la alto
4. <i>Chaetodon sedentarius</i> Poey 1860	Reef, Painted or Least Butterflyfish
5. <i>Chaetodon aya</i>	Deepwater butterflyfish
6. <i>Prognathodes aculeatus</i> (Poey) 1860	Longsnout butterflyfish
7. <i>Pomacanthus arcuatus</i> (Linnaeus) 1758	Gray angelfish, black angel, pot-cover, steamfish, mud-angel, Portuguese, Portugais, Chirivita
8. <i>Pomacanthus paru</i> (Bloch) 1787	French angelfish, Paru, Indian fish, flatfish
9. <i>Holacanthus tricolor</i> (Bloch) 1795	Rock beauty, "None-so-pretty", Catelineta, Vaqueta de dos colores
10. <i>Holacanthus ciliaris</i> (Linnaeus) 1758	Queen angelfish, Isabelita
11. <i>Holacanthus isabelita</i> (Jordan and Rutter) 1896	Blue angelfish
12. <i>Centropyge argi</i> Woods and Kanazawa 1891	Cherubfish, Pygmy angelfish

evidence from gonadal material indicated that the hybrids were potentially viable and the observations on behavior indicate that cross-spawning is likely to occur. *H. isabelita* is a continental species, and no evidence of hybridization in Jamaican waters has been found during this study.

Although *Pomacanthus arcuatus* and *P. paru*, which

commonly occur together with no apparent habitat preference, seem as closely related to each other as *H. ciliaris* and *H. isabelita*, no hybrids have been found and all specimens can be reliably identified (Feddern 1968). There is no evidence at present of hybridization between any of the chaetodontids in Jamaican waters.

Distribution

GEOGRAPHICAL DISTRIBUTION

Notes on distribution are given by Jordan and Evermann (1898), Jordan, Evermann and Clark (1930), Longley and Hildebrand (1941), Duarte-Bello (1959), Caldwell (1961), Hubbs (1963), Caldwell and Caldwell (1964), Caldwell (1966), Feddern (1967), Randall (1968), Bohlke and Chaplin (1968), Kuhlmann (1970) and Post (1971) from whose work the following has been compiled.

In general, the chaetodontids have a range of distribution from as far north as New England and south to Brazil. *Pomacanthus arcuatus* and *P. paru* have been introduced to Bermuda. *H. isabelita* is restricted to the continental shelf of the United States. *Centropyge argi* was not taken in any of the study areas but is unconfirmedly reported from Negril in western Jamaica. *Chaetodon aya*, a deep-water butterflyfish is recorded for the first time from Jamaica. This species was identified from photographs taken from a submersible at depths between 90 to 210 m off Discovery Bay (Woodley, pers. comm.). *Prognathodes aculeatus* was found to be rare in the areas investigated and was collected only from Pedro Bank.

In the western Atlantic, the distribution of the chaetodontids corresponds roughly with the distribution of hermatypic corals.

HABITATS AND DEPTH DISTRIBUTIONS

There is no previously recorded information on the spawn or larvae of the chaetodontids and there is very

little recorded information on habitats of the juvenile chaetodontids. Bohlke and Chaplin (1968) give excellent photographs of juveniles but omit collection sites and depths. Longley and Hildebrand (1941) recorded the young of *Chaetodon capistratus* from grass flats near a reef in the Florida Keys. The same has been observed on several occasions in Jamaican waters. Juveniles of this species ranging in length (TL) from 3 to 6 cm have been seen around isolated coral heads and wharf pilings at the Port Royal Marine Laboratory.

Feddern (1968) reported that juvenile *Holacanthus isabelita* were most abundant in certain inshore channels and occurred less commonly under coral heads in the Florida Keys. They were rare on the reef top and on the deep reef. Juvenile *H. ciliaris* on the other hand, were most abundant on the reef top and the deep reef, less common in the inshore channels and rare on the coral heads. Feddern (1968) also reported that in the Bahamas, where the inshore water has a more oceanic character, juvenile *H. ciliaris* were very commonly found along-shore. He also stated that juveniles of both these species lived primarily in and around colonies of finger sponge and *Millepora*. According to Feddern (1968) "they stay within the confines of sponge or coral colonies, seldom venturing into open water."

Juvenile *C. striatus* have not previously been reported in the literature. A few (about 8 cm TL) have been taken from shallow water (about 3 m) in a fine-meshed (12 mm) "mini" trap set off the jetty at the Port Royal Marine Laboratory. A few juvenile *Pomacanthus arcuatus* and *P. paru* about 10 cm TL were collected in Antillean traps at the Port Royal reefs. A few individuals of *H.*

tricolor with yellow coloration about 2 to 3 cm TL have been observed around small coral heads in shallow, sandy areas in back-reef zones of the Port Royal Reefs on several occasions. A juvenile *H. ciliaris* (10.3 cm TL) was captured in a trap set off the jetty at the Port Royal Marine Laboratory at about 2 m deep.

From the information that is available, it would seem that the young of the Chaetodontidae tend to inhabit shallow, fairly sheltered areas of the reef and coastal environments, but almost all of the species were also

captured on California Bank, an isolated oceanic bank with a least depth of about 35 m, and shallow environments are therefore not essential for completion of the life cycle.

Longley and Hildebrand (1941), Randall (1968) and Bohlke and Chaplin (1968) all record that adult chaetodontids as reef fishes. In general, observations made during the present study agreed with the above statement.

Bionomics and Life History

REPRODUCTION

Sexuality and Sexual Maturity

Table 12.2 summarizes the data on the size distributions of samples of male and female chaetodontids of six species. The samples of *C. capistratus*, *C. striatus* and *C. ocellatus* showed that males and females were of very similar mean sizes. The sample sizes for *C. sedentarius* (N = 43), *P. aculeatus* (N = 3) and *P. paru* (N = 4) were too small for comparisons to be made.

Female *P. arcuatus*, *H. tricolor* and *H. ciliaris* were several centimeters smaller than males.

Table 12.3 shows the sizes of the smallest mature male and female chaetodontids in samples taken from the various areas investigated. Many more sexually mature females than males were observed. Males appear to tend to mature at a larger size than males. The numbers examined were not sufficient to estimate the mean size at maturation of the gonads.

Information on mating in this family is lacking but repeated observations of pairs suggests that they are probably monogamous. No large spawning aggregations have been reported in the literature.

As the chaetodontids lack intromittent organs, fertilization is probably external.

Fecundity

Table 12.4 shows estimates of the number of eggs in ovaries of seven species of chaetodontids. The number of

eggs/g body wt is much less in the angelfishes than in the butterflyfishes.

Spawning

Munro et al. (1973) provide the only previous information on spawning seasons of the chaetodontids, based on sampling by the Fisheries Ecology Research Project up to June 1971. The following is based on all data collected between September 1969 and February 1973.

Chaetodon capistratus (N = 658): Table 12.5 shows the monthly percentage distribution of sexually inactive, active and ripe (includes spent) gonads in samples examined during the present study. Ripe fishes occurred in every month except April. There are no data for October. Peaks of spawning occurred between December and March.

Chaetodon striatus (N = 154): Table 12.6 shows that the greatest proportion of ripe fishes was collected in January-February, but more than 40% were ripe in all months. The proportion of inactive fishes was greatest in September to December,

Chaetodon ocellatus (N = 56): Small numbers of ripe fishes were taken in all months. There are no data for March, April and June. The greatest proportions of ripe fishes were found in January and May.

Table 12.2. Mean sizes of males and females in samples of six species of the Chaetodontidae.

Species	Males		Females	
	No. examined	Mean size (cm, TL)	No. examined	Mean size (cm, TL)
<i>Chaetodon capistratus</i>	576	8.8	238	9.2
<i>C. striatus</i>	49	13.2	100	12.4
<i>C. ocellatus</i>	23	13.4	42	13.9
<i>Pomacanthus arcuatus</i>	88	26.9	221	22.6
<i>Holacanthus tricolor</i>	52	19.0	97	15.8
<i>H. ciliaris</i>	38	24.3	79	22.0

Table 12.3. Observed sizes of the smallest mature male and female chaetodontids from all areas investigated.

Species	No. of females examined	Smallest female (cm, TL)	No. of males examined	Smallest male (cm, TL)
<i>Chaetodon capistratus</i>	71	7	1	9
<i>C. striatus</i>	63	10	1	13
<i>C. ocellatus</i>	33	11	-	-
<i>C. sedentarius</i>	7	8	-	-
<i>Prognathodes aculeatus</i>	1	8	-	-
<i>Pomacanthus arcuatus</i>	69	13	5	20
<i>P. paru</i>	9	23	-	-
<i>Holacanthus tricolor</i>	42	10	1	17
<i>H. ciliaris</i>	16	13	-	-

Table 12.4. Estimated egg numbers and eggs per gram body weight for *Chaetodon capistratus*, *C. striatus*, *C. ocellatus*, *C. sedentarius*, *Pomacanthus arcuatus*, *P. paru* and *Holacanthus tricolor*.

Species and total length (cm)	Weight (g)	Estimated number of eggs	Eggs/gram weight
<i>C. capistratus</i>			
8.0	16	2,900	181
8.8	20	7,100	355
9.4	20	7,700	385
9.5	22	6,500	295
10.4	27	12,900	478
<i>C. striatus</i>			
11.0	39.5	19,900	481
11.7	42	25,200	600
13.2	48	14,800	308
13.9	52	11,450	220
<i>C. ocellatus</i>			
11.2	90	24,500	272
13.4	110	12,500	114
14.1	120	18,000	150
15.5	138	64,000	464
<i>C. sedentarius</i>			
6.5	18	7,800	433
8.0	22	21,800	990
8.0	27	22,900	848
<i>P. arcuatus</i>			
19.9	320	16,150	50
22.6	380	21,650	57
29.7	1,025	126,000	123
<i>P. paru</i>			
28.4	685	31,400	46
30.7	730	37,000	51
<i>H. tricolor</i>			
12.0	75	12,100	161
15.4	125	9,900	79

Chaetodon sedentarius (N = 15): A few ripe fishes were found in January, May and September.

Pomacanthus arcuatus (N = 318): Table 12.7 shows that the greatest proportions of ripe fishes were collected in October and January, but there is no discernible seasonal trend in the data.

Pomacanthus paru (N = 21): Ripe fishes were collected in May, July, August, October and November.

Holacanthus tricolor (N = 148): Table 12.8 shows that samples were small in March, April and November-December. The greatest proportions of ripe fishes were collected between January and February, but ripe fishes

Table 12.5. Seasonal variations in the percentage of ripe (R), active (A) and inactive (I) *Chaetodon capistratus* in Jamaican waters. Data for 1968-1973 combined on a monthly basis.

Months	Number examined	Percent I	Percent A	Percent R
January	71	59	10	31
February	22	59	18	23
March	13	38	31	31
April	78	100	0	0
May	33	58	21	21
June	67	92	0	8
July	13	69	8	23
August	128	94	0	6
September	164	96	2	2
October	0		No data	
November	47	81	9	10
December	22	45	25	32
Total	658			

were found in all months, with the exception of December for which there are no data.

Holacanthus ciliaris (N = 111): Munro et al. (1973) found ripe fishes at the Port Royal Reefs "from January to August 1970, with a maximum proportion in April." Table 12.9 shows that the maximum proportions of ripe fishes were collected between September and October and that ripe fishes were collected throughout the year except between November and December.

Spawn

The unfertilized spawn of the chaetodontids has not been described in the literature to date.

Bardach (1958) collected fertilized eggs of *H. tricolor* in Bermuda. He noted that they were relatively large, just over 1 mm in diameter and had neither oil inclusions nor hairlike or other obvious holdfast mechanism. They sank to the bottom when released. Nothing is known of

Table 12.6. Seasonal variations in the percentage of ripe (R), active (A) and inactive (I) *Chaetodon striatus* in Jamaican waters. Data for 1968-1973 combined on a bi-monthly basis.

Months	Number examined	Percent I	Percent A	Percent R
January-February	43	33	16	51
March-April	6		Insufficient data	
May-June	27	37	15	44
July-August	13	39	15	46
September-October	10	60	0	40
November-December	55	51	9	40
Total	154			

Table 12.7. Seasonal variations in the percentage of ripe (R), active (A) and inactive (I) *Pomacanthus arcuatus* in Jamaican waters. Data for 1968-1973 combined on a monthly basis.

Months	Number examined	Percent I	Percent A	Percent R
January	28	46	18	36
February	22	100	0	0
March	2	}10		
April	8			
May	77	46	14	26
June	20	100	0	0
July	20	85	0	15
August	11	64	9	27
September	18	100	0	0
October	45	53	4	42
November	30	83	7	10
December	36	81	8	11
Total	317			

the nature of the eggs of the other species found during the present study.

PRE-ADULT PHASE

Embryonic Phase

No features of the development of chaetodontid embryos have been described. The survival rates, parasites or predators, the effects of environment and mode of hatching are unknown.

Larval Phase

Scotton and de Sylva (1972) mention that "larval butterflyfish occur in the upper waters of the open ocean."

It is hypothesized that the chaetodonts have pelagic larval stages and also that they have oceanic larval and pre-juvenile stages. Caldwell (1966) states that "fishes collected at the offshore banks consisted predominantly of groups having pelagic larvae or pre-juveniles or of species which are not bound to the shallows as adults." (During the present study chaetodontids were taken from depths ranging from 5 m to 48 m in most areas investigated.)

Juvenile Phase

During this study, the juvenile stages of all species of chaetodontids have been seen in the back reef and lagoon zone areas of coral reefs. They seem to prefer fairly sheltered water. Juvenile *C. capistratus* have been collected from the shallows at the Port Royal Marine Laboratory. Early juveniles may also be pelagic as Dragovich (1969) found juvenile chaetodontids among food items in Atlantic tuna stomachs.

Table 12.8. Seasonal variations in the percentage of ripe (R), active (A) and inactive (I) *Holacanthus tricolor* in Jamaican waters. Data for 1968-1973 combined on a bimonthly basis.

Months	Number examined	Percent I	Percent A	Percent R
January-February	32	53	3	44
March-April	9	(44)	(33)	(22)
May-June	27	59	19	22
July-August	17	18	53	29
September-October	53	60	13	26
November-December	10	80	10	10
Total	148			

Table 12.9. Seasonal variations in the percentage of ripe (R), active (A) and inactive (I) *Holacanthus ciliaris* in Jamaican waters. Data for 1968-1973 combined on a bimonthly basis.

Months	Number examined	Percent I	Percent A	Percent R
January-February	17	53	35	12
March-April	14	50	21	29
May-June	30	77	13	10
July-August	15	86	7	7
September-October	22	64	9	64
November-December	13	100	0	0
Total	111			

ADULT PHASE

Competitors

There is no direct evidence of competition in the chaetodontids. From work on food material of coral reef fishes by Randall (1967) it would seem that *Pomacanthus arcuatus* and *P. paru* may compete against each other as both feed almost entirely on sponges. It is also possible that the triggerfish, *Melicthys niger*, may compete with *P. arcuatus* and *P. paru* for food as it also feeds to a large extent on sponges.

Predators

Dragovich (1969, 1970) reported that juvenile chaetodontids were included in the food of seven species of Atlantic tunas and found that chaetodontids were among the three highest-ranking families of fish (by occurrence) eaten by skipjack and yellowfin tuna. In skipjack tuna (*Katsuwonus pelamis*) the genus *Holacanthus* comprised less than 47%, and *Chaetodon* spp. comprised less than 1%. In yellowfin tuna (*Thunnus albacares*), *Holacanthus* spp. comprised over 20% with *Chaetodon* spp. again forming less than 1% in frequency of occurrence.

Hamilton and Peterman (1971) reported that in a number of Pacific species of *Chaetodon* the dorsal lines are oriented towards predators approaching from above, and stated that "this exposes only their darkly patterned and narrow dorsal surface to view." The abovementioned authors based this conclusion upon hundreds of field observations. They also state that "the usual response to a sudden attack by a predator in the field is to dart forward then hook about to face the flank of the predator." They conclude that this behavior along with "angular swimming," "provides a smaller target and may make the fish less conspicuous especially against dark substrates."

Parasites, Diseases, Injuries and Abnormalities

Soganderes-Bernal and Soganderes (1961) reported digenic trematodes (Platyhelminthes) of the genus *Multitestis* from *Chaetodon capistratus* and *C. ocellatus*. The genus *Chaetodon* was sometimes parasitized by the trematode *Hurleytremaoides*.

Straughan (1959) reported that in captivity both *P. arcuatus* and *P. paru* sometimes contract "skin blotch" or "white patch" disease. In extreme cases the entire fish will turn white but usually a mottled effect results. The causal organism is thought to be a protozoan. This disease may be cured in captivity by treatment with sulphathiazole sodium (Straughan 1959). No diseased or abnormal chaetodontids were captured or observed during the present study.

Serology

Some work has been done by Saunders (1966) on the blood of Caribbean species of chaetodontids. The eosinophils, leucocytes, erythroblasts and erythrocytes were examined. The low numbers of leucocytes found in *C. sedentarius* was thought to be a species characteristic. *C. capistratus* had unusually large eosinophils.

NUTRITION AND GROWTH

Feeding

Feddern (1968) observed that in his study area in the Florida Keys, every specimen of *H. ciliaris* and *H. isabelita* examined (caught during the day) contained large amounts of food showing that they are diurnal feeders. The other species of chaetodontids are probably also diurnal feeders.

Food

The food habits of the Caribbean species of Chaetodontidae have been studied by Randall (1967). Much of the data presented in Table 12.10 are taken from this source except for those for *Chaetodon ocellatus*, of which five specimens were examined.

Table 12.10. Food of Chaetodontidae (in part from Randall 1967). X denotes main food material.

	<i>Chaetodon capistratus</i>	<i>C. striatus</i>	<i>C. sedentarius</i>	<i>C. ocellatus</i>	<i>Prognathodes aculeatus</i>	<i>Holacanthus tricolor</i>	<i>H. ciliaris</i>	<i>Pomacanthus arcuatus</i>	<i>P. paru</i>
Algae				x		x	x	x	x
Spermatophytes								x	x
Sponges						X	X	X	X
Bryozoans							x	x	x
Anthozoa	x	x				x		x	x
Gorgonians	x							x	x
Hydroids			x				x	x	x
Polychaetes	X	X	x	x	x				
Mollusc eggs		x							
Echinoids								x	x
Echin. tube feet				x					
Copepods		x			x				
Amphipods				x					
Shrimps			x		x				
Tunicates	x						x	x	x
Unident. crustaceans		x		x	x				
Unident. eggs	x			x					

In Randall's study (1967), coral polyps were not found in the stomachs of the butterflyfishes, although individuals of the genus *Chaetodon* were observed feeding on them in aquaria in Puerto Rico. This has also been observed for the species *C. capistratus* and *C. striatus* in aquaria in Jamaica. Straughan (1959) also reported seeing this. The Chaetodontidae also ingest inorganic material such as sand and coral fragments and thus play a direct role in the transport of calcareous fragments by reef fishes (Bardach 1961).

Randall (1967) records that the butterflyfishes (subfamily Chaetodontinae) in the West Indies "seem to feed primarily on the tentacular crowns of polychaetes and anthozoans, especially on *Zooanthus*, and that the angelfishes (Pomacanthinae) feed mostly on sponges and occasionally on algae" (see Table 12.10). From personal observations while diving around the coast of Jamaica, *Chaetodon capistratus* in particular feeds at least to some extent on the tips of live coral. This has also been observed by Reese (1973) in a Pacific species of *Chaetodon*. Randall (1967) has also observed species of *Chaetodon* feeding on coral in aquaria in Puerto Rico (see Table 12.10).

Randall and Hartmann (1968) mention that sponges comprise over 95% of the food of angelfishes of the genus *Holacanthus* and over 70% of the food of the species of *Pomacanthus*.

Growth

Maximum size

C. capistratus: Randall (1968) reports that this species reaches a maximum size of 6 in (15 cm TL) but rarely exceeds 4 in (10 cm). Bohlke and Chaplin (1968) record that they are "supposed to reach 6 inches" (15 cm TL). The largest male captured during the present study measured 14 cm TL and the largest female 13 cm TL. It appears therefore that the asymptotic length of the males is not less than 14 cm and about 1 cm less for females.

C. striatus: This species is reported by Randall (1968) and Bohlke and Chaplin (1968) to attain 6 in (15 cm). The largest specimen recorded during this study was also of 15 cm TL.

C. ocellatus: Randall (1968) states that this species reaches 7 to 8 in (17.7 to 20.3 cm) while Bohlke and Chaplin (1968) state that in the Bahamas, although "said to reach 8 in, none over 6 in (15.2 cm) were taken." The largest individual taken during this study was 16 cm TL.

C. sedentarius: Bohlke and Chaplin (1968) report that this species "grows to at least 6 inches" (15 cm) while the largest collected by Randall (1968) was 5.5 in (14 cm). The largest collected during this study was 13 cm TL.

Prognathodes aculeatus: Bohlke and Chaplin (1968) state that this species "grows to nearly 3.5 inches" (8.9 cm) and the largest specimen collected by Randall (1968) was of this size. The maximum size collected during this study was 8.8 cm (15.2 g).

Pomacanthus arcuatus: Both Randall (1968) and Bohlke and Chaplin (1968) report that this species grows to about 2 ft (61 cm) although the largest individual collected by Randall (1968) measured 17 in (43 cm). The largest specimen collected during this investigation was much smaller than the maxima stated in the literature and measured only 35 cm TL. The asymptotic length may be about 60 cm TL but more sampling with different gear, e.g., by spearfishing, is needed before a definite figure can be stated.

P. paru: Randall (1968) states that the largest specimen collected measured 16 in (40.5 cm). Bohlke and Chaplin (1968) state that 36 cm is about the maximum size. Catches of *P. paru* taken in traps set by R.V. *Alcyon* on Salmon Bank in February 1970 yielded a specimen measuring 37.5 cm. The largest taken during this study measured 36.0 cm (1,625 g).

Holacanthus tricolor: Both Randall (1968) and Bohlke and Chaplin (1968) state that this species grows to about one foot (30.5 cm). However, the largest individual captured during this study measured 34.4 cm (1,140 g), somewhat larger than that mentioned in the literature.

H. ciliaris: Randall (1968) states that this species is "reported to reach 18 inches" and the largest collected by him was "16.8 inches" (42.5 cm TL). Bohlke and Chaplin (1968) state that it "grows to one foot, and

probably larger." The largest specimen collected during this study measured 33.3 cm (13.2 in). This seems to be well under the asymptotic length of this species which might be in the region of 40 cm.

H. isabelita: Randall (1968) reports that this species "reaches 18 inches" (45.7 cm). Bohlke and Chaplin (1968) who called this species *H. bermudensis*. Jordan and Rutter, also state that it "grows to about 18 inches." None were collected during this study.

Age and growth

Randall (1962) reported that a tagged *C. capistratus* grew 13 mm in three months (about 4.3 mm per month), and specimens of *P. arcuatus* (which he termed *P. aureus*, a synonym) "grew at a decreasing rate from 6.47 mm per month for a 144 mm fish to 1.56 mm per month for a 280 mm fish." It should be noted, however, that the Petersen tags used by Randall suffer from the great disadvantage of causing actual physical damage to the fish. The fishes thus injured in this manner may contract infections and thus grow at abnormally slow rates.

Monthly length-frequency histograms of species of chaetodontids captured in traps during study showed no evidence of modal progression. Examination of scales of some chaetodontids (*P. arcuatus*, *P. paru*, *H. tricolor*, *H. ciliaris* and *C. ocellatus*) showed that rings or marks were present, but no interpretable pattern was discernible. The "rings" that could be seen might have been due to one or more of several factors such as spawning, physical condition or temperature changes. It is possible that large samples of scales collected on a regular basis could yield estimates of age and growth. Length-weight and length-depth relationships were not established for any of the chaetodontids.

BEHAVIOR

Migration and Local Movements

Tagging experiments conducted on tropical Atlantic reefs (Bardach 1958; Randall 1962; Springer and McEarlean 1962; Moe 1972) have all shown that angelfishes and butterflyfishes tend to remain on their "home reef" for very long periods. Feddern (1968), quoted by Moe (1972), reported that although these fishes are non-migratory, a variation in the habitat of juvenile and adult *H. isabelita* (near Florida) indicates a movement of juveniles into the adult range when maturity is attained.

Randall (1962) found that no tagged *C. capistratus*, *H. ciliaris* or *P. paru* moved more than 1,000 yards from the reefs where they were tagged. Springer and McEarlean (1962) found that tagged *P. arcuatus* showed a strong affinity for their home reefs and none were recaptured on other than their home reefs. Reese (1973) found that some Pacific species of *Chaetodon* were resident on a reef for up to four years.

These observations are generally in agreement with

Bardach's (1958) conclusion from tagging experiments at Bermuda that the chaetodontids in general spend their entire lives associated with a relatively small portion of the reef environment.

Schooling

There are no reports of schooling in any of the species of western Atlantic chaetodontids that occur in Jamaican waters. However, Hobson (1969) has noted that some of the Pacific butterflyfishes, notably *Heniochus nigrivittatus* Gill, often form large aggregations or schools around the cleaning stations that they operate. No such schooling around cleaning stations in the western Atlantic species of *Chaetodon* has been reported; instead, only a few aggregate nearby.

Reproductive Behavior

Bardach (1958) observed that butterflyfishes of the genus *Chaetodon* usually occurred in pairs. He captured several pairs of *C. striatus* and *C. capistratus* and the members of the pair were identified as male and female. Adult angelfishes are sometimes solitary, but more often form pairs and small groups, or rarely large aggregations (Fedderm 1968). Sylvester and Dammann (1972) in the Virgin Islands noted that butterflyfish entered fish traps in pairs. In the Pacific, Hobson (1972) observed that the butterflyfishes which are paired "as during midday," often remained paired into the early night at least. Reese (1973), also working in the Pacific, observed the same in three species of *Chaetodon*. Observations while diving on

the Port Royal reefs and also from trap catches tend to agree with those in the literature.

Cleaning Symbiosis

Bohlke and Chaplin (1968) reported that "a young *P. paru* was stationed over a period of weeks over the same rock prominence, picking at the skins of various fishes which had called at the station for that service. Another was seen cleaning the teeth of a large needlefish which was lying motionless near the bottom, its mouth wide open." Straughan (1959) reported that "in turn angelfish will be sometimes seen hovering near the cleaning stations of the cleaning Gobies (*Gobiosoma genie*) to have their parasites picked." Hobson (1969) noted that butterflyfishes in the Pacific notably *Heniochus nigrivittatus* are also cleaners and also operate cleaning stations.

Some adult butterflyfishes and most young angelfishes thus exhibit cleaning symbiosis with other fishes on coral reefs.

Aggression

Hamilton and Peterman (1971) made observations on displays of aggression in a Pacific species of *Chaetodon*, (*Chaetodon lunula*). The authors reported observing various intensities of aggressive interactions in *C. lunula* associated with color displays and changes as well as movements. Observations of captive *C. capistratus* at the Port Royal Marine Laboratory are similar to a great degree to those made by Hamilton and Peterman (1971). Similar intensities of aggressive interactions were observed both within and between species.

Populations

POPULATION STRUCTURES

Sex Ratios

Sex ratios of the various species of chaetodontids caught in traps from all the areas investigated show that females outnumber the males of the species (Table 12.11). This is very marked in *Pomacanthus arcuatus* and *P. paru* which had ratios of male to female (M:F) of 1:2.51 and 1:3.28, respectively. *Chaetodon capistratus* shows variation between the sex ratios at the Port Royal Reefs and at Pedro Bank (Table 12.11). It is possible that this variation in ratios may be due to differences in depth, because the Port Royal reef sampling was done in depths of 5 to 21 m while at Pedro Bank the depth of sampling increased to between 10 to 45 m.*

*Moyer (1978; *Jap. J. Ichthyol.* 25, 25-39) has demonstrated protogynous sex reversal for the angelfish *Centropyge interruptus*. The sex ratios (Table 12.11) and mean sizes of male and female pomacanthids (Table 12.2) might be indicative of the same phenomenon in the Caribbean species. (Ed.)

Size and Age Composition

It has not been possible to determine the ages of any of the chaetodontids taken during this study.

Table 12.11. Sex ratios of samples of chaetodontids taken from all areas investigated.

Species	No. of Males	No. of Females	Male:Female Sex ratios
<i>Chaetodon capistratus</i>			
Port Royal	392	106	1.00:0.27
Pedro Bank	66	99	1.00:1.50
<i>C. striatus</i>	49	100	1.00:2.04
<i>C. ocellatus</i>	23	42	1.00:1.83
<i>C. sedentarius</i>	5	10	1.00:2.00
<i>Prognathodes aculeatus</i>	2	1	—
<i>Pomacanthus arcuatus</i>	88	221	1.00:2.51
<i>P. paru</i>	7	23	1.00:3.28
<i>Holacanthus tricolor</i>	52	97	1.00:1.87
<i>H. ciliaris</i>	38	79	1.00:2.08

Chaetodon capistratus: The percentage frequency of successive length groups captured in traps at the Port Royal Reefs, California Bank and in the unexploited parts of Pedro Bank are compared in Fig. 12.1. Relatively more large fishes (over 10 cm TL) were taken from the unexploited parts of Pedro Bank than were caught in the other two areas. The size distributions of catches from the Port Royal Reefs and California Bank are very similar, except for a slightly greater number of larger fishes (over 10 cm TL) from the latter area. This probably results from the relatively deeper zones (31 to 45 m) at which the traps were set while traps at the Port Royal Reefs were set at a shallow depths between 5 to 21 m.

Samples of this species taken in traps at Lameshur Bay, St. John, U.S. Virgin Islands totalled 24 specimens. Total length range was 8 to 11 cm with a mean length of 10.2 cm. Eighteen specimens examined from the Jamaica south coast shelf had a total length range from 9 to 13 cm with a mean length of 11 cm.

On the basis of the California Bank sample, the sizes at first retention, mean retention and full retention are 8 cm, 8.5 cm and 9 cm TL, respectively. The minimum size caught was 7 cm TL.

Chaetodon striatus: Figure 12.2 shows the percentage length-frequency distributions of catches taken in traps at the unexploited parts of Pedro Bank in the depth range 10 to 45 m. It appears that this species fully recruited to the fishery at 13 cm TL. The samples from the Port Royal reefs and California Bank had modes at 10.5 cm TL and 12.5 cm TL. However, the temporal

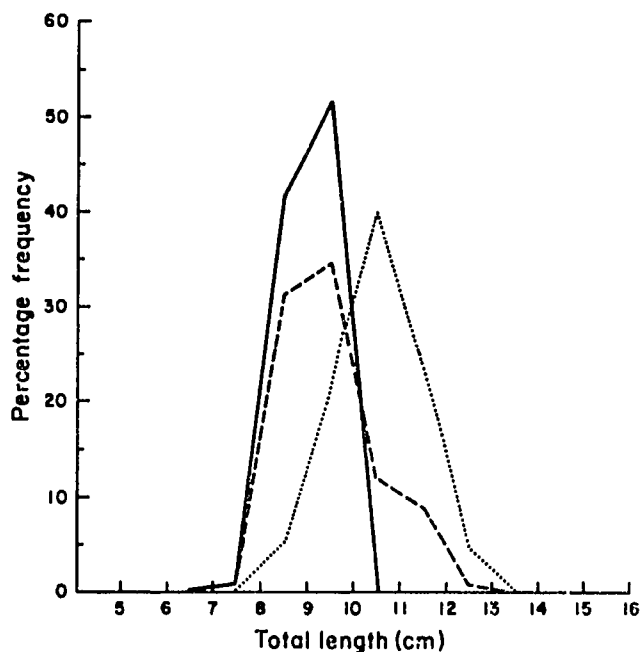


Fig. 12.1. Length-frequency distributions of trap (4.13 cm mesh) catches of *Chaetodon capistratus* from the Port Royal Reefs (—), California Bank (---), and unexploited parts of Pedro Bank (· · · · ·). Port Royal reefs: N = 498, time period = 36 months. California Bank: N = 228, time period = 12 months. Pedro Bank: N = 377, time period = 6 months.

distribution of catches was uneven and the sample sizes were small.

On the basis of the Pedro Bank sample, the sizes at first retention, mean retention and full retention are 8 cm, 12 cm and 13 cm TL, respectively.

Chaetodon ocellatus: The percentage length-frequency distributions of trap catches taken at the unexploited parts of Pedro Bank in the depth range 10 to 45 m were examined. This species appears to be fully recruited to the fishery at 13.0 to 13.9 cm TL. The samples from the other areas investigated were too small for use in size distributions. The sizes at first and mean retention are 9 cm and 12 cm TL, respectively.

Pomacanthus arcuatus: Figure 12.3 shows the percentage length-frequency distributions of catches taken in traps at the Port Royal Reefs, compared with the percentage length-frequency distributions of catches taken in traps at the unexploited parts of Pedro Bank. Relatively more of the larger fishes (over 20 cm TL) were taken at the unexploited parts of Pedro Bank compared with the size distribution of the Port Royal reef catches.

On the basis of the Pedro Bank sample, the sizes at first retention, mean retention and full retention are 9 cm, 18 cm and 21 cm TL, respectively.

Holacanthus tricolor: Figure 12.4 shows the percentage length-frequency distributions of catches taken in traps at the unexploited parts of Pedro Bank. The mean length was 18.9 cm TL and the range from 10 to 23 cm TL. A sample of 29 specimens were taken in traps at the Port Royal Reefs. In contrast to the sample from the unexploited parts of Pedro Bank, several specimens exceeding 23 cm TL were taken. The length range was 10 to 34 cm TL and the mean length was 17.0 cm TL.

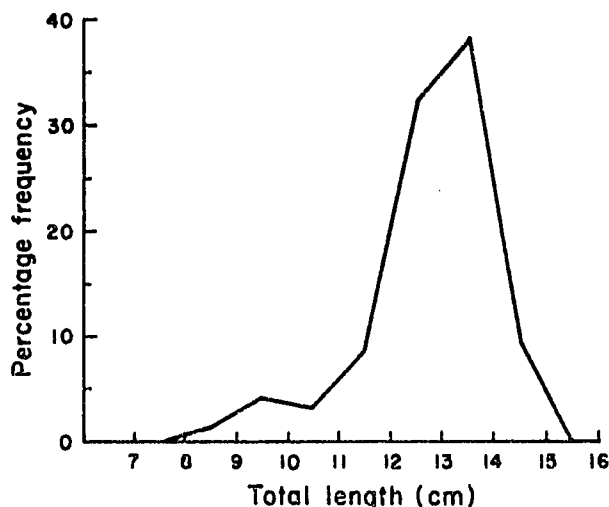


Fig. 12.2. Length-frequency distributions of trap (4.13 cm mesh) catches of *Chaetodon striatus* from unexploited parts of Pedro Bank. N = 266, time period = 6 months.

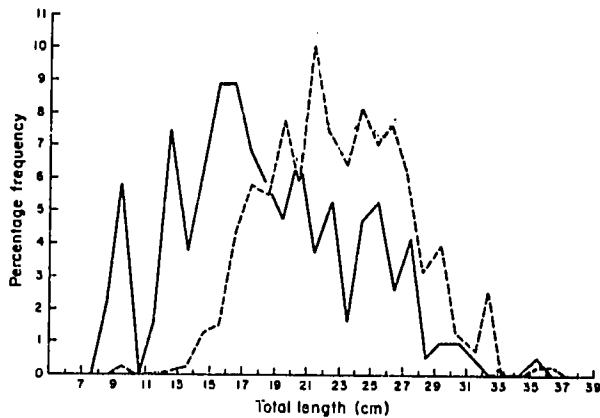


Fig. 12.3. Comparison of gross length-frequency distributions of trap (4.13 cm mesh) catches of *Pomacanthus arcuatus* from the Port Royal Reefs (N = 190; solid line) and from unexploited parts of Pedro Bank (N = 320; broken line).

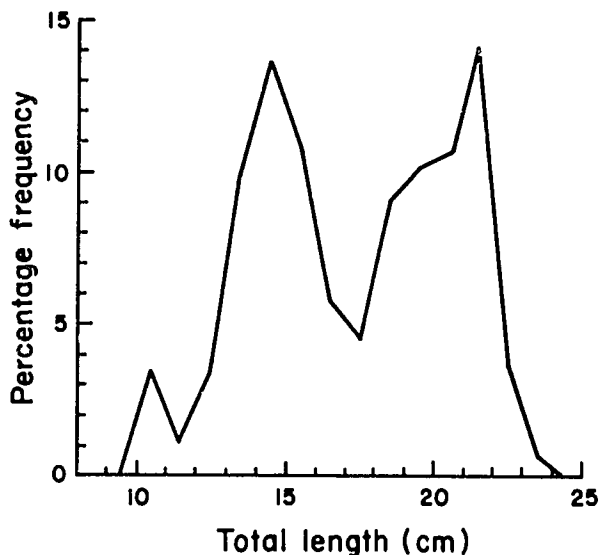


Fig. 12.4. Gross length-frequency distribution of trap (4.13 cm mesh) catches of *Holacanthus tricolor* at unexploited parts of Pedro Bank. N = 177.

At California Bank a sample of eleven specimens examined ranged in length from 10 to 20 cm TL with a mean length of 13.8 cm TL.

There is no satisfactory explanation at present as to why the larger-sized specimens were found in the relatively shallow waters (5 to 21 m) around the Port Royal Reefs and not in deeper waters offshore. The minimum mean and maximum retention lengths are 12 cm and 14 cm TL, respectively.

Holacanthus ciliaris: A sample of 47 specimens taken from all sections of Pedro Bank had a length range from 13 to 32 cm TL and a mean length of 24 cm TL. The mean length of the sample (N=95) from the Port Royal Reefs was 20.4 cm TL. This may be as a result of commercial fishing effort on the reefs there. The minimum retention size is 9 cm TL.

Chaetodon sedentarius: Seventeen specimens taken in traps at the unexploited parts of Pedro Bank had a length range from 9 to 13 cm and a mean length of 10.4 cm. Another 17 specimens (length range 8 to 10 cm; mean TL 9.4 cm) were examined from California Bank and six (length range 8 to 10 cm; mean TL 9.5 cm) were examined from the Port Royal Reefs.

Prognathodes aculeatus: Five specimens from 5.0 to 5.9 cm and mean length of 5.3 cm were taken from Eastern Pedro Bank in 1972.

Pomacanthus paru: A sample of 34 specimens taken from both the unexploited and exploited areas of Pedro Bank ranged in length from 12 to 34 cm and had a mean length of 22.9 cm. Seventeen specimens (length range 9 to 36 cm; mean length 20.1 cm) were examined from the Port Royal Reefs.

MORTALITY AND MORBIDITY

Predators probably contribute to mortality of all stages in unexploited areas. In nearshore Jamaican waters, trap and spearfishing undoubtedly cause much mortality. They are never taken on hook and line.

The absolute ages of the species of chaetodontids dealt with are not known and the estimates of mortality rates are based entirely upon the length distribution of samples taken during this study. Such estimates are probably open to fairly wide margins of possible error.

The size distributions of trap catches of *P. arcuatus* based on moderate samples from the unexploited parts of Pedro Bank and from the Port Royal Reefs are shown in Fig. 12.3.

The asymptotic length, L_{∞} , is about 60 cm TL but K is unknown. The decline in abundance of successive length groups after full recruitment at 20.0 to 20.9 cm TL is shown in Table 12.12.

The calculated value of Z/K ($= M/K$) at the unexploited parts of Pedro Bank is 8.1.

ABUNDANCE AND DENSITY

Relative Abundance

Data on relative abundance of the two commercially important chaetodontids are listed in Table 12.13. The largest trap catches of *P. arcuatus* by number and weight were made at Banner Reef at the south side of Pedro Bank. Greatest catches by weight of *P. paru* were made at 20 m Bank and SW Pedro Bank.

NATALITY AND RECRUITMENT

Chaetodontids are deep-bodied fishes which should theoretically become vulnerable to capture in small-

meshed (4.13-cm aperture) traps at a very small size. However, Figs. 12.3 to 12.4 indicate that in the case of the angelfishes, most fishes do not become fully vulnerable to traps until about 14 to 16 cm TL is attained

and it is presumed that behavioral changes are responsible.

Recruitment indices cannot be calculated because there is no information on mortality rates.

Table 12.12. Derivation of relative mortality rates from relative abundance of successive length groups of *Pomacanthus arcuatus* beyond full recruitment at 20.0 cm TL at Pedro Bank.

Length group cm TL	No. captured	Relative abundance
20.0-20.9	34	1.00
21.0-21.9	24	.71
22.0-22.9	21	.62
23.0-23.9	27	.79
24.0-24.9	23	.68
25.0-25.9	25	.74
26.0-26.9	20	.59
27.0-27.9	11	.32
28.0-28.9	13	.38
29.0-29.9	4	.12
30.0-30.9	3	.01
31.0-31.9	6	.18
32.0-32.9	0	0
33.0-33.9	0	0
34.0-34.9	1	.03
35.0-35.9	1	.03
Mean TL	=	24.4 cm
If $L_{\infty} = 60$ cm		
Z/K	=	$\frac{60.0 - 24.4}{24.4 - 20.0}$
	=	8.1 = M/K
F	=	0
E	=	0

Table 12.13. Mean catch rates of angelfishes in baited traps (4.13 cm mesh) at Pedro Bank and California Bank, expressed as numbers per 1,000 trap-days.

Species	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank	Pedro Cays area	California Bank
<i>Pomacanthus arcuatus</i>	172	408	57	237	3
<i>P. paru</i>	24	62	18	18	3

**CHAPTER 13:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE PARROTFISHES, SCARIDAE**

by
P.H. Reeson
(June 1975)

Identity

The Scaridae are oblong, slightly compressed fishes with large cycloid scales covering their body in regular rows. They have a discontinuous lateral line. The head is rounded in front and their teeth are completely or incompletely fused anteriorly to form dental plates in each jaw. Their popular name (parrotfishes) derives from the beak-like structure of the dental plates. The Scaridae have been divided into two subfamilies, the Sparisomatidae, represented in the Atlantic by *Sparisoma*, *Nicholsina* and *Cryptotomus* and the Scarinae, which contains only one genus in the Atlantic, *Scarus*.

Schultz (1958) and Smith (1956, 1959) have reviewed the classification of the Scarinae with differing results. More recently the species within that subfamily have been rearranged into two genera whilst the classification of the Sparisomatidae by Schultz is considered satisfactory (Rosenblatt and Hobson 1969).

Characters of the genera and species found in the Caribbean are given by Bohlke and Chaplin (1968) and Randall (1968).

Randall (1968) lists 14 species in 4 genera from the Caribbean and Bohlke and Chaplin (1968) found 13 species in the Bahamas. Caldwell (1966) listed 13 species from Jamaica but includes *Sparisoma abildgaardii* which had previously been shown to be in synonymy with

Sparisoma viride (Winn and Bardach 1957). Species known from Jamaica are listed in Table 13.1.

Table 13.1. Scientific and common names of scarids reported from Jamaican waters.

Scientific name	Common name
1. <i>Sparisoma rubripinne</i> (Cuvier and Valenciennes) 1839	Yellowtail parrotfish
2. <i>Sp. chrysopterus</i> (Bloch and Schneider) 1801	Redtail parrotfish
3. <i>Sp. viride</i> (Bonnaterre) 1788	Stoptlight parrotfish
4. <i>Sp. aurofrenatum</i> (Cuvier and Valenciennes) 1839	Redband parrotfish
5. <i>Sp. radians</i> (Cuvier and Valenciennes) 1839	Bucktooth parrotfish
6. <i>Sp. atomarium</i> (Poey) 1860	Green Blotch parrotfish
7. <i>Scarus vetula</i> Bloch and Schneider 1801	Queen parrotfish
8. <i>S. croicensis</i> Bloch 1790	Striped parrotfish
9. <i>S. taeniopterus</i> Desmarest 1831	Princess parrotfish
10. <i>S. coeruleus</i> (Bloch) 1786	Blue parrotfish
11. <i>S. guacamaia</i> Cuvier 1829	Rainbow parrotfish
12. <i>S. coelestinus</i> Cuvier and Valenciennes 1839	Midnight parrotfish

Distribution

The parrotfishes are tropical shallow-water fishes that abound on coral reefs and adjacent areas. They also occur over rocky shores and substrates. Most of the

species listed above are relatively common and range throughout Bermuda, southwestern coast of U.S.A., Bahamas, western coast of Central America, West Indies

and Brazil. Bauchot and Blanc (1961, quoted by Randall and Randall 1963) recorded *Sp. rubripinne* from San Thome off the west coast of Africa.

Sp. radians, *S. guacamaia* and *S. croicensis* are said to occur in the eastern Atlantic (Bohlke and Chaplin 1968) but due to past confusion over the identities of *S. croicensis* and *S. taeniopterus* the range of these two species is not certain. *Sp. atomarium* is found in deep water (15 to 76 m; Randall 1968) and is the only species listed in Table 13.1 that was not caught during the

course of this study. It has, however, been trawled from 19 fm (about 35 m) south of Alligator Pond Bay, Jamaica (Caldwell 1966).

The eggs of several species are known to be pelagic and this is probably true for the family. There are few reports of capture of the larvae.

All of the species caught during the period of this study were from coral-reef habitats or oceanic bank facies with the exception of *Sp. radians* which is common in seagrass beds.

Bionomics and Life History

REPRODUCTION

Gonads

The paired, elongated gonads lie along the dorsal wall of the abdominal cavity.

Data on gonad size or the number of eggs relative to body size and fecundity were not collected during this study.

Sexuality

Most Atlantic species of scarids exhibit sexual dichromatism (Longley and Hildebrand 1941; Winn and Bardach 1957, 1960; Randall 1963) with juveniles, females and small males exhibiting a drab-color phase while terminal-phase males are more brightly colored. During this study, drab-phase specimens of sexually dichromatic species were either male, female or immature whereas the colorful specimens were all males. The terminal-phase male-coloration pattern of *Scarus croicensis* and *S. vetula* can be induced by injecting the corresponding females with testosterone (Winn and Bardach 1957; Ogden and Buckman 1973). Winn and Bardach suggested that the females underwent a sex-reversal into the colorful male phase at a certain stage of maturity, presumably related to testosterone levels. The factors regulating the transformation are not known but it may be due to the carrying capacity of the reef for terminal-phase males (Ogden and Buckmann 1973). Randall and Randall (1963) noted that the attainment of the terminal-phase coloration by the male *Sparisoma rubripinne* is associated with a change in their spawning behavior. Buckman and Ogden (1973) have suggested that gonadal transformation probably occurs before the color change.

Scarus guacamaia and *S. coeruleus* do not show sexual dichromatism but large individuals of *S. coeruleus* have a pronounced gibbous forehead which may be a feature of the males (Randall 1968). Rosenblatt and Hobson (1969) have pointed out that in two eastern Pacific scarid species the possession of a hump on the forehead is a feature of sub-adults and adults and is due to allometric growth, although "in those species in which the males attain a larger size, (it) is more prominent in males than in females".

Maturity

The size at sexual maturity for *Sp. aurofrenatum*, *S. taeniopterus* and *S. croicensis* is indicated in Tables 13.2 to 13.4. Few ripe fishes of other species were observed but these are mentioned below.

Sparisoma aurofrenatum: Ripe fishes of this species were caught at the Port Royal reefs and on the oceanic banks. The smallest ripe male and ripe female recorded measured 15.1 cm FL and 14.6 cm FL, respectively. It is likely that the females of this small species begin to mature at a size smaller than that retained by the mesh covering the trap as shown by Table 13.2.

Table 13.2. Percentages of mature male and female *Sparisoma aurofrenatum* in successive length groups. All specimens were captured in traps at the Port Royal Reefs and at Pedro Bank.

Length group (cm, FL)	Males		Females	
	No. examined	% ripe	No. examined	% ripe
14.0-14.9	2	0	7	14.3
15.0-15.9	35	2.9	22	22.7
16.0-16.9	78	0	68	26.5
17.0-17.9	101	2.0	57	29.8
18.0-18.9	75	5.3	33	42.4
19.0-19.9	41	2.4	19	26.3
20.0-20.9	19	10.5	12	25.0
21.0-21.9	9	0	1	0
22.0-22.9	3	0	1	(100)
Total	363		220	

Sp. viride: Only 3 ripe females were caught at the Port Royal Cays of which the smallest was 17.9 cm FL. Ripe specimens were not caught on the oceanic banks. Winn and Bardach (1960) reported that males mature at 16.0 to 20.0 cm SL and females at 16.3 cm SL in Bermuda.

Sp. chrysopterus: One ripe female, which measured 24.9 cm FL, was trapped at the Port Royal Reefs. Ripe fishes were not caught on the oceanic banks.

Scarus taeniopterus: One ripe fish, a male measuring 29.1 cm FL, was caught at the Port Royal Reefs but no ripe males were caught offshore. The smallest mature female, caught offshore, measured 17.2 cm FL and full

Table 13.3. Percentages of mature female *Scarus taeniopterus* in successive length groups. All specimens were captured in traps on the oceanic banks.

Length group (cm, FL)	No. examined	% ripe
15.0-15.9	2	0
16.0-16.9	2	0
17.0-17.9	23	26.0
18.0-18.9	57	14.0
19.0-19.9	46	28.3
20.0-20.9	52	9.6
21.0-21.9	42	11.9
22.0-22.9	30	13.3
23.0-23.9	16	12.5
24.0-24.9	12	8.3
Total	282	

maturity was probably reached before 17.5 cm FL as shown by Table 13.3.

S. croicensis: Ripe females were not found at the Port Royal Reefs nor offshore. The smallest ripe male, caught at Port Royal, measured 15.5 cm FL and Table 13.4 indicates that this species matures at a size smaller than that retained by the trap-mesh. It is also a small species and individuals, approximately 10 to 12 cm in length, have been observed to engage in spawning activity. In Bermuda, the size at maturity of males is 11.0 to 13.0 cm SL and that of females is 9.0 to 10.0 cm SL (Winn and Bardach 1960).

Other species: The smallest mature *S. coeruleus* female measured 30.5 cm FL and the smallest ripe male and female of *Sp. rubripinne* measured respectively 27.0 cm FL and 16.1 cm FL. Winn and Bardach (1960) reported that around Bermuda *S. vetula* matured as males between 21.0 and 24.5 cm SL.

Mating and Fertilization

Two types of reproductive behavior have been recognized within the same species of the sexually dichromatic scarids (Randall and Randall 1963) and the type of reproductive behavior exhibited is related to the color phase of the males involved. Parrotfishes do not have intromittent organs and fertilization is external.

Spawning aggregations

The observations of Randall and Randall (1963) on spawning aggregations of drab-phase *Sp. rubripinne* may be summarized as follows: Incipient spawning is indicated by the increased activity of small groups of parrotfish amongst the larger school. These small groups rise higher in the water column, then incline their bodies upward, hesitate briefly and shoot diagonally upwards and release their milt at the peak of their upward movement. Subsequently they descend and disperse. About 4 to 11

Table 13.4. Percentages of mature male *Scarus croicensis* in successive length groups. All specimens were captured in traps at the Port Royal Reefs or at Pedro Bank.

Length group (cm, FL)	No. examined	Males	
		No.	% ripe
14.0-14.9	3		0
15.0-15.9	14		14.3
16.0-16.9	52		3.8
17.0-17.9	58		8.6
18.0-18.9	22		4.5
19.0-19.9	3		33.3
20.0-20.9	1		0
Total	153		

fishes are involved in the spawning runs which last about 2 seconds. The Randalls believe that each group consists of a single female with the rest being males. They also suggest that the sudden upward rush helps to expel the gametes by causing expansion of the airbladder as would the sharp flexure of the body at the apex of the spawning run. Similar spawning behavior by aggregations of *S. croicensis* have been observed (Ogden and Buckman 1973). This author also witnessed spawning of *S. croicensis* at Discovery Bay, in August 1972 at 1530 hours. Over 400 drab-phase individuals (approx. 10 to 12 cm) were associated together over a thicket of *Acropora cervicornis*, near the edge of a buttress spur. The aggregation milled around about 2 m above the coral. Within the school small groups of fishes swam together of which a few would suddenly dart 0.5 to 1.0 m upwards expelling a cloud of milt at the apex of their spawning run. About 10 of these spawning runs were witnessed over the 10-min period of observation. At the same time, other fishes in the aggregation were seen grazing on fine algae on dead coral at the bottom. The presence of terminal-phase males in the aggregation was not noted.

Spawning of pairs

Observations on spawning acts between individual male and female *Sp. rubripinne* and *S. croicensis* were also made by Randall and Randall (1963) in the Virgin Islands. The males display, by vibrating the posterior part of body and tail over the female, and spawning occurs by both fish dashing a few feet upwards, releasing the eggs and sperm as they turn sharply and swim downwards. Paired-spawning of *Sp. aurofrenatum* has been observed by Winn and Bardach (1960) in Bermuda and by Randall and Randall (1963) in the Virgin Islands. Suspected pre-spawning behavior of *S. coelestinus* was observed by a colleague (David Allard) in February 1970 at the Port Royal Cays. About fifty pairs of fishes were seen in which the larger fish swam behind and to one side of the smaller fish. The larger fish (possibly males) had reddish, bulging abdomens, the

dorsal and anal fins often raised and the dental plates exposed. In the eastern Pacific, pair-spawning has been observed for *S. ghobban* and *S. rubroviolaceus* (Rosenblatt and Hobson 1969).

Randall and Randall (1963) suggested the possibility that pair-spawning between fishes of different color is the basic reproductive pattern of parrotfishes and that aggregate spawning is secondary, related to the attainment of sexual maturity by males before the color change has been effected. Ogden and Buckman (1973) question the secondary role of aggregate-spawning as their observations showed it to be the most common pattern of reproduction for *S. croicensis*. Randall and Randall (1963) and Smith (1972) suggest that the aggregation of species for spawning increases its reproductive potential and has an adaptive value in enhancing the chances of fertilization.

Time of day of spawning

The observations of Randall and Randall (1963) on *Sp. rubripinne* showed that spawning commenced between 1125 to 1345 hours and continued through the afternoon until 1700 to 1740 hours. Ogden and Buckman (1973) noted that *S. croicensis* spawned in the afternoon off Panama as was also observed at Discovery Bay for this species.

The diving activities of the project at Port Royal usually took place between 1000 to 1300 hours and more than 120 hours were personally spent scuba-diving in the same area. Definite spawning behavior by scarids was never observed by any member of the diving teams during this time. If the spawning of scarids, or at least of certain species, commonly occurs in the afternoon, then it is possible that we missed the phenomenon. However, it is also possible that scarids at the Port Royal Reefs migrate to the exposed reef front on the surrounding barrier reef for spawning.

Spawning

Spawning seasons

Initial information regarding the spawning seasons of parrotfishes around Jamaica has been reported by Munro et al. (1973).

Sparisoma aurofrenatum: Catches of this species at the Port Royal Reefs (n = 509) indicate that spawning takes place throughout the year, with a peak in April (Fig. 13.1a). On the oceanic banks, ripe fishes were caught in all months (n = 103) except May. It would seem that this species spawns year round with higher activity in April. Spawning was observed in the Virgin Islands by Randall and Randall (1963) in March, April, June and August. Winn and Bardach (1960) found ripe fish in Bermuda from June to August.

Sparisoma viride: Although 890 fishes caught at the

Port Royal Reefs were examined, only 3 were ripe and these were captured in February and April. However, the proportions of active fishes captured suggest that the breeding season extends from October through May, perhaps with a peak in February as shown in Fig. 13.1b. Only a few fishes of this species were caught on the oceanic banks, one of which had gonads in the active stage and this was caught in February. Randall and Randall (1963) observed a pair spawning in the Virgin Islands during May and Winn and Bardach (1960) found ripe females at Bermuda during June, July and August.

Sparisoma chrysopterym: Only 1 ripe fish was found in a total of 512 fishes examined for gonad activity and this was caught in March. As shown in Fig. 13.1c, fishes with active gonads were found from February to March and again in September with a suggestion of peak gonad

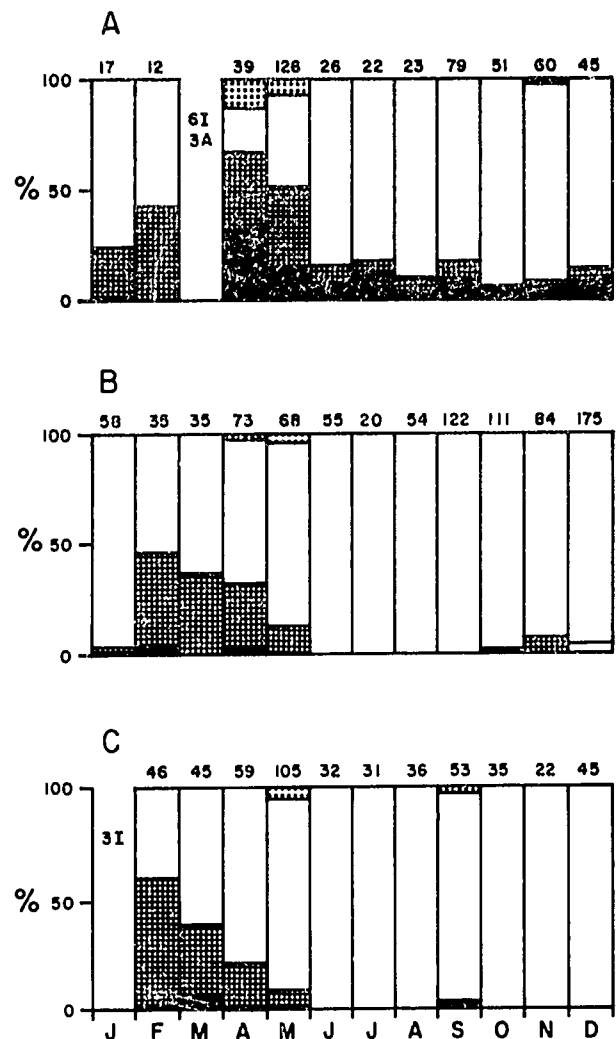


Fig. 13.1. Monthly percentages of ripe (shaded), active (cross-hatched), inactive (blank) and spent (stippled) gonads of parrotfishes at the Port Royal Reefs: (a) *Sparisoma aurofrenatum*, (b) *Sp. viride* and (c) *Sp. chrysopterym*. The numbers of fishes examined are given above each respective month. I = inactive; A = active.

activity in February. Only 3 fishes were caught offshore and all had inactive gonads.

Scarus croicensis: Six specimens were caught offshore and all had inactive gonads. Gonads of 175 fishes caught at the Port Royal Reefs were examined and active and ripe fishes were found in January, April and May (Fig. 13.2a). Randall and Randall (1963) observed this species spawning in the Virgin Islands in February, March, April, June and August. Spawning of *S. croicensis* was observed at Discovery Bay, Jamaica in August 1972, and this behavior had been noted throughout the summer (P. Dustan, pers. comm.). Ogden and Buckman (1973), working on the eastern coast of Panama from May 1970 to February 1971, observed group- and pair-spawning "often during the study" but did not specify the months.

Scarus taeniopterus: One ripe male was caught at the Port Royal Reefs in January 1970. Ripe fishes were found on the oceanic banks every month during which samples were obtained. The highest proportion of ripe fishes occurred in December and January as shown in Fig. 13.2b.

Other species: Ripe *S. vetula* were caught at the Port Royal Reefs in January and May 1970. Randall and Randall (1963) observed a spawning pair during August in the Virgin Islands and another pair in January at Puerto Rico. *Sp. rubripinne* with ripe gonads were caught during November 1969 and January and February 1970 at the Port Royal Cays. Randall and Randall (1963)

collected ripe males and females in all months of the year in the Virgin Islands. Ripe female *S. coeruleus* were caught on Pedro Bank in January 1973. The spawning of *S. guacamaia* and *S. coelestinus* seems to be confined to the warmer months of the year in Bermuda (Winn et al. 1964). Longley (in Longley and Hildebrand 1941) noted that the female *Sp. radians* are ripe in July and August in the Tortugas, Florida. Erdman (cited by Winn and Bardach 1960) collected ripe eggs from this species in November at Puerto Rico.

Factors influencing spawning seasons

Sp. aurofrenatum and *S. taeniopterus* appear to spawn throughout the year whereas for the other species illustrated, the highest proportion of active and ripe fishes were confined to the period between January and May.

Randall and Randall (1963) suggested that seasonal spawning occurs in regions where there is a wide seasonal range in water temperature and length of day. Munro et al. (1973) have shown that the expected abundance of reef-fish eggs is greatest during the cooler months (February to April) than in the remaining months around Jamaica where the range of temperature is 26.5 to 29.5°C. In the Caribbean spawning probably occurs throughout the year for some, if not all, parrotfish species with more intense spawning activity being confined to the cooler months of the year.

Location of spawning ground

Randall and Randall (1963) have pointed out that deeper reef fronts (15 to 20 m) appear to be the focal points for spawning groups of *Sp. rubripinne*, and suggest that such sites are more exposed to water currents which afford more opportunity for dispersal of the pelagic eggs. A similar observation has been made for *S. croicensis* in Jamaica.

Spawn

Female parrotfishes release transparent pelagic eggs. Winn and Bardach (1960) showed that the eggs of *Sparisoma* species are round whereas those belonging to species of *Scarus* are a modified fusiform shape. These authors also gave length measurements of ripe eggs of *S. croicensis* (2.4 to 2.6 mm), *S. guacamaia* (2.9 to 3.1 mm), *S. vetula* (2.8 to 2.9 mm) and diameter measurements of eggs of *Sp. aurofrenatum* (0.9 to 1.1 mm) and *Sp. chrysopterus* (0.6 to 0.7 mm).

PRE-ADULT PHASES

Little or nothing is known about the developmental stages of scarids through adolescence. Randall and Randall (1963) have described the development of artificially fertilized *Sparisoma rubripinne* eggs up until the 6 day post-larval stage. Metamorphosis probably

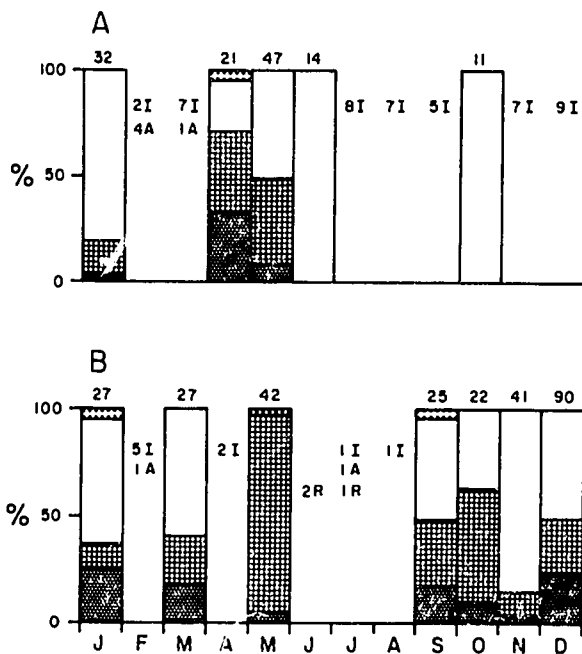


Fig. 13.2. Monthly percentages of ripe (shaded), active (cross-hatched), inactive (blank) and spent (stippled) gonads of *Scarus croicensis* at the Port Royal Reefs (a) and *S. taeniopterus* from the oceanic banks (b). The numbers of fishes examined are given above each respective month. I = inactive; A = active; R = ripe.

takes place when the larvae are carried by currents over suitable habitats. At the Port Royal Reefs, juvenile *Scarus croicensis* (2 to 3 cm), *Sp. viride* (3 to 5 cm) and *Sp. aurofrenatum* (4 to 5 cm) are commonly found amongst corals in shallow water, although juveniles of certain species may be encountered on deep reefs.

ADULT PHASE

Competitors

There are no data regarding the degree of intraspecific competition amongst the scarids or of interspecific competition with the other major groups of herbivorous fishes at Port Royal, namely the acanthurids, pomacentrids and monacanthids.

Predators

Moray eels (Muraenidae) are commonly caught in traps around Jamaica and often are found to contain whole parrotfishes in their stomachs. This is not to say that this situation exists in the normal reef environment, but the many observations made suggest that morays are important predators of parrotfishes. The role of the mucous envelope, produced at night by species of *Scarus*, in reducing predation by moray eels has been discussed by Winn and Bardach (1959). Ogden and Buckmann (1973) have observed predation by *Epinephelus striatus*, *Scomberomorus regalis* and *Caranx ruber* on foraging groups of *S. croicensis*. Randall (1963) recorded scarids in the stomach contents of *Gymnothorax vicinus* and in addition from the Serranidae (*Cephalopholis fulva*, *Epinephelus striatus*, *E. adscensionis*, *E. guttatus*, *Mycteroperca tigris*, *M. venenosa*); the Lutjanidae (*Lutjanus apodus*, *L. cyanopterus*, *L. jocu*) and the Carangidae (*Caranx bartholomaei*, *C. ruber*). *Lutjanus griseus* is also a predator of parrotfishes (Starck and Davis 1966; Starck and Schroeder 1970).

Parasites and Diseases

Saunders (1966) has reported the presence of the blood parasite *Haemogregarina bigemina* in *S. croicensis* and *Sp. aurofrenatum*. The large parasitic isopod, commonly found on the heads of many reef fishes, e.g., holocentrids, pomacanthids and acanthurids, has never been observed attached to parrotfishes.

NUTRITION AND GROWTH

Feeding

Parrotfishes feed intermittently and Bakus (1967) has estimated that they spend 30 to 40% of their active period in feeding. They are grazers and browsers, using the fused beak to rasp filamentous algae growing on

dead coral and other hard substrates or on the blades of *Thalassia testudinum*. They also feed directly on *T. testudinum* taking characteristic scalloped bites from the edges of the leaf blades. Bakus (1964, 1966, 1967) and Randall (1961c, 1965) have pointed out the importance of herbivorous fishes on the settlement and growth of benthic primary producers and invertebrates. Smith and Paulson (1974) suggested that ingested calcium carbonate is dissolved in the intestine, thus possibly making the interstitial algae growing in coral substrate available for nutrition.

Randall (1967) has reported the food habits of *Scarus coelestinus*, *S. croicensis*, *S. guacamaia*, *S. taeniopterus*, *S. vetula*, *Sparisoma aurofrenatum*, *Sp. chrysopterus*, *Sp. rubripinne*, *Sp. viride* and *Sp. radians*. In the absence of suitable data from parrotfishes caught in our traps, Randall's results are referred to below.

More than 85% of the food content of the stomachs of most of these species was comprised of algal material with seagrasses making up the majority (1.3 to 17.3%) of the remaining items. Algae was the only item of food found in *S. croicensis*. The young of this species have been observed to browse epiphytes on *Thalassia* blades at the Port Royal Reefs.

Longley (in Longley and Hildebrand 1941) has observed *S. coeruleus* and *S. guacamaia* ingesting mouthfuls of fine sand which was ground to a fine powder by the pharyngeal mill, and he presumed that they were feeding on microscopic organisms. Randall (1967) estimated that approximately 70% of the dried stomach contents of most of the above species was residual inorganic material and further suggested that the inorganic sediment serves to grind plant tissues thus rendering them more digestible. Ogden and Buckman (1973) reported that *S. croicensis* ingested large amounts of sediment whilst foraging.

Sp. radians is restricted to seagrass beds and, correspondingly, 88% of its food was *Thalassia* and 12% was algae. It ingests very little inorganic sediment (Randall 1967). Greenway (1973) has estimated the amount of *Thalassia* grazed by fishes in Kingston Harbour at 0.06 g/m²/week. *Sp. radians* is the species largely responsible as indicated by the scarid bite marks on the blades. Randall (1965) has pointed out that the scalloped edges of *Thalassia* blades mentioned by Thomas et al. (1961) were probably due to this species.

Other items of food found in the stomachs of West Indian scarids were gorgonians, sponges, corals and fragments of molluscs, crustaceans and echinoids, but these constituted, at most, less than 3% of the stomach contents of any one species.

Although parrotfishes are herbivorous grazers and browsers utilizing benthic algae and marine angiosperms as a source of food, it has also been reported that Indo-Pacific scarids feed on living coral. Hiatt and Strasburg (1960) considered parrotfishes, in the Marshall Islands, as either grazing herbivores or grazing omnivores depending on the relative amounts of algae or coral polyps that were consumed. The corals that were rasped were largely

Table 13.5. Relationships between fork lengths (FL) and maximum body depth (D) for three species of parrotfishes. Measurements are expressed in centimeters.

Species and formula	Number of fishes	Length range (cm, FL)
<i>Sparisoma aurofrenatum</i> D = $-0.90 + 0.36$ (FL) FL = $2.54 + 2.78$ (D)	43	14.5-19.5
<i>Sparisoma viride</i> D = $0.10 + 0.33$ (FL) FL = $-0.40 + 3.06$ (D)	79	13.5-25.5
<i>Sparisoma chrysopterygum</i> D = $-1.38 + 0.36$ (FL) FL = $3.76 + 2.79$ (D)	44	17.5-23.5

massive glomerate forms. Talbot (1965) also classified the Scaridae off East Africa as coral-feeders, but Bakus (1967) suggested that parrotfishes "consume mostly dead coral in the process of rasping algae and sessile invertebrates from the substratum". Parrotfishes studied at Madagascar (Vivien 1973), the Great Barrier Reef, Australia (Choat, cited by Randall 1967), Hawaii (Hobson 1974), Marshall Islands (Smith and Paulson 1974), and the eastern Pacific (Rosenblatt and Hobson 1969) were considered to be strictly herbivorous. In Florida, Starck (cited by Randall 1967) observed that insignificant amounts of live coral were occasionally scraped by parrotfishes, but Randall (1967) did not observe such feeding in the Virgin Islands nor saw any evidence of scarid beak marks on living coral. Parrotfishes have never been observed to feed on live coral by this author.

Recent studies show that different species of scarids utilize different vegetative resources. Vivien (1973) has recognized two feeding patterns amongst parrotfishes: those that browse on soft algae and phanerogams and those that scrape epiphytes on dead coral. Hobson (1974) distinguished species that mainly scraped coral substrate and those that preferred rocky substrate. Different life stages of the same species may also utilize different resources. Observations at the Port Royal Reefs indicate that juvenile and subadult *S. croicensis* over the reef flat feed on epiphytic algae growing on *Thalassia* blades whilst schools of larger individuals, foraging over the reef, scrape dead coral substrate as well as ingest fine sediments.

Metabolism

The relationship between the high calcium content of the diet and the metabolism of calcium in parrotfishes has been recently studied. Fontaine et al. (1973) suggest that the comparatively high level of activity of the ultimobranchial bodies and the corpuscles of Stannius, glands which cause a lowering of the blood calcium level, is attributable to the calcium-rich diet of these fishes.

Table 13.6. Relationships between fork lengths (FL) and weight (W) for four species of parrotfishes. Lengths and weights are expressed in centimeters and grams respectively.

Species and formula	Number of fishes	Length range (cm, FL)
<i>Sparisoma aurofrenatum</i> Log W = $-1.89 + 3.11$ (Log FL)	100	14.5-22.5
<i>Sparisoma viride</i> Log W = $1.27 + 2.74$ (Log FL)	145	13.5-31.5
<i>Sparisoma chrysopterygum</i> Log W = $-2.03 + 3.21$ (Log FL)	126	16.5-27.5
<i>Scarus croicensis</i> Log W = $-1.78 + 3.02$ (Log FL)	78	8.5-19.5

Smith and Paulson (1975) found high levels of intestinal carbonic anhydrase activity in *Scarus jonesii*, as well as in *Acanthurus triostegus*, and hypothesized that ingested calcium carbonate dissolves in the gut and that this enzyme was involved in the carbon dioxide transport mechanism.

Growth

Relative growth patterns

The relationships between fork length and maximum body depth for *Sp. aurofrenatum*, *Sp. viride* and *Sp. chrysopterygum* are shown in Table 13.5. Given that the maximum aperture of the wire mesh commonly used on Jamaican fish traps is 4.13 cm, then the fork lengths of *Sp. aurofrenatum*, *Sp. viride* and *Sp. chrysopterygum* at that body depth are 14.0 cm, 12.2 cm and 15.3 cm, respectively.

Table 13.6 gives the relationships between fork length and weight of *Sp. aurofrenatum*, *Sp. viride*, *Sp. chrysopterygum* and *S. croicensis*. Growth is isometric for these four species. The length-weight relationship of *Sp. rubripinna* is illustrated by Randall (1961c; Fig. 6).

Maximum size

The maximum lengths recorded for each species caught during this investigation are given in Table 13.7. Except in the case of *Sp. aurofrenatum* and *S. taeniopferus*, these values do not closely approach the values given by either Bohlke and Chaplin (1968) or Randall (1968). In most of the observed cases the males had attained a greater size than the females.

Age and growth

During his reef-fish tagging experiments in the Virgin Islands, Randall (1962) found that parrotfishes showed

Table 13.7. Maximum observed fork lengths of parrotfishes from Jamaican waters and the maximum total lengths reported in the literature.

Species	Maximum observed fork length (cm)		Maximum reported total length (cm)*
	Male	Female	
<i>Sparisoma viride</i>	32.0	31.0	50.8-53.3
<i>Sp. aurofrenatum</i>	24.2	22.2	25.4-27.9
<i>Sp. chrysopterum</i>	27.5	27.0	45.7
<i>Sp. rubripinne</i>	34.5	22.7	44.2-45.7
<i>Scarus croicensis</i>	20.8	19.7	25.4-27.9
<i>S. taeniopterus</i>	35.5	24.7	30.5-33.0
<i>S. vetula</i>	28.6	24.8	51.0-61.0
<i>S. coeruleus</i>		44.5	58.4-121.9
<i>S. guacamaia</i>	-	45.7	93.9-121.9
<i>S. coelestinus</i>	29.5	32.1	76.2

*Values obtained from Bohlke and Chaplin (1968) and Randall (1968).

the fastest growth rates. He reported that 14 *S. coeruleus* (13.3 to 18.8 cm FL) had an average growth rate of 7.2 mm per month. Three *S. vetula* showed growth rates between 11 to 18 mm per month, 3 *Sp. chrysopterum* grew at rates between 8.7 to 20 mm per month and the growth rates of 9 *Sp. rubripinne* averaged 8.1 mm per month. Three *Sp. viride* ranging in length between 18.7 to 23.6 cm had growth rates of 7.7 to 3.5 mm per month.

Length-frequency histograms of *Sp. viride*, *Sp. chrysopterum* and *Sp. aurofrenatum* caught in traps set at the Port Royal Reefs did not appear to show any consistent pattern of modal progression.

BEHAVIOR

Recent studies have paid attention to the diurnal or nocturnal pattern of activity amongst many coral reef fishes (Hobson 1972, 1973; Starck and Davis 1967; Collette and Talbot 1972). Parrotfishes are diurnally active commencing their activity around the time of sunrise and retiring to sleep on the reef at sunset.

Migrations and Local Movements

Scarids undertake daily migrations between their diurnal feeding areas and their nocturnal resting sites. Near dusk they tend to aggregate in the shallow waters and then move to deeper areas before nightfall but whether they reform into groups before they ascend the reef at dawn is not known. Ogden and Buckman (1973) were able to identify specific routes along which schools of *Scarus croicensis* migrate daily, and Winn et al. (1964) found that sexually mature *S. coelestinus* and *S. guacamaia* use sun-navigation in order to return to their home caves. It has not been established whether scarids occupy the same sleeping site each night.

It has been indicated that scarids have a tendency to

be associated with the same area of "home" reef for variable periods of time but they may move over distances of up to several hundred meters during feeding (Bardach 1958; Randall 1961c; Winn et al. 1964). Ogden and Buckman (1973) noted that terminal-phase males of *S. croicensis* have a stronger tendency to home than the striped phase.

Ogden and Buckman (1973) have also recognized three behavioral patterns in *S. croicensis*. Individuals or small groups of both striped-phase and terminal-phase fishes may repeatedly be found in the same area of reef and apparently use the area for feeding. In contrast to the stationary category, striped-phase fishes and terminal-phase males may actively defend a territory in shallow water (Buckmann and Ogden 1973). The third category includes the large foraging groups which move and feed over the reef all day.

Schooling

Winn and Bardach (1966) noted that during the day species of the genus *Sparisoma* tended to be found individually or in small groups, in contrast to the species of *Scarus* which tend to form large groups or schools. However, in view of the recognition of the three types of dispersion in a single species (*S. croicensis*) by Ogden and Buckman (1973) and Buckman and Ogden (1973), this generalization may not be valid.

Mixed-species aggregations may occur, e.g., *S. coelestinus* and *S. guacamaia* (Winn et al. 1964), *S. croicensis* and *S. taeniopterus* (Stark and Davis 1967), or the schools may additionally contain representatives of other families. It is common around Jamaica to find members of the Acanthuridae (surgeonfishes), Mullidae (goatfishes), Pomadasyidae (grunts) and Labridae (wrasses) along with the usually numerically dominant *S. croicensis*. Itzkowitz (1974) discusses these groupings in further detail.

Mucous Envelope and "Sleep"

Several observations have shown that parrotfishes remain motionless in crevices and holes in the reef at night. Winn (1955) and Stark and Davis (1967) noted the formation of a mucous envelope at night by species of *Scarus* but Collette and Talbot (1972) also observed *Sparisoma viride* within a mucous envelope on one occasion. The mucous envelope has anterior and posterior openings and is produced into a cocoon around the body of the fish by opercular glands (Byrne 1970). In the eastern Pacific, only small individuals of *Scarus* regularly produce the mucous envelope (Rosenblatt and Hobson 1969), and Hobson (1965, 1974) has suggested that mucous envelopes are most commonly produced by small individuals or those that are injured.

Winn and Bardach (1959) have discussed the possible role of the mucous envelope in reducing predation by moray eels, fishes which seek out their prey by olfactory or gustatory senses.

Behavior in Relation to Fish Traps

Within traps, weak or injured parrotfishes were often seen to be chased and attacked by the same species, and

they also often nipped at dead conspecifics. Similar observations have been noted by High and Beardsley (1970). The significance of this behavior is not understood but it has not been observed amongst free individuals.

Populations

POPULATION STRUCTURES

Sex Ratios

Randall and Randall (1963) found that the male to female ratio of a spawning aggregation of *Sparisoma rubripinne* was 1:0.3 as compared with a ratio of 1:1 obtained from the fishes in their usual shallow habitat.

The sex ratio of parrotfishes caught in traps varied according to the species, but all differed from the 1:1 ratio as shown in Table 13.8. Except in the cases of *Sp. aurofrenatum* and *Scarus croicensis* at the Port Royal Reefs there was a predominance of females in the catches of the other species. *Sp. aurofrenatum* and *S. croicensis* are small species and the predominance of males in the catches probably relates to the retention of the larger sized males in the traps. Buckmann and Ogden (1973) have reported that approximately one fifth of the migratory population of *S. croicensis* were terminal-phase males.

The relative abundance of female *Sp. viride*, *Sp. aurofrenatum* and *S. taeniopterus* decreased with increasing size with a corresponding increase in the relative number of males. Randall and Randall (1963) similarly found that drab-phase males and females of *Sp. rubripinne*

were smaller than the terminal-phase males. *Sp. chrysopterus* appeared to be the exception.

Age and Length Compositions

There was no success in establishing the absolute age of parrotfishes at given sizes and, therefore, there is no information regarding the age composition of the catches. Parrotfishes scales are fairly deciduous and the majority of scales obtained for age determination were regenerated.

The size compositions of *Sp. viride*, *Sp. chrysopterus* and *Sp. aurofrenatum* from the Port Royal Reefs were estimated by combining the length-frequency distributions, obtained during 1970 and 1971 as shown in Figs. 13.3 and 13.4a. The estimated mean annual length-frequency distributions of *Sp. aurofrenatum* and *S. taeniopterus* on the oceanic banks are shown in Figs. 13.4b and 13.5.

Sp. viride and *S. chrysopterus* are fully recruited to the traps at the Port Royal Reefs at sizes 20.5 cm FL and 21.5 cm FL, respectively, as shown by Fig. 13.3. Figure 13.4a shows that *Sp. aurofrenatum* are fully recruited at 17.5 cm FL. The smallest individuals of these three species recorded from the traps were 13.1 cm FL, 15.8

Table 13.8. Sex ratio and percentage females of parrotfishes caught at the Port Royal Reefs and on the oceanic banks.

Length class (cm, FL)	Port Royal								Oceanic banks			
	<i>Sp. viride</i>		<i>Sp. chrysopterus</i>		<i>Sp. aurofrenatum</i>		<i>S. croicensis</i>		<i>Sp. aurofrenatum</i>		<i>S. taeniopterus</i>	
	No. fishes	% female	No. fishes	% female	No. fishes	% female	No. fishes	% female	No. fishes	% female	No. fishes	% female
14.0-14.9					12	41.7						
15.0	48	85.4			54	37.0	14	0				
16.0	68	86.8			137	43.0	52	3.8				
17.0	75	88.0	19	57.9	141	29.8	59	6.9	16	87.5	21	100.0
18.0	86	86.0	29	44.8	91	22.0	22	0	17	70.6	55	98.2
19.0	103	85.4	58	58.6	45	15.5			15	80.0	50	88.0
20.0	117	89.7	97	56.7	13	23.0			18	50.0	57	91.2
21.0	95	86.3	109	67.9					10	10.0	53	79.2
22.0	90	85.5	79	70.9							42	71.4
23.0	56	76.8	45	82.2							22	72.7
24.0	44	68.2	14	85.7							19	63.1
25.0	30	63.3										
26.0	22	50.0										
27.0	10	50.0										
Overall ratio of Male:Female	1:4.6 n = 866		1:1.9 n = 466		1:0.5 n = 492		1:0.5 n = 161		1:2.1 n = 92		1:4.6 n = 334	

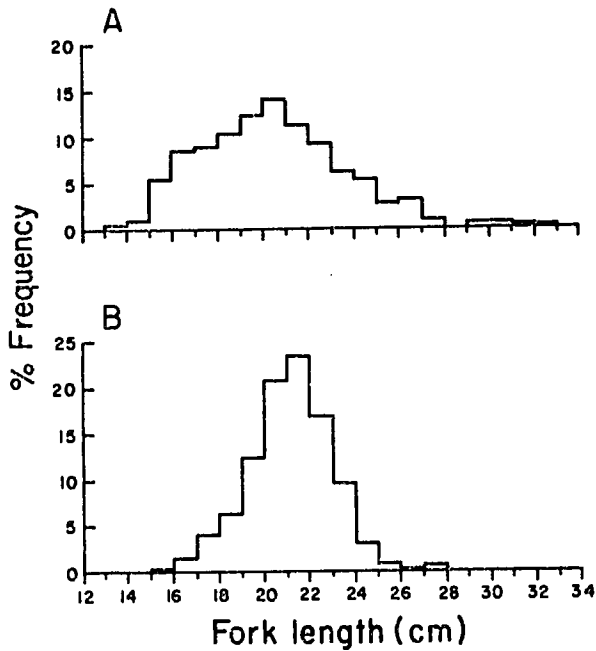


Fig. 13.3. Annual length-frequency distribution of (a) *Sparisoma viride* and (b) *Sp. chrysopterygum* caught in traps set on the Port Royal Reefs (mean of annual data collected in 1970 and 1971).

cm FL and 14.0 cm FL, respectively, values which more or less correspond to the calculated size at retention. Figure 13.4 shows a complete overlap in the length ranges of *Sp. aurofrenatum* from the Port Royal reefs and the oceanic banks, but the modal size at the oceanic banks (19.5 cm FL) is 2 to 3 cm larger than that at the Port Royal Reefs. This either indicates that smaller specimens of *Sp. aurofrenatum* are to be found in shallower areas, or it indicates that exploitation at the Port Royal Reefs is so heavy that most individuals are captured while still within the selection ogive of the 4.13-cm mesh. The latter appears most likely, but the small size of the sample from the oceanic banks precludes any definite conclusions.

S. taeniopterus is fully recruited to the traps at the exploited Pedro Cays at a size of 18.5 cm FL as compared with the recruitment size of 20.5 cm FL obtained from the unexploited areas (Fig. 13.5).

MORTALITY AND MORBIDITY

Factors Affecting Mortality

Those species which prey on parrotfishes have been discussed previously, but otherwise direct evidence of the factors affecting mortality in adolescent or adult parrotfishes is not available. Parrotfishes are not readily caught on hand-lines but are important components of trap catches from coastal areas.

Mortality Rates

The age composition of the catches of parrotfishes

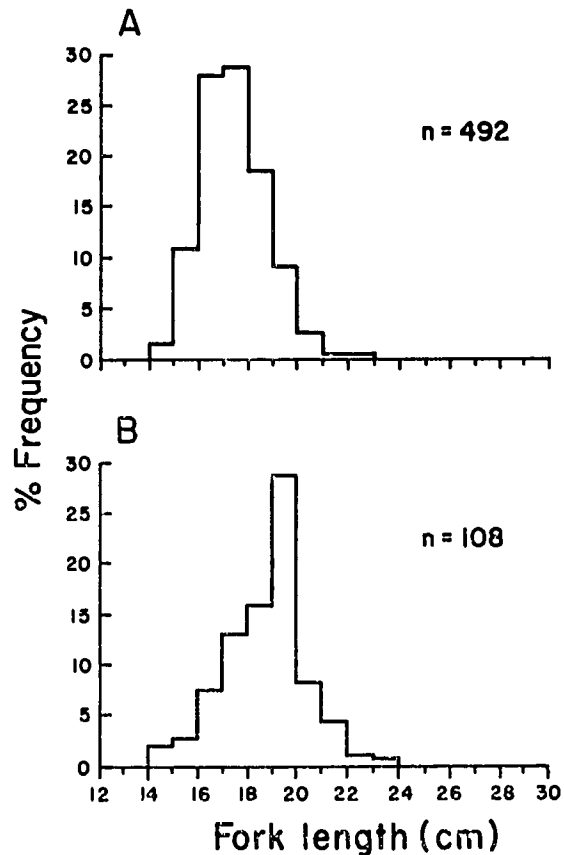


Fig. 13.4. Annual length-frequency distribution of *Sparisoma aurofrenatum* caught in traps set on (a) the Port Royal Reefs (mean of annual data collected in 1970 and 1971) and (b) California Bank and Pedro Bank (data collected between May 1971 and February 1973).

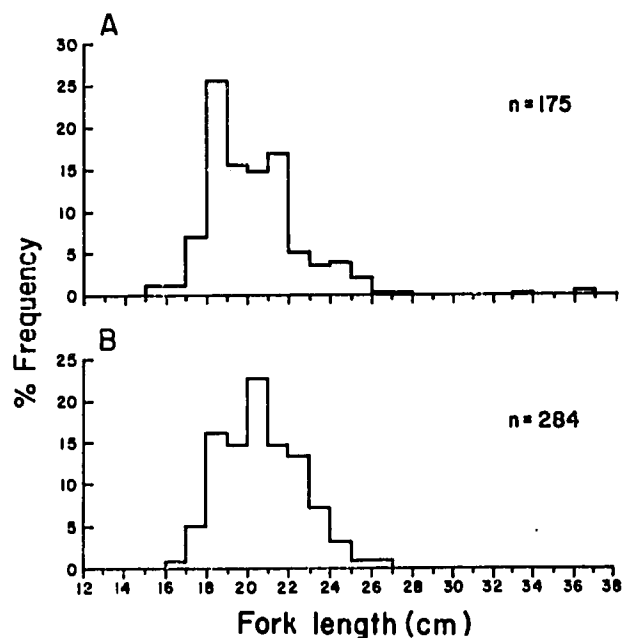


Fig. 13.5. Annual length-frequency distribution of *Searus taeniopterus* caught in traps set on (a) the Pedro Cays and (b) the unexploited portions of Pedro Bank.

Table 13.9. Relative abundances of successive length groups of fully recruited *Sparisoma viride* at the Port Royal Reefs with computation of mortality rate. $L_{\infty} = 50.0$ cm FL. Data for both sexes combined.

Length class (cm, FL)	Port Royal Reefs	
	% frequency	Relative frequency
13.0-13.9	.41	.03
14.0-14.9	.86	.06
15.0-15.9	5.49	.39
16.0-16.9	8.60	.62
17.0-17.9	8.82	.63
18.0-18.9	10.33	.74
19.0-19.9	12.34	.88
20.0-20.9	13.95	1.00
21.0-21.9	11.29	.81
22.0-22.9	9.24	.66
23.0-23.9	6.03	.43
24.0-24.9	5.17	.37
25.0-25.9	2.65	.19
26.0-26.9	2.83	.20
27.0-27.9	.91	.06
28.0-28.9	.04	+
29.0-29.9	.32	.02
30.0-30.9	.46	.03
31.0-31.9	.18	.01
32.0-32.9	.09	+

$$l_c = 20.5$$

Mean FL (\bar{l}) = 22.6
If $L_{\infty} = 50$ cm

$$Z/K = \frac{50.0 - 22.6}{22.6 - 20.0} = 10.5$$

Table 13.11. Relative abundances of successive length groups of fully recruited *Sparisoma aurofrenatum* at the Port Royal Reefs with computation of mortality rate. $L_{\infty} = 26.0$ cm FL. Data for both sexes combined.

Length class (cm, FL)	Port Royal Reefs	
	% frequency	Relative frequency
14.0-14.9	1.42	.05
15.0-15.9	10.97	.38
16.0-16.9	27.84	.97
17.0-17.9	28.66	1.00
18.0-18.9	18.49	.64
19.0-19.9	9.15	.32
20.0-20.9	2.64	.09
21.0-21.9	0.41	.01
22.0-22.9	0.41	.01

$$l_c = 17.5$$

Mean length = 18.3
If $L_{\infty} = 26$ cm

$$Z/K = \frac{26.0 - 18.3}{18.3 - 17.0} = 5.9$$

Table 13.10. Relative abundances of successive length groups of fully recruited *Sparisoma chrysopterum* at the Port Royal Reefs with computation of mortality rate. $L_{\infty} = 40.0$ cm FL. Data for both sexes combined.

Length class (cm, FL)	Port Royal Reefs	
	% frequency	Relative frequency
15.0-15.9	.43	.02
16.0-16.9	1.50	.06
17.0-17.9	4.08	.17
18.0-18.9	6.22	.26
19.0-19.9	12.45	.53
20.0-20.9	20.81	.89
21.0-21.9	23.39	1.00
22.0-22.9	16.95	.92
23.0-23.9	9.66	.41
24.0-24.9	3.00	.13
25.0-25.9	.86	.04
26.0-26.9	.21	.01
27.0-27.9	.43	.02

$$l_c = 21.5$$

Mean length = 22.5
If $L_{\infty} = 40$ cm

$$Z/K = \frac{40.0 - 22.5}{22.5 - 21.0} = 11.7$$

has not been determined and their mortality rates cannot be calculated directly. However, estimates of relative mortality rates were obtained from length composition data as described in Chapter 3.

The relative abundance of successive length groups of *Sparisoma viride*, *Sp. chrysopterum* and *Sp. aurofrenatum* at the Port Royal Reefs and *Scarus taeniopterus* from the exploited and unexploited portions of Pedro Bank are given in Tables 13.9 to 13.12. The ratio of Z/K for each of these species is calculated below their respective tables. In the case of *S. taeniopterus* from the unexploited Pedro Bank, the ratio of Z/K is taken as equal to the ratio M/K.

ABUNDANCE AND DENSITY

No measure of the absolute abundance or population density of parrotfishes was obtained during this study.

Relative Abundance at the Port Royal Reefs

Munro (1974) has described a measure termed 'availability' to estimate the relative abundance of fishes taken in trap catches. The mean monthly availability values of *Sparisoma viride*, *Sp. chrysopterum* and *Sp. aurofrenatum* at the Port Royal Reefs were plotted as shown in Fig. 13.6. The figure shows that the relative abundances of *Sp. viride* and *Sp. chrysopterum* were highest during the earlier months of the year. The

Table 13.12. Comparison of the relative abundance of successive length-groups of *Scarus taeniopterus* beyond full recruitment at the Pedro Cays (N = 175) and at unexploited portions of Pedro Bank (N = 284). Data for both sexes combined. L_{∞} = 35.0 cm FL.

Length class (cm, FL)	Unexploited Pedro Bank		Pedro Cays	
	No. captured	Relative frequency	No. captured	Relative frequency
15.0-15.9			1	.05
16.0-16.9	1	.02		
17.0-17.9	12	.20	8	.42
18.0-18.9	43	.70	17	.89
19.0-19.9	47	.77	19	1.00
20.0-20.9	61	1.00	14	.74
21.0-21.9	40	.65	18	.95
22.0-22.9	35	.57	8	.42
23.0-23.9	24	.39	6	.32
24.0-24.9	14	.23	5	.26
25.0-25.9	3	.05	3	.16
26.0-26.9	3	.05	1	.05
27.0-27.9			1	.05
l_c	20.0		19.0	
Mean length If L_{∞} = 35 cm	22.0		21.6	
Z/K	$\frac{35.0 - 22.0}{22.0 - 20.0}$		$\frac{35.0 - 21.6}{21.6 - 19.0}$	
	= 6.5 (= M/K)		= 5.2	

availability of *Sp. aurofrenatum* was generally very low. The figures also show that these species were present on the reefs throughout the year. As cited before, workers have shown that reef fishes tend to remain within limited tracts of reef.

Relative Abundance on the Oceanic Banks

The relative abundance of parrotfishes on the oceanic banks are given in Table 13.13. In contrast to the catches at the Port Royal Reefs, *S. taeniopterus* was the most important parrotfish in the trap catches from

the oceanic banks. Apart from *Sp. aurofrenatum*, catches of the other parrotfishes were poor.

NATALITY AND RECRUITMENT

Information regarding the rates of reproduction of the three species studied is not available.

Sparisoma viride and *Sp. aurofrenatum* smaller than 15 cm FL and *Sp. chrysopterus* smaller than 17 cm FL were caught in the traps between May and December. However, there is no well-defined recruitment period to the trap fishery.

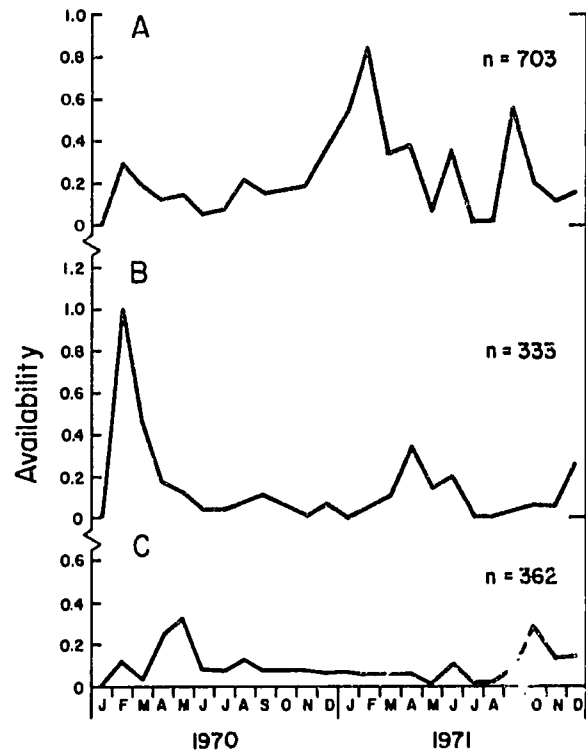


Fig. 13.6. Monthly availability of (a) *Sparisoma viride*, (b) *Sp. chrysopterus* and (c) *Sp. aurofrenatum* caught in unbaited traps set at the Port Royal Reefs.

Table 13.13. Mean catch rates of parrotfishes in baited traps (4.13 cm mesh) at Pedro Bank and California Bank expressed as numbers per 1,000 hexagonal trap-days.

Species	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank	Pedro Cays area	California Bank
<i>Scarus taeniopterus</i>	47	422	23	244	149
<i>S. croicensis</i>	0	10	0	9	0
<i>S. vetula</i>	0	6	0	6	0
<i>S. coelestinus</i>	0	0	0	9	0
<i>S. coeruleus</i>	2	0	13	0	0
<i>Sparisoma viride</i>	0	5	0	4	0
<i>Sp. chrysopterus</i>	0	1	0	4	0
<i>Sp. aurofrenatum</i>	14	19	13	84	74

CHAPTER 14:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE SURGEONFISHES, ACANTHURIDAE

by
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(June 1975)

Identity

The surgeonfishes are oblong, high-bodied, compressed and covered with small scales. The eye is placed laterally high on the head; mouth small and low with non-protractile upper jaw. The teeth are small, close-set, spatulate, with denticulate edges. The preorbital is very narrow and deep. The family receives its common name from the one or more modified spinous scales borne laterally on the caudal peduncle. The spines are hinged posteriorly and contained in a horizontal groove.

The family contains 6 genera with about 75 species. Five species in a single genus, *Acanthurus*, occur in the

Atlantic and the genus has been reviewed by Randall (1956). Caldwell (1966) included the following species known from Jamaica:

Acanthurus coeruleus Bloch and Schneider 1801.
Blue tang.

Acanthurus chirurgus (Block) 1787. Doctorfish.
Acanthurus bahianus Castelnau 1855. Ocean surgeon.

The other two Atlantic species are *Acanthurus monroviae*, which is known only from West Africa, and *Acanthurus randalli*, a species found in the Gulf of Mexico (Briggs and Caldwell 1957).

Distribution

The surgeonfishes are circumtropical, herbivorous fishes but apparently absent from the Mediterranean. Most species are wide-ranging, probably due to a long pelagic larval life. They are fishes commonly found on coral reefs. *Acanthurus coeruleus* is known from New York and Bermuda to Brazil, including the central American coast, Gulf of Mexico and the Bahamas. *A. chirurgus* occurs in West Africa and in the Western Atlantic from Massachusetts and Bermuda, Bahamas, West Indies, Gulf of Mexico, Panama, Venezuela and

Brazil. *A. bahianus* is found from New England and Bermuda to Brazil as well as being recorded from Ascension and St. Helena.

All the specimens of these species found in extreme northern localities were juveniles or sub-adults, and their range extension probably resulted from the transport of larvae by the Gulf Stream (Randall 1956).

The three species occur on the inshore reefs around Jamaica as well as on adjacent oceanic banks.

Bionomics and Life History

REPRODUCTION

Gonads

The paired gonads lie on either side of the midline in the ventroposterior part of the coelom. The sexes are

macroscopically distinguishable except when the fish are immature. The testes are white, elongated and separated dorsally. The ovaries are pink but the color is often masked by the silvery black peritoneum. In shape the ovaries are rounded and lie close together.

Table 14.1. Percentages of mature male and female *Acanthurus coeruleus* in successive length groups. All specimens were captured in traps at the Port Royal Reefs or at Pedro Bank.

Length group (cm, FL)	Males		Females	
	No. examined	% ripe	No. examined	% ripe
8.0-8.9	4	0	1	0
9.0-9.9	15	0	13	0
10.0-10.9	41	0	29	0
11.0-11.9	65	1.5	35	0
12.0-12.9	72	—	61	0
13.0-13.9	55	1.8	57	5.3
14.0-14.9	67	3.0	64	0.9
15.0-15.9	60	6.7	92	20.6
16.0-16.9	75	4.0	64	18.7
17.0-17.9	51	7.8	60	20.0
18.0-18.9	30	3.3	52	26.9
19.0-19.9	18	16.7	24	16.7
20.0-20.9	14	7.1	15	13.3
21.0-21.9	16	18.7	14	4.3
22.0-22.9	5	0	10	20.0
23.0-23.9	1	0	7	28.6
24.0-24.9	2	0	4	25.0
25.0-25.9	2	0	1	0
26.0-26.9	0	0	1	0
27.0-27.9	0	0	0	0
28.0-28.9	1	0	0	0
Totals	594		604	

Sexuality

The sexes are separate amongst the acanthurids and there is no evidence of sexual dimorphism.

Maturity

The length-frequency distributions and the percentages of mature surgeonfishes in successive length groups are given in Tables 14.1 to 14.3. The sizes at full maturity are difficult to define as are the sizes at which the average fish matures. *Acanthurus coeruleus* appears to normally mature at about 13 cm FL and most fishes probably mature within a few cm of this size. In the case of *A. bahianus*, first maturity is at about 11 cm FL, and most fishes are probably mature at 15 to 16 cm FL. Only one ripe male *A. chirurgus* (14.0 to 14.9 cm group) was ever captured, but quite large numbers of ripe females were found, first maturing at about 17 cm FL. The reasons for this are unknown.

Fertilization

Randall (1961a and b) witnessed the spawning behavior of three acanthurid species. The eggs and sperm are shed into the water simultaneously and fertilization is external.

Table 14.2. Percentages of mature male and female *Acanthurus bahianus* in successive length groups. All specimens were captured in traps at the Port Royal Reefs or at Pedro Bank.

Length group (cm, FL)	Males		Females	
	No. examined	% ripe	No. examined	% ripe
9.0-9.9	0	0	1	(100.0)
10.0-10.9	6	0	7	0
11.0-11.9	33	3.0	37	2.7
12.0-12.9	63	3.2	91	13.2
13.0-13.9	82	1.2	99	10.1
14.0-14.9	84	4.8	144	39.6
15.0-15.9	59	11.9	101	62.4
16.0-16.9	51	19.6	48	60.4
17.0-17.9	47	29.8	34	67.6
18.0-18.9	38	21.0	16	56.2
19.0-19.9	12	16.7	5	40.0
20.0-20.9	12	41.7	2	0
21.0-21.9	3	33.3	1	0
22.0-22.9	3	33.3	0	0
23.0-23.9	1	0	0	0
Totals	494		586	

Table 14.3. Percentages of mature male and female *Acanthurus chirurgus* in successive length groups. All specimens were captured in traps at the Port Royal Reefs or at Pedro Bank.

Length group (cm, FL)	Males		Females	
	No. examined	% ripe	No. examined	% ripe
10.0-10.9	1	0	1	0
11.0-11.9	4	0	11	0
12.0-12.9	13	0	17	0
13.0-13.9	18	0	30	0
14.0-14.9	32	3.1	38	0
15.0-15.9	38	0	45	0
16.0-16.9	45	0	59	0
17.0-17.9	45	0	54	1.8
18.0-18.9	44	0	38	5.3
19.0-19.9	20	0	22	4.5
20.0-20.9	22	0	21	14.3
21.0-21.9	14	0	24	29.2
22.0-22.9	20	0	15	20.0
23.0-23.9	10	0	8	62.5
24.0-24.9	9	0	5	(40.0)
25.0-25.9	4	0	2	(50.0)
26.0-26.9	0	0	0	0
27.0-27.9	2	0	1	0
28.0-28.9	1	0	1	(100.0)
29.0-29.9	2	0	0	0
30.0-30.9	0	0	0	0
31.0-31.9	1	0	0	0
32.0-32.9	0	0	0	0
33.0-33.9	0	0	1	(100.0)
Totals	345		393	

Fecundity

Data on gonad size or number of eggs relative to body size were not collected during this study. It is not known whether individual surgeonfishes spawn more than once a year.

Estimates of fecundity were not obtained during this study.

Mating and fertilization

Randall (1961a and b) reports a spawning behavior pattern for acanthurids that is similar to the spawning aggregation pattern of parrotfishes and the wrasse, *Thalassoma bifasciatum*. The fish mill together constantly in small or large schools. A few spawning individuals swim rapidly upwards, above the school, and then down again flexing their bodies at the apex of their movement. The decrease in pressure and consequent expansion of the airbladder caused by the upward dash as well as the sharp flexure of the body at the apex of the spawning run are believed to assist in the extrusion of eggs and sperm.

Spawning occurred in localities where the set of the current was towards the sea which would be advantageous to dispersal of the fertilized eggs.

Randall originally thought that the upward rush of the spawning fish served to confuse would-be predators but he has subsequently abandoned this idea. Jones (1968) maintains it has a possible secondary advantage in that the eggs are placed out of reach of predators.

The spawning of acanthurids was never witnessed during the course of this study. Randall (1961a and b) has observed the spawning behavior of three Pacific species (*A. triostegus sandvicensis*, *Ctenochaetus striatus* and *Zebrasoma scopas*) for each of which spawning occurred at dusk. Randall (1961b) also reported observing what he believed to be a prespawning aggregation of *A. coeruleus* in the Bahamas late in the day.

Randall (1961a and b) noted from his observations that acanthurid spawning occurred around full moon.

Spawning Seasons

Initial data on the spawning seasons of surgeonfishes around Jamaica have been reported by Munro, Gaut, Thompson and Reeson (1973).

Acanthurus coeruleus: Monthly data on the state of the gonads of fishes caught at the Port Royal Reefs and on adjacent oceanic banks have been combined and are presented for each of the above areas in Fig. 14.1. Very few ripe fishes were caught at the Port Royal Reefs but the highest proportion of fishes with active gonads appeared in April. High proportions of active and/or ripe fishes were caught during most months on the oceanic banks.

Acanthurus bahianus: Active and/or ripe fishes were

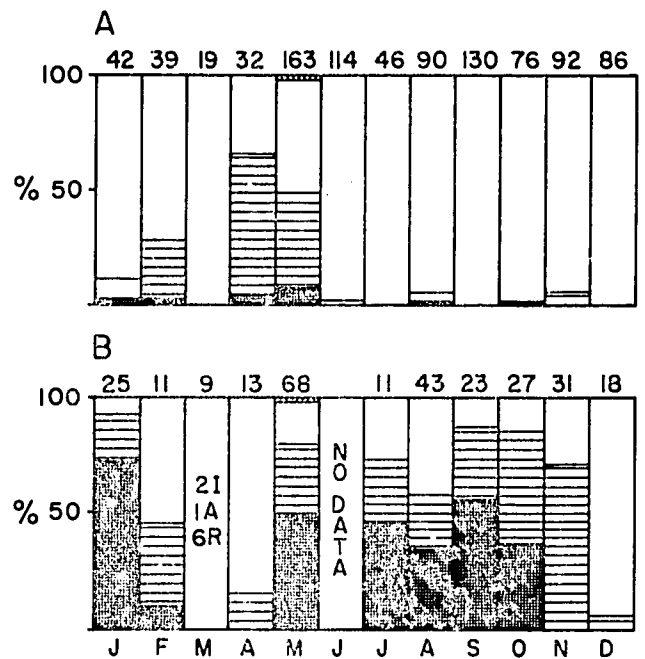


Fig. 14.1. Monthly percentages of ripe (shaded), active (cross-hatched), inactive (blank) and spent (stippled) *Acanthurus coeruleus* in Jamaican waters. Monthly data was combined for all localities at (a) the Port Royal Reefs and on (b) the oceanic banks. The number of fishes examined is given above each month. I = inactive; A = active; R = ripe.

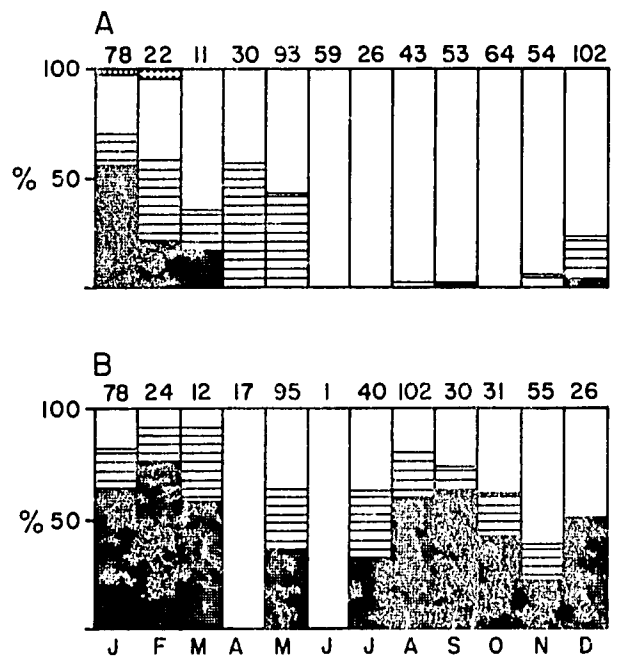


Fig. 14.2. Monthly percentages of ripe (shaded), active (hatched), inactive (blank) and spent (stippled) *Acanthurus bahianus* in Jamaican waters. Monthly data was combined for all localities at (a) the Port Royal Reefs and on (b) the oceanic banks. The number of fishes examined is given above each month.

taken in all month except June, July and October at the Port Royal Reefs as shown in Fig. 14.2. The highest

proportion of ripe fishes occurred in January. Active and ripe fishes were found offshore during most months which indicates that this species also has a year round breeding season with peaks in spawning activity during January to February and August to September.

Acanthurus chirurgus: Data from the Port Royal Reefs (Fig. 14.3) indicate that active gonads were found from December to June with the highest proportions of active fish occurring between January and May. A few ripe fishes were caught in May 1970. Only a few specimens obtained from the oceanic banks were examined. Ripe fishes were caught during September to November.

As shown by Table 14.4, higher proportions of ripe acanthurids were caught on the oceanic banks than at the Port Royal Reefs. This may be due to a lack of spawning activity around the lagoon patch reefs at Port Royal, and spawning aggregations may be migrating to the exposed windward slopes of the surrounding barrier reef. Alternatively, as discussed in a later section, the modal size of the fishes captured at the Port Royal Reefs is smaller than that of fishes trapped on the oceanic banks and thus fewer fishes are reaching sexual maturity at the exploited Port Royal Reefs.

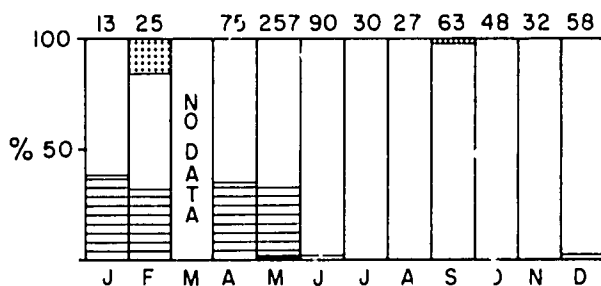


Fig. 14.3. Monthly percentages of ripe (shaded), active (cross-hatched), inactive (blank) and spent (stippled) *Acanthurus chirurgus* in Jamaican waters. Monthly data were combined for all localities at the Port Royal reefs. The number of fishes examined is given above each month.

Spawn

Unfertilized eggs of the three species of acanthurids are spherical, less than 1 mm in diameter, and transparent. The eggs float in sea water and are not adhesive. Randall (1961a) reports similar characteristics for the eggs of *A. triostegus sandvicensis* from Hawaii.

PRE-ADULT PHASE

Randall (1961a) estimated the length of the pelagic larval life of *A. triostegus sandvicensis* around Hawaii to be 2 1/2 months. The post-larval stage is reached 5 days after fertilization. Transformation into the juvenile form

Table 14.4. Percentages of ripe fishes caught at the Port Royal Reefs and at Pedro Bank.

Species	Location	No. of fishes examined	% ripe
<i>A. coeruleus</i>	Port Royal	920	1.8
	Pedro Bank	278	30.9
<i>A. bahianus</i>	Port Royal	646	7.7
	Pedro Bank	434	49.1
<i>A. chirurgus</i>	Port Royal	678	0.8
	Pedro Bank	60	36.7

occurs at night when the characteristic late post-larval stage, the acronurus, moves inshore. Transformation in this species takes 4 to 5 days. The early developmental stages of the Caribbean species have been described by Burgess (1965). Acronurus larval stages have been found in plankton tows taken around Jamaica and are reported from Barbados (Powles 1975), and Burgess (1965) has shown that acanthurid larvae are mainly found above 100 m. Lutken (1880, cited by Randall 1961a) identified post-larval *A. coeruleus* and observations on the transformation of *A. hepatus* (= *A. chirurgus*) were made by Breder (1949). Sale (1969) concluded that the presence of substratum, cover, food and a suitable depth of water were the major environmental characters that acted as stimuli for habitat selection by juvenile *A. triostegus sandvicensis*.

Juvenile *A. chirurgus* and *A. bahianus* have the same coloration pattern as the adults. The juveniles of *A. coeruleus*, however, are a bright yellow and may be found at various sizes in this color or in intermediate patterns of yellow and blue, with the caudal fin becoming blue last. Observations show that the change in color occurs when the juveniles are between 4 to 9 cm FL.

ADULT PHASE

Competitors

The most important potential competitors for algae on the Port Royal Reefs are the parrotfishes, various pomacentrid species and the filefishes, notably *Canthorhines pullus*. There is no available information on the relative degree of intraspecific or interspecific competition or whether in fact the several populations are sufficiently abundant that the food resources are in short supply. Jones (1968) has suggested habitat selection, foraging methods, food habits and modifications of the alimentary canal as possible factors that would reduce interspecific competition amongst the more diverse acanthurid fauna of Hawaii and Johnson Island in the Pacific Ocean.

Predators

Predatory attacks by any species upon acanthurids were not witnessed during this study but a young *Synodus intermedius*, approximately 9 cm FL, was observed resting on the bottom with a juvenile *Acanthurus chirurgus* (3 to 4 cm FL) between its jaws. In his extensive study of the food habits of West Indian reef fishes, Randall (1967) reported the presence of adult or young acanthurids in the stomachs of *Ginglymostoma cirratum*, *Dasyatis americana*, *Sphyræna barracuda*, *Alphesthes afer*, *Cephalopholis fulva*, *Epinephelus striatus*, *Mycteroperca venenosa*, *M. tigris*, *Lutjanus analis* and *Caranx ruber*. Randall (1961a) has noted that predation on *A. triostegus sandvicensis* "is probably most acute during the early stages of the life history". Larval acanthurids have been found in the stomach contents of skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) (Dragovich 1970; Dragovich and Potthoff 1972) as well as blackfin tuna (*T. atlanticus*) (Bone 1965).

Parasites

Ectoparasitic isopods are frequently found on the heads of all three species of acanthurids.

Longevity and Hardiness

It was not possible to establish the age at a given length for the species under study and, thus, the average life expectancy and maximum age attained are not known. Surgeonfishes have been kept alive for up to 20 years in aquaria (Randall 1961a).

Surgeonfishes are able to withstand a minimal amount of handling. Their tolerances to salinity and temperature are not known.

NUTRITION AND GROWTH

Feeding and Food

Surgeonfishes are diurnal feeders, almost entirely herbivorous and well adapted for browsing and grazing algae by means of spatulate teeth. All three species have a long intestine, generally typical of herbivores. Although the stomach contents of fishes caught in traps were examined during the initial phases of the study, in the majority of cases the stomachs were empty or else the contents had been digested beyond identification. Randall (1967) has analyzed the food habits of many West Indian reef fish species and his data are incorporated below.

Acanthurus bahianus and *A. chirurgus* have thick-walled stomachs, tend to feed close to the bottom (Longley and Hildebrand 1941) and consume much inorganic material along with algae. Randall (1967) reported that 5 to 8% of the stomach contents of *A.*

bahianus consisted of sand, small shells, etc. and similarly, 25 to 75% of the stomach contents of *A. chirurgus* examined was inorganic matter. It is believed that the inorganic material ingested aids in grinding the algal cells, allowing their contents to be digested. Algae and organic detritus comprised 91.8% of the diet of *A. bahianus* and the remainder consisted of seagrasses. Likewise for *A. chirurgus*, algae and organic detritus comprised 93.9% by volume of their diet with seagrasses making up 5.7%. On the other hand, *A. coeruleus* has a thin-walled stomach, and does not ingest much calcareous material. Its diet is also made up of algae and organic detritus (92.8%) and seagrasses (6.8%). Longley and Hildebrand (1941) observed that *A. coeruleus* swam higher in the water column than either of the other species, which suggests a possible mechanism by which *A. coeruleus* may be ecologically separated from *A. bahianus* and *A. chirurgus*. However, this behavior has not been noted by this author, and Earle (1972) did not distinguish differences in the food habits of the three species.

Although there is no doubt that these surgeonfishes are primarily herbivorous, *A. bahianus* have been observed feeding on dead fish both in traps and in a fish pen. In the latter case, these acanthurids were also observed to feed on several species of fleshy and filamentous algae that were growing on the sides of the pen.

Growth Rates

Relative growth patterns

The relationships between fork lengths and total lengths of *A. coeruleus* and *A. bahianus* are given in Table 14.5.

Table 14.6 shows the relationships between fork length and maximum depth for the above species. Maximum depth was measured as the perpendicular distance between the dorsal edge of the fish and a point between the anus and the insertion of the anal fin. The mean maximum aperture of the wire mesh commonly used on Jamaican fish traps is 4.13 cm, and the fork lengths

Table 14.5. Relationships between fork length (FL) and total length (TL) of two species of surgeonfishes. Measurements are expressed in centimeters.

Species and formula	Number of fishes	Length range FL, cm
<i>Acanthurus coeruleus</i> FL = 0.55 + 0.89 (TL) TL = -0.60 + 1.12 (FL)	101	14.5-21.5
<i>A. bahianus</i> FL = 1.61 + 0.84 (TL) TL = -1.70 + 1.18 (FL)	110	14.5-20.5

Table 14.6. Relationships between fork lengths (FL) and maximum body depth (D) of two species of surgeonfishes. Measurements are expressed in centimeters.

Species and formula	Number of fishes	Length range FL, cm
<i>Acanthurus coeruleus</i> D = 1.98 + 0.42 (FL) FL = -4.75 + 2.38 (D)	91	14.5-21.5
<i>A. bahianus</i> D = 2.33 + 0.27 (FL) FL = -8.44 + 3.64 (D)	109	14.4-20.5

of *A. coeruleus* and *A. bahianus* at that body depth are 5.08 and 6.59 cm respectively.

The relationships between fork lengths and weights of *A. coeruleus*, *A. bahianus* and *A. chirurgus* are given in Table 14.7. In all three cases the exponent *b* has a value approximating 3.0, and it is concluded that growth is isometric in these species.

Maximum size

Table 14.8 shows the maximum fork lengths measured for both sexes of *A. coeruleus*, *A. bahianus* and *A. chirurgus* caught during the present investigations. The maximum total lengths recorded for these species from the western Atlantic (Randall 1968) are also included.

Age and growth

Randall (1961a) estimated that juveniles of the Pacific species, *A. triostegus sandvicensis* grew at the rate of about 12 mm per month, while adults of 100 to 120 mm SL and 120 to 141 mm SL grew at rates of more than 1.0 mm and 0.8 mm per month respectively. Using a mark and recapture method around the Virgin Islands and ignoring individuals that showed no growth, Randall (1962a) found that specimens of *A. bahianus* between 97 and 137 mm FL, had a mean growth rate of 2.7 mm per month while larger fishes, between 140 and 180 mm FL, grew at a rate of 1 mm per month. Ten individuals of *A. chirurgus*, between 86 and 181 mm FL, grew at 2.3 mm per month and *A. coeruleus* had a growth rate of 1.3 mm per month.

Length frequency distributions of acanthurids at the Port Royal Reefs and on the unexploited portions of Pedro Bank showed no interpretable modal progressions.

The absence of well-defined modal progressions in the length frequencies of the three species is perplexing. The sample sizes are admittedly small for many of the periods but this reflects the great amount of trap fishing effort that is required to obtain statistically satisfactory sample of a single species from a community that is very diverse. Little is known about the biology of most coral reef

Table 14.7. Relationships between fork lengths (FL) and weights (W) of three species of surgeonfishes. All lengths are expressed in centimeters and weights are given in grams.

Species and formula	Number of fishes	Length range FL, cm
<i>Acanthurus coeruleus</i> Log W = -1.556 + 3.022 (Log FL)	276	8.5-24.5
<i>A. bahianus</i> Log W = -1.719 + 3.080 (Log FL)	142	10.5-18.5
<i>A. chirurgus</i> Log W = -1.655 + 3.009 (Log FL)	271	6.5-24.5

Table 14.8. Maximum observed fork lengths of surgeonfishes from Jamaican waters and the maximum total lengths reported in the literature.

Species	Maximum observed fork length (cm)*		Maximum reported total length (cm)**
	Male	Female	
<i>A. coeruleus</i>	21.5	23.6 (25.8)	36.6
<i>A. bahianus</i>	22.1 (24.4)	17.3	25.6
<i>A. chirurgus</i>	35.0	25.0	34.3

*Calculated total lengths are given in brackets.

**Randall (1968)

species and it is not known whether several schools of surgeonfishes exist on the reefs at Port Royal, each with their own size structure, or whether the population structure of the surgeonfishes in this area is stable and that the samples represent estimates of a stable population structure. In the latter case recruitment and mortality rates would be continuous and constant. It is later noted that recruitment to the trap fishery appears to take place throughout the year.

BEHAVIOR

Surgeonfishes are active during daylight hours (Stark and Davis 1966; Hobson 1972; Collette and Talbot 1972), during which time they engage in feeding, moving slowly over the substrate, usually in small groups or in larger aggregations. The three species were observed associated with larger mixed-species aggregations of other species of reef fishes such as parrotfishes, grunts, goatfishes and wrasses as noted by Luckhurst (1972) and Collette and Talbot (1972) and studied from a behavioral viewpoint by Itzkowitz (1974). Earle (1972) has noted that *Acanthurus bahianus* and *A. chirurgus* may be encountered on the reef as well as over adjacent algal

plains and seagrass beds, whereas *A. coeruleus* is commonly seen on the reef but does not often venture far from it. As previously noted by Longley and Hildebrand (1941), Randall (1956) and Collette and Talbot (1972), *A. chirurgus* commonly schools with *A. bahianus*.

During the evening acanthurids seek cover and remain inactive at night. *A. bahianus* and *A. chirurgus* nest in groups near open shelter whilst *A. coeruleus* are found individually in more confined locations (Stark and Davis 1966). Randall (1961a) noted that *A. triostegus sandvicensis* rested on the bottom at night. Juvenile and

adult *A. coeruleus* adopt a nocturnal pattern of pale bars on the sides whilst *A. bahianus* may become paler at night (Stark and Davis 1966; Collette and Talbot 1972).

Studies by Bardach (1958) and Randall (1961a and b) indicated that acanthurids are permanent residents in the same general location on a reef. More recently Smith and Tyler (1973b) have categorized *A. bahianus* as a benthic resident whilst *A. coeruleus* and *A. chirurgus* are considered as suprabenthic nomads. Detailed studies have yet to be done in order to properly define the extent of home or feeding ranges of these species.

Populations

POPULATION STRUCTURES

Sex Ratios

The sex ratio of fishes caught in traps at the Port Royal Reefs is approximately 1:1 for the three species as shown in Table 14.9. There was no apparent variation in the sex ratio with size or preferential selection of either sex by the traps within the size range of fishes caught.

The ratios of males to females caught on the exploited

Table 14.9. Sex ratio and percentage of female surgeonfishes caught at the Port Royal Reefs. Sample size within each length class = > 30 fishes.

Length class (cm)	<i>A. coeruleus</i> % female	<i>A. bahianus</i> % female	<i>A. chirurgus</i> % female
10	41		
11	51	51	
12	47	56	
13	51	52	62
14	45	56	54
15	54	43	54
16	40	30	57
17	57		54
18	56		45
19			52
20			47
21			62
Overall ratio of Male:Female	1:0.89 (n = 920)	1:1.04 (n = 646)	1:1.12 (n = 678)

Table 14.10. Sex ratio of surgeonfishes caught on Pedro Bank.

Species	Pedro Cays			Unexploited Pedro Banks		
	No. Male	No. Female	M:F	No. Male	No. Female	M:F
<i>A. coeruleus</i>	19	22	1:1.2	77	114	1:1.5
<i>A. bahianus</i>	17	52	1:3.0	150	177	1:1.2
<i>A. chirurgus</i>				38	29	1:0.8

(Pedro Cays) and unexploited portions of Pedro Bank are shown in Table 14.10.

Age and Length Compositions

The age at any given size of individual was not established for any of the surgeonfishes. There is thus no information regarding the age composition of the populations. The scales of the three species dealt with in this report were small and the circuli were very regular and closely spaced. Marks that could be used for age determination were not noticeable and a high percentage of the scales were regenerated. Randall (1961a) reported that annular marks could not be detected on the scales, otoliths or vertebrae of *A. triostegus sandvicensis*.

The estimated mean annual length frequency distributions of surgeonfishes caught in traps at the Port Royal reefs and on the oceanic banks are shown in Figs. 14.4 to 14.9. The length frequency estimates pertaining to the Port Royal reefs were derived from the length frequencies obtained in 1970 and 1971. The length frequencies at the oceanic banks were estimated from monthly data collected between May 1971 and February 1973 at the unexploited portions of Pedro Bank; between July 1971 and June 1972 at the Pedro Cays and between October 1971 and March 1972 at Serranilla Bank. The catches from the oceanic banks were expressed as percentage frequencies.

Acanthurus coeruleus: As shown in Fig. 14.4a and b, there is an almost complete overlap in the length range of the catches from the Port Royal Reefs and the unexploited portions of Pedro Bank. The modal size of *A. coeruleus* in the traps at the Port Royal Reefs was 12.5 cm FL whilst they were fully recruited at 15.5 cm FL on the unexploited parts of Pedro Bank. Further data regarding the size composition of catches of *A. coeruleus* were obtained from commercial catch samples (Fig. 14.5a and b). The estimated modal lengths of the catches from the exploited Pedro Cays area and the relatively unexploited Serranilla Bank are 17.5 cm FL and 19.5 cm FL, respectively. Fishes smaller than 13.5 cm FL were not encountered in the commercial catches and this is believed to be due to the size selection of fishes by fishermen who often discard the smaller fishes

or retain them for their own purposes.

The minimum size of *A. coeruleus* theoretically retainable by the 4.13-cm mesh used in the trap fishery is 5.01 cm FL. Based on the size composition of the catches from the Port Royal Reefs the minimum length at retention is 8.5 cm FL. In the absence of body depth measurements at the smaller length sizes, one is

not able to exclude the possibility that the length/depth relationship is not linear over a wider range of length groups. Assuming that the relationship is linear however, then the available data would indicate that the smaller fishes are unavailable to the traps below 8.5 cm FL. This is possibly due to the absence of the smaller fishes at depths greater than 7.6 m, the depth below which traps were most commonly set, or to different behavior patterns relative to traps.

Acanthurus bahianus: Fishes caught at the Port Royal Reefs and on Pedro Bank fall within the length range of 9.5 to 23.5 cm FL as shown in Figs. 14.6 and 14.7. The modal size caught at the Port Royal reefs (12.5 cm FL) is smaller than that at Pedro Bank (15.5 cm FL) as shown in Figs. 14.6a, b and c. The commercial catches taken at the exploited Pedro Cays and at Serranilla Bank had modal sizes of 16.5 cm FL and 18.5 cm FL, respectively as shown in Figs. 14.7a and b.

The minimum length at retention of fishes caught on the Port Royal Reefs is 9.5 cm FL as compared with a theoretical minimum retainable size of 6.59 cm FL by a mesh size of 4.13 cm. As with *A. coeruleus*, it appears that *A. bahianus* is unavailable at sizes smaller than 9.5 cm FL at depths below 7.6 m.

Acanthurus chirurgus: Figure 14.8 shows the estimated size compositions of catches of *A. chirurgus* at the Port Royal Reefs and the unexploited portions of Pedro Bank. The modal size at the Port Royal Reefs was 16.5 cm FL compared to 22.5 cm FL at Pedro Bank.

The estimated annual size compositions of commercial catches from the Pedro Cays and Serranilla Bank are shown in Fig. 14.9. The modal size at the Pedro Cays is 17.5 cm FL. The first mode of the polymodal length distribution at Serranilla Bank occurred at 18.5 cm FL.

Although insufficient data were collected to establish a length:body depth relationship for this species it is likely that the minimum size retained by the traps at the Port Royal Reefs (= 9.0 cm FL) is greater than the theoretical minimum retainable size, as would seem to be the case for *A. coeruleus* and *A. bahianus*.

The modal lengths of catches of the three species from Pedro Bank are greater than the corresponding modal lengths from the Port Royal Reefs. This is attributed to the greater degree of exploitation by the trap fishery at the Port Royal Reefs resulting in a smaller size structure of the populations.

The mean weights of samples of the three surgeonfishes taken at different depths on the oceanic banks, presented in Table 14.11 show that the larger fishes tend to be found at greater depths.

MORTALITY AND MORBIDITY

Factors Affecting Mortality

Direct evidence of factors affecting mortality in

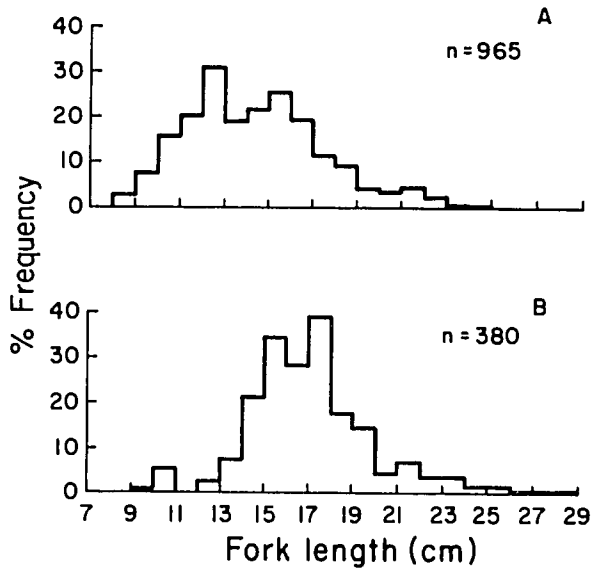


Fig. 14.4. Annual length-frequency distribution of *Acanthurus coeruleus* caught in traps set on (a) the Port Royal Reefs (mean of annual data collected in 1970 and 1971) and (b) the unexploited portions of Pedro Bank (data collected between May 1971 and February 1973).

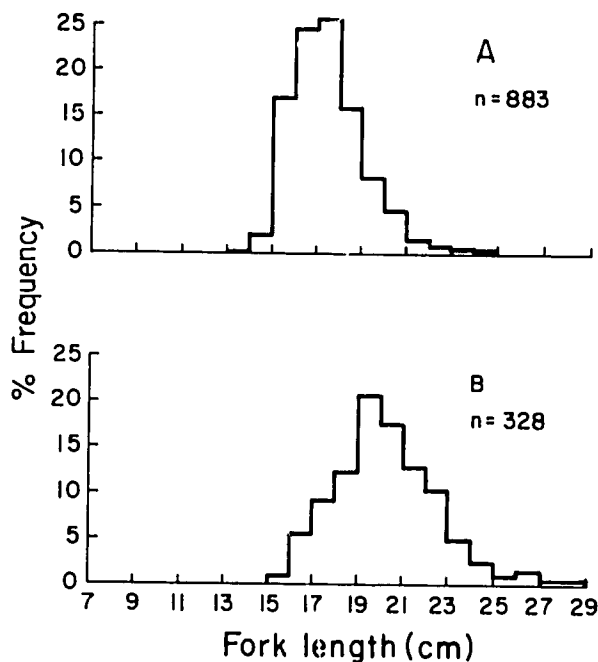


Fig. 14.5. Annual length-frequency distribution of *Acanthurus coeruleus* caught in traps by the commercial fishery at (a) the Pedro Cays and (b) Serranilla Bank.

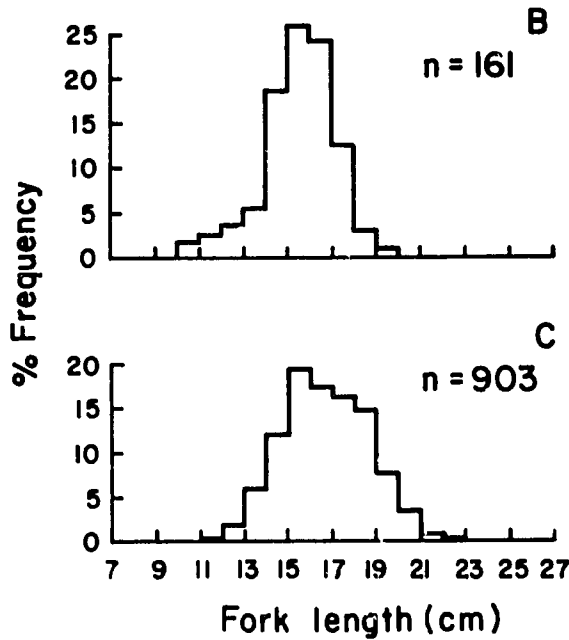
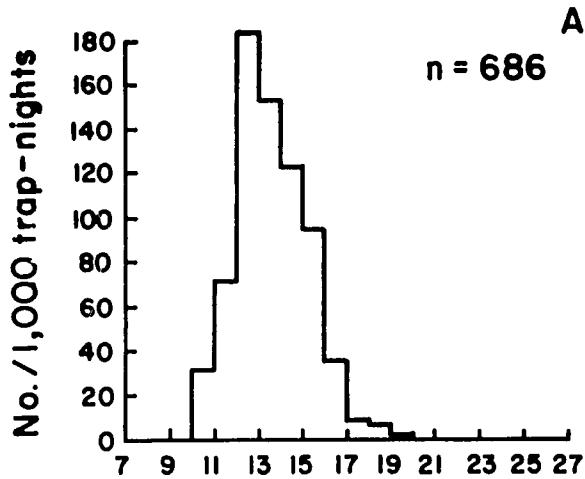


Fig. 14.6. Annual length-frequency distribution of *Acanthurus bahianus* caught in traps set at (a) the Port Royal Reefs (mean of annual data collected in 1970 and 1971), (b) the Pedro Cays (data collected between February 1971 and February 1973) and (c) the unexploited portions of Pedro Bank (data collected between May 1971 and February 1973).

adolescent or adult surgeonfishes is unavailable. Predatory species have been discussed previously. Surgeonfishes are not caught by hand-lines but they contribute substantially to the catch of the trap fishery both inshore and on the oceanic banks.

Mortality Rates

Mortality rates of the surgeonfishes cannot be cal-

Table 14.11. Mean weight of acanthurids taken from different depth zones on the oceanic banks.

Species	Depth zone (m)	Number of fishes	Mean weight (kg)
<i>A. coeruleus</i>	11-20	379	0.12
	21-30	204	0.14
	31-45	25	0.21
<i>A. bahianus</i>	11-20	1,402	0.10
	21-30	1,849	0.11
	31-45	85	0.12
<i>A. chirurgus</i>	11-20	112	0.20
	21-30	100	0.27
	31-45	27	0.36

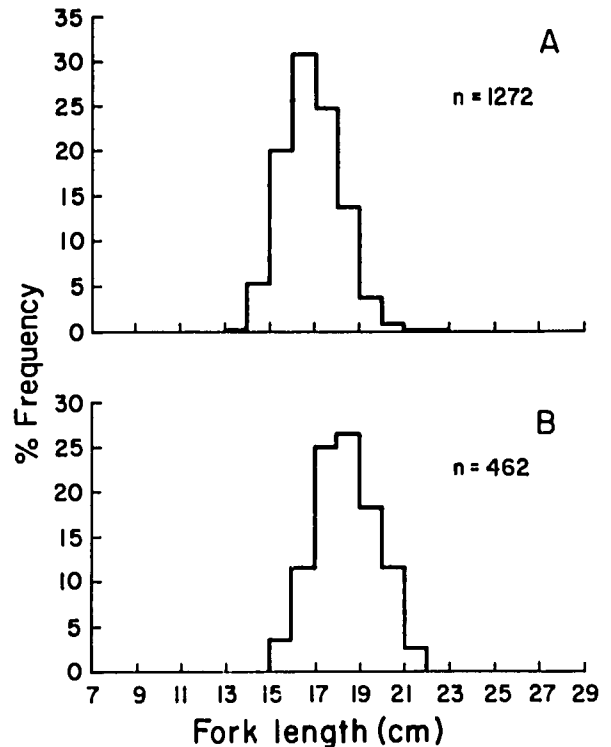


Fig. 14.7. Annual length-frequency distribution of *Acanthurus bahianus* caught in traps by the commercial fishery at (a) the Pedro Cays and (b) Serranilla Bank.

culated directly as the age composition of samples of the three species is unknown. Assuming that growth and mortality rates conform with theoretical patterns, estimates of relative mortality rates can be made from data on size composition.

Tables 14.12 to 14.14 show the relative abundances of successive length groups of the three species and calculations of mortality rates. As the growth rates and asymptotic lengths are unknown, the ratio Z/K may be estimated, given approximated asymptotic lengths, and

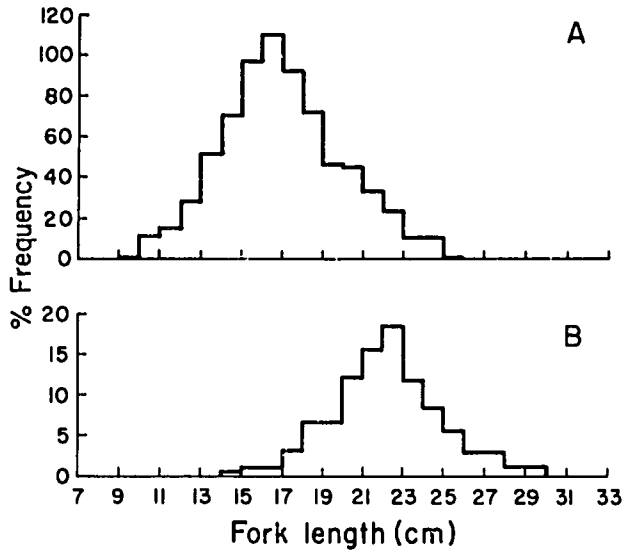


Fig. 14.8. Annual length-frequency distribution of *Acanthurus chirurgus* caught in traps set on (a) the Port Royal Reefs (mean of annual data collected in 1970 and 1971) and (b) the unexploited portions of Pedro Bank (data collected between May 1971 and February 1973).

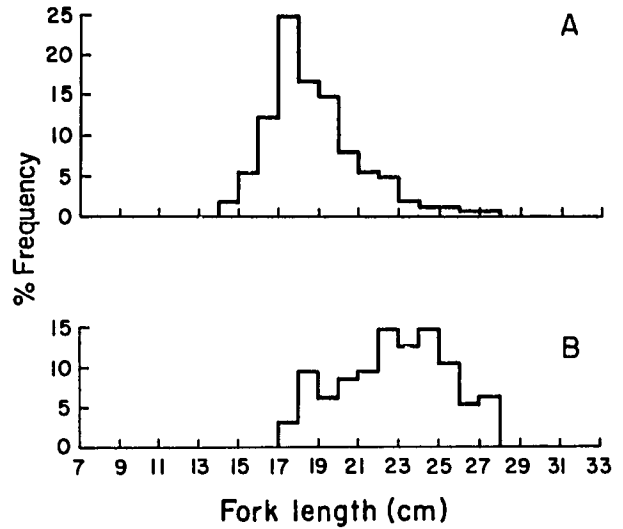


Fig. 14.9. Annual length-frequency distribution of *Acanthurus chirurgus* caught in traps by the commercial fishery at (a) the Pedro Cays and (b) Serranilla Bank.

Table 14.12. Relative abundances of successive length groups of fully recruited *Acanthurus coeruleus* at the Port Royal Reefs and the unexploited parts of Pedro Bank with computations of mortality rates. $L_{\infty} = 30.0$ cm FL.

Length class (cm, FL)	Unexploited Pedro Bank		Port Royal Reefs		
	% frequency	Relative frequency	% frequency	Relative frequency	Adjusted frequency
8.0-8.9	0		1.36		
9.0-9.9	.55		3.70		
10.0-10.9	2.77		7.91		
11.0-11.9	.27		10.35		
12.0-12.9	1.38	.07	15.47	1.00	14.3
13.0-13.9	3.88	.20	9.74	.63	3.1
14.0-14.9	10.80	.54	10.91	.70	1.3
15.0-15.9	17.45	.89	12.07	.78	.9
16.0-16.9	14.40	.73	9.84	.64	.9
17.0-17.9	19.67	1.00	5.88	.38	.4
18.0-18.9	9.14	.46	4.72	.30	.6
19.0-19.9	7.48	.38	2.13	.14	.4
20.0-20.9	2.22	.11	1.88	.12	1.1
21.0-21.9	3.60	.18	2.43	.16	.9
22.0-22.9	1.94	.10	1.17	.07	.7
23.0-23.9	1.94	.10	.20	.01	.1
24.0-24.9	.83	.04	.15	+	+
25.0-25.9	.83	.04	0	0	0
26.0-26.9	.27	.01	0	0	0
27.0-27.9	.27	.01	0	0	0
28.0-28.9	.27	.01	0	0	0
l_c		17.0		12.0	
Mean length if $L_{\infty}=30$ cm		19.3		14.3	
Z/K		$= \frac{30.0 - 19.3}{19.3 - 17.0} = 4.7 (= M/K)$		$= \frac{30.0 - 14.3}{14.3 - 12.0} = 6.8$	

Table 14.13. Relative abundances of successive length groups of fully recruited *Acanthurus bahianus* at the Port Royal Reefs, the exploited Pedro Cays and the unexploited parts of Pedro Bank with computations of mortality rates. $L_{\infty} = 28.0$ cm FL.

Length class (cm, FL)	Unexploited Pedro Bank		Pedro Cays		Port Royal Reefs		Adjusted frequency
	% frequency	Relative frequency	% frequency	Relative frequency	% frequency	Relative frequency	
9.0-9.9	.11	+	0	0	.07	+	
10.0-10.9	.11	+	1.86	.07	4.46	.17	
11.0-11.9	.22	.01	2.48	.09	10.04	.39	
12.0-12.9	1.66	.09	3.73	.14	25.73	1.00	11.1
13.0-13.9	5.87	.30	5.59	.21	21.41	.83	2.8
14.0-14.9	11.96	.62	18.63	.71	17.22	.67	1.1
15.0-15.9	19.37	1.00	26.08	1.00	13.32	.52	.5
16.0-16.9	17.39	.90	24.22	.93	5.02	.19	.2
17.0-17.9	16.28	.84	12.42	.48	1.32	.05	.1
18.0-18.9	14.73	.76	3.10	.12	.98	.04	+
19.0-19.9	7.64	.39	1.86	.07	.28	.01	+
20.0-20.9	3.43	.18	0	0	.07	+	+
21.0-21.9	.77	.04	0	0	0	0	0
22.0-22.9	.33	.02	0	0	.07	+	+
23.0-23.9	.11	+	0	0	0	0	0
\bar{l}_c	15.0		15.0			12.0	
Mean length	17.4		16.5			13.0	
If $L_{\infty}=28$ cm							
Z/K	$= \frac{28.0 - 17.4}{17.4 - 15.0} = 4.4$ (M/K)		$= \frac{28.0 - 16.5}{16.5 - 15.0} = 7.7$		$= \frac{28.0 - 13.0}{13.0 - 12.0} = 15.0$		

Table 14.14. Relative abundances of successive length groups of fully recruited *Acanthurus chirurgus* at the Port Royal Reefs and the unexploited Pedro Bank with computations of mortality rates. $L_{\infty} = 35.0$ cm FL.

Length class (cm, FL)	Unexploited Pedro Bank		Port Royal Reefs		Adjusted frequency
	% frequency	Relative frequency	% frequency	Relative frequency	
9.0-9.9			.07		
10.0-10.9			.52		
11.0-11.9			2.08		
12.0-12.9			3.95		
13.0-13.9			7.07		
14.0-14.9	.56		9.70		
15.0-15.9	1.12		13.44		
16.0-16.9	1.12	.06	15.25	1.00	16.7
17.0-17.9	3.35	.18	12.75	.84	4.7
18.0-18.9	6.70	.36	9.98	.65	1.8
19.0-19.9	6.70	.36	6.37	.42	1.2
20.0-20.9	12.29	.67	6.31	.41	0.6
21.0-21.9	15.64	.84	4.64	.30	0.4
22.0-22.9	18.43	1.00	3.26	.21	0.2
23.0-23.9	11.73	.64	1.39	.09	0.1
24.0-24.9	8.38	.45	1.39	.09	0.2
25.0-25.9	5.59	.30	.83	.05	0.2
26.0-26.9	2.79	.15	0	0	0
27.0-27.9	2.79	.15	0	0	0
28.0-28.9	1.11	.06	0	0	0
29.0-29.9	1.11	.06	0	0	0
30.0-30.9	0	0	0	0	0
31.0-31.9	.56	.03	0	0	0
\bar{l}_c	= 22.0		= 16.0		
Mean length	= 24.2		= 17.3		
If $L_{\infty} = 35$ cm					
Z/K	$= \frac{35.0 - 24.2}{24.2 - 22.0} = 4.9$ (= M/K)		$= \frac{35.0 - 17.3}{17.3 - 16.0} = 13.6$		

for unexploited areas where $Z = M$, M/K can also be estimated.

It was noted previously that the populations at the Port Royal Reefs are virtually extinct whilst still within the recruitment ogive as exemplified by the unexploited populations on Pedro Bank. Therefore, for the purposes of computing mortality rates the observed length frequencies of the Port Royal populations have been adjusted by dividing by the probability of capture indicated by the recruitment ogive of the populations on Pedro Bank (see Chapter 3).

ABUNDANCE AND DENSITY

No information was obtained on the absolute abundance or the population density of the acanthurids.

Relative Abundance at the Port Royal Reefs

A measure of the relative abundance of trap-caught fishes was described by Munro (1974) and termed "availability". This measure takes into account the tendency for the catch to accumulate in traps over time in the form of an asymptotic curve.

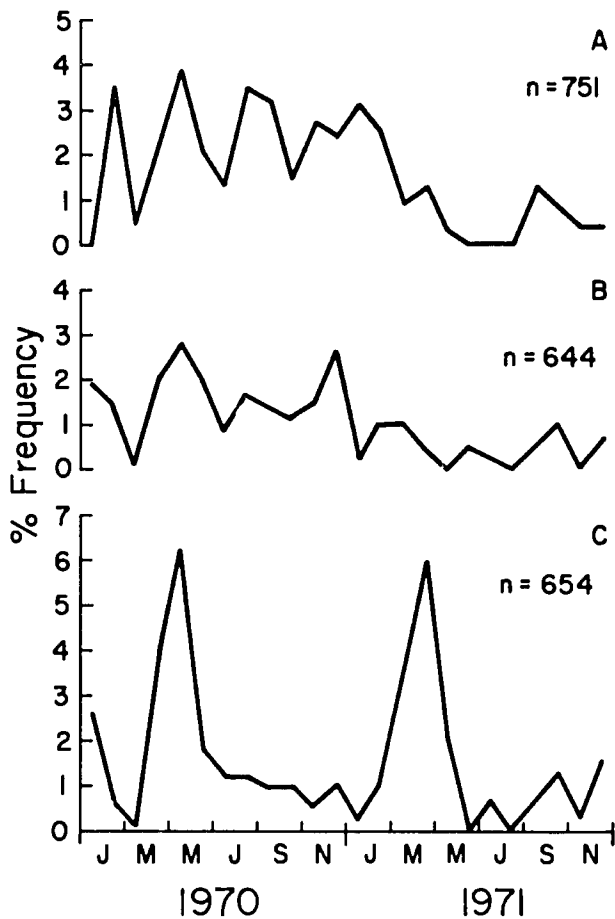


Fig. 14.10. Monthly availability of (a) *Acanthurus coeruleus*, (b) *A. bahianus* and (c) *A. chirurgus* caught in unbaited Z and S traps set at the Port Royal Reefs.

The monthly availability values of surgeonfishes caught throughout the Port Royal Reefs are shown in Figs. 14.10a, b and c. *Acanthurus coeruleus* and *A. bahianus* showed a decline in abundance throughout 1970 and 1971 while *A. chirurgus* was annually more abundant between March and June.

Most of the trap fishing effort at the Port Royal reefs was expended at two large patch reefs, Nassau Reef and Yahoo Reef, and the monthly availability value of each species at these reefs is plotted in Figs. 14.11 to 14.13. As shown in Figs. 14.11a and b, there was a decline in

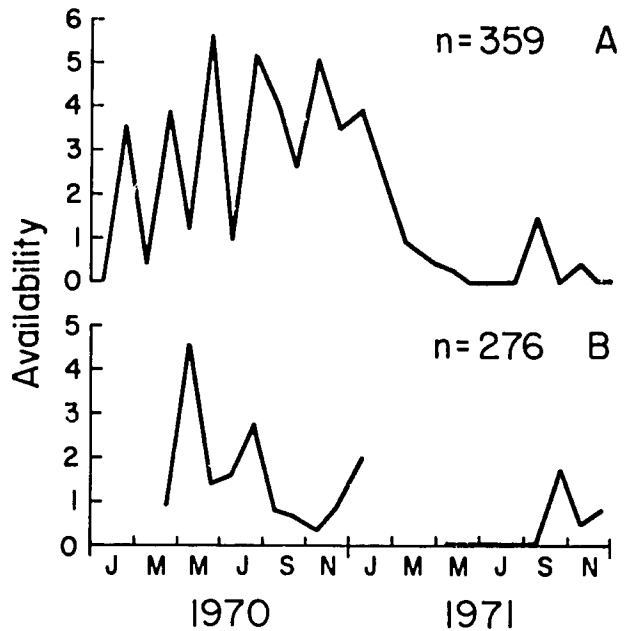


Fig. 14.11. Monthly availability of *Acanthurus coeruleus* at (a) Nassau Reef and (b) Yahoo Reef. Traps were not set at Yahoo Reef between February and April 1971.

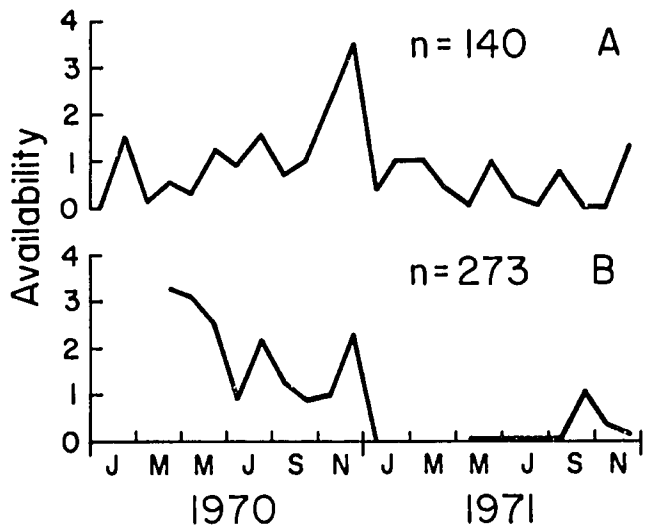


Fig. 14.12. Monthly availability of *Acanthurus bahianus* at (a) Nassau Reef and (b) Yahoo Reef. Traps were not set at Yahoo Reef between February and April 1971.

the abundance of *A. coeruleus* during 1971 at both reefs. At Nassau reef the abundance of *A. bahianus* remained comparatively stable throughout the two year period except for a peak in December 1970 whereas there was a general decline in abundance at Yahoo reef (Figs. 14.12a and b). Only a few *A. chirurgus* were caught at Nassau reef but they were caught throughout the two year sampling period. At Yahoo reef (Fig. 14.13) there was a decline in catches of this species following initially very high catches.

The data shows that these species are present on the patch reefs throughout the year and no seasonal fluctuations in abundance are apparent except possibly in the case of *A. chirurgus*. It is felt that the decline in catches of these species was due, in part at least, to the fishing activities of the project and that this may have maintained these populations at low levels of availability.

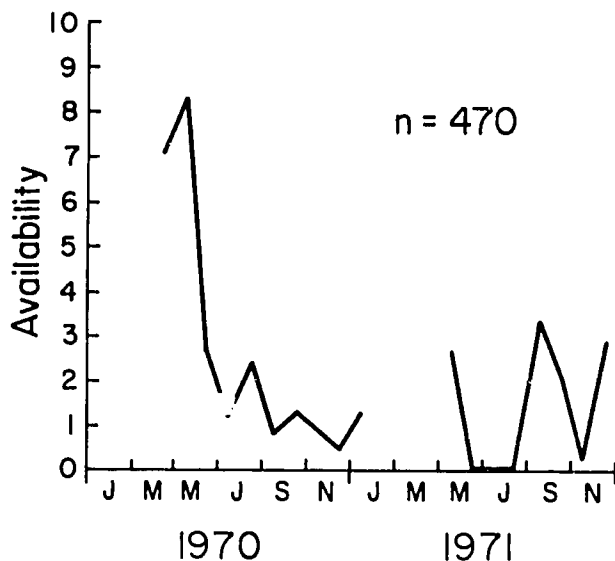


Fig. 14.13. Monthly availability of *Acanthurus chirurgus* at Nassau Reef.

Relative Abundance at Oceanic Banks

The catch rates obtained at the locations sampled on the oceanic banks is presented in Table 14.15. No surgeonfish were caught at Central Pedro Bank.

A. bahianus was the most common acanthurid caught offshore followed in abundance by *A. coeruleus* and *A. chirurgus*, respectively. At Pedro Bank, relatively high catch rates of each species were obtained at SE Spur and 20 meter Bank. Also *A. coeruleus* was abundant at Banner Reef, *A. chirurgus* was abundant at SW Pedro and *A. bahianus* was abundant at Portland Rock. Although less sampling effort was expended at Central Pedro and along the northern edge it is noteworthy that only poor catches of *A. bahianus* were made at the northern edge. The bottom substrate type is not well-known in either of these areas but certainly these are not the reef formations that are found along the southern side of the bank. It is suggested that the lack of cover limits the abundance of the acanthurids in these areas.

The catch rates of the three species at California Bank were comparatively low. The depth of this bank ranges from 35 to 45 meters and there are no shallow reefs or cays such as are found on Pedro Bank. The presence of acronurus larvae can occur at that depth. Due to light attenuation, algal growth may be somewhat limited on this bank and the possible scarcity of food resources could be the reason for the low catch rates.

NATALITY AND RECRUITMENT

There is no available information regarding the rates of reproduction of the three species studied.

The presence of small *Acanthurus coeruleus* (8.0-9.9 cm FL) in each bimonthly period during 1970 suggests that recruitment to the trap fishery at Port Royal occurs throughout the year. *A. bahianus* appears to be similar in this respect.

In Jamaica, juveniles of the three species of surgeonfishes have been observed throughout the year in shallow reef areas, beds of *Thalassia testudinum* and along rocky shorelines.

The mean lengths at recruitment (l_r) for traps with 4.13 cm mesh are 14.4 cm for *A. coeruleus*, 14.7 cm for *A. bahianus* and 20.6 cm for *A. chirurgus* (Tables 14.12 to 14.14).

Table 14.15. Mean catch rates of surgeonfishes (*Acanthurus* sp.) in baited traps (4.13 cm mesh) at Pedro Bank and California Bank, expressed as numbers per 1,000 hexagonal trap-days.

Species	Eastern Pedro Bank	Southern Pedro Bank	Western Pedro Bank	Pedro Cays area	California Bank
<i>A. coeruleus</i>	180	374	12	270	55
<i>A. chirurgus</i>	59	125	33	20	23
<i>A. bahianus</i>	1,608	1,426	134	549	96

**CHAPTER 15:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF THE TRIGGERFISHES, BALISTIDAE**

by
K.A. Aiken
(October 1975)

Identity

TAXONOMY

Suprageneric Affinities

The taxonomy of the Balistidae according to Smith (1965) is as follows:

- Family — Balistidae
- Genus — *Balistes*
- Melichthys*
- Xanthichthys*
- Canthidermis*

The presently accepted valid scientific names for those species included in the present study are included in Table 15.1, together with their common names.

Jordan and Evermann (1898), Meek and Hildebrand (1928), Longley and Hildebrand (1941), Duarte-Bello (1959), Moore (1967), Randall (1968) and Bohlke and Chaplin (1968) give synonyms for these species.

The triggerfishes (Balistidae) are one of several families of the Order Tetradontiformes (Plectognathi). They are very distinctive and often colorful shore and oceanic fishes of the tropical seas which appear to be derived from the surgeonfishes or acanthurid-like stock (Randall 1968). Randall (1968) describes them as having a body which is relatively deep and moderately laterally compressed; the eye is high on the head and the preorbital deep, the snout is long but not attenuate and the mouth is terminal or directed slightly upwards. The jaws are short but strong; there are eight long, close-set protruding incisiform teeth in each jaw, the upper with

six inner reinforcing teeth. The gill opening is restricted to a short slit. There are two dorsal fins, the first of two or three spines; the first spine is the longest and is very stout. The pelvic fins are replaced by a single small spinous knob termed the "pelvic terminus" (Randall 1968) or "ventral apparatus" (Bohlke and Chaplin 1968) which is articulated to the long pelvis. The skin is tough; the scales are modified to platelike structures, the basal plate often being rhomboid in shape, with the outer surface roughened or armed with one or more small

Table 15.1. Scientific and common names of Caribbean balistids.

Scientific names	Common names
1. <i>Balistes capricus</i> Gmelin 1788	Gray or Common triggerfish, Leatherjacket, Filefish, Sabaco.
2. <i>Balistes vetula</i> Linnæus 1758	Queen triggerfish or turbot, Oldwife, Old wench, Blue striped triggerfish, Bessy corca, Bastard turbot, Alewife, Peje puerco, Cochino.
3. <i>Canthidermis sufflamen</i> (Mitchill) 1815	Ocean triggerfish, Sobaco.
4. <i>Canthidermis maculatus</i> (Bloch) 1786	Rough triggerfish.
5. <i>Melichthys niger</i> (Bloch) 1786	Black triggerfish, durgeon or oldwife, Fanny Corker, Negrito, Galafate, Ocean tolly.
6. <i>Xanthichthys ringens</i> (Linnæus) 1758	Sargassum or Redtail triggerfish.

spines or tubercles (Randall 1968; Norman and Greenwood 1963).

The triggerfishes are noted for possessing a locking mechanism (trigger) in the spinous dorsal fin. When the first largest dorsal spine (which has a deep V-shaped furrow along most of its hind surface) is erected, the small second spine (which is wedge-shaped) moves forward, fitting into the groove in the first. When the first spine is fully erect and the second is pushed home,

the first spine cannot be depressed by external force and can only be depressed if the second spine is pulled back. When depressed the second fits into the first and both lie flat in a deep furrow along the dorsal. The second spine is the trigger, hence the name "trigger" fish (Smith 1965; Bohlke and Chaplin 1968).

Thus far there is no record of hybridization among the Balistidae and no hybrids were found during the course of this study.

Distribution

GEOGRAPHICAL DISTRIBUTION

Notes on distribution are given by Jordan and Evermann (1898), Longley and Hildebrand (1941), Duarte-Bello (1959), de Sylva (1963b), Caldwell (1966), Berry and Baldwin (1966), Moore (1967), Randall (1968) and Bohlke and Chaplin (1968).

The Balistidae are tropical fishes. Most Atlantic Ocean species are circumtropical except *Balistes capricus* and *Canthidermis sufflamen*, which are known only from that ocean.

HABITS AND DEPTH DISTRIBUTION

Areas Occupied by Spawn, Larvae, Juveniles

Cousteau (1971) has briefly described the spawn of two tropical Pacific triggerfishes and states that it is attached to coral.

There is very little information in the literature on the areas occupied by very young balistids. Longley and Hildebrand (1942) state that young *Balistes capricus*, up to 100 mm in length are common in floating sargassum and about bits of flotsam. Some young were observed accompanying a piece of bamboo, in the hollow of which they hid when alarmed. Observations made during the present study confirm that post-larval *B. capricus* are common in floating sargassum and flotsam. Also some post-larval *B. capricus* up to 10 mm FL have been captured in plankton nets from among mangrove (*Rhizophora mangle*) prop roots in the shallow swamp near Port Royal, Jamaica, during another study and several juvenile *B. capricus* up to 35 mm were captured from floating sargassum and *Thalassia testudinum* blades in shallow water in the Port Royal area, Jamaica. Three 80 mm juveniles were taken in traps set in 20 m on a sandy bottom at Pedro Bank.

No larval *B. vetula* were seen or captured during the present study but other information (see Section 3.1.6) suggests that they are pelagic.

No larval *Canthidermis sufflamen* were seen or captured but it is thought that the larvae would be pelagic in distribution.

Xanthichthys ringens juveniles are said to be common under sargassum weed patches on the surface (Randall 1968), hence their common name "*Sargassum trigger-*

fish." None were taken but several were seen at California Bank, south of Port Royal.

No larval *Melichthys niger* were seen or taken during the present study and some doubt remains as to whether the juveniles of this species are pelagic or benthic in distribution.

Areas Occupied by Adults

Adult *B. vetula* are found near the bottom on most coral reef environments ranging from shallow sandy or grassy areas (Randall 1967) to the upper slope of the deep reef (100 m). During this study adult *B. vetula* were caught both by traps and lines in depths ranging from 6 m to about 100 m. *B. vetula* adults thus cover the full range of the coral reef complex. There is some evidence that the smaller individuals tend to be found in shallower water than the larger ones.

B. capricus adults were taken from Pedro Bank on only one occasion and nothing definite is known about the areas occupied by this species. They seem to inhabit the same areas as *B. vetula* but are far less abundant in number. Randall (1968) records them as "rare in the West Indies but may be common in higher latitudes."

Adults of *C. sufflamen* are found in mid-water or at the surface below floating objects. They have commonly been taken by hook-and-line in mid-water and just below the surface near drop-offs and over deep water (Randall 1967). This is related to their plankton-feeding habits. However, Randall (1967) reports this species feeding on *Diadema* in only 3 m of water in Puerto Rico. On one occasion during the study a single individual was seen hiding within an over-turned floating plastic crate in deep oceanic water south of Kingston. On another occasion at California Bank a group of about three large *C. sufflamen* were seen at the surface (in 40 m of water) feeding on bread thrown overboard.

Randall (1967) reports adult *M. niger* as a species typical of outer reefs and clear water at depths exceeding 15 m. However, he also reported that occasionally individuals may be seen inshore in as little as 3 or 4 m. Like *C. sufflamen*, adults of *M. niger* are usually seen well above the bottom (Randall 1967, 1968). Randall (1967) also reported that individual fish may rise from the bottom in 20 m or more of water to feed at the surface. Berry and Baldwin (1966) state that *M. niger* "is primarily an inhabitant of oceanic islands, and

may be locally abundant in that environment.”

X. ringens adults may be found beneath floating mats of sargassum weed or other floating objects often over deep water. A few have also been taken in traps from 20 m on Pedro Bank. Randall (1968) reports that “adults are rarely encountered in less than 100 feet of water, but

beyond this depth they become one of the most abundant West Indian reef fishes.”

According to Berry and Baldwin (1966) *Canthidermis maculatus* “is primarily a surface oceanic species that occasionally occurs in inshore waters.” None were caught during the present study.

Bionomics and Life History

REPRODUCTION

Sexuality

Evidence of hermaphroditism, heterosexuality or intersexuality has not been reported for the Balistidae. Moore (1967) records that *Melichthys niger* shows morphological sexual dimorphism in which the lower jaw projects antero-ventrally in adult males while that of females does not.

Data gathered on the length distributions of male and female *Balistes vetula* during the present study are shown in Figs. 15.1a and b. The length distributions of males and females taken by *R. V. Caranx* are very similar and suggest that size differences between both sexes are

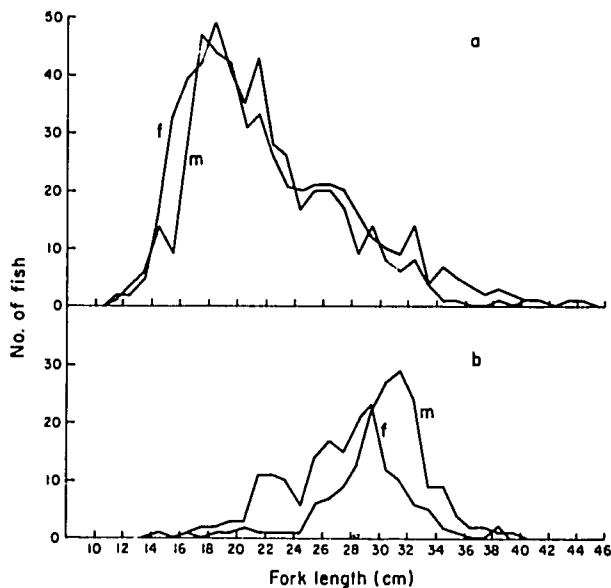


Fig. 15.1. Length-frequency distribution of trap catches (4.13 cm mesh) of male (m) and female (f) *Balistes vetula* (a) from all sampling areas, (b) from *R. V. Alcyon* cruise 70-2 (Eastern Pedro, Salmon and Albatross Banks).

slight, but that males might attain a larger maximum size. Catches of *B. vetula* taken by *R. V. Alcyon* contained larger males and females than did those obtained by *R. V. Caranx*. This is probably because traps set from the *R. V. Alcyon* were usually set as deep as possible (100 m) on the outer edge of the sill reefs. The larger size of the males is apparent in this sample. Samples of other balistids were too small from which to deduce any conclusions.

Maturity

A sample of 642 male and 661 female *B. vetula* taken from all areas and in all months of the year, showed that the minimum size at maturity of males is 17.5 cm FL (Table 15.2). Females attained maturity at a minimum size of 16.5 cm FL (about 150 g). The mean size at maturity is found to be 26.5 cm for males and 23.5 cm for females.

The sample sizes for the other four species *B. capricus*, *Canthidermis sufflamen*, *M. niger* and *Xanthichthys ringens* were too small for accurate estimate of sizes at maturity.

Fecundity

There is no previous information on fecundity of the balistids. Egg counts for two species of triggerfishes are

Table 15.2. Length distributions of male and female *B. vetula* and percentages of fishes with ripe gonads (samples from all areas combined). Lengths are FL in cm.

Median of length group	Males		Females	
	No. examined	% ripe	No. examined	% ripe
16 and under	33	0	58	0
16.5	28	0	40	12.5
17.5	48	2.0	44	20.4
18.5	45	6.6	51	9.8
19.5	43	0	44	11.3
20.5	33	3.3	40	30.0
21.5	35	5.7	52	23.0
22.5	27	3.7	40	30.0
23.5	22	4.5	36	27.7
24.5	21	19.0	23	39.1
25.5	27	44.4	34	50.0
26.5	27	29.6	38	55.2
27.5	29	51.7	31	61.2
28.5	29	44.8	31	58.0
29.5	34	58.8	26	42.3
30.5	37	59.4	20	45.0
31.5	38	52.6	16	56.2
32.5	38	52.6	14	50.0
33.5	14	28.5	9	33.3
34.5	16	25	3	66.6
35.5	11	36.3	1	0
36.5	2	0		
37.5	4	0		
38.5	4	25		
39.5	3	67		

Table 15.3. Estimated egg numbers and eggs per gram body weight for (a) *Balistes vetula* and (b) *Canthidermis sufflamen*.

Species and fork length (cm)	Total weight (g)	Estimated no. of eggs	Eggs/gram weight
(a) <i>Balistes vetula</i>			
32.0	800	52,000	65
37.0	1,200	83,000	69
28.0	570	49,000	86
(b) <i>Canthidermis sufflamen</i>			
38.7	1,350	219,700	163
40.7	1,600	332,000	208
40.2	1,500	427,170	285
50.1	2,950	620,000	210

Table 15.4. Monthly distribution of gonad development stages for *Balistes vetula* from all areas, February 1969 to February 1973. I—inactive; A—active; R—ripe.

Month	No. examined	Percentage		
		I	A	R
January	164	53	10	37
February	152	71	13	17
March	50	69	22	8
April	99	95	5	—
May	231	84	7	9
June	27	100	—	—
July	34	88	3	9
August	58	78	3	20
September	107	74	1	25
October	54	69	9	22
November	116	93	2	5
December	59	83	7	10
Total	1,151			

listed in Table 15.3. The average number of eggs produced by the three *B. vetula* in the table is 73 eggs per gram body weight. *C. sufflamen* yielded an average of 217 eggs per gram body weight.

Mating and Fertilization

There is no information on mating in the balistids.

As the balistids lack intromittent organs it is concluded that fertilization is external.

Spawning

There are relatively few publications on the spawning of Caribbean reef fishes. Randall and Randall (1963) and Munro et al. (1973) provide some information on this topic.

Balistes capriscus (N = 3): There is no previous information on the spawning of this species in the literature and no information was obtained during this study as only juveniles of this relatively rare fish were caught.

Balistes vetula (N = 1,147): Munro et al. (1973) reported having found fishes with ripe gonads in February and May. Table 15.4 shows that ripe fishes were collected all through the year except in April and June. Maxima of spawning were found between January and February and the period August to October. No ripe fishes were taken from the Port Royal Reefs during the period November 1969 to February 1972, although fishes with active gonads were captured between January to February and April to May. Most of the fishes of this species from these reefs were small maturing individuals, suggesting perhaps a movement into deeper water on maturation.

Canthidermis sufflamen (N = 49): Ripe fishes were taken in January, May, August, September and December with a maximum in September.

Melichthys niger (N = 58): During this study ripe fishes were taken in March and August to November.

Xanthichthys ringens (N = 4): Ripe fishes were collected in March and November.

LARVAL AND JUVENILE PHASES

Eggs and Larvae

Cousteau (1971) observed the actual spawning site of a Pacific triggerfish, *Balistes conspicillum* (Bloch and Schneider 1801), which was seen on several occasions watching over the eggs which were deposited in an opening in the coral. It is not known whether the mid-water and pelagic triggerfish such as *Canthidermis sufflamen*, *Xanthichthys ringens* and *Melichthys niger* spawn on the bottom but it seems probable that *B. vetula* and *B. capriscus* may do so. However, there is no evidence for this at the present time.

Randall (1961), Da Cruz (1965) and Bane (1965, quoted by Beardsley 1969, 1970) all found larvae and early juvenile specimens in the stomachs of several species of nearshore-feeding tunas. Specimens of *B. vetula* about 20 mm long were obtained from mid-water trawls in areas east of Jamaica some 80 miles from the nearest land lying up-current (Munro et al. 1972). It is hypothesized that Jamaican waters and the western Caribbean oceanic banks are dependent to some extent for their recruitment of *B. vetula* on those which spawn in southern Hispaniola, Puerto Rico and the Lesser Antillean chain far to the east. It is thought that the eggs and larvae might be transported westwards by the trans-Caribbean Current (an off-shoot of the South Equatorial Current) and taken to suitable habitats which lie in its path. These areas probably include Jamaica, Pedro Bank

and the Cayman Islands.

Large sexually mature fishes were absent from trap samples of *B. vetula* from the Port Royal reefs. This may be explained by the heavily exploited nature of the area or by the larger fishes going into deeper water as they reach maturity.

Adolescent Phase

There is no information in the literature on the adolescent phase of balistids. A few were caught during the present study. They would seem to occur in roughly the same areas as the adult fishes. Small adolescents, however, are very seldom seen by divers and it is not known when they settle out of the plankton.

ADULT PHASE

Competitors

The species captured during this study differed in food habits (Table 15.5), size and ecological distribution, so it is doubtful if interspecific competition occurs.

Interspecific competition may occur between *Melichthys niger* and the angelfishes *Pomacanthus arcuatus* and *P. paru* as these species feed mainly on sponges (Randall 1967).

Predators

Dragovich (1969) studied the food of Atlantic tunas, and found post-larval and juvenile balistids in the stomachs of *Euthynnus alletteratus*, *Katsuwonus pelamis*, *Thunnus albacares* and *T. alalunga*. Specimens of *Balistes capriscus* (listed by Dragovich as *B. forcipatus*, a synonym) were positively identified from two species of tuna.

Bane (1965) quoted by Dragovich (1969) found that balistids ranked third, numerically, in the stomach contents of *E. alletteratus* collected near Puerto Rico. Most of the balistids were small. Da Cruz (1965) quoted by Dragovich (1969), noted large numbers of small balistids in the stomachs of *E. alletteratus* taken off the Brazilian coast.

Caldwell (1966) reported that De Syiva (1963b) found a specimen of *B. capriscus* in a blue marlin (*Makaira nigricans*) stomach captured off Port Antonio, Jamaica.

Dragovich (1970) in a further study of tuna food items showed that balistids were one of the major fish families preyed upon by them. Balistids ranged from less than 1% to over 18% by frequency of occurrence. Two species, *B. vetula* and *Xanthichthys ringens* were identified from stomach contents. Randall (1961) showed that in the Pacific, *T. albacares* fed on balistids to some extent.

Dolphinfish (*Coryphaena hippurus*) are also predators of balistids. Gibbs and Collette (1959), quoted by Beardsley (1967), examined the stomach contents of a

Table 15.5. Food of Balistidae (in part from Randall 1967). Note: X denotes the major food item.

	<i>Balistes vetula</i>	<i>B. capriscus</i>	<i>Canthidermis sufflamen</i>	<i>Melichthys niger</i>	<i>Xanthichthys ringens</i>
Foraminifera				x	
Algae	x	X	x	x	x
Seagrasses				x	
Sponges				X	
Anthozoa (Exc. Corals)	x				
Corals	x			x	
Polychaetes	x				
Sipunculids	x				
Pelecypods	x				
Gastropods	x				
Echinoids	X	x	x		
Ophiuroids	x				
Asteroids	x				
Chitons	x				
Amphipods	x		x		
Shrimps	x			x	x
Stomatopods	x				
Crabs	x				
Hermit Crabs				x	
Scyllarid Lobster	x				
Unident. Crustaceans	x	x		x	
Fishes	x	x		x	x
Tunicates	x			x	
Siphonophores			x	x	
Pelecypod Larvae				x	
Gastropod Larvae			x	x	
Isopod Larvae			x		
Pteropods			x	x	
Barnacle Larvae			x	x	x
Copepods				x	
Crab Larvae			x	x	x
Shrimp Larvae			x	x	
Unident. Eggs		x			x

sample of 46 dolphin fish taken off the coast of Florida and found balistids in 47% of them.

Ovchinnikov (1971) investigating the feeding of Xiphoid fish, found that 7.7% of blue marlin (*M. nigricans*) stomach samples from the Gulf of Mexico and the Caribbean contained balistids. The Atlantic sailfish (*Histiophorus americanus*) was found to be another predator on balistids, and stomachs of specimens taken from waters off northeastern Brazil contained 34% of the genus *Balistes*.

The species of parasite found in *B. vetula* indicate that sharks may also prey upon the balistids. Few fish

stomachs were examined during this study and no balistids were found in them.

Parasites, Diseases, Injuries and Abnormalities

Sogandares-Bernal (1959) in his study of digenetic trematodes of marine fishes from the Gulf of Panama and from Bimini, Bahamas, found three species of the trematode platyhelminth genus *Apocreadium* and two species of *Pseudocreadium* within the digestive tracts of *B. vetula* and *B. capriscus*. The species of *Apocreadium* live in a particular section of the intestine. *B. vetula* was found to be parasitized by *A. coili* (which inhabits the region 1/3 the way down the intestine). *A. uroproctoferum* was found 2/3 distance down the intestine as was *Pseudocreadium lamelliforme*. *B. capriscus* was parasitized by *A. balistis*, *A. coili* and *P. biminensis*. *M. niger* was found to harbor an unidentified lepecreadid trematode.

Specimens of an otobothrid cestode larva were found (sometimes in large numbers) at various times in the abdominal cavity of *B. vetula* from the Pedro Bank. These were identified at the British Museum as possibly being *Otobothrium (Pseudobothrium) dipsaeum* (Linton 1897), the final hosts of which are sharks.

On a single occasion, two specimens of *B. vetula* each over 30 cm FL were taken by hook and line from 42 meters at Pedro Bank and both had their body surfaces irregularly spotted with small subepidermal "bumps," which appeared to be cysts which had come to lie just under the tough "leathery" modified scales covering the body.

A 41 cm FL *C. sufflamen*, from Pedro Bank was found to have 15 to 20 white circular bodies about 1 mm in diameter in each of the ripe female ovaries. These bodies may be encysted reproductive stages of a parasite. No gonadal infection was noted for males of any balistid species.

On several occasions specimens of *B. vetula* and *C. sufflamen* (usually the larger ones more than 30 cm) had parasitic isopods attached to the anus, especially in *C. sufflamen*, and around the eye membranes of *B. vetula*. It should be noted here that these isopods may have only a nuisance value and not have a true parasitic relationship.

Only a few injured balistids were seen in catches made during this study. The majority of these were *B. vetula* and had much of the caudal fin lobes missing or shredded. The cause may be attacks by other fishes or a "fin-rot" disease. On one occasion a large (36 cm TL) *B. vetula* from Pedro Bank was seen with the caudal fin reduced to a stump.

NUTRITION AND GROWTH

Feeding

The balistids are diurnal feeders (Randall 1968). *Balis-*

tes vetula is a bottom feeder (Randall 1963, 1967, 1968) rummaging for its food. It has been seen by Randall (1967) to feed on *Diadema antillarum*, an echinoid, by gripping a single spine and flipping the urchin over to expose its oral surface. The spines are shorter on this surface and it attacks the urchin there. There is no information on the feeding of *B. capriscus* in the literature. Specimens captured during this study appeared to be bottom feeders.

Canthidermis sufflamen is a zooplankton-feeder in midwater and the surface (Randall 1967). *Melichthys niger* often feeds well above the bottom (Randall 1967) and also to a considerable extent on the bottom.

Food

The types of food eaten by most balistids have been described to some extent by Randall (1967). However Randall gave no information on food items eaten by two species, *B. capriscus* and *Xanthichthys ringens*.

The results of Randall's investigations (1967) and data obtained during this study are listed in Table 15.5.

It may be observed from the table and from Randall (1967) that *B. vetula* consumes a wide variety of food while *C. sufflamen* and *M. ringens* are fairly restricted in their diets. *C. sufflamen* and *M. niger* consume mainly planktonic forms. Food items listed for *B. capriscus* were taken from juvenile forms only.

Growth

Relative growth patterns

Randall (1962) presented a length-weight curve for *B. vetula* from the Virgin Islands, West Indies, but did not calculate the length-weight relationship. A sample of 190 *B. vetula* examined during this study gave the following expression for the fork length-weight relationships of both sexes within the length range of 19 to 31 cm FL:

$$W = 0.05164 L^{2.875}$$

where W is the weight in grams and L is the fork length in centimeters.

For *C. sufflamen* the fork length/weight relationship within the length range of 35 to 47 cm FL is described by the following equation:

$$W = 0.05985 L^{2.817}$$

The exponents for both *B. vetula* and *C. sufflamen* indicate that there is a relative decrease in weight with increasing length.

The relationship of fork length (FL) to standard length (SL) in *B. vetula* in the size range 14 to 38 cm FL

is expressed by the formulae

$$\begin{aligned} \text{SL} &= 0.940 \text{ FL or} \\ \text{FL} &= 1.063 \text{ SL} \end{aligned}$$

The relationship between fork length and maximum body depth (MD) in *B. vetula* in the size range 14 to 33 cm FL is expressed by the formulae

$$\begin{aligned} \text{MD} &= 0.7804 \text{ FL or} \\ \text{FL} &= 1.281 \text{ MD} \end{aligned}$$

The FL:SL relationship in *C. sufflamen* within the size range 37 to 45 cm is expressed by the formulae

$$\begin{aligned} \text{SL} &= 0.9503 \text{ FL or} \\ \text{FL} &= 1.052 \text{ SL} \end{aligned}$$

The FL:MD of *C. sufflamen* within the size range 37 to 45 cm is expressed by the formulae

$$\begin{aligned} \text{MD} &= 0.7556 \text{ FL or} \\ \text{FL} &= 1.323 \text{ MD} \end{aligned}$$

There were insufficient data to determine morphometric relationships of *B. caprisus*, *M. niger* and *X. ringens*.

Maximum size

Randall (1968) and Bohlke and Chaplin (1968) record that a fork length of about a foot (30.5 cm) is the maximum size of *B. caprisus*. Moore (1967) found several individuals of 32 cm FL on the U.S. east coast during a study of the western Atlantic Balistidae. The asymptotic length is probably about 31 cm FL.

Randall (1968) records *B. vetula* of up to 57 cm (22.5 in) FL from the U.S. Virgin Islands. Bohlke and Chaplin (1968) state that *B. vetula* grow a little longer than 43 cm (17 inches) FL. The largest male captured during these investigations measured 44.7 cm FL and the largest female, 39.6 cm FL. It seems therefore that the median asymptotic length (L_{∞}) of *B. vetula* is about 45 cm FL, that of females being somewhat less than the abovementioned figure and that of males somewhat larger.

Using the length-weight conversion the calculated asymptotic weight is 2920 g.

C. sufflamen is reported by Bohlke and Chaplin (1968) to reach a maximum size of 2 feet (61 cm). Randall (1968) reports that it attains a length of "at least 22 inches" (56 cm). The largest specimen recorded during this study was 50 cm FL (2,950 g) from Pedro Bank. Some specimens measuring 53 cm FL (3,000 g) were seen in commercial catches from Serranilla Bank. It therefore appears that the asymptotic size is about 55 cm FL.

Bohlke and Chaplin (1968) record that in the west Pacific *M. niger* grows "up to 20 inches" (51 cm) in length. However, most specimens seen by them in the

Bahamas were slightly less than a foot (30 cm) long. Randall (1968) reported *M. niger* "attains 14 inches" (35 cm). The maximum size captured in this study was 32 cm (13 inches).

Bohlke and Chaplin (1968) recorded specimens of *X. ringens* of up to 25.5 cm FL and Randall (1968) reported the same length for this species. The largest specimen captured during this study was 20 cm FL. The asymptotic length for this species appears to lie in the region of 25 cm FL.

Age and growth

During this study, analysis of modal progressions in length-frequency distributions was possible only for *Balistes vetula* as samples of other species were too small and irregularly distributed spatially to yield reliable information.

Randall (1962) tagged *B. vetula* in the U.S. Virgin Islands and found that the average growth rate of fishes ranging from 192 to 304 mm fork length was 4.4 mm per month. The specimen at large the longest increased in size at a rate of 6.8 mm per month.

The length distributions of catches of male and female *B. vetula* suggest that there is only slight sexual dimorphism in growth rates (Table 15.2).

Monthly length-frequency distributions of samples taken at Pedro Bank between May 1971 and April 1972 show some evidence of modal progression (Fig. 15.2) and modes are quite discrete in most samples. The calculation of the values of $\log_e (L_{\infty} - l_t)$ against t and plotted as a regression against a monthly time scale gives two similar regressions, (Fig. 15.3) when an asymptotic length, L_{∞} , of 45.0 cm FL is used. The mean slope (K) of the regression lines on an annual basis is 0.57. These values derived are the best estimates from available data on *B. vetula*.

BEHAVIOR

Migration and Local Movements

Several tagging studies of balistids on tropical Atlantic reefs (Bardach 1958; Randall 1962; Springer and McErlean 1962 and Moe 1972) have been conducted, and no indications of migration found. However, the size compositions of samples of *Balistes vetula* seems to indicate movement to deeper waters with increasing size.

Hobson (1972) noted that two related species of triggerfishes in the Hawaiian Islands which had remained close to the substrate throughout their active periods during daylight and early twilight, sought shelter 15 to 20 minutes after sunset and vacated the water column (along with other diurnal species).

In the mornings, Hobson noted the appearance on Hawaiian reefs of what he termed "milling assemblages" mainly of herbivorous fishes. Also swimming in and around these assemblages were a number of larger

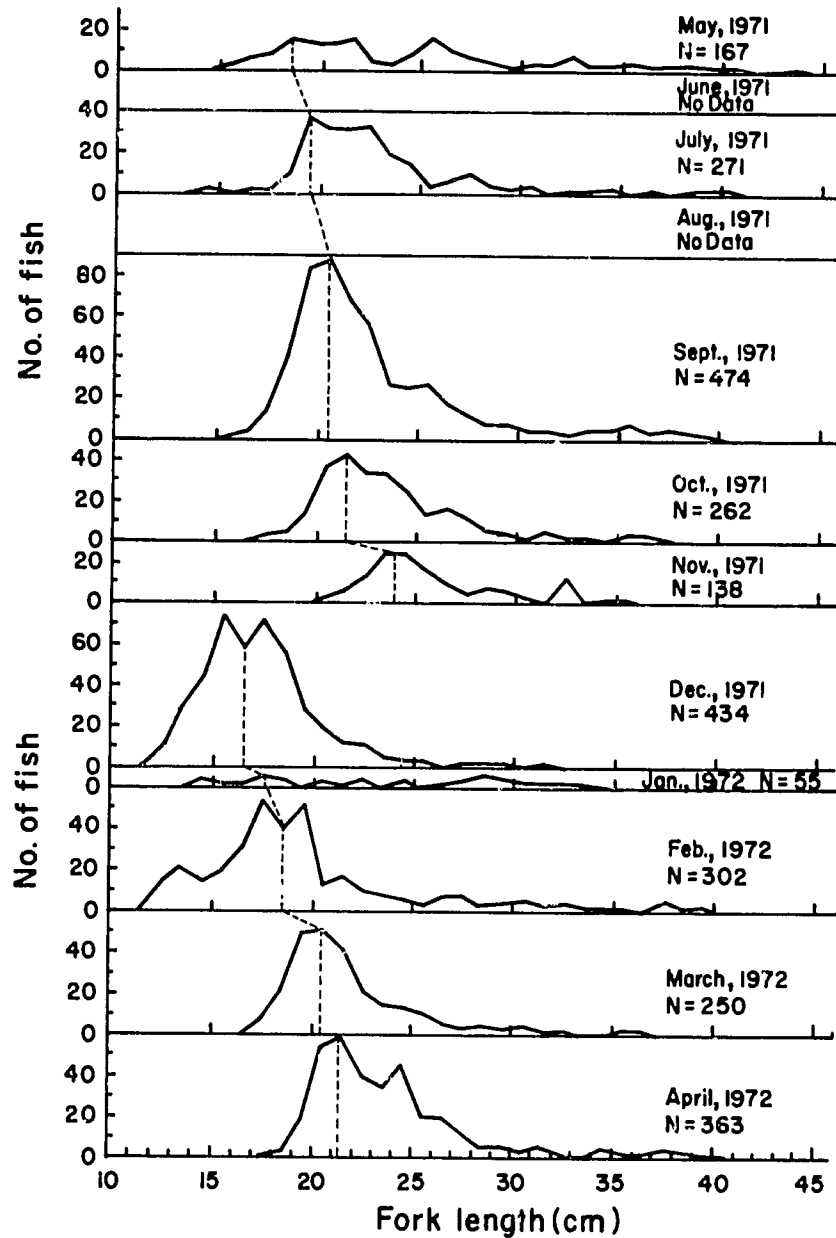


Fig. 15.2. Monthly length-frequency distributions of trap samples of *Balistes vetula* from Pedro Bank, May 1971 to April 1972. Broken lines show the modal progressions utilized in estimating the growth rate.

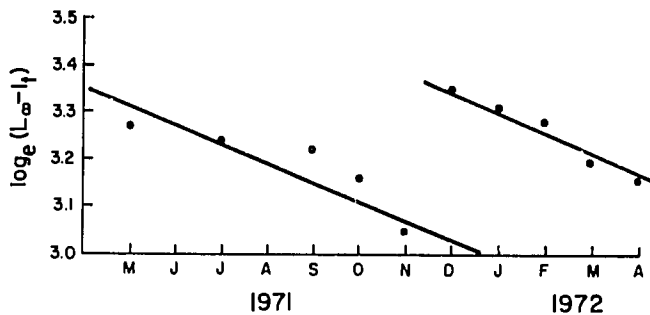


Fig. 15.3. Modal lengths of monthly samples of *Balistes vetula* from Pedro Bank expressed as values of $\log_e(L_\infty - l_t)$. Data from Fig. 15.2. Best fit of regression is obtained when $L_\infty = 45.0$ cm FL. Mean slope, $K = 0.57$ per 12 months.

diurnal fishes that occur as individuals or groups of two or three fishes: these included two species of triggerfishes, one of them *Melichthys niger* which ranges circumtropically.

Schooling

B. vetula has been said to be solitary (Randall 1968) but groups of one to four fish have been observed around Jamaican reefs. Also, Bohlke and Chaplin (1968) reported that Beebe (1933) observed "a school at 150 feet," from his bathysphere off Bermuda.

According to Bohlke and Chaplin (1968) *Canthidermis sufflamen* forms loose groups of about six individuals and that sometimes this species and *M. niger* are seen together. A school of well over 50 individuals was ob-

served on one occasion near the bottom (in 8 to 10 m) on the reef at the U.W.I. Discovery Bay Marine Laboratory, Jamaica (M. Itzkowitz, pers. comm.)

On a few occasions during this study loose aggregations of *C. sufflamen* were seen just below the surface on the deep side of the reef drop-off on some areas of Pedro Bank.

Xanthichthys ringens forms small schools under floating *Sargassum* weed patches. The size of the schools is thought to be related to the area of the weed patch. The reason for this correlation lies in the fact that the weeds offer shelter from predators.

Responses to Stimuli

There are only a few brief references to balistid responses to stimuli (Moulton 1958; Steinberg et al. 1965).

Steinberg et al. (1965) observed a small *B. vetula* to produce a "rattling" sound as it swam after intruding fishes. The intruding fishes included snowy groupers (*Epinephelus niveatus*) and slippery dicks (*Halichoeres bivittatus*).

Steinberg et al. (1965) observed a large *B. vetula* which progressively undermined an acoustic instrument placed on the bottom. It did this by "lying on its side and fanning vigorously with its body." The instrument eventually had to be righted by divers (Steinberg et al. 1965).

POPULATION STRUCTURES

Sex Ratios

There is no previous information regarding sex ratios in the balistids. The sex ratios observed in samples during these investigations are summarized in Table 15.6. Sex ratios of male and female *Balistes vetula* samples taken in traps (4.13-cm mesh) are very nearly equal. Female *Canthidermis sufflamen* outnumber males in the samples by more than two to one, while in *Melichthys niger* samples the situation is apparently reversed. These deviations from the usual may be due to male *C. sufflamen* attaining a retainable size before the females, and the converse in *M. niger*.

Age and Length Compositions

It has not been possible to determine the ages of any species of balistids and consequently there is no information on the age compositions of catches or of the populations.

Balistes vetula: The percentage frequency of successive length-groups captured on hook-and-line are shown in Fig. 15.4. Data were gathered from cruises of the

Other Aspects of Behavior

Cousteau (1971) mentions that in the Indian Ocean triggerfish are "particularly ferocious while their eggs are incubating. The female stands guard over her nest and defends it against all comers (including divers) regardless of their size, with a vigor and disregard for her own safety that it would be difficult to match with any land animal." From photographs in Cousteau (1971), at least two of the balistids have been identified as the big-spotted triggerfish *Balistes conspicillum* (Bloch and Schneider 1801) and the yellow-spotted triggerfish *Pseudobalistes fuscus* (Bloch and Schneider 1801) both from the tropical Pacific and Indian oceans (Marshall 1965).

Cousteau also reports (1971) that divers have seen female triggerfishes, possibly of the two abovementioned species, fanning eggs which are laid among the corals in clumps. This is the first account of a triggerfish incubating eggs by fanning to maintain water circulation. No such observations have yet been made in any of the western Atlantic species of balistids.

Clark (1950) and Marshall (1972) mention that triggerfishes may be observed sleeping or resting lying flat on their sides on the bottom. Clark (1950) stated that in captivity, in the daytime *B. vetula* may be seen to rest for up to one minute on their sides on the bottom and at night resting or sleeping in a vertical or near vertical position against the side wall of their container or flat on the bottom. *M. niger* have also been observed by Clark (1950) to sleep in a vertical position against the sides of their container.

Populations

R.V. Caranx where hook-and-line gear was used for fishing at all parts of Pedro Bank. The mean size caught was 27 cm FL.

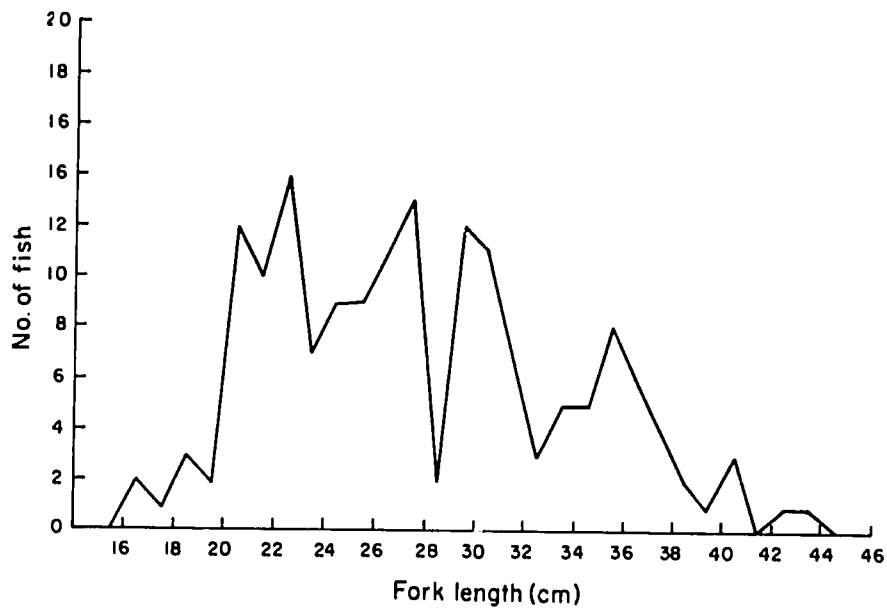
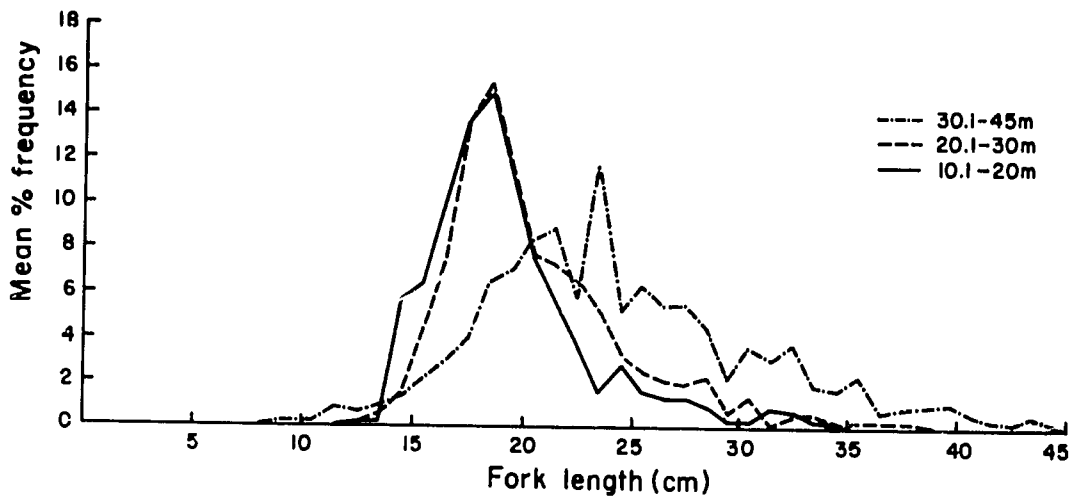
Figure 15.5 shows the mean percentage frequency distributions of catches taken in traps in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones on unexploited Pedro Bank. Relatively more larger fishes (above 25 cm FL) were taken in the 30.1 to 45 m zone and the mean size increased by several centimeters. Fishing effort was similar in the zones 20.1 to 30 m and 30.1 to 45 m, and so it is thought that this increase in mean size of the samples implies that *B. vetula* seeks deeper water as it increases in size.

Figure 15.6 shows the gross length-frequency distributions of trap catches of *B. vetula* at the exploited parts of Pedro Bank (the Pedro Cays) and at California Bank. Relatively more small fishes (less than 18 cm FL) were taken at the Pedro Cays than at California Bank. This may be as a result of the traps at the Pedro Cays being set in shallower water (10 to 20 m) than those at California Bank (31 to 45 m).

Figure 15.7 shows the percentage length-frequency distributions of trap catches of *B. vetula* taken by commercial fishermen operating mainly around the Pedro Cays. When compared with catches taken during this study from the unexploited parts of Pedro Bank (10

Table 15.6. Sex ratios of balistid samples taken from all areas.

Species	Area	No. of Males	No. of Females	Male:Female Sex ratio
<i>Balistes vetula</i>	Port Royal Reefs	26	29	1.00:1.12
	Unexploited Pedro Bank	268	274	1.00:1.02
	Pedro Cays (exploited)	79	87	1.00:1.10
	California Bank	67	71	1.00:1.06
<i>Canthidermis sufflamen</i>	all	14	36	1.00:2.57
<i>Melichthys niger</i>	all	35	15	1.00:0.43

Fig. 15.4. Length-frequency distributions of catches of *Balistes vetula* at Pedro Bank on hook and line.Fig. 15.5. Length-frequency distributions of catches of *Balistes vetula* caught in traps (4.13 cm mesh) in the 10.1 to 20 m, 20.1 to 30 m and 30.1 to 45 m depth zones of unexploited parts of Pedro Bank.

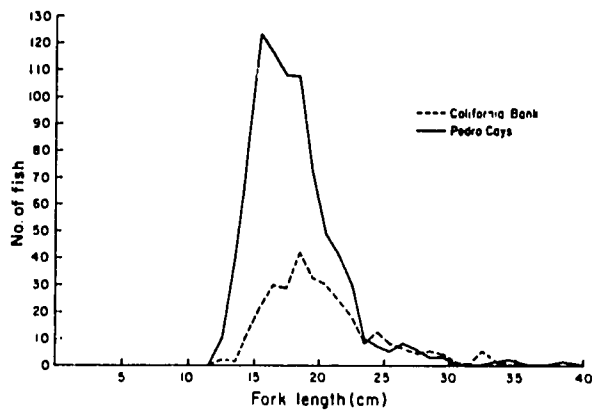


Fig. 15.6. Length-frequency distribution of catches of *Balistes vetula* caught in traps (4.13 cm mesh) at Pedro Cays (exploited parts of Pedro Bank) and California Bank (exploited). Pedro Cays—N = 821; California Bank—N = 295.

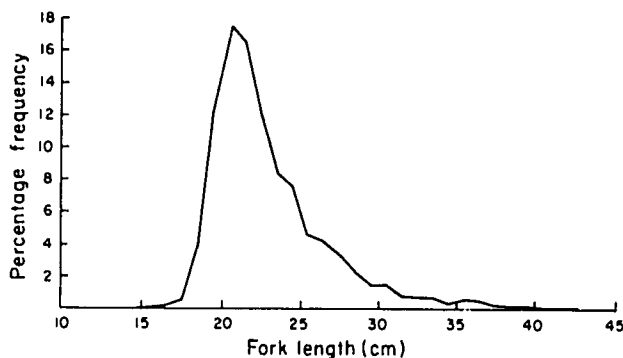


Fig. 15.7. Length-frequency distributions of commercial trap (4.13 cm mesh) catches of *Balistes vetula* from the Pedro Cays. N = 1982.

to 45 m) (Fig. 15.5), any deductions should be made with some caution as the commercial fishermen usually dispose of the smaller length groups (i.e., those less than about 17 cm FL) prior to shipment from the Pedro Cays.

Figure 15.8 shows the percentage length-frequency distributions of commercial catches taken in traps at the Honduras-Nicaragua shelf and at Serranilla Bank. The distributions are very similar. The mean size of catches at the Honduras-Nicaragua shelf was 22 cm FL while that of Serranilla Bank catches was 21 cm FL.

Figure 15.9 shows the percentage length-frequency distributions of successive length-groups of trap (4.13 cm mesh) catches taken by the UNDP/FAO vessel *R. V. Alcyon* at eastern Pedro Bank, Salmon Bank and Albatross Bank. Relatively larger fishes were taken at Salmon and Albatross Banks (over 30 cm FL) than at Pedro Bank on this cruise (70-2). The mean sizes of catches on Salmon and Albatross Bank are 29 cm and 28 cm FL, respectively. Catches at eastern Pedro Bank had a mean size of 23 cm FL by comparison.

The catches at Salmon and Albatross Banks have a far greater proportion of the larger length groups (over 25 cm FL) than do any of the samples taken from all other

areas. This may probably be due to the fact that the traps used on *M. V. Alcyon* were set much deeper (about 100 m) than were those at the other areas (maximum depth 45 m). This may also imply that the larger length groups of this species are found in deeper water.

On the basis of the sample taken from the unexploited parts of Pedro Bank (10 to 30 m) the sizes at first retention, mean retention and full retention are 9 cm, 15 to 16 cm and 18 cm, respectively. At depths below 30 m the size at full recruitment (l_r) is 23 to 24 cm FL.

Canthidermis sufflamen: The frequency of successive length groups captured with hook-and-line on unexploited Pedro Bank in 10 to 45 m depth is shown in Fig. 15.10. A mean size of 39 cm FL was calculated from 65 individuals measured.

Table 15.7 lists the size range (in cm FL), mid-range mode and mean size of those captured by the same gear on California Bank. A mean size of 38 cm FL was calculated.

Melichthys niger: The frequency of successive length groups captured with hook-and-line on the unexploited parts of Pedro Bank is shown in Fig. 15.11. A mean size of 27 cm FL was calculated from 32 specimens measured.

Table 15.7 lists the size composition data gathered for this species from California Bank hook-and-line catches.

Xanthichthys ringens: Table 15.7 lists the size composition of a sample of 23 specimens taken in traps at the unexploited parts of Pedro Bank. The mean size calculated was 17 cm FL. Four specimens (length range 16 to 19 cm FL; mean FL 17.3 cm) were examined from hook-and-line catches at California Bank.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

There is no direct evidence concerning natural factors responsible for mortality of adolescent or adult balistids. One of the major sources of mortality would be predation probably by tunas on the pelagic species or stages (Dragovich 1969, 1970) or by groupers and sharks upon the demersal species. Heavy infestations of the otobothrid cestode parasite *Otobothrium (Pseudobothrium) dipsaeum* Linton 1897 have been observed in *Balistes vetula* only. It is possible that extreme cases of infestation result in death.

In the nearshore areas of the Jamaican shelf at California Bank and the Port Royal Reefs, trap fishing is undoubtedly a major cause of mortality. Balistids are also readily caught with hook-and-line.

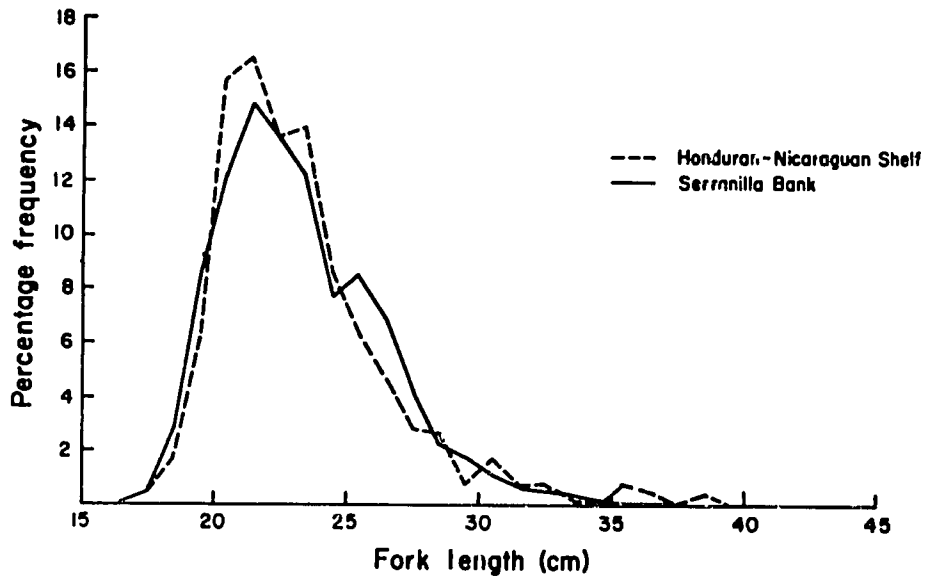


Fig. 15.8. Length-frequency distributions of commercial trap (4.13 cm mesh) catches of *Balistes vetula* from Serranilla Bank and the Nicaraguan-Honduran Shelf. N = 381.

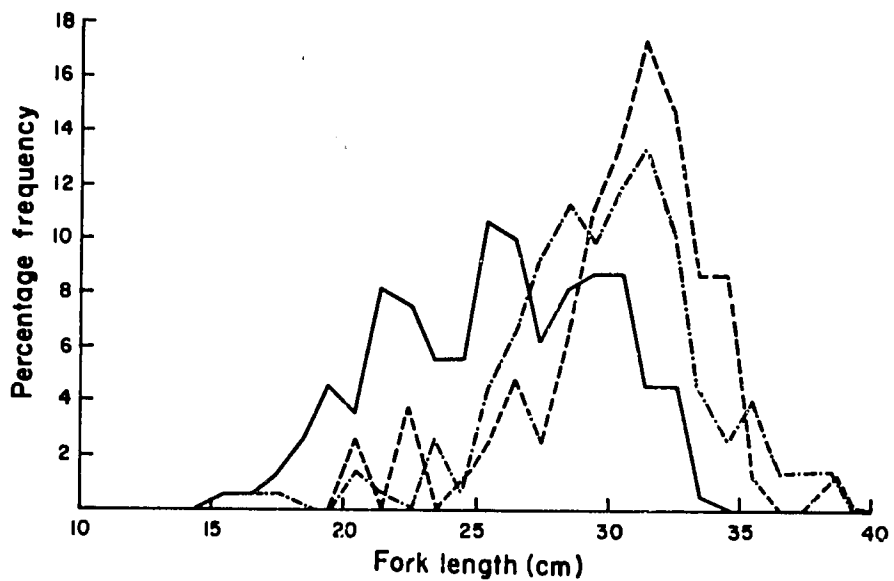


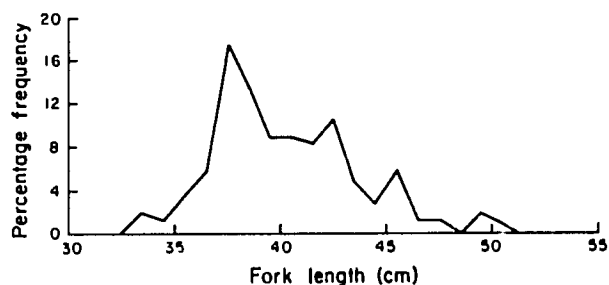
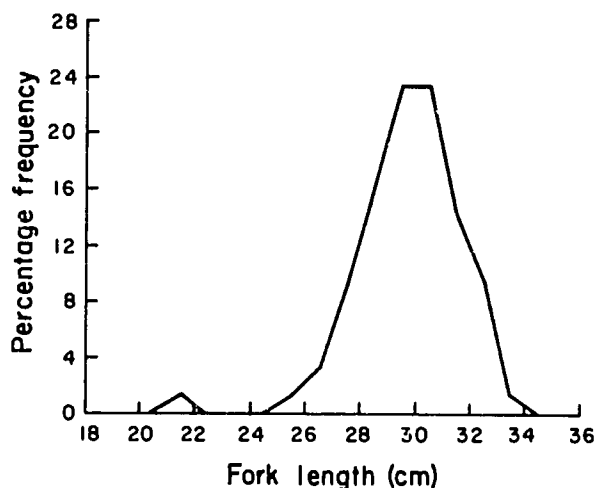
Fig. 15.9. Length-frequency distributions of *M.V. Alcyon* trap (4.13 cm mesh) catches of *Balistes vetula* from Pedro Bank (—), Salmon Bank (----) and Albatross Bank (- · - ·). Pedro Bank-N = 161; Salmon Bank-N = 81; Albatross Bank-N = 152.

Table 15.7. Size composition of Balistid samples taken by traps and lines.

Species and area	Size range (cm FL)	Mid-range (cm FL)	Modal size (cm FL)	Mean size (cm FL)	Sample size	Depth (m)
<i>Canthidermis sufflamen</i> California Bank (H.L.)	35-43	39.5	–	38	22	31-45
<i>Melichthys niger</i> California Bank (H.L.)	26-32	29.5	–	29	27	31-45
<i>Xanthichthys ringens</i> Pedro Bank (Unexploited Traps)	13-20	16.5	–	17	23	10-45

Table 15.8 Relative density of *Balistes vetula* populations in various depth zones of Pedro Bank.

Depth zone	Total trap catch	Adjusted effort (hexagonal trap days)	C/f	Area of zone (km ²)	Relative abundance (C/f̄ x km ²)
10.0-20 m	3,846	562.3	6.84	2,219	15,180 (1.00)
20.1-30 m	982	773.7	1.27	3,700	4,700 (0.31)
30.1-45 m	1,122	785.6	1.43	1,948	2,790 (0.18)

Fig. 15.10. Percentage frequency of 83 specimens of *Canthidermis sufflamen* all taken with hook and line, mainly from Pedro Bank.Fig. 15.11. Percentage frequency of 63 specimens of *Melichthys niger* captured in traps (4.13 cm mesh) from all areas investigated.

Mortality Rates

The absolute ages of the species of balistids dealt with are not known and the following estimates of mortality rates are based entirely upon the length distribution of samples taken during this study. The accuracy of such estimates is probably dependent upon the size and representativeness of the samples.

Balistes vetula: Estimates of the mortality rate of this species are based on large samples from the unexploited parts of Pedro Bank. There is a very marked movement from the shallows to deeper water with increasing size and any estimates of mortality must take this movement into account. This has been done by weighting the length distributions according to relative population density (= catch/1,000 hexagonal trap-days) and the area of each depth zone. The product (C/f x area) gives an index of relative abundance (Table 15.8). This table shows that the ratio of relative abundance in 20 to 30 m is only 0.31 of that in 10 to 20 m. In 30 to 45 m the figure is 0.18.

Table 15.9 shows the length-frequency distributions in each depth zone reduced by 0.31 (for 20 to 30 m) and by 0.18 (for 30 to 45 m) and then summed to get the best overall estimate of the decline in abundance of successive groups. If $L_{\infty} = 45$ cm FL and $K = 0.57$, the best resulting estimates are $M/K = 4.58$ and $M = 2.6$.

The population length structure at California Bank which is uniformly deep and level, indicates a total mortality rate of $Z = 3.2$. The derivation of fishing mortality rates and catchabilities is described in Chapter 17.

Table 15.9. Relative abundance of unexploited stocks of *Balistes vetula* adjusted for population density and area of depth zone at Pedro Bank.

Median of length group	10.2-20 m	20.1-30 m	30.1-45 m	Relative abundance
21.5	1.00	.31	.18	1.49
22.5	.44	.32	.12	.88
23.5	.59	.27	.11	.97
24.5	.41	.16	.11	.68
25.5	.26	.13	.15	.54
26.5	.24	.10	.12	.46
27.5	.21	.08	.13	.42
28.5	.03	.09	.10	.22
29.5	.03	.06	.06	.15
30.5	.12	.02	.08	.22
31.5	.12	.03	.07	.22
32.5	.06	.03	.09	.18
33.5		.02	.05	.07
34.5	.03	.01	.04	.08
35.5		.02	.05	.07
36.5			.01	.01
37.5		.02	.02	.04
38.5			.02	.02
39.5			.02	.02
40.5			.01	.01
41.5			.01	.01
43.5			--	
44.5			.01	.01

$$l_c = 2.10$$

$$\text{Mean FL} = 25.3 \text{ cm FL}$$

$$\text{If } L_{\infty} = 45 \text{ cm FL}$$

$$Z/K = \frac{45.0 - 25.3}{25.3 - 21.0}$$

$$= 4.58 = M/K$$

$$\text{If } K = 0.57, Z = 2.6 = M$$

Other species: Catches of other species of balistids were not sufficiently large to yield estimates of mortality rates.

ABUNDANCE AND DENSITY

There is no information on the absolute size of the populations which were studied nor of the effect of ecological factors on population density and abundance.

Relative Abundance

Catch rates of *Balistes vetula* in traps during this study are listed in Table 15.10. Highest catch rates (C/f) were found at the Pedro Cays but the average weight of individual fishes was low.

Table 15.11 lists data on the abundance of *B. vetula* relative to depth at Pedro Bank. Highest catch rate for this species was at the Pedro Cays between 11 to 20 m depth where it comprised nearly 60% of the total catch by number and 52.41% by weight. Greatest mean weights were found at western Pedro Bank between 31 to 60 m depth.

In general *B. vetula* comprised, by both number and weight, the most abundant of all species caught in traps (4.13 cm mesh) at all parts of Pedro Bank.

NATALITY AND RECRUITMENT

There appears to be no information on any aspect of the natality of any species of Balistidae.

As previously mentioned the minimum size at which *B. vetula* is recruited to the trap (4.13 cm mesh) fishery is about 9 cm and mean and full recruitment generally occur at about 16 and 21 cm FL respectively at most areas investigated.

Owing to the very marked movement into deeper waters with increasing size and the uncertain nature of

Table 15.10. Mean catch rates, percentages of *Balistes vetula* (by wt) and mean weights of individuals in the catch (\bar{W}_c) in various areas. Catch rates expressed as numbers (C) or weight (W) per 1,000 hexagonal trap-nights (f).

Area	Effort trap-nights	C/f	W/f kg	\bar{W}_c g	% wt
N.W. Pedro (incl. N. edge)	648.6	1,385	587	424	35
S.W. Pedro	170.4	968	195	202	11
20m Bank	387.3	8,102	1,529	189	34
Banner Reef	307.6	2,799	423	151	23
S.E. Spur (incl. E. Pedro)	577.7	2,024	572	283	19
Central Pedro	91.8	1,318	230	175	38
Pedro Cays area	403.6	9,568	1,317	136	52
Morant Cays	19.6	1,786	357	200	32
California Bank	390.0	1,232	222	175	38
South Jamaica Shelf	122.1	270	83	307	12

Table 15.11. Relative abundance and mean weight of individual *Balistes vetula* captured in traps (4.13 cm mesh) in various areas and depth zones of Pedro Bank. Catch rates expressed as numbers (C) or weight (W) per 1,000 hexagonal trap-nights (f).

Area	Depth (m)	C/f	W/f (kg)	Average weight
Pedro Cays	11-20	9,200	1,261	137
Southern Pedro	11-20	6,315	1,122	177
Southern Pedro	21-30	448	129	287
Western Pedro	21-30	753	151	201
Western Pedro	31-60	970	475	489
East Pedro	21-30	1,287	371	288
East Pedro	31-60	3,185	852	267

the mortality estimates, estimates of recruitment indices are rather speculative. A very rough estimate of numerical catch per unit effort in unexploited areas averaged in terms of depth zones amounts to 2,900 fishes/1,000 hexagonal trap-nights. If the natural mortality rate, M , is 2.6, the mean recruitment index, R , for Pedro Bank is about 7,500 fishes.

Table 15.12. Summary of estimated population parameters for *Balistes vetula* exploited by traps with 4.13 cm wire mesh. All lengths are fork length in cm.

	Males	Females	Both sexes
Minimum retainable length, l_1	9	9	
Mean retention length, l_T	16	16	
Full retention length, l_C	21	21	
Asymptotic length, L_∞			45
Asymptotic weight (g), W_∞			2,920
Coefficient of growth, K			0.57
Coefficient of natural mortality, M			2.6
M/K			4.6
Length at maturity, l_m	17.5	16.5	
l_m/L_∞	0.39	0.37	

DYNAMICS OF THE POPULATION

The biological and population parameters estimated for male and female *Balistes vetula* are summarized in Table 15.12.

CHAPTER 16:
THE BIOLOGY, ECOLOGY AND BIONOMICS
OF SPINY LOBSTERS (PALINURIDAE),
SPIDER CRABS (MAJIIDAE) AND OTHER
CRUSTACEAN RESOURCES

by
J.L. Munro
(November 1974)

Introduction

Various species of crustaceans comprise a very valuable portion of the catches of the trap fisheries of Caribbean coral reefs. Spiny lobsters (Palinuridae) are of particular importance and spider crabs (Majidae) and species of the family Xanthidae (the stone crabs and queen crabs) are also important in some areas.

In most parts of the Caribbean the common spiny lobster, *Panulirus argus*, is the most important species of crustacean. In some areas (Florida, the Bahamas, Cuba and the Turks and Caicos Islands, and most Central and South American countries bordering the Caribbean) they are the object of specific fisheries, using wooden refuge traps of several designs, spears or bully nets. In the Antilles, where there is an almost unlimited demand for fish, *P. argus* is mostly captured concurrently with reef fishes, in Antillean fish traps constructed of wire mesh supported by a wooden frame. There appears to be no indication that wooden slat-traps are superior to Antillean traps in catching spiny lobsters and it appears that the wooden designs are only popular where there is a limited market for trap-caught fishes.

There is a voluminous, rather repetitive, literature describing the fisheries for *P. argus* in the Caribbean and west Atlantic, but few of the biological and ecological details necessary for rational management are available.

However, this has not prevented the imposition of quotas, closed seasons, minimum size limits, prohibition of certain fishing gear, or restrictions upon the capture of berried female lobsters in many areas. Some of these measures have been of rather dubious value, while others appear to have needlessly restricted development of the fisheries.

Fishing techniques for spiny lobsters in the Caribbean and catch statistics are given by Idyll (1971) and a very comprehensive account of the Cuban fishery, together with much biological detail, by Buesa Mas (1965). The overall status of biological knowledge of *P. argus* was reviewed by Smith (1959) and Idyll (1971). Fishing methods have been reviewed by Cope (1966). A very extensive annotated bibliography by Sims (1966) covers almost all literature concerning the Palinuridae and Scyllaridae published between 1900 and 1965.

In the area exploited by the Jamaican fisheries (Fig. 2.1), only *Panulirus argus*, *P. guttatus* and the Majid spider crab, *Mithrax spinosissimus*, are of importance and are considered in detail in the following pages. Other species of edible crustaceans which are of potential importance or presently occur in limited numbers in the trap catches are mentioned in the last part of this chapter.

A. PANULIRUS ARGUS (LATREILLE): PALINURIDAE

Identity

The spiny lobsters are a clearly defined group of decapod Crustaceans. On a world-wide basis various problems of taxonomic detail have still to be resolved, but only a limited number of species occur in the Caribbean and western Atlantic.

Panulirus argus is readily distinguishable from *P. guttatus* and *P. laevicauda*, which are the only species with which it might be confused (Holthuis and Zaneveld 1958).

Distribution

The common spiny lobster, *Panulirus argus* is found along the western Atlantic coasts from Rio de Janeiro, Brazil to Beaufort in North Carolina, at Bermuda, and throughout the Bahamas and the islands of the Caribbean. The depth range is from the extreme shallows of the littoral fringe, particularly around mangroves and

seagrass (*Thalassia testudinum*) beds which are inhabited by the post-larval and early juvenile stages, to depths of at least 100 m. There are few records of *P. argus* captured in depths exceeding 50 m but this is possibly a consequence of limited fishing effort with suitable traps in such depths.

Bionomics and Life History

REPRODUCTION

Gonads

The gonads lie in the postero-dorsal part of the carapace and are connected to paired gonopores situated at the base of the third pair of legs of the female and on the last pair of legs of the male.

The ovaries undergo progressive color changes as maturation proceeds and their colors have been described by Buesa Mas and Mota Alves (1971) and may therefore be used for elucidating aspects of the reproductive cycle.

Sexuality

There is no evidence of any hermaphroditism, heterosexuality, or intersexuality in the Palinuridae. The sexes are anatomically distinct. Sexual dimorphism is apparent in the relative size and shape of the tail and the males have a relatively larger and heavier carapace and relatively lighter and shorter tails.

Maturity

Smith (1948) reported that a female *Panulirus argus* of 45 mm carapace length (CL: the distance from the anterior margin of the carapace, between the horns, to the posterior margin of the carapace measured in the mid-dorsal line) was found carrying eggs, but the smallest sizes reported by other authors are somewhat larger: 54 mm CL in British Honduras (FAO 1968a), 57 mm CL in Cuba (Buesa Mas and Mota Alves 1971) and 65 mm CL in Venezuelan waters (Cobo de Barany et al. 1972). Elsewhere, the smallest berried females have usually been in the 80- to 90-mm CL size range (Creaser 1950; Sutcliffe 1952; Feliciano 1958; Dawson 1949; Peacock

1974) and smaller berried females have not been found despite the examination of many individuals.

Weber (FAO 1968b) used the presence or absence of setae on the abdominal pleopods of a large sample ($N > 720$) of females as an indicator of maturity and on this basis, the smallest mature females were about 60 mm CL and full maturity was at 88 mm CL. The mean size at maturity would be 74 mm CL.

During the present investigations, the smallest female found carrying eggs measured 83 mm CL and weighed 580 g. Table 16.1 shows that most females are mature at 110 to 119 mm CL and the mean size at maturity in Jamaican waters might be about 95 mm CL.

This is a larger mean size than that estimated by Weber for the British Honduras stock, and the difference is difficult to explain. Over half of the 248 females examined during this study were less than 80 mm CL

Table 16.1. Proportions of female *Panulirus argus* in successive size classes which were found to be bearing spermathecae or fertilized eggs. All specimens from Jamaican waters.

Carapace length (mm)	No. examined	No. mature	Percentage mature
50-59	7	0	0
60-69	30	0	0
70-79	79	0	0
80-89	43	3	7
90-99	45	23	51
100-109	28	22	79
110-119	13	8	69
120-129	2	2	
130-139	1	1	
Total	248	59	

but none carried eggs or spermathecae.

There is no information on the sizes at which males become mature, but Berry (1970) has suggested that the male *P. homarus* must be larger than the female in order to mate successfully and the males therefore probably attain maturity at a larger size than the females.

Fecundity

No fecundity estimates were made during this study, but a number of investigators have previously made limited numbers of counts of the numbers of eggs carried by female *P. argus* of various sizes (Creaser 1950; Crawford and de Smidt 1922; FAO 1965a). A compilation of the results indicates that egg production per unit body weight varies over a fairly narrow range from about 670 to 1,210 eggs/g of total body weight, with an average of 830 eggs/g.

Creaser (1950) stated that female *P. argus* in Bermuda spawn at least twice between May and August, but the numbers of broods produced in Caribbean waters, where the spawning period appears to be more extended, are not known. Peacock (1974) observed that large females were less frequently found carrying eggs than were smaller individuals and suggested that the frequency of broods might decline with age. As it has been reported that female spiny lobsters normally molt before mating (Berry 1970, for *P. homarus*; Buesa Mas 1965, for *P. argus*) it is possible that decreased frequency of molting in older females results in a decrease in the frequency of spawning.

Mating, Fertilization and Spawning

The mating of *P. argus* has been briefly described by Buesa Mas (1965) and appears to be similar to that of *P. homarus* which has been described in detail by Berry (1970). Males are strongly attracted to females with ripe ovaries and which are usually recently molted but hard-shelled. After a vigorous and prolonged courtship, copulation takes place in a frontal position and the male deposits a spermatophoric mass on the sternum of the female. The spermatophoric mass contains a pair of spermatophores which are simultaneously extruded from the paired gonophores during copulation. The spermatophoric mass consists of an outer protective matrix, a spermatophoric matrix containing the spermatophores and spermatozoa and an adhesive matrix. The protective matrix hardens immediately after deposition and the spermatophores and sperm are protected by the matrix until the spawning process commences, after an interval ranging from 1 to 42 days (Berry 1970, for *P. homarus*).

The process of fertilization and spawning of spiny lobsters is initiated when the female commences scratching at the protective outer matrix of the spermatophoric mass, using the dactyls of the fifth legs (Berry 1970). This exposes the spermatophores in which the sperm are embedded in a gel. Oviposition occurs with the female resting in a vertical position or lying partly or entirely on

her back, with the abdomen flexed to form a chamber (Berry 1970; Sutcliffe 1952). Beating of the pleopods creates a current passing from the gonopores, over the spermatophoric mass and into the brood chamber. It is likely that an enzyme released with the eggs dissolves the gel in which the sperm are embedded and eggs and sperm are together drawn into the brood chamber where fertilization occurs and the eggs become attached to the endopodites of the pleopods (Berry 1970). When oviposition is completed the spermatophores are empty and the remnants of the spermatophoric mass are picked off by the female.

Buesa Mas (1965) reported that eggs of *P. argus* are laid in three batches at daily intervals, with each spawning lasting about 2 1/2 hours.

Spawning Seasons

A large number of investigators have reported on the seasonal occurrence of berried female *P. argus* in the western Atlantic and Caribbean. For most territories within the Caribbean Sea, berried females have been observed in all months of the year but with greatest frequency in the months from February to August (Buesa Mas 1965; Buesa Mas and Mota Alves 1971; Mattox 1952; Feliciano 1958; Peacock 1974). However, the observations are not entirely consistent. Year-round spawning but with maxima in February-March and August-September has been reported by Cobo de Barany et al. (1970) at the Los Roques Islands off Venezuela. In Florida and the Bahamas, spawning is said to occur only between March and July or early August (Sweet 1968; Dawson and Idyll 1951). At Bermuda, mating occurs from mid-May onwards and two broods are produced in rapid succession in June and July and no berried females are found after August (Sutcliffe 1952).

During the present investigations berried female *P. argus* were captured in all months, and no seasonal maxima were apparent.

Spawn

The fertilized eggs of *P. argus* adhere to hairs on the endopodites of the pleopods. The incubation period is about 4 weeks (Buesa Mas 1965) and the females tend to move towards deeper water when the eggs are ready to hatch. It appears that no account of the embryology of any species of spiny lobster has been published.

PRE-ADULT PHASES

Spiny lobsters normally appear to hatch as first stage phyllosoma larvae, but some authors have reported hatching at the naupliosoma stage, with rapid transformation to the first phyllosoma stage (Sims 1965; Baisre 1964).

The larval and post-larval stages of *Panulirus argus* have been described and illustrated by Lewis (1951) and

Lewis, Moore and Babis (1952). Larvae have not yet been reared in the laboratory from egg to the post-larval puerulus stage (Provenzano 1969). The actual duration of the larval life has not been determined, but the available evidence indicates that larval life extends through at least twelve stages and might last from six months to one year (Lewis 1951; Chittleborough and Thomas 1969, for *P. longipes cygnus*). Relative to the prevailing speeds of ocean currents this would permit extremely wide dispersal of the larvae and it appears most likely that larvae spawned in the Caribbean could, for example, settle at Bermuda. During their planktonic phase they are preyed upon by pelagic fishes, including the tunas, *Katsuwonus pelamis* and *Thunnus atlanticus* (Baisre 1964). Provenzano (1969) has suggested that medusae might be an important element in the diet of the late phyllosoma stages.

After transformation to the puerulus stage, the post-larvae settle in suitable environments, and it is likely that shallow mangrove-fringed lagoons offer the most favorable habitats, (Ingle and Witham 1969; Peacock 1974; Witham, Ingle and Sims 1964; Lewis et al. 1952). However as *P. argus* also occurs on isolated oceanic banks such as Rosalind Bank, which has a least depth of about 10 m, and Pedro Bank, of which only about 2.1% of the area is less than 10 m deep (see Chapter 3), it is clear that shallow environments are not essential for completion of the life cycle. Metamorphosis to the puerulus stage occurs in the pelagic environment. It is not known whether the pueruli are able to survive for an appreciable time if suitable shallows are not encountered soon after metamorphosis.

The earliest pueruli have been captured moving shorewards with the flood tide in Florida (Sweat 1968) and later stages have most commonly been found concealed in algae and other marine growth attached to mangrove roots and pilings (Witham, Ingle and Sims 1964; Ingle and Witham 1969). After the pigmentation is fully developed, rocky shallow-water habitats and seagrass (*Thalassia testudinum*) beds are the most favored environment.

Peacock (1974) found that *P. argus* of from 10 to 90 mm CL inhabited the shallow (less than 3 m) Barbuda lagoon, but moved out of the lagoon when 60 to 90 mm CL was attained, and no sexually mature lobsters were found in this habitat. Likewise few small *P. argus* were encountered in deeper reef or offshore areas.

It is therefore likely that shallow areas with mangroves and seagrass serve as nursery areas for pre-adult populations of *P. argus* wherever such habitats are available. However, it is not clearly established that such habitats are essential to the development of abundant populations of this species.

ADULT PHASE

There is no direct evidence concerning the longevity of adult *Panulirus argus* under natural conditions.

The species is found on most shelf areas which offer adequate shelter in the form of reefs, wrecks or other forms of cover. As they have few defences other than the heavily armoured carapace it is likely that they rely upon their nocturnal habits and upon access to shelter by day in order to escape predation.

The major predators of adult and sub-adult stages are skates (*Dasyatis* spp.), sharks (especially the nurse shark, *Ginglylostoma cirratum*), various species of snappers (Lutjanidae) and groupers (Serranidae) and the octopus (Buesa Mas 1965). Other predators include dolphins and loggerhead turtles. A small whelk (*Murex pomum*) is reported to kill lobsters in traps and presumably in nature, by boring through the carapace (FAO 1968a).

Barnacles (*Balanus ebureus* Coull) settle on the carapace of large *P. argus* and could serve as indicators of habitat and of the intermolt period (Buesa Mas 1965).

There are no reports of parasitized, diseased or abnormal spiny lobsters in the literature and none were encountered during this study.

NUTRITION AND GROWTH

Feeding and Food

Panulirus argus feeds only at night. Lobsters captured by day invariably have empty guts. Bivalve molluscs are the main food but small crustaceans are also taken. In aquaria they have been observed to attempt to capture small fishes. Several lobsters were caught on baited hooks during this study. The massive mandibles with grinding molar surfaces are clearly adapted for crushing hard-shelled animals or plants (Peacock 1974).

Peacock (1974) found that *P. argus* in the Barbuda lagoon appeared to feed only on molluscs, but in the reef habitat the guts contained algae, foraminifera, sponge spicules, polychaetes and sand, in addition to bivalve and gastropod mollusc and crustacean remains. In Belize, *P. argus* was found to consume fish, crustaceans (including other lobsters) and molluscs, particularly the turkey wing clam, *Arca zebra* (FAO 1968a).

Growth Rates

Relative growth patterns

Numerous authors have commented on or illustrated aspects of the relative growth patterns of *P. argus*, but few accurate or mathematically correct regression equations have been given for the length:weight relationships and other morphometric features.

Male and female *P. argus* differ in the relative sizes of their carapaces and tails. Females of a given carapace length (CL) have heavier tails than males of the same carapace length and the tail of a female is longer and narrower than that of a male of the same tail weight (FAO 1968b). However, the relationships between total length and total weight are very nearly identical for males and females.

During this study samples of 50 male and 50 female *P. argus* from the Port Royal Reefs yielded identical carapace length:weight regressions (W expressed in g and CL in mm):

$$W = 0.00271 CL^{2.738}$$

The average relationship between carapace length (CL) and total length (TL) is given by Peacock (1974) as follows:

$$\begin{aligned} \text{males : } TL &= 2.61 CL \text{ or } CL = 0.383 TL, \\ \text{females: } TL &= 2.91 CL \text{ or } CL = 0.344 TL. \end{aligned}$$

The average relationship between tail weight (AW) and total weight (W) is given by Pinto Paiva (1960) as follows:

$$\begin{aligned} \text{males : } W &= 3.36 AW \text{ or } AW = 0.298 W \\ \text{females: } W &= 2.74 AW \text{ or } AW = 0.365 W \end{aligned}$$

The maximum carapace width is about 0.78 CL for males and 0.73 CL for females. The maximum depth of the cephalothorax is about 0.88 CL.

Age and growth

The growth rate of *Panulirus argus* has been investigated in detail by several authors, with fairly divergent and sometimes conflicting results. Dawson (1949), Smith (1959) and Buesa Mas (1965) have provided estimates of age and/or growth but do not give any details of the methods employed. Ting (1973), Witham, Ingle and Joyce (1968) and Travis (1954) studied the growth of the species under aquarium conditions and Eldred, Futch and Ingle (1972) studied the growth of juvenile *P. argus* using the Petersen method. Peacock (1974) has recently made estimates of the growth rate based upon the recovery of 32 marked individuals from the Barbuda lagoon.

During these investigations, *P. argus* formed a significant proportion by weight of the total trap catch at the Port Royal Reefs. Year classes were recruited to the Port Royal fishery at a length of 65 to 69 mm CL in the mid-summer months of 1970 and 1971. The modal progression of the cohorts could be followed (Fig. 16.1) as they increased from a modal size of 67.5 mm CL in May-June of 1970 to 82.5 mm CL by November-December. The 1971 cohort likewise attained 82.5 mm CL in November-December of that year, at which time the 1970 cohort appeared to have attained 102.5 mm CL. The numbers of lobsters decreased rapidly with increasing size, presumably as a result of emigration from the reef areas to the offshore shelf (as observed by Peacock 1974, at Barbuda) and the modal progression beyond 82.5 mm CL is not clearly discerned.

During 1969 and 1970 mark and recapture programs were undertaken by the Florida State Board of Conservation (Little 1972) and by the Fisheries Unit of the

Department of Agriculture of British Honduras (Belize). Details of the sizes and dates at marking and at recovery of 70 specimens of *P. argus* have been published by Little (1972). Similar data for 86 specimens marked and recaptured in British Honduras waters have been supplied to the author by Mr. G.W. Miller. The data show similar increases in size per unit time, but differ in that the data from Florida have a preponderance of recaptures after periods exceeding 50 days, whereas most recaptures in British Honduras were taken within 50 days and had not molted. Consequently, neither set of data provides sufficient information upon which to estimate the mean intermolt period and the mean growth per molt.

The abovementioned data have therefore been combined in an attempt to produce an adequate representa-

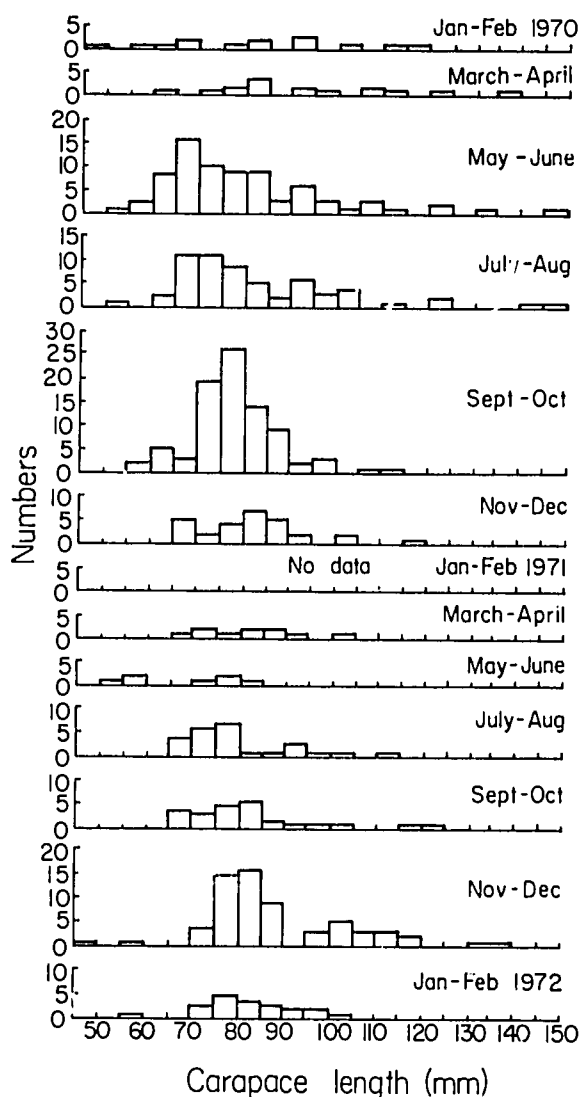


Fig. 16.1. Carapace length-frequency histograms of samples of *Panulirus argus* captured in traps (4.13 cm mesh) at the Port Royal Reefs, between January 1970 and February 1972.

tion of the growth rate of *P. argus*. The combined data show the following trend:

- 6.7% of recaptures (N = 60) effected in 0-19 days had molted
- 23.8% of recaptures (N = 21) effected in 20-39 days had molted
- 58.8% of recaptures (N = 17) effected in 40-59 days had molted
- 80.0% of recaptures (N = 15) effected in 60-79 days had molted
- 88.9% of recaptures (N = 27) effected in 80-139 days had molted
- 94.0% of recaptures (N = 16) effected after more than 140 days had molted.

Of 28 specimens free for more than 120 days only one (which was free for 161 days) had not molted. The trend of the above data indicates that 50% of the specimens had molted within 45 days of marking and the mean intermolt is therefore about 90 days.

The basic assumption in this method for estimating the intermolt period is that at the time of tagging, individuals are randomly distributed throughout their molting cycle, and that 50% will therefore have molted when half of their intermolt period has elapsed. Most investigators have reported that recently molted lobsters occur throughout the year, with the exception of Bermuda waters where Travis (1954) reported that molting ceased when water temperatures fell below 17 to 18° and all molting occurred between May and October. Nevertheless, Travis observed an average of four molts per year.

The estimated intermolt period of 90 days is based upon specimens in the 50 to 120 mm CL size range. There is no evidence to indicate that the intermolt period is constant throughout the growth span. On the contrary, smaller individuals might be expected to molt more frequently and Witham et al. (1968) observed a juvenile that grew from the puerulus stage to a 15 mm CL juvenile in seven molts over 183 days—a mean intermolt period of only 26 days. Likewise it is possible that large adults might molt with decreasing frequency.

If the growth pattern conforms with the von Bertalanffy growth equation, plots of the length at marking against the length at recapture of individuals which showed an increase in size should produce several discrete regressions when separated according to the time free; those free for 0 to 89 days should have molted once, those free for 90 to 179 days should have molted twice and those free for 180 to 269 days should have molted three times.

Figures 16.2a, b and c show Walford plots of the combined Florida and Belize data. There are not sufficient data to enable the sexes to be treated separately, even though it is well established that males attain a larger size than females and must therefore have a slightly different pattern of growth (Creaser 1952; Sutcliffe 1957; Buesa Mas 1965). The asymptotic length is unknown but males are commonly reported to attain 200 mm CL and females 180 mm CL and the asymptotic

length might be about 190 mm CL. The regression lines shown in Figs. 16.2a, b and c are simply drawn through the estimated L_{∞} of 190 mm and through the means of the lengths at marking and recapture in each case. The resulting lines have slopes of

$$k_1 \text{ (1 molt in 0-89 days)} = 0.9456 = e^{-K_1} \text{ and } K_1 = 0.05594$$

$$k_2 \text{ (2 molts in 90 to 179 days)} = 0.9090 = e^{-K_2} \text{ and } K_2 = 0.09545$$

$$k_3 \text{ (3 molts in 180 to 269 days)} = 0.8422 = e^{-K_3} \text{ and } K_3 = 0.17176$$

If K_2 and K_3 are divided by two and by three respectively the resulting estimates of the coefficient of growth per molt (per 90 days) are 0.05594, 0.04773 and 0.05725, with a mean of $K_1 = 0.05364$. If there are four molts per year, the annual coefficient of growth is derived as

$$K = 0.05364 \times 4 = 0.2146 \text{ when } L_{\infty} = 190 \text{ mm CL}$$

The studies of Witham et al. (1968), Eldred et al. (1972) and Ting (1972) have all suggested that a size of 40 to 50 mm CL is attained one year after settlement of the puerulus from the plankton. Using the median value of 45 mm CL attained at one year, and the values of K and L_{∞} above, a growth curve has been calculated and is shown in Fig. 16.3, together with indications of growth obtained by other workers. When the calculated growth curve is used as a reference point, there is close agreement between the calculated curve, and the estimates given by Sutcliffe (1957), Ting (1973), Peacock (1974) and those derived from the present investigations at the Port Royal reefs. The early estimates given by Smith (1959) and Travis (1954) and the recent estimates by Buesa Mas (1965) indicate much slower growth. In the latter case this is probably because Buesa Mas (1965) estimates that molting occurs only twice per year, in contrast to the present estimate of four molts per year.

BEHAVIOR

There is much evidence that indicates that spiny lobsters have complex, seasonal and diurnal behavior patterns, but many aspects of the observed behavior are not yet well understood.

There appears to be little doubt that *Panulirus argus* moves progressively from shallow-water juvenile habitats to relatively deep shelf areas when adult (Sutcliffe 1952). Tagging experiments have indicated that with few exceptions adult lobsters do not usually undertake extensive movements. For example, Buesa Mas (1965) reports that 5,203 tagged and recaptured *P. argus* moved only an average 0.16 kilometers per day and the movement appeared to be at random. However, Buesa

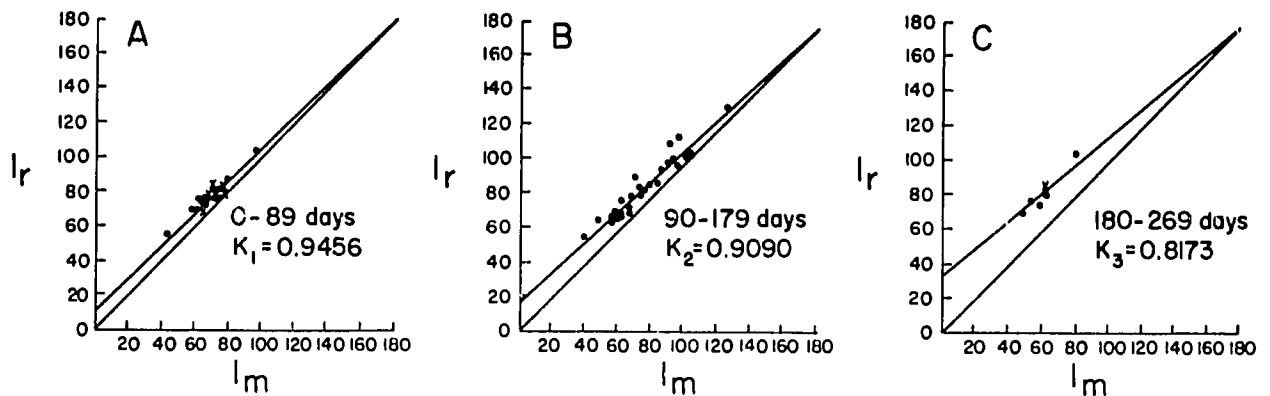


Fig. 16.2. Walford graphs showing carapace length at marking (l_m) and recovery (l_r) of *Panulirus argus*. Solid circles—Florida data; crosses—Belize. (a) 35 specimens recovered within 0 to 89 days; (b) 27 specimens recovered within 90 to 179 days; and (c) 6 specimens recovered within 180 to 269 days.

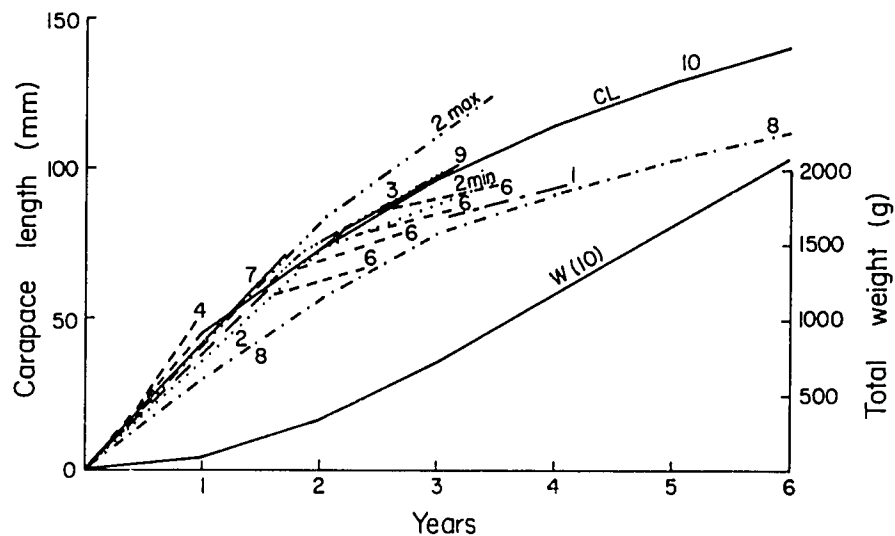


Fig. 16.3. Growth of *Panulirus argus* estimated from tagging data (line 10), compared with estimates given by (1) Smith 1979; (2) Ting 1972; (3) Peacock 1974; (4) Eldred et al. 1972; (5) Witham et al. 1968; (6) Travis 1954; (7) Sutcliffe 1957; (8) Buesa Mas 1965 and with (9) modal progression of length-frequency distributions at the Port Royal Reefs. Lower line, W (10) shows equivalent growth in weight.

Mas (1965) also reports that in fall and early winter, large, dark-colored *P. argus* approach the coast and Dawson (1949) also found indications of seasonal inshore movements by this species. Sutcliffe (1952) found that greater numbers of large individuals (over 145 mm CL) were found in the lagoon areas at Bermuda than on the outside reefs.

Mass migrations by this species have been reported by a number of authors and the whole phenomenon exhaustively discussed by Herrnkind et al. (1973). During the migratory phase the spiny lobsters emerge from their usual refuges and form very long queues which normally move purposefully in a given direction. The phenomenon has been reported most often from Florida and the Bahamas, where the movement is usually southwards and appears to be possibly related to the onset of autumnal storms. Within the Caribbean Sea it appears to

have been reported only from Belize (British Honduras). No such migrations have ever been reported in Jamaican waters.

Davis (1971) reported that juvenile *P. argus* (26 mm CL) at the U.S. Virgin Islands sheltered in daytime aggregations of the sea-urchin *Diadema antillarum* and thus gained access to extensive feeding areas which were otherwise devoid of shelter. This phenomenon was not observed in Jamaican waters.

The species normally emerges from shelter and feeds only at night. By day, groups of adult *P. argus* aggregate in holes and crevices in reefs or other refuges. A strong "pecking-order" is rapidly established in any group and the largest dominant male usually occupies the most favored and safest position deep within the refuge (J. Strangways-Dixon, pers. comm.).

Populations

POPULATION STRUCTURES

Sex Ratios

The sex ratio in populations of *Panulirus argus* appears usually to be close to unity (Creaser 1952; Feliciano 1958; Buesa Mas 1965).

During this investigation, samples from the Port Royal Reefs totalled 242 males: 188 females, (56.3% males) while samples from Pedro Bank totalled 245 males: 169 females or 59.2% males.

Age and Size Compositions

As the absolute age of individual crustaceans cannot be determined, there is no information on the age compositions of populations of *P. argus*. Details of the size composition of commercial catches in Florida and at Barbuda have been given by Robinson and Dimitriou (1963) and Peacock (1974) respectively.

Figure 16.4 shows the estimated mean annual size compositions of *P. argus* at the exploited Port Royal reefs and at unexploited parts of Pedro Bank. The data show that the males are consistently larger (in carapace length) than the females, the modal lengths being 80 to 89 mm CL and 70 to 79 mm CL, respectively at the Port Royal Reefs and 110 to 119 mm CL and 90 to 99 mm CL, respectively at Pedro Bank. Female *P. argus* enter the Port Royal fishery at a mean recruitment length, l_1 , of 71.2 mm CL and males are recruited at a mean length of 76.3 mm CL. Males at Pedro Bank become available to the traps at a mean size of 106.3 mm CL, and females at a mean size of 92.3 mm CL. These sizes are well in excess of the minimum sizes retainable by the 4.13 cm mesh of the traps which will theoretically retain lobsters of about 45 mm CL. The largest males captured at Pedro

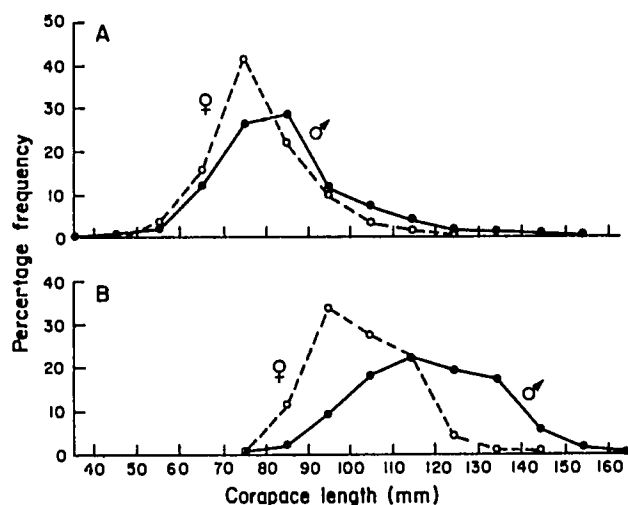


Fig. 16.4. Estimated mean annual carapace length-frequency distributions of male and female *Panulirus argus* at (a) the Port Royal Reefs and (b) unexploited parts of Pedro Bank.

Bank measured 150 to 154 mm CL, substantially smaller than the largest sizes reported elsewhere, or the estimated asymptotic carapace length. Females were likewise much smaller than the reported maximum sizes.

Peacock (1974) reported that male *P. argus* become fully recruited to the diving fishery at the reefs around Barbuda at a modal length of 70 to 79 mm CL, and to the offshore trap fishery at 100 to 109 mm CL. These sizes are 10 mm less than those found in the Port Royal Reefs and at Pedro Bank, respectively.

Buesa Mas (1965) reported that both male and female *P. argus* are fully recruited to the Cuban fishery at 230 mm TL (equivalent to 88 mm CL in the case of males and 79 mm CL in the case of females), and that the males were of substantially larger average size. The length distributions shown by Buesa Mas are very similar in terms of mode, median and range to those found at the Port Royal Reefs.

MORTALITY AND MORBIDITY

Factors Causing or Affecting Mortality

There is little direct evidence concerning the causes of mortality in *Panulirus argus*. Predators undoubtedly cause substantial mortality of all stages in unexploited areas. In nearshore Jamaican waters large predators are not abundant (owing to the intensive fishery for all species) and trap and spearfishing are undoubtedly the major causes of mortality.

Chittleborough (1970) has shown that the natural mortality of pre-recruit *P. longipes cygnus* in Western Australian waters is directly related to the density of the pre-recruit populations, and postulated that the amount of shelter on a given reef area might be a limiting factor, leading to high mortality amongst individuals which are unable to find a safe refuge by day. However, in coralline areas it seems unlikely that the amount of shelter offered by a reef would ever be a limiting factor but this might be important in shelf areas which have a sparse coral cover.

Mortality Rates

The only previous estimates of mortality rates in populations of *P. argus* are given by Buesa Mas (1965) who calculated that annual total mortality in Cuban waters amounted to 56-78%, varying somewhat with age.

Tables 16.2 and 16.3 show the relative abundances of the successive length groups (CL) of *P. argus* at the Port Royal Reefs and at unexploited parts of Pedro Bank, together with calculations of the values of the coefficient of mortality, Z , derived from Beverton and Holt's (1956) formulation: $Z = K(L_{\infty} - \bar{l})/(\bar{l} - l_c)$. At unexploited parts of Pedro Bank, the calculated values of Z (= M) are 0.81 and 1.25 for males and females respectively.

Table 16.2. Relative abundances of successive length groups of male and female *Panulirus argus* at unexploited parts of Pedro Bank (12-45 m depth), and computations of the mortality rates.

Length group (CL, mm)	Males		Females	
	% frequency in catch	Relative abundance	% frequency in catch	Relative abundance
7.0-7.9	0.4		0.6	
8.0-8.9	2.0		11.3	
9.0-9.9	9.8		34.0	1.00
10.0-10.9	18.3		27.7	.81
11.0-11.9	22.0	1.00	22.0	.65
12.0-12.9	19.1	.87	3.8	.11
13.0-13.9	17.5	.80	0.6	.02
14.0-14.9	5.3	.24	0	0
15.0-15.9	1.6	.07	0	0
Mean CL of recruited stock	126.7 mm when $L_{\infty} = 190$ mm		104.7 mm when $L_{\infty} = 190$ mm	
	$M/K = \frac{190.0 - 126.7}{126.7 - 110.0}$		$M/K = \frac{190.0 - 104.7}{104.7 - 90.0}$	
	If $K = 0.215$		If $K = 0.215$	
	$M = 0.81$		$M = 1.25$	

Table 16.3. Relative abundances of successive length groups of male and female *Panulirus argus* at the Port Royal Reefs (7-14 m depth) and computations of the mortality rates.

Length group (CL, mm)	Males		Females	
	% frequency in catch	Relative abundance	% frequency in catch	Relative abundance
4.0-4.9	0.9		0	
5.0-5.9	2.1		3.7	
6.0-6.9	12.9		16.0	
7.0-7.9	26.9		42.0	1.00
8.0-8.9	28.9	1.00	22.4	.53
9.0-9.9	11.4	.39	9.6	.23
10.0-10.9	7.9	.27	3.7	.09
11.0-11.9	4.2	.15	2.1	.05
12.0-12.9	2.0	.07	.5	.01
13.0-13.9	1.7	.06	0	0
14.0-14.9	1.2	.04	0	0
Mean CL of recruited stock	96.0 mm when $L_{\infty} = 190$ mm		83.0 mm when $L_{\infty} = 190$ mm	
	$Z/K = \frac{190.0 - 96.0}{96.0 - 80.0}$		$Z/K = \frac{190.0 - 83.0}{83.0 - 70.0}$	
	= 5.88		= 8.23	
	If $K = 0.215$		If $K = 0.215$	
	$Z = 1.26$		$Z = 1.77$	

However, as it is most likely that the males grow more rapidly and to a larger asymptotic size than females, the median estimates of L_{∞} and K used in the calculations will lead to mortality coefficient for females being slightly overestimated and that for the males being underestimated. The median estimates for both sexes will be $M/K = 4.80$ and $M = 1.03$.

The estimated values of Z at the exploited Port Royal Reefs are 1.26 and 1.77 for males and females, respectively (median 1.52) and these values are compounded of natural mortality, M , fishing mortality, F , and emigration from the reefs to the South Jamaica Shelf.

It is argued in Chapter 17 that it is most likely that natural mortality results very largely from predation and

$$M = M_x + gP$$

in which P is the biomass of predators and g is the mortality generated in the prey species by one unit of biomass of predators. Mortality caused by other factors, M_x , is probably negligible except in communities where predators are extremely rare. At the Port Royal reefs, the biomass of predators amounts to only about 14% of that at unexploited parts of Pedro Bank (see Chapter 17 for details). It is therefore likely that the natural mortality rate is about 0.11 for males and 0.18 for females (median 0.14).

The emigration rate from the Port Royal Reefs is indeterminate, but if it can be presumed that few lobsters survive to attain the size at which emigration usually occurs, then the fishing mortality rate will be close to and not more than $Z - M$:

$$\begin{aligned} \text{for males} & : F < 1.26 - 0.11 = 1.15 \\ \text{for females} & : F < 1.77 - 0.18 = 1.59 \\ \text{both sexes} & : F < 1.52 - 0.14 = 1.38 \end{aligned}$$

On the basis of the foregoing, and of data given in Chapter 17 the following estimates can be derived:

$$\begin{aligned} \text{Port Royal Reefs: } & M = 0.14, F = 1.38, Z = 1.52, E = 0.91 \\ \text{South Jamaica Shelf: } & M = 0.23, F = 1.3 \times 0.206 = 0.27, \\ & Z = 0.50, E = 0.54 \\ \text{Pedro Cays area: } & M = 0.52, F = 0.5 \times 0.206 = 0.10, \\ & Z = 0.62, E = 0.16 \end{aligned}$$

ABUNDANCE AND DENSITY

Catches of *Panulirus argus* in the areas investigated were too sparse or too sporadic to show any consistent seasonal variations in availability.

Peacock (1974) estimated the stock in the shallow Barbuda lagoon to amount to $10,800 \pm 3,360$ individuals at a mean weight of 216 g each. This is a density of 290 to 550 lobsters, or 63 to 119 kg/km². This concentration yielded a catch rate of 5.25 lobsters per week in the local rectangular Antillean trap. Buesa Mas

(1965) estimated the "reserves" of *P. argus* in Cuban waters to amount to 26,000 tonnes in an area of about 100,000 km², or an average of about 260 kg/km².

Cobo de Bañany et al. (1972) found that lobster production at the Los Roques islands amounted to 90 metric tons p.a. from an area of about 1,000 km², or about 90 kg/km². Similarly, the total Jamaican production in 1968 amounted to 293 metric tons (Vidaeus 1970) from an area of 3400 km², or 86 kg/km².

The total catch taken at Pedro Bank during these investigations amounted to only 120 *P. argus* from a total fishing effort (expressed in terms of hexagonal traps set for one day each) of 2,064 trap-nights or an average of 58 spiny lobsters per 1,000 trap-nights. The deeper eastern and western portions of the bank yielded the greatest catch rates (104 and 66 lobsters/1,000 trap-nights respectively), confirming the observations of Chislett and Yesaki (1974) that these areas are more productive of spiny lobsters. The shallower southern margins of the bank produced only 22 lobsters/1,000 trap-nights and the exploited Pedro Cays area only 3 lobsters/1000 trap-nights.

At the Port Royal Reefs, *P. argus* were captured at a rate of 52/1,000 hexagonal trap-nights, and limited fishing effort on the South Jamaica Shelf produced *P. argus* at a rate of 81/1,000 hexagonal trap-nights. None were caught at California Bank.

NATALITY AND RECRUITMENT

Data on the fecundity of *Panulirus argus* is given in the section on reproduction. The number of spawnings per year and absolute abundances of populations are unknown, and it is therefore not possible to calculate the natality of any population.

The product of the mean stock density and the coefficient of total mortality is equal to the initial stock density of any population. Likewise, the product of the mean catch per unit effort (\bar{C}/\bar{f}) and the mortality rate (Z) will yield an index of recruitment (R') equal to the theoretical number of recruits at the mean recruitment length which are required to produce the observed catch per unit effort. Thus $R' = (\bar{C}/\bar{f})Z$.

For the Port Royal reefs, $\bar{C}/\bar{f} = 52$ and $\hat{Z} = 1.52$, thus $R' = 52 \times 1.52 = 79$ spiny lobsters at a mean recruitment length of 71.2 - 76.3 mm CL (according to sex).

At Pedro Bank, the mean catch rate was 58 *P. argus* per 1,000 trap-nights and $Z = M = 1.03$, thus $R' = 60$ spiny lobsters at a mean recruitment length of 92.3 mm CL in the case of females and 106.3 mm CL in the case of males. It is therefore likely that recruitment rates are basically similar in the two areas.

Calculations given in the following section show that the population on the South Jamaica Shelf is presently yielding about 480 g/recruit. If the 1968 yield of *P. argus*, amounting to 293,000 kg (Vidaeus 1970), was taken mostly from the South Jamaica Shelf, then recruitment in that year amounted to at least 600,000 recruits at 60 mm CL.

DYNAMICS OF THE POPULATIONS

The various population parameters estimated in the preceding pages are summarized in Table 16.4, and are sufficient to permit the formation of some opinions regarding the exploitation of the species.

It has been shown in the preceding pages that the natural mortality rate, M , of the unexploited Pedro Bank stock is about 1.03, and the growth rate, K , in the Caribbean area is about 0.215. The ratio M/K is 4.80. Additionally, it has been argued that the natural mortality rate is probably proportional to the biomass of predators, and that in the most heavily exploited areas with the lowest stock densities of predatory reef fishes, natural mortality rates of prey species will be correspondingly reduced. If, as seems likely (see Chapter 17 for details), this is essentially correct, then the ratio of $M/K = 4.80$ will be reduced as follows:

$$\text{Pedro Cays area, } M/K = 4.80 \times 0.50 = 2.40$$

$$\text{South Jamaica Shelf, } M/K = 4.80 \times 0.22 = 1.06$$

The biomass of predatory species at the Port Royal Reefs is only about 14% of that at Pedro Bank, but these reefs are contiguous with the South Jamaica Shelf and should not be treated separately, other than to note that the natural mortality rate affecting the stocks in the reef areas might be expected to be very low ($M = 1.03 \times 0.14 = 0.14$). Likewise, it is to be expected that natural mortality rates in the heavily exploited, narrow shelf areas of the north, southeast and southwest coasts of Jamaica will be even lower than that prevailing at the Port Royal Reefs.

Figure 16.5 shows eumetric yield curves calculated by use of Beverton and Holt's (1964) "Tables of yield functions for fishery assessment" and which represent the various areas.

It has been estimated that the rates of exploitation ($E = F/Z$) at the Pedro Cays and the South Jamaica Shelf are equal to, or slightly less than, 0.16 and 0.54, respectively, and at the Port Royal Reefs might be as much as 0.90. On this basis, several pertinent observations can be made:

i) The mean size of recruitment to the Port Royal reefs is 71.2 mm CL for females and 76.3 mm CL for males and these same stocks are exploited at ever smaller sizes by the local fishery in the seagrass beds and mangrove areas. The mean sizes of recruitment to the South Jamaica Shelf fishery is therefore substantially less than that mentioned above, and perhaps around 60 mm CL. The rate of exploitation is estimated to be 0.54. Reference to curve C in Fig. 16.5 shows that the present size at first capture is probably less than half of that required to maximize the yield from the South Jamaica Shelf.

ii) The fishing intensity on the north, south-east and southwest coasts is even greater than that on the South Jamaica Shelf. Small-meshed traps (3.30 cm) are very widely used, and the recruits to the fishery are harvested at an extremely early stage, often at carapace lengths of

Table 16.4. Summary of estimated biology and fishery parameters of populations of *Panulirus argus* captured in Antillean fish traps (4.13 cm mesh) at unexploited parts of Pedro Bank and at the exploited Port Royal Reefs.

	Both sexes	Males	Females
L_{∞} (mm CL)	190		
W_{∞} (g)	4,700		
K	0.215		
a (in $W = aCL^b$)	0.00271		
b (in $W = aCL^b$)	2.738		
M (Pedro Bank)		0.81	1.25
M/K (Pedro Bank)		3.79	5.80
l_m (mm CL)		?	95
l_m/L_{∞}		?	0.50
e (eggs/g body wt.)		—	830
R (Jamaican shelf)	600,000		
Port Royal Reefs			
(7-14 m depth)			
l_1 (mm CL)		40-49	50-59
l_r (mm CL)		76.3	71.2
l_c (mm CL)		80-89	70-79
l_r/L_{∞}		0.40	0.37
Z/K		5.88	8.23
Pedro Bank			
(12-45 m depth)			
l_1 (mm CL)		70-79	70-79
l_r (mm CL)		106.3	92.3
l_c (mm CL)	-	110-119	90-99
l_r/L_{∞}		0.56	0.49

only 30 to 40 mm. These stocks are represented by Curve D in Fig. 16.5.

iii) Curve B of Fig. 16.5 represents the stocks in the Pedro Cays area. The fishing effort per unit area is estimated to be 0.15 canoes/km²) and the rate of exploitation is not more than 0.16. The stocks of *P. argus* are only recruited to the trap fishery at a fairly large size, about 92 mm CL for females and 106 mm CL for males. Consequently, they are underexploited, and eumetric yields can only be achieved by increasing the fishing effort. Such a move would also result in a decreased biomass of predators, a decrease in the value of M/K and a further increase in the potential yield per recruit of *P. argus*.

Figure 16.6 shows yield per recruit curves for the *P. argus* stocks of the South Jamaica Shelf ($M/K \cong 1.00$) for various sizes at recruitment, ranging from $l_c = 60$ mm CL (the approximate size at which the stock is presently recruited) to $l_c = 125$ mm CL, a size which probably represents the upper limit of that which can readily be marketed. The curves indicate that if the present fishing effort on the South Jamaica Shelf generates a fishing mortality rate, F , of 0.27, then yields would be increased by about 13% if the minimum size were set at 95 mm

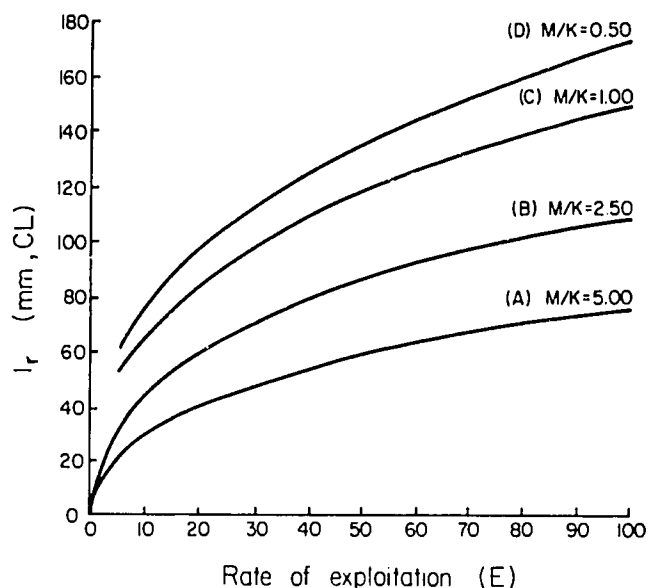


Fig. 16.5. Eumetric fishing curves for *Panulirus argus* populations subjected to different natural mortality rates (M) and a constant growth rate, $K = 0.215$. Curve A ($M/K = 5.0$) represents the unexploited stock at Pedro Bank; Curve B ($M/K = 2.5$) represents the stock at the Pedro Cays area; Curve C ($M/K = 1.0$) represents the stock on the South Jamaica Shelf and Curve D ($M/K = 0.5$) represents the stock on the heavily-exploited northern, southwestern and southeastern shelves of Jamaica.

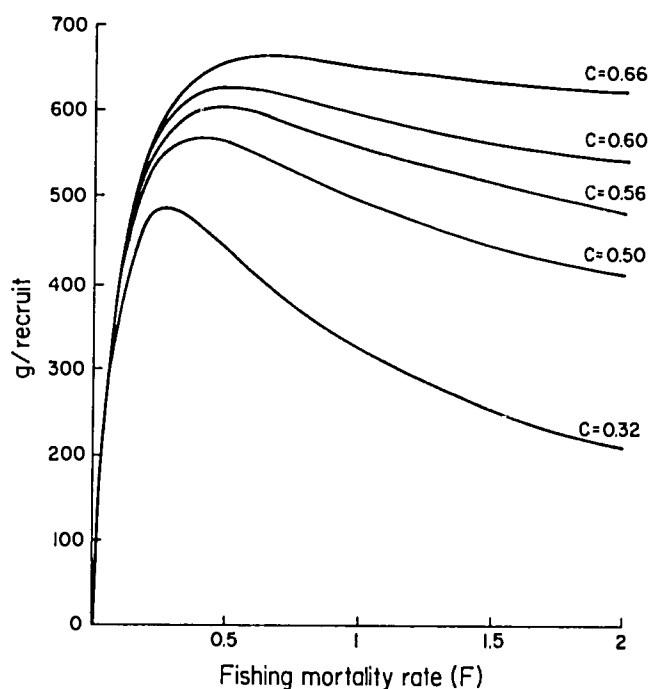


Fig. 16.6. Theoretical yield per recruit from the stock of *Panulirus argus* on the South Jamaica Shelf ($M/K = 1.0$, $F = 0.27$, $l_r = 60$ mm CL, $c = 0.32$) compared with potential yield per recruit if recruitment were at a mean carapace length of 95 mm ($c = 0.50$), 106 mm ($c = 0.56$), 114 mm ($c = 0.60$) or 125 mm ($c = 0.66$).

CL, and by 18%, 21% or 22% if the minimum CL were set at 106 mm, 114 mm or 125.4 mm, respectively.

It is also important to note that any increase in fishing effort will result in decreases in the catch of *P. argus*. Yields from the more heavily exploited northern, southwestern and southeastern shelves would increase by approximately 100% if the mesh size was increased.

Thus, any restraint on the harvesting of small sizes of *P. argus* will result in substantial increases in yield.

It is also likely that enforcement of a minimum size regulation would result in increased recruitment, by effectively protecting the very young stages which are indiscriminately harvested in nursery areas at the present time and which have not been considered in arriving at the present estimate of mean length at recruitment of 60 mm CL.

The species of crustaceans which are represented in the Jamaican trap fishery can be managed by means of minimum size regulations, whereas regulation of the fish stocks cannot be undertaken on the same basis because most fishes are mortally harmed by the abrupt pressure change which they undergo when traps are hauled to the surface.

In addition to questions relating to gross yield per recruit (discussed in the previous pages), several factors require consideration in arriving at a suitable minimum size.

1) The mean size at maturity of females is about 95 mm CL and this should represent the lowest acceptable limit under any circumstances.

2) For the fishery on the South Jamaica Shelf, a minimum size of at least 110 mm CL would appear to be commensurate with the present rates of exploitation and even larger sizes would be indicated for the northern, southeastern and southwestern shelf areas.

3) It must be borne in mind that if minimum size regulations are enforced, the average size of individuals in the catch should not be substantially in excess of that which is normally acceptable to purchasers. However, it should also be observed that the demand is so greatly in excess of the supply that this is unlikely to be a major constraint.

4) On theoretical grounds, different sizes should be set for areas which differ in the intensity of fishing. A very large minimum size would be appropriate to the north, southeast and southwest coasts where the fishing intensity (canoes/km²) is up to fourteen times greater than that on the South Jamaica Shelf, and the rate of exploitation undoubtedly approaches unity. A lesser minimum size would be appropriate to the South Jamaica Shelf, and an even smaller size for the Pedro Cays fishery. However, variable limits might lead to false claims regarding the origin of undersized catches and thus lead to difficulties in enforcement of the regulations.

It appears likely that a minimum size limit of 108.0 mm (4½ in) carapace length would be most realistic in the light of the circumstances outlined above, despite the fact that this would be substantially below the eumetric size limit appropriate to the most heavily

exploited areas. The equivalent total weight is 1,000 g (2.2 lb.). The equivalent tail size is about 174 mm (298 g) for males and 206 mm (365 g) for females. Tail weights vary by about $\pm 15\%$ of the average of any given

length and lose weight on freezing or cooking, and regulations specifying minimum weights might be difficult to enforce and should be avoided if possible.

B. PANULIRUS GUTTATUS (LATRIELLE): PALINURIDAE

This small spiny lobster occurs on the coasts of Florida and Bermuda, in the Bahamas, throughout the West Indies and as far south as Brazil.

The species appears to be confined to relatively shallow water and was not captured in depths exceeding about 20 m during this study, and appeared to be most common in fairly exposed areas near or behind the reef crest. During the day they are usually observed hiding deep within crevices in stands of *Acropora palmata*, but at night may be seen wandering over shallow sand and coral-rubble flats in the lee of the Port Royal barrier reef. Caillouet, Beardsley and Chitty (1971) observed that this species concealed itself by day amongst boulders at Government Cut, Miami, Florida, but emerged at night and moved around over boulders and along the sides of jetties, usually in depths of 1.5 m to 3 m.

As with other species of palinurids, the sexes are morphologically distinct, and the males are of larger average size than the females. The smallest mature (berried) female captured by Caillouet et al. (1973) measured 36 mm CL and weighed 45.8 g.

Berried females have been found by Caillouet et al. (1971) in Florida in greatest abundance in June, and in declining numbers to October, but there are no data for November-May. Sutcliffe (1953) found berried females in August, September and October in Bermuda. They were taken in June, November and March during this study. It is therefore likely that spawning occurs in all months in Jamaican waters.

Caillouet et al. (1971) found a sex ratio approaching

unity, when sampling was done by hand, but Sutcliffe (1953) obtained a sex ratio of $\delta:\text{♀} = 10:1$ in Bermuda and during this study our samples totalled 77 males:37 females. In both of the latter cases the mesh sizes of the traps probably precluded complete sampling of the female populations.

Sutcliffe (1953) reported maximum sizes of males and females of 88 mm CL and 72 mm CL, respectively. Caillouet et al. (1971) captured males of up to 85 mm CL and females of 77 mm CL. In contrast, the largest male taken during this study was only 70 mm CL and the largest female 61 mm CL and this perhaps is indicative of the heavy rates of exploitation.

There is no information on the growth rates of this species. Caillouet et al. (1971) determined the carapace length (mm), weight (g) relationships to be as follows:

$$\begin{aligned} \text{males: } W &= 0.00126 L^{2.85} \\ \text{females (non-ovigerous): } W &= 0.00069 L^{3.01} \end{aligned}$$

At the Port Royal Reefs, this species is first recruited to the fishery at 43 to 44 mm CL and the catches have modal lengths of 55 to 59 mm CL (males) and 50 to 54 mm CL (females).

As this is a small species, which matures well before it reaches its mean retention length of about 50 mm CL in the 4.13-cm mesh traps, it is unlikely that any conservation measures are necessary at the present time, and it is likely that the present yields are close to the eumetric requirements.

C. MITHRAX SPINOSISSIMUS (LAMARCK): MAJIIDAE

There appears to be no account in the literature of any aspects of the biology and ecology of this species and the genus appears not to have previously been reported as being of importance in any fishery. Several species of spider crabs of the northern Pacific and north Atlantic (*Chionocetes* spp., *Maja squinado*) are important

fishery resources but no comparable tropical species are known to exist.

Accounts of the biology and ecology of spider crabs are few, the most comprehensive accounts being those of Hartnoll (1963 and 1965).

Identity

A number of species of the genus *Mithrax* (Majidae, Brachyura, Decapoda) occur in the Caribbean. Keys to the western Atlantic species and descriptions are given by Rathbun (1902, 1925, 1933) and Williams (1965).

Mithrax spinosissimus is distinguished from other species of the genus by its large size, nearly naked carapace without oblique parallel branchial sulci and the absence of spines or spinules from the manus.

Distribution

According to Rathbun (1925) and Williams (1965), *Mithrax spinosissimus* occurs from the Caribbean to the

Bahamas and the Florida Keys and in the West Indies. During this investigation most specimens were taken

at the Port Royal Reefs in depths of 7 to 14 m but were also captured in depths of 10 to 45 m at Pedro Bank and at California Bank which has a depth range of 35 to 45 m.

Specimens have been observed at locations all around the Jamaican coast and are usually seen in exposed positions, clinging motionless to coral heads in depths of 5-15 m. Specimens have also occasionally been seen hiding under ledges or coral outcrops. The relatively large numbers captured in traps during this investigation suggests that the species is far more abundant than underwater observations would indicate and, presumably, most specimens are overlooked as a result of their

cryptic coloration and very slow movements. Juveniles were never observed by divers, nor captured in traps, despite the fact that traps would retain any specimens exceeding about 40-mm carapace width. It is therefore possible that the immature stages have different habits or live in depths or habitats other than those occupied by the adults. However, several juveniles, tentatively identified as belonging to this species, were recovered from stomachs of the red hind, *Epinephelus guttatus*, captured in reef areas at Pedro Bank.

Williams (1965) states that this species is often found around rocks, in shallow water and to depths of 179 m.

Bionomics and Life History

The only comprehensive accounts of the biology and life history of tropical majiids, of which the present author is aware, are those by Hartnoll (1963, 1965). There is no previous account of the biology of *Mithrax spinosissimus*, but one of the species studied by Hartnoll (*M. sculptus*) appears to conform to the general characteristics of the family and it might therefore be presumed in the absence of evidence to the contrary that the biology and life history of *M. spinosissimus* might likewise follow the same basic pattern. Nevertheless, it should be emphasized that *M. spinosissimus* is by far the largest species of tropical spider crab and for this reason might differ in some important respects.

REPRODUCTION

Hartnoll (1965) has pointed out that, as far as is known, species of spider crabs undergo a molt of puberty which is the final molt and thereafter the crabs enter a terminal anecdyosis and no further growth occurs. He shows that the size at which this terminal molt occurs can vary very widely in a population. Copulation can take place at any time after the terminal molt has occurred, and it is not necessary that the female be in the "soft-shelled" condition for this to be successful. The females are able to produce several batches of eggs in rapid succession, fertilized by sperms which are stored in spermathecae. The sperm remain viable for an extended period and it is therefore likely that it is necessary for these species to mate only once in their lifetime.

The incubation periods of the species studied by Hartnoll (1965) in Jamaican waters varied between 11 and 14 days, but these included only one species of *Mithrax* (*M. sculptus*) and all were very much smaller than *M. spinosissimus*. Hatching of the eggs occurred at night.

The sexes are separate and strongly dimorphic: the males are larger and have larger chelae than the females. Table 16.5 shows the size frequency distributions of male and female *M. spinosissimus* captured in fish traps (4.13 cm mesh) at the Port Royal reefs, and the percentage of each size class (carapace width or CW) of females found carrying eggs. The males had a mean size

of 133.4 mm CW and a modal size of 135 mm CW. Individuals of up to 160 mm CW are very common and the largest specimen observed measured 175 mm CW and weighed 2,425 g. In contrast, the mean size of females was 122.8 mm CW, but the modal size of the females was the same as that of the males. The largest female (which had only recently molted) measured 154 mm CW and weighed 1,140 g.

Table 16.5. Length-frequencies of male and female *Mithrax spinosissimus* and the proportion of egg-bearing females in successive size-classes. All specimens from Jamaican waters.

Carapace width (mm)	No. captured		Berried females	
	Males	Females	Number	Percentage of total
60-69	1	0	—	—
70-79	0	0	—	—
80-89	3	2	0	0
90-99	5	2	0	0
100-109	3	9	2	22
110-119	15	13	9	69
120-129	20	20	12	60
130-139	32	22	10	55
140-149	27	2	2	100
150-159	24	1	0	0
160-169	6	—	—	—
170-179	5	—	—	—
Totals	141	71	35	

The smallest berried female measured 106 mm CW and weighed 540 g. However, as only a few females smaller than this size were ever captured this is not necessarily the smallest size at which the species matures. No observations were made of the state of maturity of males.

Berried females were found in every month with no discernable maxima and spawning might therefore be continuous after the terminal molt is completed.

The fertilized spawn, which are about 1 mm in diameter, are attached to the pleopods and are deep red in the early stages of development and change to an

orange-brown color as embryogenesis proceeds. The incubation period was not determined. The fecundity was not estimated, but is likely in excess of 50,000 for an average-sized female.

PRE-ADULT PHASE

Spider crabs appear to normally undergo a fairly abbreviated larval life, hatching as a pre-zoeal stage, and passing through two zoeal stages and one megalopa stage before settlement as small crabs.

There is no information whatever on the pre-adult life history of *Mithrax spinosissimus*. The smallest individual captured was a male of 66 mm CW (100 g) and, as stated previously, it appears possible that the juveniles occupy a different habitat from that of the adults, and only enter the coral reef environment at sizes approaching maturity. Alternatively, the juveniles might live in the reef environment but have different habits which preclude their capture in traps. Several juveniles (20 to 30 mm CW) were recovered from stomachs of the red-hind *Epinephelus guttatus*, and presumably might fall prey to other predators of similar size and habits.

ADULT PHASE

There is no information concerning competitors and predators, parasites, longevity or other aspects of the life history of adult *Mithrax spinosissimus*. It is most likely that, like spiny lobsters, they fall prey to nurse sharks, turtles, groupers and other large predators, but there is no direct evidence on this point.

NUTRITION AND GROWTH

Feeding and Food

There appears to be no information on the feeding and food habits of tropical species of majid crabs. *M. spinosissimus* is presumably a nocturnal feeder and its slow movements suggest that it is not an active predator.

Hartnoll (1963) found that majids in British waters were highly omnivorous and algae, hydroids, "crustaceans", amphipods and decapods were all major components in the diets of various species. Polychaetes, gastropods, lamellibranchs and ophiuroids were also important.

Growth Rates

Hartnoll (1963, 1965) has discussed molting and aspects of the relative growth of a number of species of majid crabs. In all of the species studied by him it appears that after the molt of puberty, no further molting or growth occurs. Specimens which have entered the terminal anecdyosis (i.e., mature specimens) are

unable to replace autotomized limbs or chelae.

The molt of puberty is usually accompanied by distinct morphological changes in the chelae of the males and by a variety of changes in the shape of the abdomen, pleopods, sternum and genital apertures of the females. Hartnoll observed that the terminal molt might be attained over a very wide size range, and differences of 162% and 314% between the minimum and maximum sizes (carapace length) of mature males and females were found in the case of *M. sculptus*.

During the course of this study, the author was unaware that spider crabs could be classified as pre- or post-puberty according to external morphological criteria and such data were therefore not sought when catches were examined. However, if *M. spinosissimus* conforms in its characteristics with other species of the genus then the molt of puberty is attained by females at sizes between 106 mm CW (the smallest berried female) and 154 mm CW (the largest "soft" or recently molted female; incidentally, also the largest female captured). The mean size of berried females was 125.3 mm CW.

Relative growth patterns

The relationships between carapace width (CW) in mm and total weight (W) in g are described by the following equations:

$$\text{males : } W = 0.000181 \text{ CW}^{3.1654}$$

$$\text{females: } W = 0.000280 \text{ CW}^{3.0515}$$

Growth of the females is thus very nearly isometric but that of males is slightly allometric, probably mostly as a result of the development of the massive chelae in the later stages of growth. Rathbun (1902) states that young specimens are relatively more elongate and have longer horns than the adults.

Maximum size

The largest male measured 175 mm CW and weighed 2,425 g. The largest female, which was recently molted and still "soft-shelled", measured 154 mm CW and weighed 1,140 g. Williams (1965) states that males attain 184 mm CW and 170 mm carapace length. The largest female reported by him was only of 80 mm CW.

Age and growth

There is no previous information on the age and growth of this species. The size-frequency distributions of male and female *M. spinosissimus* captured at the Port Royal Reefs showed no discernible modal progression between November 1969 and February 1972. This is not unexpected as most of these specimens had presumably reached the terminal anecdyosis.

BEHAVIOR

Only limited numbers of solitary *Mithrax spinosissimus* were seen on reefs during the course of this study. None showed any reaction to the presence of divers, and

all could be picked up without eliciting any response other than slow movements of the limbs when raised clear of the substratum. The only strong response evoked was that of a large male which retaliated by vigorous use of the large chelae when the author attempted to forcibly dislodge it from a coral crevice.

Populations

POPULATION STRUCTURES

Sex Ratios

A total of 131 males and 71 females were captured at the Port Royal reefs: a ratio of males to females of 1.99:1. The reasons for such a large preponderance of males is not understood. The size ranges represented in the samples are well above the minimum retainable size and the divergence from unity is therefore not a result of any gear selection factors. Behavioral factors or a true biological imbalance must therefore account for the observed sex ratio.

Age and Size Compositions

The absolute age of specimens of *M. spinosissimus* cannot be determined and there is no information on the age composition of the catches.

If this species resembles other majids and reaches a terminal anecdyosis coincident with maturity, the ascending limb of the size frequency distribution of the catch (Table 16.5) shows the sizes at which the species is recruited to traps in the particular habit which was fished, but the descending limb is compounded of the range of sizes at which the final molt is attained and the size frequency distribution of that portion of the population which is immature and is still actively growing. As immatures were not distinguished in this study, the two components of the size frequency distribution cannot be separated.

The mean size at recruitment to the Park Royal fishery is 122 mm CW (males 727 g, females 651 g) for both males and females, and both sexes are fully recruited to the fishery at 135 mm CW.

Forty-nine per cent of the females carried eggs and the size distribution of these mature females was similar to that of the non-berried females—most of which were presumably immature. This suggests that recruitment to the fishery is related to the initiation of maturation of the gonads.

ABUNDANCE AND DENSITY

Seasonal Abundance

A marked seasonal trend in the relative abundance of *M. spinosissimus* is apparent in the data. Catches were zero or negligible in January and February of 1970,

1971 and 1972, and the availability index (Munro 1974) reached maxima in March or April, June or July and November or December in 1970 and 1971. There is no known factor which might be responsible for such an annual cycle, and the coincidence of the maxima in the two years might be fortuitous.

Relative Abundance

The total catch of *M. spinosissimus* at the Port Royal Reefs amounted to 219 crabs weighing 213.4 kg, from a total effort of 14,066 trap-days (Z and S traps) equivalent to a catch rate of 27 crabs per 1,000 hexagonal trap-nights.

The catch rates at Pedro Bank were very low, being zero at the Pedro Cays area and Eastern Pedro Bank and 2.9 and 2.7 crabs/1,000 hexagonal trap-nights at Southern and Western Pedro Bank, respectively. California Bank yielded 13.1 crabs/1,000 h. t-n and the South Jamaica Shelf 20.4 crabs/1,000 h. t-n.

Catch rates were generally greatest in the most intensively exploited areas, with the exception of the Pedro Cays area where none were taken. It appears likely that the difference is caused by reduced predation in areas subjected to heavy exploitation.

NATALITY AND RECRUITMENT

There is no information concerning natality and the recruitment rates to the fishery.

DYNAMICS OF THE POPULATIONS

Data for this species are inadequate to make any sort of assessment of the dynamics of the populations. It appears possible that the relatively great abundance of the species in nearshore Jamaican waters is a direct result of reduced predation, caused in turn by the intensive fisheries.

Males outnumber females in the catch by about 2:1 and are the most sought-after components of the populations; the fishery would therefore not suffer greatly from conservation measures directed at protection of the females. If, as is the case with other majiids, a single mating is all that is required to ensure fertilization of successive batches of eggs, then protection of all berried females would be worthwhile and could serve to enhance recruitment rates.

As there is no information on mortality rates, it is not possible to assess the optimum sizes at which the species should be harvested, but the species only becomes available to the fishery at a mean size of 122 mm CW

and growth probably ceases soon thereafter, and it therefore seems likely that the fishery is to a large extent self-regulatory.

D. OTHER CRUSTACEAN RESOURCES

Several species of crustaceans are either of minor importance or of potential major importance in the Jamaican trap fisheries and are discussed below. They include *Justitia longimana* (Palinuridae) and *Scyllarides aequinoctialis* (Scyllaridae). A large, unidentified species of xanthid crab, known locally as the "queen crab", occasionally yields modest catches, and caridean prawns, which have not been identified beyond the family Pandalidae, appear to be very abundant on the deep slopes below the drop-off in depths exceeding 200 m.

Several specimens of *Justitia longimana* (40 to 50 mm CL) were taken at Discovery Bay, on the south coast of Jamaica at depths of 30 to 170 m. All were captured in traps, and none have ever been observed by divers. Presumably they secrete themselves deep within the reef by day. Nothing is known of the biology of this small species. Its large raptorial chelae suggest that it might be an active predator.

Specimens of *Scyllarides aequinoctialis* were occasionally captured in traps at the Port Royal Reefs, but only three were taken at Pedro Bank and none at California Bank. The depth range was from 1 m to 45 m. The species is not sufficiently abundant to be of much commercial importance in any of the areas investigated.

Specimens of the "queen crab" were captured in quantity at Pedro Bank and on the South Jamaica Shelf in depths of 25 to 45 m on several occasions. They are edible, but do not appear to be marketed by the fishermen, and are most often crushed and left in the traps as bait.

It appears possible that caridean prawns (family Pandalidae) could become an important resource if appropriate techniques are developed for their exploitation in depths of over 200 m. Several species may be present in Jamaican waters. The prawns were captured on all occasions with traps set in depths of 200 to 400

m on the slope below the drop-off of the northern and southern Jamaican shelves. In most cases the traps were of 4.13 cm mesh and the only shrimp retained were those which had become entangled in the mesh work, but on two occasions a trap covered with an outer layer of 1.27 cm mesh was set in these depths and produced modest catches of shrimps despite the fact that most of the shrimps escaped from the trap and could be seen dropping through the meshes when the trap was hauled to the surface.

The stomachs of specimens of *Epinephelus mystacinus*, *Brotula barbata* and various sciaenids captured in these depths often contained caridean prawns which are clearly a major food resource for such predators.

In the Indian Ocean, at Reunion Island, trap fishing for species of *Parapandalus*, *Plesionika* and *Heterocarpus* in depths of 100 to 800 m, has been shown by Lebeau (unpublished report) to have some commercial potential, and there are reports of similarly promising investigations undertaken in the Pacific at the Hawaiian Islands, Guam and the New Hebrides. *Heterocarpus ensifer* appears to be the most abundant species. Lebeau found that catches of about 1 to 8 kg of pandalid shrimps per m³ of trap size (most traps had a volume of about 0.5 m³) could be taken in all depths from 105 to 795 m in waters around Reunion, and most depths yielded about 3 kg/m³.

Various set-line systems using strings of small light-weight traps and a mesh size of not more than 10 mm should be tested in Jamaican waters at the earliest opportunity. This aquatic resource, if shown to be of significant size, lies within reach of the unmechanized canoe fleets of the north, southwest and southeast coasts of Jamaica, and even if only modest catch rates are possible could result in the development of an economically viable fishery.

CHAPTER 17:
BIOLOGICAL AND ECOLOGICAL
CHARACTERISTICS OF
CARIBBEAN REEF FISHES

by
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(March 1975)

Introduction

The purpose of this chapter is to summarize the basic features of the biological and ecological data on commercially important Caribbean reef fishes which have been presented in the preceding chapters, with the final objective of utilizing these data to assess potential yields and to evaluate possible management techniques for the multispecies Caribbean coral-reef fisheries, which are exploited mainly by means of wire-meshed Antillean fish traps (Munro 1969; Munro et al. 1971) and secondarily by means of hand-lines, seine nets and by spearfishing.

It is also of interest to attempt to ascertain the degree to which species, groups or families of fishes have characteristics in common such as common spawning seasons, catchabilities, natural mortality rates, growth rates, fecundities, sizes at maturity, or juvenile nursery grounds, or, conversely, to examine the degree to which such features differ within the exploited section of the coral-reef fish community. It appears likely that the differences in the compositions of various exploited reef fish communities (described in Chapters 4 and 5), are the result of the biological or ecological characteristics and of differential fishing mortalities of the constituent species, and that a complete understanding of the dynamics of the exploited communities will only be achieved when these features have been exhaustively studied.

In perusing the data presented in the following pages, it is most important that the reader bears in mind that the estimates of biological, ecological and fishery parameters are almost entirely based upon the results of a

3 1/2-year research program and virtually no previous data, other than of a most generalized nature, have been available. Sample sizes have varied widely, and, even for the most abundant species, many of the estimates of biological parameters can only be regarded as approximations. Sample sizes and the general adequacy of the sampling program for each species are discussed in Chapters 6 to 16, from which the reader might make his or her own evaluations. Additionally, in the tables which accompany this chapter, some indication is given of the degree of confidence which might be attached to the various estimates.

Over 200 species of fishes are landed and marketed by Caribbean fishermen and most of these species are associated with reefs or coralline areas. About seventy of these species, in ten families, have been discussed in some detail in Chapters 6 to 16 and these species collectively constitute over 90% of all landings from the coralline shelves of most parts of the Caribbean and adjacent regions. The most important reef fish species in Jamaican waters are listed in Table 17.1, the rough criterion for inclusion in this list being that each species constituted more than 1.0% by weight of the total catch in traps or on lines in at least one of the areas investigated, and that they have some commercial value.

The greatest part of the shelf area over which commercially valuable species are distributed lies in depths of less than 40 m. Most of the area lying below 40 m and above the edge of the bathyal zone at about 300 m is

comprised of very steep slopes and is located beneath a very narrow strip of surface water. This habitat is occupied by a fish fauna in which snappers, groupers, jacks and sharks are predominant (see Chapter 4), and few of the species found in this region are also found on the shelf in depths of less than 40 m (with the exception of juveniles of a few species).

The shelf fauna appear to be quite generally distributed, both in a geographical sense and with respect to depth. Few species appear to be confined to either the shallows or to the deeper portions of the shelf although

habitat or depth preferences are apparent in a number of species. A large proportion of the species appear to move progressively into deeper water with increasing size, but shallow waters are not essential as nursery areas in most species. This is shown by the fact that isolated oceanic banks having least depths of about 30 m are inhabited by most of the economically important demersal species. The parrotfishes (Scaridae) are the only group in which most of the species appear to be confined to depths of less than about 20 m.

The Biological Characteristics

The various biological parameters estimated for each species are listed in Table 17.1. These include estimates of asymptotic sizes, length:weight relationships, coefficients of growth (K) and natural mortality (M), the ratio M/K , fecundity (e) (eggs per gram body weight) and size at maturity.

The fishery parameters, including calculated size retainable in 4.13-cm mesh traps, observed mean lengths at recruitment to that mesh size, mortality rates in exploited areas and estimates of catchabilities are given in Table 17.2 for species for which such data are available. Parameters shown in brackets can only be described as informed guesses and all parameters require further investigation.

REPRODUCTION

A high degree of uniformity in reproductive patterns is apparent in the species. With the exception of the groupers and angelfishes, which are protogynous hermaphrodites (Chapters 7 and 12), all commercially important species appear to be bisexual. Most species, with the possible exception of the balistids, appear to have externally fertilized planktonic spawn, produced by aggregations of spawning fishes (Randall and Randall 1963). These spawning aggregations appear to often be located on promontories on the seaward edge of a reef system, as far out in open water as is possible without actually leaving the reef.

Almost all of the species have a main spawning season in Jamaican waters from January to May, with the maximum in March or April and a second, much less intensive, spawning in September to October. The groupers spawn exclusively in the period from December to April. These spawning periods have not been correlated with environmental factors (Munro et al. 1973).

The mean size at sexual maturity has been determined for most of the species listed in Table 17.1. Although the age at maturity is not known with any precision for any species, it seems likely on the basis of known growth rates that most of the small species mature for the first time at the end of their first year of life and that some of the larger species such as snappers, jacks, and groupers might mature in their second or third years. For those

species for which the mean length at maturity has been accurately determined, the ratio l_m/L_∞ lies between 0.37 and 0.76. The average value is about 0.5, and there is some tendency towards an inverse relationship between this ratio and the asymptotic length.

The few fecundity estimates which have been made do not permit the formation of any general conclusions regarding reef fish fecundity, other than to observe that for most of the species considered, mean fecundity counts of 200 to 500 eggs/g body weight appear to be the most usual order of magnitude (Table 17.1). This is not strikingly different from that of many demersal species inhabiting temperate waters.

GROWTH

Growth rates have been estimated by conventional techniques such as the Petersen method and in a few cases by proportionality of marks on scales and otoliths.

In the case of length frequency data for estimation of modal progressions, the main problem was the acquisition of sufficiently large samples of individual species, regularly spaced over extended time periods. The numbers of fishes measured were fully adequate for only a few species, and in most cases the data had to be analyzed on a bi- or tri-monthly basis in order to obtain length-frequency distributions based on reasonable numbers of fishes.

There was some evidence that marks on scales and otoliths could be utilized for estimation of age and growth of a substantial proportion of the species encountered. However, such marks are, with a few exceptions, not nearly as clearly discernible as those found in temperate waters, and would require very detailed and laborious studies to produce useable estimates of age and growth. The scientific manpower available during these investigations was insufficient to permit such studies but, given the basis provided by the present investigations, could be expected to form an important part of any future studies.

The estimates of the coefficient of growth, K , indicate that growth is relatively rapid in comparison with temperate-water species. However, none of the species considered here have the exceptionally rapid

rates of growth which are found, for example, in the tropical freshwater groups such as *Tilapia* spp. or the Indian and Chinese carps.

MORTALITY

Estimates of the mortality rates of the species captured during these investigations have been based on the length-frequency distributions of catches by using the Beverton and Holt (1956) formulation

$$Z = K (L_{\infty} - \bar{l}) / (\bar{l} - l_c)$$

in which

- Z is the coefficient of total mortality,
- K is the coefficient of growth
- L_{∞} is the asymptotic length
- l_c is the smallest size at which the fishes are fully represented in the catch and
- \bar{l} is the mean length of all fishes between l_c and L_{∞} .

This formulation has not been widely used. Most investigators have preferred the more laborious, but perhaps more accurate, method of deriving estimates of mortality rates from the age compositions of samples of catches, where such data have been available. Some doubts have also been cast upon the validity of such an "elementary" method of estimating Z. However, Le Guen (1971) has shown that estimates of Z based upon age compositions and upon length-distributions of samples of *Pseudotolithus elongatus* from the Gulf of Guinea are nearly identical and, provided that growth over the exploited range is reasonably well described by the von Bertalanffy growth equation, the above equation will yield quite accurate estimates of Z. As with any other estimate based upon samples, it is likely that very large samples will enhance the accuracy of the estimates.

Additionally, estimates of Z have been derived from the mean weights of individuals in the catches. These estimates are not included in Chapters 6 to 16 because the compilation of data on trap catches in various areas (Chapter 5) was not complete at the time that the bulk of these chapters were in preparation.

The equation for deriving the mean weight of individuals in the catch is

$$\bar{W}_c = W_{\infty} \sum_0^3 \frac{U_n Z e^{-nK(t_c - t_0)}}{Z + nK}$$

(Gulland 1969)

in which the mean weight (\bar{W}_c) is a function of the asymptotic weight (W_{∞}), the growth rate (K), the total

mortality rate (Z) and the age at entry to the exploited phase (t_c). U_n is the summation variable in which $U_0 = 1$, $U_1 = -3$, $U_2 = 3$ and $U_3 = -1$.

Curves or tabulations showing the relationships between \bar{W}_c and Z have been prepared for those species for which the growth rates are known and estimates of Z then derived from the observed mean weight of individuals in catches from various areas. Estimates so derived are indicated by an asterisk in Table 17.2. The accuracy of such estimates of Z is much dependent upon the estimates of \bar{W}_c having been based upon catches which were evenly distributed throughout the year or which have been appropriately weighted to allow for seasonal changes in condition and the growth of year classes. However, condition factors are not subject to very large variation in tropical waters. For the species listed in Table 17.2 there are, with some notable exceptions, large measures of agreement between the estimates of Z derived from length distributions and those derived from mean weights.

Natural Mortality Rates

A coral-reef fish community normally contains a complete spectrum of fish species, ranging from major predators such as sharks, mainly piscivorous species such as groupers, snappers and jacks, omnivores such as grunts and purely herbivorous or at least non-piscivorous groups such as parrotfishes and surgeonfishes. Most species are resident upon the reefs from a very small size and are liable to predation by larger fishes throughout most of their lives, but the likelihood of death by predation will decrease with increasing size. Predatory species will themselves be liable to predation throughout all of their life cycle, the only likely exceptions being the largest adult sharks. Most species will therefore suffer great reductions in their numbers as a result of predation.

The traditional concept of trophic structure is therefore largely inapplicable and, with the exception of the herbivorous species, the position of a fish in the trophic pyramid is largely determined by its size. Most species contribute to the biomass of predators in accordance with their numbers, average size and their proclivity to the piscivorous habit. All species form part of the pool of prey in accordance with their numbers and average size.

Beverton and Holt (1957, p. 169) have considered in some detail the theoretical basis for calculating the effect of exploiting two interdependent populations either in competition with each other or in a predator-prey system. However, their equations are not suitable for application to a highly complex coral reef community and cannot be used in the present analysis, mostly because of the large numbers of species involved.

The present estimates of natural mortality rates

Table 17.1. Biological characteristics of selected species of Caribbean reef fishes. Notation is as follows: a and b, respectively the constant and the exponent in the length/weight equation ($W = aL^b$) when weight (W) is measured in grams and length (L) is measured in cm; K, the coefficient of growth; L_{∞} and W_{∞} , the asymptotic length and weight; M_0 , the coefficient of natural mortality in an unexploited population (at Pedro Bank); \bar{e} , the average number of eggs produced per gram of total body weight; \bar{L}_m , the mean length at maturity of females; R' , the recruitment index at Pedro Bank and at the South Jamaica Shelf; l_r , the mean length at recruitment to traps with 4.13 cm mesh. Values in brackets are approximations.

	a	b	K	L_{∞} (cm)	W_{∞} (g)	M_0	M_0/K	\bar{e}	\bar{L}_m (cm)	l_m/L_{∞}	Pedro Bank R'	Pedro Bank \bar{l}_r	Jamaica Shelf R'	Jamaica Shelf \bar{l}_r
Serranidae														
<i>Cephalopholis fulva</i>	.0729	2.574	.63	34	640	1.95	3.09	677	< 16	< 0.47	1,121	23	810	23
<i>Epinephelus guttatus</i>	.0176	2.960	.24	52	1,880	.68	2.83	458	< 25	< 0.48	240	31	130	31
<i>E. striatus</i>	.0107	3.112	.09	90	12,900	(.21)	2.33	—	< 48	< 0.53	12	57	(12)	(57)
<i>Petrometopon cruentatum</i>	.0076	3.237	.34	34	690	—	—	639	< 16	< 0.47	80	20	30	20
<i>Mycteroperca venenosa</i>	—	—	.17	86	(12,000)	.38	2.25	—	< 51	< 0.59	10	57	(10)	(57)
Carangidae														
<i>Caranx ruber</i>	.0083	3.191	.24	52	2,490	1.51	6.3	(520)	24	0.46	240	22.5	75	16
<i>C. bartholomaei</i>	.0063	3.368	—	(85)	19,900	—	—	—	> 45	> 0.53	25	26	(8)	(26)
<i>C. latus</i>	—	—	—	(70)	—	—	(2.5)	—	37	(0.53)	—	—	—	—
<i>C. lugubris</i>	—	—	—	(82)	—	—	—	—	> 38	(> 0.46)	—	—	—	—
<i>C. fuscus</i>	.0065	3.302	—	(62)	(5,400)	—	—	—	> 20	(> 0.32)	—	—	—	—
Lutjanidae														
<i>Lutjanus apodus</i>	.0089	3.204	(.18)	57	3,800	(.54)	3.00	—	25	.44	(9)	(27)	(40)	19.5
<i>L. buccanella</i>	♂ —	—	(.70)	54	(3,200)	2.24	3.20	—	26	.48	—	—	—	—
	♀ —	—	(.35)	48	(1,890)	1.83	5.23	—	24	.52	—	—	—	—
<i>L. vivanus</i>	—	—	—	(72)	(8,000)	—	—	—	52	.72	—	—	—	—
<i>Apsilus dentatus</i>	♂ —	—	.65	(58)	(4,500)	1.90	2.92	—	44	.76	—	—	—	—
	♀ —	—	.30	(56)	(4,000)	.83	2.76	—	40	.71	—	—	—	—
<i>Ocyurus chrysurus</i>	.0145	3.032	.25	60	3,600	.62	2.50	—	30	.50	(7)	(25)	(40)	18
Pomadasyidae														
<i>Haemulon album</i>	.0144	3.07	.20	65	5,300	.79	3.93	220	24	.37	12	28	(12)	(28)
<i>H. flavolineatum</i>	.0107	3.25	—	(25)	(370)	—	4.88	284	16	(.64)	1,980	17	1,000	14
<i>H. sciurus</i>	.0314	2.84	.26	40	1,110	—	—	113	20	.50	0	—	140	19
<i>H. plumieri</i>	.0238	2.93	.35	42	1,360	1.77	5.12	600	22	.52	490	26	1,870	15
<i>H. melanurum</i>	.0557	2.63	—	(30)	(430)	—	3.50	—	> 19	(> .63)	100	21	0	—
<i>H. aurolineatum</i>	.0298	2.79	—	(23)	(190)	—	6.78	434	> 13	(> .57)	330	23	330	23

Continued

Table 17.1 (continued)

	a	b	K	L_{∞} (cm)	W_{∞} (g)	M_0	M_0/K	\bar{e}	$l_m^{\text{♀}}$ (cm)	l_m/L_{∞}	Pedro Bank R'	\bar{I}_r	Jamaica Shelf R'	\bar{I}_r
Mullidae														
<i>Pseudupeneus maculatus</i>	♂ .0099	3.210	(.70)	27	360	1.89	2.70	—	18	.67				
	♀ .0552	2.626	(.35)	25	260	—	—	—	< 16	< .64	790	19	(790)	(19)
<i>Mulloidichthys martinicus</i>	♂ .0820	2.493	(.40)	29	360	1.70	4.29	—	19	.66				
	♀ .0089	3.223	(.40)	30	520	1.70	4.29	—	18	.60	340	19	(340)	(19)
Chaetodontidae														
<i>Holacanthus tricolor</i>	—	—	—	(35)	(1,400)	—	—	120	>10	(>.29)	—	22	—	—
<i>H. ciliaris</i>	—	—	—	(40)	(2,400)	—	—	—	>13	(>.33)	—	26	—	21
<i>Pomacanthus arcuatus</i>	—	—	—	(60)	(2,700)	—	8.1	77	>13	(>.22)	—	21	—	17
Scaridae														
<i>Scarus taeniopterus</i>	—	(2.74)	—	35	(900)	—	6.5	—	—	—	(490)	19	0	—
<i>Sparisoma chrysopterus</i>	.0093	3.21	—	40	1,300	—	—	—	—	—	—	—	(950)	20
<i>S. aurofrenatum</i>	.0129	3.11	—	26	324	—	—	—	—	—	(80)	17	(470)	17
<i>S. viride</i>	.0537	2.74	—	50	2,430	—	—	—	—	—	(6)	17	(1,030)	18
Acanthuridae														
<i>Acanthurus coeruleus</i>	.0278	3.022	—	30	810	—	4.7	—	—	—	(440)	14	(1,180)	11
<i>A. chirurgus</i>	.0221	3.009	—	35	980	—	4.9	—	—	—	(190)	21	(960)	15
<i>A. bahianus</i>	.0191	3.080	—	28	550	—	4.4	—	—	—	(2,440)	15	(780)	12
Balistidae														
<i>Balistes vetula</i>	.0516	2.875	.57	45	2,920	2.6	4.6	73	25	0.56	7,500	16	2,900	16
<i>Canthidermis sufflamen</i>	.0599	2.817	—	(55)	(4,790)	—	—	217	—	—	—	—	—	—

Note: Parameters for *C. fulva* changed in this edition. See Table 7.17.

Table 17.2. Summary of fishery parameters estimated for the commonest species in the Jamaican trap fishery. Notation is as follows: \bar{l}_r , calculated and observed mean lengths at recruitment to traps with 4.13 cm wire mesh; M_0 , coefficient of natural mortality in unexploited stocks at Pedro Bank; Z, coefficient of total mortality; F, coefficient of fishing mortality; q, the catchability (the amount of fishing mortality generated by a fishing intensity of 1 canoe/km²). Values in brackets are approximations. Mortality estimates marked with an asterisk have been derived from the mean weights of individuals in the catches.

	Calculated \bar{l}_r	Observed \bar{l}_r	M_0	Pedro Cays f = 0.15 canoes/km ²			California Bank f = 0.38 canoes/km ²			Port Royal reefs f = 1.52 canoes/km ²			Best estimate of q
				Z	F	q	Z	F	q	Z	F	q	
Serranidae													
<i>Cephalopholis fulva</i>	17	23	1.95	.84*-1.83	0-0.86	? -5.7	2.15-3.2*	1.64-2.69	4.3-7.1				5.7
<i>Epinephelus guttatus</i>	17	31	.68	.87	.53	3.5	0.90-1.1*	0.72-0.92	1.9-2.4	5.5*	5.4	3.6	3.4
<i>E. striatus</i>	15	57	.1*(-.21)	.38-0.60*	-	-	-	-	-	-	-	-	-
<i>Mycteroperca venenosa</i>	16	57	.38	-	-	-	-	-	-	-	-	-	-
Carangidae													
<i>Caranx ruber</i>	13	16	1.50*-1.51	1.32	0.57	3.8	-	-	-	8.66	8.55	5.6	4.1
Lutjanidae													
<i>Lutjanus apodus</i>	14	19.5	.54	-	-	-	-	-	-	-	-	-	-
<i>Ocyurus chrysurus</i>	14	18	.62	-	-	-	-	-	-	-	-	-	-
Pomadasyidae													
<i>Haemulon album</i>	12	28	0.79-0.93*	-	-	-	-	-	-	-	-	-	-
<i>H. flavolineatum</i>	13	14	(1.71)	(2.34)	(1.49)	(9.9)	-	-	-	6.07	(5.83)	(3.8)	(4.5)
<i>H. sciurus</i>	13	19	-	-	-	-	-	-	-	(1.60)	(1.35)	(0.9)	(4.5)
<i>H. plumieri</i>	13	15	1.77-1.8*	-	-	-	-	-	-	6.90	6.65	4.5	4.5
<i>H. melanurum</i>	(14)	21	(0.88)	(1.22)	(0.78)	(5.2)	-	-	-	-	-	-	-
<i>H. aurolineatum</i>	14	23	-	-	-	-	-	-	-	-	-	-	-
Mullidae													
<i>Pseudupeneus maculatus</i>	16	19	1.5*-1.89	-	-	-	-	-	-	5.22	4.98	3.3	3.3
<i>Mulloidichthys martinicus</i>	17	19	1.6*-1.70	1.90	1.05	7.0	-	-	-	-	-	-	7.0
Scaridae													
<i>Scarus taeniopterus</i>	12	17	(4.35)	-	-	-	-	-	-	-	-	-	-
<i>Sparisoma chrysopterygum</i>	15	17	(4.0)	-	-	-	-	-	-	(9.0)	(8.4)	(5.5)	(4.1)
<i>S. aurofrenatum</i>	14	17	(4.0)	-	-	-	-	-	-	(4.8)	(4.2)	(2.8)	(4.1)
<i>S. viride</i>	12	17	(4.0)	-	-	-	-	-	-	(6.5)	(5.9)	(3.9)	(4.1)
Acanthuridae													
<i>Acanthurus coeruleus</i>	(5)	15	(2.97)	-	-	-	-	-	-	(4.36)	(3.9)	(2.6)	(6.5)
<i>A. chirurgus</i>	(5)	15	(3.15)	-	-	-	-	-	-	(15.00)	(14.6)	(9.6)	(6.5)
<i>A. bahianus</i>	7	15	(2.79)	-	-	-	-	-	-	11.05)	(10.7)	(7.0)	(6.5)
Balistidae													
<i>Balistes vetula</i>	9	16	2.6	-	0.82	5.5	3.22	2.54	6.7	-	-	-	6.2

Note: Mortality rate of *C. fulva* changed in this edition. See Table 7.17.

(Table 17.2) have been based upon the length frequency compositions of catches taken at unexploited parts of Pedro Bank. The mortality rates are relatively high and undoubtedly reflect the great abundance of predatory species in such areas. As a general case it can be suggested that the following equation adequately describes the situation:

$$M = M_x + gP$$

in which M is the natural mortality from all causes, M_x is natural mortality caused by factors other than predation, P is the biomass of predators and g is the amount of mortality generated in the prey population which is caused by one unit of biomass of predators. With the exception of communities from which predators are virtually absent, the value of M_x will usually be extremely small, as any fish which is stricken a result of disease, injury or lack of food becomes highly vulnerable to predation. Thus, for most natural communities, $M \cong gP$. The above equation is directly analogous to the expression, $F = qf$, used for describing fishing mortality, F , in which q is the catchability, or amount of mortality generated by one unit of fishing effort, f . Thus the mortality rates in a population of prey are directly proportional to the abundance or biomass of the predators. When predator and prey are concurrently exploited, the biomasses and abundances of both groups will decline exponentially in response to increases in fishing effort. The natural mortality rate of the prey species will therefore also decline exponentially. However, certain compensatory effects will occur:

(a) The numbers of the prey species will not decline as rapidly as those of the predators, because the natural mortality of prey will have decreased.

(b) The growth rates of the prey species will be enhanced as a result of decreased competition.

(c) The ratio of predators to prey will decrease thus reducing competition between predators for the available prey and possibly enhancing growth rates of predators.

(d) The predators will be of smaller average size and survival of the largest prey species will be differentially improved, thus producing relative increases in the biomass of prey species.

As a result of the complexity of these interactions the exact magnitude of the changes in natural mortality rates which might result from exploitation are not calculable. However, it is possible to make generalized estimates of the magnitude of the decreases in natural mortality rates in exploited areas by comparing the relative abundances of predatory species in various areas. The trap catch rates of predatory species have therefore been calculated, and expressed as catch in kg per 1,000 hexagonal traps (Munro 1973) set for one night. Groups classed as major predators for this purpose include all species of sharks, lizardfishes (*Synodontidae*), eels (*Gymnothorax* spp.), the trumpetfish (*Aulostomus maculatus*), *Sphyrna barracuda*, hinds and groupers

(*Epinephelus* spp., *Cephalopholis fulva*, *Petrometopon cruentatum* and *Mycteroperca* spp.), the tilefish (*Malacanthus plumieri*) and all species of jacks (*Caranx* and *Seriola* spp.) and snappers (*Lutjanus* spp. and *Ocyurus chrysurus*). The relative total biomasses of these species were as follows:

Area	Kg/1,000 hexagonal trap-nights	Relative biomass
Unexploited Pedro Bank	718.3	1.00
Pedro Cays area	355.8	0.50
California Bank	188.9	0.26
S. Jamaica Shelf	161.0	0.22
Port Royal reefs (unbaited traps)	53.7	0.14 (0.07 x 2)*

* (The adjustment of the Port Royal Reefs catch rate allows for the fact that unbaited traps were used and that baiting doubles availability; Munro 1974).

It should be noted that the Port Royal Reefs are contiguous with the S. Jamaica Shelf, and it is likely that many species move onto the shelf and thus into an area which has more predators. For the purpose of estimating the relative amounts of fishing and natural mortalities in exploited areas, the natural mortality rates determined for unexploited parts of Pedro Bank have been reduced by a factor of 0.50 for the Pedro Cays area, 0.26 for California Bank, 0.22 for the South Jamaica Shelf, and 0.14 for the Port Royal Reefs.

The estimated natural mortality rates in the unexploited reef environment are remarkably high in comparison with those commonly found in temperate waters but this is not surprising when due recognition is paid to the trophic structure of the reef fish community and the relatively great biomass of predatory species (Talbot 1965; Odum and Odum 1955; Hiatt and Strasberg 1960).

Fishing Mortality Rates

Figure 17.1 illustrates the relationships which exist between natural mortality rates (M), fishing mortality rates (F), and total mortality rates (Z), at different levels of fishing effort, if natural mortality rates in the reef fish community change in the manner suggested previously.

It is clear from this figure that fishing mortality rates and catchability cannot be derived from conventional techniques of regression of estimates of Z against fishing effort (Widrig 1954). Instead, estimates of F must be derived as $F = Z - M$ for each level of fishing effort. Results of such calculations are given in Table 17.2.

Estimation of Fishing Effort

Figure 2.3 shows that there is a negative linear relationship between the logarithm of the annual catch

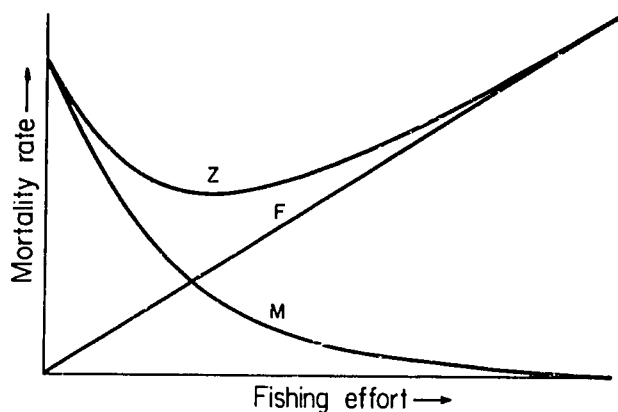


Fig. 17.1. Theoretical interrelationships between natural mortality rate (M), fishing mortality rate (F) and total mortality rate (Z) which will exist if natural mortality rates in an exploited community decline as a result of concurrent exploitation of predatory species.

(of all neritic species) per canoe (C_w/f) and the fishing intensity, f , expressed as canoes/ km^2 , i.e.

$$\log_{10} (C_w/f) = -mf + c$$

in which m , the slope of the regression is -0.1468 and c , the y-axis intercept, is 3.5714 , equal to the logarithm of a theoretical initial catch of $3,727$ kg/canoe/year.

The only other indications of relative abundance of the fish stocks in the areas investigated are the "availabilities" calculated by the methods of Munro (1974). These refer to the theoretical average weight of fishes which will enter a trap which is set for one day. The calculated values are as follows:

Southern Pedro Bank	$A_w = 3,795$ g	} 3,083 g
Eastern Pedro Bank	$A_w = 3,455$ g	
Western Pedro Bank	$A_w = 1,998$ g	
Pedro Cays area	$A_w = 2,930$ g	} 934 g
California Bank	$A_w = 986$ g	
South Jamaica Shelf	$A_w = 882$ g	
Port Royal Reefs (unbaited traps)	$A_w = 317$ g x 2 = 634 g*	

*Adjusted to account for use of unbaited traps.

The only area common to the two sources of data is the South Jamaica Shelf (including California Bank) where the estimated annual catch per canoe (C_w/f) is $3,279$ kg and the availability A_w is estimated at 934 g/day. The equivalence between these relationships is $C_w/f = 3.511 A_w$.

The expected catch rate at the Port Royal Reefs is therefore $634 \times 3.511 = 2,226$ kg/canoe/year. Therefore,

fishing effort at the Port Royal Reefs,

$$f = (\log 3727 - \log 2226)/0.1468 = 1.52 \text{ canoes}/km^2$$

At unexploited parts of Pedro Bank, the mean availability, A_w , is $3,083$ g and the theoretical initial catch per canoe is $3.511 \times 3,083 = 10,824$ kg/canoe/year. This is almost three times greater than that estimated for the fishery around the coasts of Jamaica, and suggests either that recruitment to the nearshore Jamaican reefs has been adversely affected by the fishery, or that the stocks at the oceanic banks are naturally greater. The relationship shown in Fig. 2.3 should nevertheless hold and as availability at the Pedro Cays area was $2,930$ g/day, the fishing effort in the sampling area can be calculated as follows:

$$f = \frac{\log(3.511 \times 3083) - \log(3.511 \times 2930)}{0.1468} = 0.15 \text{ canoes}/km^2$$

It is most strongly emphasized that the above calculations of fishing effort cannot be regarded as definitive, and are merely useful approximations which are in rough accordance with the expected values for fishing intensity.

The approximate relative amounts of commercial fishing effort at the sampling stations are therefore as follows

Pedro Cays area	0.15 canoes/ km^2
California Bank	0.38 canoes/ km^2
South Jamaica Shelf	
Port Royal Reefs	1.52 canoes/ km^2

Catchability

Estimates of catchability, q , have simply been derived for the exploited Pedro Cays area, California Bank and the Port Royal reefs from the following formula:

$$q = \frac{Z - P_w M_o}{f}$$

in which

- Z is the total mortality rate in each area
- P_w is the relative biomass of predators
- M_o is the natural mortality rate at unexploited parts of Pedro Bank, and
- f is the estimated fishing intensity, expressed as canoes/ km^2 .

With some exceptions, the resulting estimates of q (Table 17.2) are quite variable and can only be regarded as first approximations to the true values. The estimated values lie between 3.4 and 7.0, implying that a single canoe fishing with traditional techniques, is capable of

generating mortalities per square kilometer of 97% to 100% per year in most species. As fishing intensity on the narrow northern shelf of Jamaica exceeds 5.5 canoes/km² in some areas, and averages 3.4 canoes/km², the resultant annual fishing mortality rate is in excess of 99% for all species, and the rate of exploitation approaches unity in most areas.

In contrast, fishing intensity on the wider southern shelf averages 0.38 canoes/km², but this is still sufficient to generate instantaneous fishing mortality rates, F , of 1.3 to 2.7 in most species and corresponding annual fishing mortality rates of 73% to 93%.

RECRUITMENT RATES

Estimates of annual recruitment to the stocks are not available for any species, there being no statistics of landings available. Recruitment has therefore been expressed on a relative basis, and a recruitment index (R') calculated which is equal to the theoretical number of recruits required to produce the observed catch rate

(numbers per 1,000 hexagonal traps set for one night). Such estimates are derived simply as $R' = (C/f)Z$ for various areas and the median estimates for each species at Pedro Bank and/or the South Jamaica Shelf are given in Table 17.1.

Recruitment rates tend to be greatest at Pedro Bank, but some of the smaller species such as grunts and surgeonfishes have relatively more recruits in the exploited areas. This suggests that predation upon juveniles might be an important factor determining recruitment rates and that if the Pedro Bank stocks are exploited, the patterns of recruitment will shift in favor of the prey species. This statement does not mean that ecological factors do not influence recruitment. For example, the relatively great abundance of parrotfishes on the South Jamaica Shelf undoubtedly reflects the presence of extensive shallow reefs which are absent from Pedro Bank.

It is emphasized that the estimates of the recruitment index are in no way precise measures of abundance and merely illustrate the likely relative differences between species and between areas.

The Effects of Fishing

Apart from the changes in the biomass of predators and consequent changes in natural mortality and growth rates of all species which can be expected to be generated by the fisheries, there remain other questions which need be elucidated before a full understanding of the dynamics of exploited multispecies reef fisheries can be gained.

In particular, the effect of high rates of exploitation with small-meshed traps can be presumed to adversely influence recruitment. The only available evidence that this is so is illustrated by the declining right hand arm of the surplus yield curve shown in Fig. 2.4.

A comparison of the lengths at maturity (l_m) and the mean lengths at which fishes are recruited (l_r) to the 4.13 cm fish traps currently employed in the Jamaican fishery, shows that about half of the 37 species considered in detail here become catchable well before maturity. These include all of the snappers and jacks, most of the larger species of grunts and the triggerfish, *Balistes vetula*. Most of the groupers mature before recruitment, but transformation to males (they are protogynous hermaphrodites) occurs at sizes well in excess of the mean recruitment length. If this factor is

considered in conjunction with the very high rates of exploitation mentioned in the previous section, it becomes apparent that negligible numbers of fishes survive long enough to spawn in the most heavily exploited areas, and that recruitment to these areas might be largely dependent upon spawning elsewhere around the island, or even elsewhere in the Caribbean (Munro et al. 1973).

Any increase in fishing effort in response to relative increases in the value of the catch could lead to a virtual collapse in the stocks. Indeed, it could be argued that this has already occurred on the northern Jamaican shelf, where experimental fishing yielded an average catch rate of less than 100 g/trap/day, mostly of unmarketable fishes. Rehabilitation of these stocks can only be achieved by either a reduction in the fishing effort, or an increase in the mesh size used. The prohibition of the use of traps on the narrow northern shelf might also be considered, but this would lead to herbivorous species and some of the omnivorous species, which are catchable only in traps or by spearfishing, becoming underutilized. These matters are further discussed in Chapter 18.

CHAPTER 18:
ASSESSMENT OF THE POTENTIAL
PRODUCTIVITY OF JAMAICAN FISHERIES

by
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(April 1975)

Introduction

Discussions of the comparative productivity of Jamaican fisheries, the nature of the various fisheries and an outline of the organization of the fishing industry are included in Chapters 1 to 17. A brief recapitulation of the situation is given below.

The fisheries of Jamaica can be divided into three basic groups:

(a) the nearshore fisheries in which canoes are the basic operating units, and which exploit the fish stocks of the Jamaican shelf and proximal oceanic banks (Fig. 2.2) by means of traps, hand-lines, gill-nets, seine nets and by trolling.

(b) the trap fisheries based on offshore islands (cays) at oceanic banks including Pedro Bank, Morant Bank, Bajo Nuevo, Serranilla Bank and Serrana Bank and at various cays on the Nicaragua-Honduras shelf (Fig. 2.1). These fisheries are serviced by carrier vessels which ply between Jamaica and the cays. The canoes seldom venture more than fifteen miles from their island bases and fishing gears other than traps are seldom used.

(c) the offshore fisheries which exist only in embryonic form. These fisheries will be based on decked fishing vessels operating on oceanic banks and shelves remote from any land bases. It has been demonstrated that trap fishing at Pedro Bank can be effectively pursued by using stackable fish traps (Munro 1973) but results of attempts at line fishing supplemented by trolling have not been encouraging up to the present time (Kawaguchi 1974 and Chapter 4). The evidence available at the present time suggests that economically viable fisheries in offshore areas will have to be based

upon trap catches, supplemented by high-quality hand-line and trolling catches.

The statistical information on landings and fishing effort in these fisheries is very poorly based (see Chapter 2). The most recent estimates of landings by the nearshore fishery are for 1968, when the total catch of neritic demersal and pelagic species (including crustaceans) amounted to an estimated 5,893 t. In addition, about 740 t of oceanic pelagic species were landed (Vidaeus 1970b). Estimates supplied to the author by officers of the Fisheries Division of the Jamaican Ministry of Agriculture show that the carrier vessels servicing the fisheries at the offshore cays landed about 3,650 t in 1973. Of this total, about 680 t originated from the Pedro Cays fishery, about 95 t from the Morant Cays and about 2,870 t from the cays on the Nicaragua-Honduras shelf and adjacent oceanic banks. Mr. E.L. Hamblyn (UK Ministry of Overseas Development, Fisheries Adviser in Jamaica) estimated that the landings by the Pedro Cays fishery amounted to 756 t in 1974. In addition to the foregoing, about 300 t/year are said to be landed by vessels engaged in offshore operations. The total landings by the Jamaican fishing industry therefore amounted to about 10,000-11,000 t in 1974.

It is known that almost all of the landings of the carrier vessels are derived from fishing by means of Jamaican Z traps. In the case of the nearshore fisheries, the relative contributions of the various fishing gears to the total catch are not known with any precision. The 1968 survey of this fishery indicated that trap-caught

demersal species probably contribute about 65% of the total neritic catch (excluding oceanic pelagic species) and that about 20% is taken in seine-nets and gill-nets. The remaining 15% is taken on hand-lines and a very small fraction is caught by spear fishermen.

For management purposes, the catch of demersal species in depths of 5 to 45 m can be regarded as being almost entirely harvested by means of traps and the fraction taken by means of nets or hand-lines is very small. In contrast, most of the catch taken on hand-lines is captured over the sill reefs or from the "drop-off" and deep reefs in depths of 45 to 300 m (see Chapters 3 and 4). Important exceptions to the above statement include the yellowtail snapper (*Ocyurus chrysurus*) and the black-fin snapper (*Lutjanus buccanella*). *O. chrysurus* is of major importance in both the fisheries but the greater proportion of the catch is taken in hand-lines. Juvenile *L. buccanella* inhabit the sill reef areas and are exploited by the trap fishery before they migrate down the slope to deeper waters. It is likely that the line fishery suffers a great reduction in its potential harvest as a result of this factor.

Catches in seine-nets and gill-nets are predominantly comprised of pelagic clupeids and carangids, particularly the sprat, *Harengula humeralis*, and the goggle-eye scad, *Selar crumenophthalmus*. A small part by weight and a numerically large part of the seine-net catch consists of juvenile reef fishes, and the seine-net fishery undoubtedly exerts an adverse effect on recruitment to the trap fishery. There are no statistical data and minimal biological or ecological information on the important species

in the gill-net and seine-net fisheries. Consequently, no assessment of potential harvests in this fishery is possible at the present time. Likewise, no assessment of potential harvest is possible in the case of the trolling fishery for oceanic pelagic species. The problem in this case does not stem from a lack of biological or ecological data, but relates instead to the fact that all of the species involved in this fishery undertake extensive migrations, and are subjected to exploitation on a regional basis. The harvests of the Jamaican fishery are therefore affected by events elsewhere in the western Atlantic and the Caribbean and catches will be proportional to the amount of fishing effort and the numbers of these fishes which actually pass through Jamaican waters.

The remainder of this chapter is directed towards an assessment of changes which might result in the trap and hand-line fisheries for demersal species in Jamaican waters as a result of changes in the mesh size used for traps and of changes in fishing effort. The biological and ecological data upon which the assessments are based have been detailed in the preceding chapters and summarized in Chapter 17 and will not be repeated here.

This assessment deals only with the shelf areas of Jamaica and proximal oceanic banks, and with the extensive Pedro Bank which by virtue of its size and proximity is the most valuable oceanic area in Jamaican waters. By extrapolation, the conclusions reached in this report might be applied to the other oceanic banks and shelf areas of the west-central Caribbean, but it is emphasized that no primary research has been conducted in these areas.

Assessment of Potential Yields

The basic techniques for assessing the potential harvests from single species fisheries are well established. They are largely based upon the population models developed by Beverton and Holt (1957), Schaefer (1954) and earlier workers and their validity has been proven in their application to numerous fisheries. Gulland (1969) has provided the most recent review of these techniques. The techniques are applicable to most exploited fish stocks, but in many tropical regions the problems of assessment of potential harvests are compounded by the multiplicity of species which are exploited. The same species is often exploited by a variety of techniques or a single technique might capture an enormous variety of species.

The problems of assessing the potential harvests from multispecies fisheries increase proportionately with the number of species involved and reach their maximum complexity in fisheries of coral reefs and other tropical environments. In the reef environment, the diversity of species is so great that no species is of singular importance, and a substantial portion of the catch is comprised of species which are individually of low abundance and for which even the most extensive biological sampling program is unable to produce adequate samples for the estimation of growth and mortality rates. An assessment

of such a fishery must be based upon a summation of yield curves for individual species (or the sexes if growth or mortality rates differ), starting with the most abundant species and progressing through the list of species to include all species for which there are adequate data upon which to base an assessment. The number of species included in an assessment is therefore proportional to the magnitude and effectiveness of the biological sampling program. In cases where some of the less abundant species form the basis of fisheries in other areas, biological parameters of such species might have to be determined on the basis of their characteristics in the latter areas.

However, conventional yield assessments are rendered extremely complex by a major problem which probably characterizes multispecies fisheries, in which the biomasses of the herbivorous, omnivorous or predatory species are uniformly or differentially reduced by the fishery. The difficulty results from the fact that the natural mortality rate of each species is reduced in proportion to the biomass of its predators and its growth rate might increase in response to decreased biomass of competitors. This can result in radical reductions in the ratio of natural mortality to growth rates and improvements in the yield potentially available from

a given recruitment. The proportion of non-predatory species in the catch will therefore increase disproportionately with increases in fishing effort.

The question of the extent to which natural mortality rates of individual species are decreased as a result of non-selective exploitation of the entire reef fish community has been discussed at some length in Chapter 17 and is further discussed in the following pages. It has been shown that natural mortality rates will undoubtedly fall to levels which are much lower than those which prevail in unexploited communities which contain a great abundance of predators.

Two basic techniques are available for assessing potential harvests. These are models of the type proposed by Schaefer (1954) which are based on catch and effort statistics, and the Beverton and Holt (1957) model which is based upon the biological characteristics of the species.

A rather simplistic exponential surplus yield model (e.g., Fox 1970) based upon the total neritic catch of the nearshore fisheries of the various Jamaican parishes has been presented in Chapter 2. This model is further discussed in the following pages and is useful in predicting the relationships between relative abundances of the fish stocks and fishing intensities and in giving an estimate of the yields per unit area which are potentially available. However, the model cannot be used to estimate the possible effects of changes in the fishing techniques or of adoption of different mesh sizes by the fisheries.

In order to accomplish the latter objectives the stochastic model of Beverton and Holt (1957) must be used. This model assumes recruitment to be constant and density independent. The basic equation is as follows:

$$Y = F R e^{-M(t_c - t_r)} W_{\infty} \sum_0^3 \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK} \quad (\text{Equation 1})$$

The basic yield equation can also be expressed as follows (Gulland 1969):

$$Y = R W_{\infty} e^{M(t_r - t_0)} g(1-c)^{-b} \{\beta_{1-c}(m+g, b+1)\} \quad (\text{Equation 2})$$

in which the terms are defined as follows:

- Y = yield in weight
- R = number of recruits to the fishery at age t_r and length l_r
- W_{∞} = the asymptotic weight
- M = the coefficient of natural mortality
- t_0 = the theoretical x-axis intercept of the growth curve
- b = the exponent in the length-weight relationship
- g = F/K

- F = the coefficient of fishing mortality
- K = the coefficient of growth
- c = l_c/L_{∞}
- l_c = length of first capture at time t_c
- L_{∞} = asymptotic length
- m = M/K
- Z = the coefficient of total mortality = F + M
- β = the incomplete Beta function, related to the relative size at first capture, c, the ratio of total mortality of growth ($m+g = M/K + F/K = Z/K$) and the exponent in the length-weight relationship, b.

Tables of the incomplete Beta function have been prepared by Wilimovsky and Wicklund (1963) and the values are readily determined.

The value $e^{M(t_r - t_0)}$ can be expressed in terms of length as

$$e^{M(t_r - t_0)} = 1/(1 - L_r/L_{\infty})^{M/K} \quad (\text{Equation 3})$$

thus facilitating assessments in cases where the ratio M/K is known only from the size composition of catches and the individual values of M and K and of t_r and t_0 are unknown. The yield equation then becomes:

$$Y/R = \frac{W_{\infty}}{(1 - L_r/L_{\infty})^m} g(1-c)^{-b} \{\beta_{1-c}(m+g, b+1)\} \quad (\text{Equation 4})$$

Also, values of the yield function,

$$Y' = g(1-c)^{-b} \beta_{1-c}(m+g, 4)$$

have been tabulated by Beverton and Holt (1964) for instances where the value of b, the exponent in the length-weight relationship, is equal to or is close to 3 and each value of Y' is related to particular values of c and $E = g/m + g$.

Then,

$$Y = \frac{Y' R W_{\infty}}{(1 - L_r/L_{\infty})^m} \quad (\text{Equation 5})$$

These simplified renderings of the basic Beverton and Holt yield equation are particularly useful for making rapid checks of results produced by means of a computer, or for making assessments over a narrow range of values. Production of complete series of yield curves is, however, a very laborious process which is best accomplished by programming for the computer the original yield equation. Additionally, the yield function tables can be used for making adjustments which allow for changes in the natural mortality rates.

The Trap Fishery

APPLICATION OF THE MODELS

In order to apply the Beverton and Holt yield per recruit model to the Jamaican trap fisheries and to properly evaluate the effects of changes in mesh sizes or fishing effort, various non-biological or fishery-related factors must be considered in addition to the biological characteristics of the species which have been summarized in Chapter 17 (Tables 17.1 and 17.2). These include the following:

- The species to be considered.
- Mesh sizes which might potentially be utilized by the fishery.
- Relative amounts of fishing effort required to generate an array of values of fishing mortality (F) in each species.
- The landed cash values per unit weight of each species.

The Species Assessed

A total of 130 species of fishes occurred in samples taken during the course of these investigations, and most of these species were captured, at least occasionally, in traps. However, as shown in Chapter 5, the number of species which contribute a significant part (by weight) of the trap catches, is much more limited.

Reference to Chapter 5 shows that in most of the areas which were investigated, fewer than 25 species comprised over 80% by weight of the total catch. With some exceptions (mentioned below) the species selected for inclusion in the assessment program are those which are marketable and which comprised more than 1.5% of the weight of the trap catch in any area. These areas included the Port Royal Reefs, California Bank, the South Jamaica Shelf, the Pedro Cays area and the various unexploited sections of Pedro Bank; Portland Rock, the Southeastern Spur, Banner Reef, 20 meter Bank, Southwest Pedro and Northwest Pedro (Figs. 2.2 and 3.2).

The species selected on this basis are as follows:

Serranidae	<i>Cephalopholis fulva</i> <i>Epinephelus striatus</i> <i>E. guttatus</i> <i>Mycteroperca venenosa</i>
Carangidae	<i>Caranx ruber</i> <i>C. bartholomaei</i>
Lutjanidae	<i>Lutjanus apodus</i> <i>Ocyurus chrysurus</i>
Pomadasyidae	<i>Haemulon flavolineatum</i> <i>H. melanurum</i> <i>H. album</i> <i>H. plumieri</i> <i>H. sciurus</i> <i>H. aurolineatum</i>

Mullidae	<i>Mulloidichthys martinicus</i> <i>Pseudupeneus maculatus</i>
Scaridae	<i>Scarus taeniopterus</i> <i>Sparisoma chrysopterus</i> <i>Sp. aurofrenatum</i> <i>Sp. viride</i>
Acanthuridae	<i>Acanthurus coeruleus</i> <i>A. chirurgus</i> <i>A. bahianus</i>
Balistidae	<i>Balistes vetula</i>

Of the species mentioned above, only *O. chrysurus* did not constitute more than 1.5% of the total catch in any one area and is included on the grounds that it is actively sought by Jamaican trap fishermen and is probably of greater importance to the fishery than is indicated by the experimental trap catches.

The species which comprised more than 1.5% of the marketable component of the trap catches from the Port Royal Reefs, but which have been excluded from the analysis, include *Epinephelus itajara* (2.0%), of which only a few, very large individuals were captured; *Chaetodipterus faber* (2.3%) of which large numbers were occasionally captured in a single trap but for which the biological data are inadequate; and *Abudefduf saxatilis* (2.2%) which occurred in traps in large numbers at certain times of the year, but has little market value. Species which comprised more than 1.5% of the trap catch at stations at Pedro Bank, but for which the necessary biological parameters could not be estimated, include *Scarus coeruleus*, *Seriola dumerili*, *Caranx latus*, *Holacanthus tricolor*, *H. ciliaris* and *Pomacanthus arcuatus*. Also, analyses of data on the squirrelfishes, *Holocentrus rufus* and *H. ascensionus*, were not completed at the time this chapter was prepared and have had to be excluded from the yield assessments.

The 24 species listed above collectively constitute a very substantial percentage of the total trap catches of marketable fishes (excluding crustaceans, which are dealt with separately in Chapter 16) taken in various areas: viz

Port Royal Reefs	65%
California Bank	61%
South Jamaica Shelf (limited sampling)	(52%)
Pedro Cays area	70%
Unexploited Pedro Bank —	
Portland Rock	82%
Southeast Spur	80%
Banner Reef	66%
20-meter Bank	78%
Southwest Pedro	82%
Northwest Pedro	76%

The biological and fishery parameters estimated for these species are given in Table 18.1.

Table 18.1. Summary of biological and fishery parameters used for assessment of the effects of changes in mesh size upon the potential yields of the multispecies Jamaican trap fishery. Notation is as follows: V, relative value of the species; v and d, constants in the equation $L_c = dD + v$ in which L_c is the mean length at first capture and D is the maximum aperture of the wire mesh; W_∞ and L_∞ , the asymptotic weights (g) and lengths (cm); K, the coefficient of growth; M, the notional coefficient of natural mortality (set at one half of that prevailing in an unexploited population); q, the catchability or amount of fishing mortality generated by an annual fishing intensity of one canoe per square kilometer; L_T , the mean length at recruitment to traps with 4.13 cm mesh and R' is the mean index of the relative abundance of recruits to the fisheries at Pedro Bank and on the South Jamaica Shelf. Values given in brackets are approximations and are not definitive.

Species	V	v	d	W_∞ (g)	L_∞ (cm)	K	M	q	Pedro Bank		South Jamaica shelf	
									L_T (cm)	R'	L_T (cm)	R'
Serranidae												
<i>Cephalopholis fulva</i> *	2.2	4.2	3.09	649	34	0.63	0.98	5.7	23	1,121	23	808
<i>Epinephelus striatus</i>	2.2	0	(3.5)	12,900	90	0.09	(0.11)	(6.8)	57	12	(57)	(12)
<i>E. guttatus</i>	2.2	2.5	3.43	1,880	52	0.24	0.34	3.4	31	235	31	134
<i>Mycteroperca venenosa</i>	2.2	0	(3.8)	(12,900)	86	0.17	(0.19)	(6.8)	57	10	(57)	(10)
Carangidae												
<i>Caranx ruber</i>	3.3	-1.8	3.61	2,490	52	0.24	0.76	4.1	23	240	16	75
<i>C. bartholomaei</i>	3.3	-3.6	3.60	(19,900)	(85)	(0.24)	(0.76)	4.1	(26)	(24)	(26)	(8)
Lutjanidae												
<i>Lutjanus apodus</i>	3.3	2.7	2.81	3,800	57	(0.18)	(0.27)	(4.5)	(27)	(9)	20	(40)
<i>Ocyurus chrysurus</i>	3.3	-1.2	3.69	3,600	60	0.25	0.31	(4.5)	(25)	(7)	18	(40)
Pomadasyidae												
<i>Hacmulon aurolineatum</i>	1.7	0.7	3.33	190	23	(0.35)	(1.19)	4.5	16	(330)	16	(330)
<i>H. flavolineatum</i>	1.7	1.2	2.82	(370)	(25)	(0.35)	(0.86)	4.5	17	1,980	14	1,000
<i>H. melanurum</i>	1.7	0	3.37	(430)	(30)	(0.25)	(0.44)	4.5	21	100	-	0
<i>H. album</i>	1.7	0	2.33	5,300	65	0.20	0.40	4.5	28	12	28	(12)
<i>H. plumieri</i>	1.7	1.4	2.73	1,360	42	0.35	0.89	4.5	26	490	15	1,870
<i>H. sciurus</i>	1.7	0.3	3.10	1,110	40	0.26	(0.90)	4.5	-	0	19	140
Mullidae												
<i>Mulloidichthys martinicus</i>	3.3	0	4.01	459	30	0.40	0.85	6.8	19	340	19	(340)
<i>Pseudupeneus maculatus</i>	3.3	0	3.93	331	26	0.60	0.95	3.4	19	785	19	(785)
Scaridae												
<i>Scarus taeniopterus</i>	1.0	0	2.90	(900)	35	(0.50)	(2.18)	4.1	19	(490)	-	0
<i>Sparisoma chrysopterygum</i>	1.0	3.8	2.78	1,300	40	(0.50)	(2.00)	4.1	-	0	20	(950)
<i>Sp. aurofrenatum</i>	1.0	2.5	2.78	320	26	(0.50)	(2.00)	4.1	17	(80)	17	(470)
<i>S. viride</i>	1.0	-0.3	3.03	2,400	50	(0.50)	(2.00)	4.1	-	0	18	(1,030)
Acanthuridae												
<i>Acanthurus coeruleus</i>	1.0	-4.7	2.38	810	30	(0.50)	(1.49)	6.5	14	(440)	11	(1,180)
<i>A. chirurgus</i>	1.0	-6.0	3.00	980	35	(0.50)	(1.58)	6.5	21	(190)	15	(960)
<i>A. bahianus</i>	1.0	-8.6	3.70	550	28	(0.50)	(1.40)	6.5	15	(2,440)	12	(780)
Balistidae												
<i>Balistes vetula</i>	1.0	0	2.10	2,900	45	0.57	1.30	6.2	16	7,500	16	2,900

*See Table 7.17.

Selection of Mesh Sizes

At the present time the wire mesh most commonly used for trap construction in Jamaica is a hexagonal weave with a minimum aperture of 3.18 cm (known as 1¼" mesh) and a maximum aperture of 4.13 cm (1.625"). Mesh with a maximum aperture of 3.30 cm is mostly used on the northern and western shelves of the island.

For assessing the effects of mesh sizes upon yields, the following mesh sizes have been selected:

Maximum aperture	Aperture between "knots"
3.30 cm	2.54 cm (1.00 inch)
4.13 cm	3.18 cm (1.25 inch)
4.95 cm	3.81 cm (1.50 inch)
5.78 cm	4.45 cm (1.75 inch)
6.60 cm	5.08 cm (2.00 inch)
8.25 cm	6.35 cm (2.50 inch)
9.91 cm	7.62 cm (3.00 inch)
11.56 cm	8.89 cm (3.50 inch)
13.21 cm	10.16 cm (4.00 inch)
14.86 cm	11.43 cm (4.50 inch)

Fishing Mortality Rates

The estimated amounts of commercial fishing effort in the various areas investigated by this research program are given in Chapter 17 of this series of reports, and the fishing effort on an island-wide basis is given in Chapter 2 (Table 2.1).

The fishing intensity expressed as canoes/km² of shelf area ranges from zero at unexploited oceanic banks to over 5.5 canoes/km² on parts of the northern shelf of Jamaica. Catchabilities, q , (the amount of mortality generated by one canoe/km²) range between 3.3 and 7.0 according to species or family (Table 17.2). The range of possible values of F covered by the present fishery is therefore extremely wide and the rate of exploitation undoubtedly approaches unity on the north coast of Jamaica, where fishing mortality rates, F , of 20 to 40 might prevail accompanied by negligible natural mortality rates.

Fish Prices

Trap-caught fishes marketed in Jamaica are normally sold in 4 grades; "trash", "grunt", "common" and "quality". Prices are variable, being highest in proximity to the main centers of population and on the north coast of Jamaica where demand greatly exceeds the supply. Despite the variations in absolute price, there is a fairly

constant relative price structure which even extends to the retail level. Setting the value of "trash" fish at unity, the approximate average relative values are as follows:

Trash fish	1.0 unit of value
Grunt	1.7 units of value
Common fish	2.2 units of value
Quality fish	3.3 units of value

There is some indication that the price range is narrowing, with prices of cheaper fish rising more rapidly than that of quality fish. This presumably results from high demand combined with low purchasing power or consumer resistance to the highest-priced fish. There are both local and seasonal variations in this price structure and the above weighting has been selected as being most representative of the fishery as a whole.

Recruitment Rates

There are no statistics of landings of any individual species in the Jamaican demersal fisheries, and it is therefore not possible to estimate recruitment to the fishery, other than as a relative value, R' , which is the number of recruits required to produce the observed average numerical catch per 1,000 baited hexagonal traps set for one night. Use of this value, R' , in the yield equation will therefore produce estimates of yield relative to the other species in the fishery and not estimates of absolute yield.

ESTIMATES OF RELATIVE YIELDS

In order to assess the changes in yield which might result from changes in the mesh size of traps or of fishing intensity, relative yields have been calculated for each species for a range of possible mesh sizes and fishing efforts. This has been accomplished by the following procedure.

The basic Beverton and Holt yield equation (Equation 1) has been applied to each of the species considered, for a range of mesh sizes and fishing efforts. This has been accomplished by means of a Wang computer, programmed by staff of the Computing and Statistics Unit of the MAFF Sea Fisheries Laboratory, Lowestoft, United Kingdom. The equation has been slightly modified to produce estimates of the relative value of catches for a given fishing effort, in addition to relative weights of landings. The relative values of the yields (Y_v) of each species are then summed to give the total relative value of the catch for each mesh size over the range of effort values.

All calculations have been based on estimates of natural mortality rates equal to one half of those estimated to prevail in unexploited stocks. It is therefore necessary to adjust the estimates of relative yields to allow for the fact that natural mortality rates decrease

exponentially with increasing fishing effort. Ideally, such adjustments should be made for each species by taking into account the concurrent changes in the abundance of its predators which will result from successive increases in fishing effort. However, the detailed knowledge of each species which is required in order to effect such adjustments is simply not available and, even if they were available, the procedures for calculating the adjustments are exceedingly complex. Instead, it has been necessary to adopt a more generalized approach to the problem, which is outlined as follows:

(a) The biomass of any exploited stock of predators will decrease exponentially in response to increases in fishing effort. The natural mortality rate (M) and hence the ratio of natural mortality to growth (M/K) of the prey populations which are concurrently exploited will likewise decrease exponentially.

(b) The only information that is available concerning this decrease in mortality rates is derived from the regression shown in Fig. 2.3. This shows that the biomass of fish stocks on the Jamaican shelf (as shown by the catch/canoe/year) is reduced to one half of its original value by a fishing effort of 2.05 canoes/km². If the natural mortality rates in unexploited areas and the growth rates of the stocks considered here are averaged in terms of the total number of recruits, the average original natural mortality rate (M_0) is close to 2.0, the average growth rate (K) is 0.48 (say 0.5) and the ratio M_0/K is therefore 4.0. As the decrease in the value of M/K is known to be exponential and the stocks are known to be halved by a fishing effort of 2.05 canoes/km², the M/K ratio can likewise be assumed to be halved. Then $\log_e (M/K) = bf + \log_e (M_0/K)$ in which b is the slope of the regression and represents the change in the logarithm of the ratio M/K which is induced by an increase in fishing intensity of one canoe/km². Thus $\log_e 2.0 = -2.05b + \log_e 4.0$; therefore $b = -0.3381$.

(c) Given the above information it is then possible to calculate a correction factor for the yields attained at different levels of fishing effort. This is accomplished by utilizing the tables of yield functions for fish stock assessment prepared by Beverton and Holt (1964). Values of $YW_\infty/R = Y'/(1-c)^{M/K}$ are first calculated for different levels of exploitation (corresponding to those used in the computer program) by reference to the table of Y' for the ratio $M/K = 2.0$ (that is, one half of the average of that prevailing in the unexploited stocks).

The average value of $c = L_T/L_\infty$ (the relative size of recruitment) is $c = 0.40$. The adjustments are not very sensitive to the latter factor, except at extremely small or large values of c and the value of $c = 0.40$ is well representative of the bulk of the stock. The actual values of M/K which will prevail in the stocks at different levels of fishing effort are then calculated using the equation $\log_e (M/K) = -0.099f + \log_e (M_0/K)$. The actual value of M is then calculated and the corresponding value of $E (= F/F + M)$. The values of $YW_\infty/R = Y'/(1-c)^{M/K}$ are then determined by reference to the yield tables for the appropriate values of M/K , c and E . The latter estimates

of the "correct" values of YW_∞/R are then compared with those determined when M/K was assumed to be constant and equal to one half of M_0/K , and a correction factor calculated.

(d) The correction factor is then multiplied by the estimated yields at successive levels of fishing effort. The effect of having used an estimate of $M = 0.5 M_0$ is that the uncorrected estimates overestimate yields at levels of effort up to 2.05 canoes/km² and underestimate yields at higher fishing intensities.

Alternative approaches are possible in coping with the problem of allowing for changes in mortality rates which result from exploitation. The approach suggested above is simplistic in that it deals with the fish community as a whole. More complex treatments which deal with individual species can be developed or applied but their application cannot be justified until better estimates of the biological parameters and, particularly, adequate catch statistics are gathered on a continuing basis.

An important result of the decrease in natural mortality rates with increasing fishing effort is that the yield curves for many species will tend to reach their maxima at high levels of fishing effort, unlike the yield-fishing effort curves which characterize fishes in temperate regions and which reach maxima at relatively modest fishing intensities and thereafter decline exponentially (see Beverton and Holt 1957 for example). In the latter cases, natural mortality is assumed to be constant, usually at a fairly low value.

It is important to note that conceptual difficulties will be encountered if attempts are made to apply the yield curves to areas other than the South Jamaica Shelf and Pedro Bank. The difficulties lie in the use of the recruitment index, R' , which is a measure of the relative numbers of the recruits of various species which are entering the trap fishery. For example, if the same number of recruits are concentrated or dispersed within areas of different extent, different values of R' will result, although the percentage which each value of R' contributes to the pool of all recruits will remain constant. Thus, for example, it is possible that greater concentrations of recruits will be found in narrow shelf areas with prolific coral growth (e.g., the north coast of Jamaica), and hence more favorable nursery grounds, than in an extensive area with sparse amounts of coral.

Selected examples of the computed yield (by weight) fishing effort curves for traps with 4.13 cm, 5.78 cm and 8.25 cm mesh at the Jamaica Shelf and at Pedro Bank are shown in Figs. 18.1 to 18.3 and 18.5 to 18.7. Owing to the great volume of calculated values only a representative selection are illustrated here, but the full series of computations have been deposited with the Fisheries Ecology Research Project at the Port Royal Marine Laboratory in Jamaica, and are available for inspection by interested persons.

Summations of the yield (by value) curves for all species and including all of the mesh sizes, are shown in Figs. 18.4 and 18.8 which refer respectively to the stocks of the Jamaica Shelf and of Pedro Bank.

The Jamaican Shelf

The expected relative value of catches using various mesh sizes at fishing intensities of up to 4 canoes/km² is shown in Fig. 18.4. Two points are immediately apparent:

(a) Increases in the value of the total catch, Y_v , can be achieved by adoption of mesh sizes larger than the 3.30 cm and 4.13 cm mesh commonly used in the present fishery. The 3.30 cm mesh is mostly used on the intensively exploited narrow northern shelf, while the 4.13 cm mesh is commonest on the extensive South Jamaica Shelf. However, the average fishing effort on the South Jamaica Shelf is only 0.4 canoes/km², and the increases in Y_v which could be achieved by adoption of 4.95 cm or 5.78 cm mesh are in themselves insufficient to warrant a change in mesh size. On the intensively exploited north coast, the fishing intensity averages 3.4 canoes/km² and increases in Y_v of 40% to 53% can be achieved by adoption of a mesh size of between 4.95 cm and 8.25 cm maximum aperture.

(b) The Y_v curves tend to flatten out at when fishing intensity reaches about 1.5 canoes/km² and any increase in effort beyond this point results in negligible increases

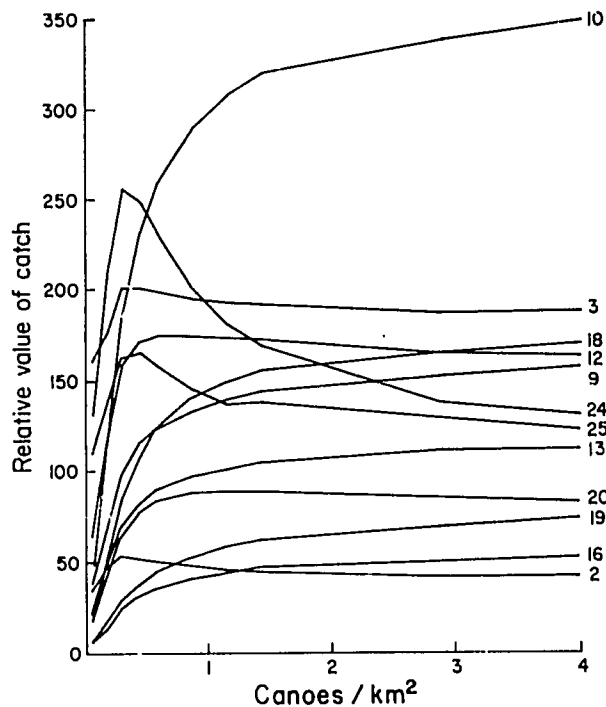


Fig. 18.1. Curves showing the relationships between fishing intensity and the calculated relative values of catches of various species on the South Jamaica Shelf when traps with 4.13 cm mesh are used. Numbers indicate the following species: 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 9 *Mulloidichthys martinicus*, 10 *Pseudupeneus maculatus*, 12 *Haemulon plumieri*, 13 *H. flavolineatum*, 16 *H. aurolineatum*, 18 *Sparisoma chrysopteron*, 19 *S. aurofrenatum*, 20 *S. viride* and 24 *Balistes vetula*. Relative yields of the remaining 11 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches using this mesh size, have been summed to give curve 25.

in the total value of the catch and substantial reductions in the value of the annual catch per canoe. Conversely any reduction in fishing effort in the heavily exploited areas will result in large increases in the profit accruing to the remaining fishermen.

Figures 18.1 to 18.3 show the relative contributions of various species to the total calculated value of catches in traps with 4.13 cm, 5.78 cm and 8.25 cm mesh. It is evident that the relative importances of various species change to varying degrees both in response to changes in mesh size and in response to increases in fishing effort.

Traps with a mesh size of 4.13 cm are used on the South Jamaica Shelf and adjacent areas, and the average fishing intensity is about 0.4 canoes/km². Table 18.2 and Fig. 18.1 show that 11 species will yield 89% and 11 other species will yield the remaining 11% of the total value of these species. However, these 22 species will collectively contribute only about 60% of the total trap catch (by weight) and presumably the same amount by value. *Balistes vetula* and *Pseudupeneus maculatus* each comprise more than 9% of the total Y_v , *Cephalopholis fulva* contributes 8% and *Haemulon plumieri* contributes 7.2%. Seven species contribute 1.2% to 4.5%

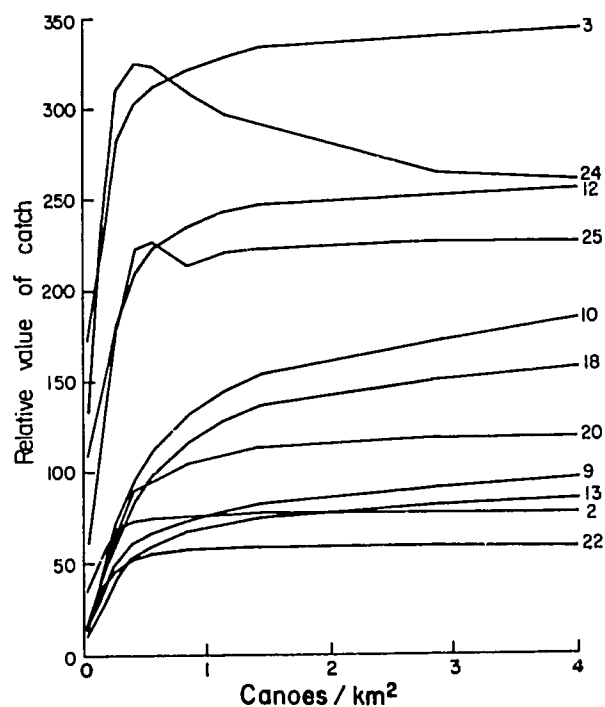


Fig. 18.2. Curves showing the relationships between fishing intensity and the calculated relative values of various species on the South Jamaica Shelf when traps with 5.78 cm mesh are used. Numbers indicate the following species: 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 9 *Mulloidichthys martinicus*, 10 *Pseudupeneus maculatus*, 12 *Haemulon plumieri*, 13 *H. flavolineatum*, 18 *Sparisoma chrysopteron*, 20 *S. viride*, 22 *Acanthurus chirurgus* and 24 *Balistes vetula*. Yield curves of the remaining 12 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches using this mesh size, have been summed to give curve 25.

of the total Y_v .

Table 18.2 also shows that the theoretical composition (by weight) of the total trap catch accords fairly well with the observed composition of catches from sampling stations within the general area, and that the theoretical catch is in most cases bracketed by the values observed at the Port Royal Reefs, the station on the South Jamaica Shelf and at California Bank. The exceptions are *Epinephelus guttatus* in which the observed percentages of the catch are somewhat greater than the theoretical value, and the goatfishes, *Mulloidichthys martinicus* and *Pseudupeneus maculatus* which contributed less than the theoretical percentages.

Figures 18.2 and 18.3 show that when the mesh sizes are increased, the yields from a given fishing effort tend to increase for those species with relatively large maximum sizes, but the yields of small species abruptly decline and some of the species disappear from the catches when the aperture of the mesh exceeds the maximum body depth attained by the species. The

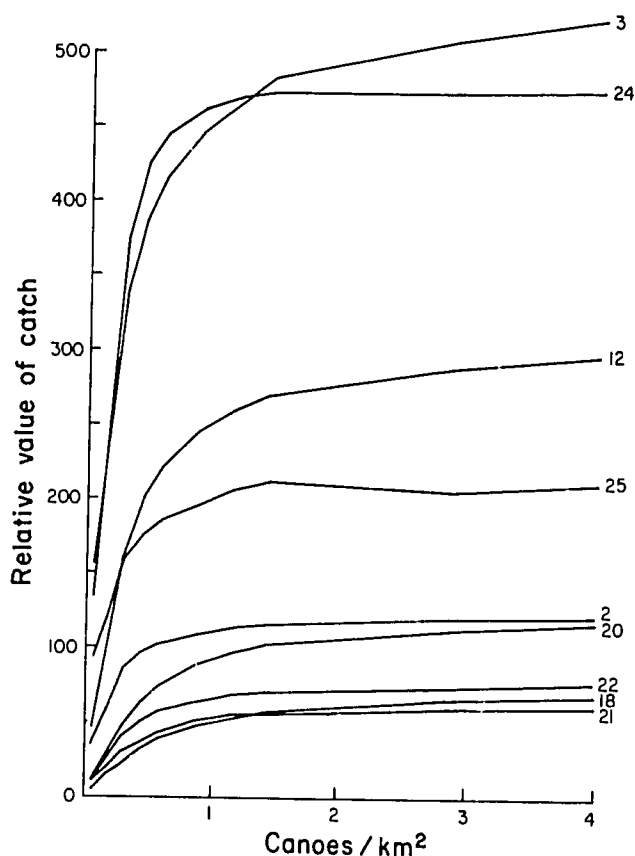


Fig. 18.3. Curves showing the relationships between fishing intensity and the calculated relative values of various species on the South Jamaica Shelf when traps with 8.25 cm mesh are used. Numbers indicate the following species: 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 12 *Haemulon plumieri*, 18 *Sparisoma chrysopterum*, 20 *S. viride*, 21 *Acanthurus coeruleus*, 22 *A. chirurgus* and 24 *Balistes vetula*. Yield curves of the remaining 14 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches using this mesh size, have been summed to give curve 25.

groupers, *E. guttatus* and *C. fulva*, the white grunt, *Haemulon plumieri* and the triggerfish, *Balistes vetula* are representative of the first group. In contrast, the maximum yields of goatfishes, *M. martinicus* and *P. maculatus* are obtained in the 4.13 cm and 4.95 cm mesh, and yields decline in larger mesh sizes and they are eliminated from the catches in meshes of greater than 6.60 cm maximum aperture.

Pedro Bank

The relative yields attainable in various mesh sizes at Pedro Bank are shown in Fig. 18.8. Details of the relative contributions of the most important species in traps with 4.13 cm, 5.78 cm and 8.25 cm mesh are shown in Figs. 18.5 to 18.7. The essential features are similar to those described for the Jamaica Shelf fishery, but owing to the relatively greater abundance of large species (particularly *Balistes vetula*) the differences between the yields in large and in small-meshed traps are greater and the total relative values of the catches are also proportionately greater. The yields in mesh sizes between 4.13 cm and 8.25 cm maximum aperture become nearly stable at fishing intensities exceeding 1.5 canoes/km² and the greatest yields are taken in mesh sizes of 4.95 cm to 8.25 cm maximum aperture.

The most important species in the Pedro Bank fishery is *Balistes vetula* which will comprise about 25% of the value of the total catch, even in the smallest mesh sizes,

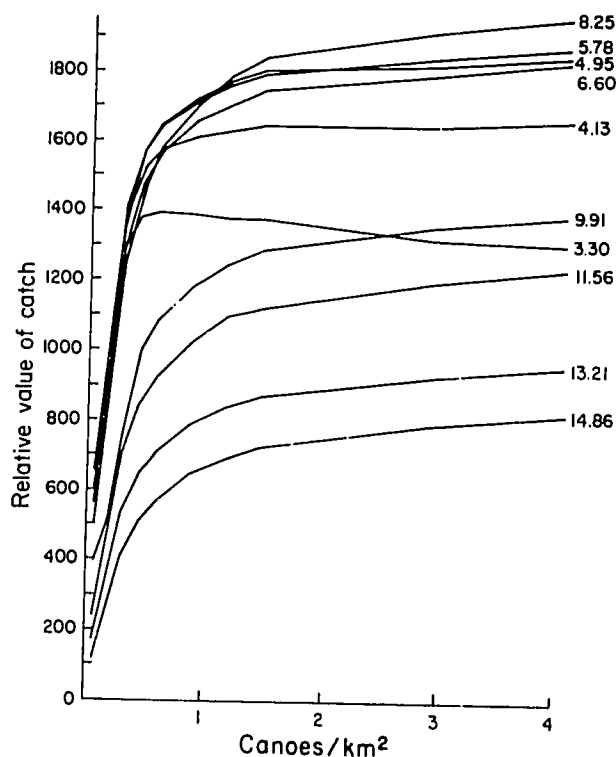


Fig. 18.4. Calculated relative total values of catches of 22 species of reef fishes (listed in Table 18.1) in various mesh sizes and at various fishing intensities on the South Jamaica Shelf.

and almost 40% in the 8.25 cm mesh. Other species of major potential importance include the French grunt, *Haemulon flavolineatum*, which is extremely abundant in some areas, the goatfishes, *Mulloidichthys martinicus* and *Pseudupeneus maculatus*, the white grunt, *Haemulon plumieri* and the groupers (*Epinephelus guttatus* and *Cephalopholis fulva*). Owing to their relatively great body depth, the surgeonfishes, particularly *Acanthurus bahianus* are favored by moderately large mesh sizes (Figs. 18.5 to 18.7).

Estimation of Potential Harvests

The yield-fishing effort curves shown in Figs. 18.4 and 18.8 serve only to show the mesh sizes which might be used in the trap fishery, and to illustrate the *relative* increases or decreases in yield which will result from changes in the mesh size. They do not provide any information on the magnitude of the catches which might be taken from a given area, and estimates of potential harvests can only be derived indirectly from other data.

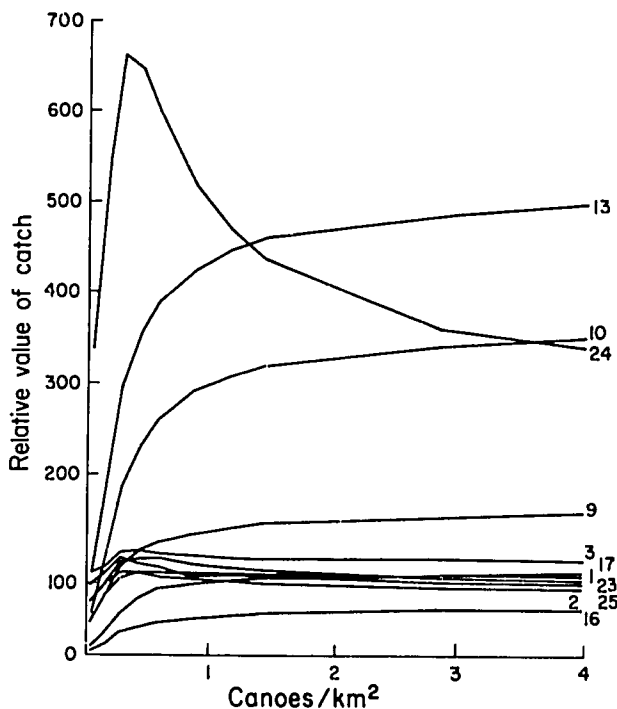


Fig. 18.5. Curves showing the relationships between fishing intensity and the calculated relative values of catches of various species at Pedro Bank when traps with 4.13 cm mesh are used. Numbers indicate the following species: 1 *Caranx ruber*, 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 9 *Mulloidichthys martinicus*, 10 *Pseudupeneus maculatus*, 13 *Haemulon flavolineatum*, 16 *H. aurolineatum*, 17 *Scarus taeniopterus*, 23 *Acanthurus bahianus* and 24 *Balistes vetula*. Relative yields of the remaining 11 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches in this mesh size, have been summed to give curve 25.

The estimates of relative yield refer to Pedro Bank as a whole, the major part of which is unexploited at the present time. It is therefore not possible to compare the estimated composition of the catches with any actual values. Catches taken at the Pedro Cays area, which is lightly exploited, also cannot be compared with the computed estimates, as the catch at the Pedro Cays station contained about 50% *Balistes vetula* juveniles, which concentrate in shallow areas and move out onto the bank at maturity (see Chapter 15).

THE NEARSHORE FISHERY

The South Jamaica Shelf

Figure 2.4 shows that the fishing intensity on the South Jamaica Shelf in 1968 was 0.38 canoes/km². However, there is reason to believe that owing to the relatively high proportion of mechanized canoes the effective fishing effort is actually somewhat in excess of this value. Traps with 4.13 cm mesh are the predominant fishing gear. The 1968 harvest of all neritic species amounted to 1,240 kg/km²/yr or 3,279 kg/canoe, of which about 60% to 70% was taken in traps. The harvest of trap-caught fishes therefore amounted to about 875 kg/km²/yr. Fig. 18.4 shows that an increase to a mesh size of 4.95 to 8.25 cm could produce a 5% increase in the harvest to about 920 kg/km²/yr. However, if recruitment patterns were enhanced as a result of an increase in the stock of fishes which were able to mature before recruitment, then further substantial increases in recruitment might occur and, if recruitment was restored to levels similar to those which prevail on Pedro Bank, a 50% increase in harvests to about 1,300 kg/km²/yr might be attainable.

The potential harvest in traps from a fishing intensity of about 0.38 mechanized canoes/km² therefore probably lies between 875 kg/km²/yr and 1,300 kg/km²/yr to which must be added about 360 kg/km²/yr of species captured by other methods. The extent to which the latter figure can be increased is unknown. Some increases in the hand-line catches of groupers, snappers and jacks might result indirectly from an increase in mesh size. At the present time, small blackfin snapper, *Lutjanus buccanella*, which reside on the sill reefs in their juvenile stages, are harvested by the small-meshed traps at sizes well before maturity. An increase in mesh size would enable more juveniles to enter the hand-line fishery for the adult stocks on the deep-reef slope and thus enhance harvest rates. Fig. 18.4 suggests that some increases in the catch would result from increasing effort up to about 1.5 canoes/km², but it seems likely that increases in effective fishing of effort will only be achieved by radical departures from present fishing practices, including the introduction of economical diesel-powered canoes or other small craft, the use of line haulers and more efficient and cheaper traps such as Cuban S-traps,

improved marketing systems (possibly including higher prices to the fishermen and a reduction of the role of the middlemen) and technological innovations. An effective doubling of effort as a result of such innovations seems not to be impractical. Development of the fishery for neritic pelagic clupeids (mainly *Harengula* spp.) and carangids (mainly *Selar crumenophthalmus*) might also result in increases in the total.

On a conservative basis, it is therefore estimated that potential yields lie between 1,235 kg/km²/yr and 1,660 kg/km²/yr. The total area of the South Jamaica Shelf is 2,760 km² and the total potential catch from the area is therefore 3,400 to 4,600 metric tons.

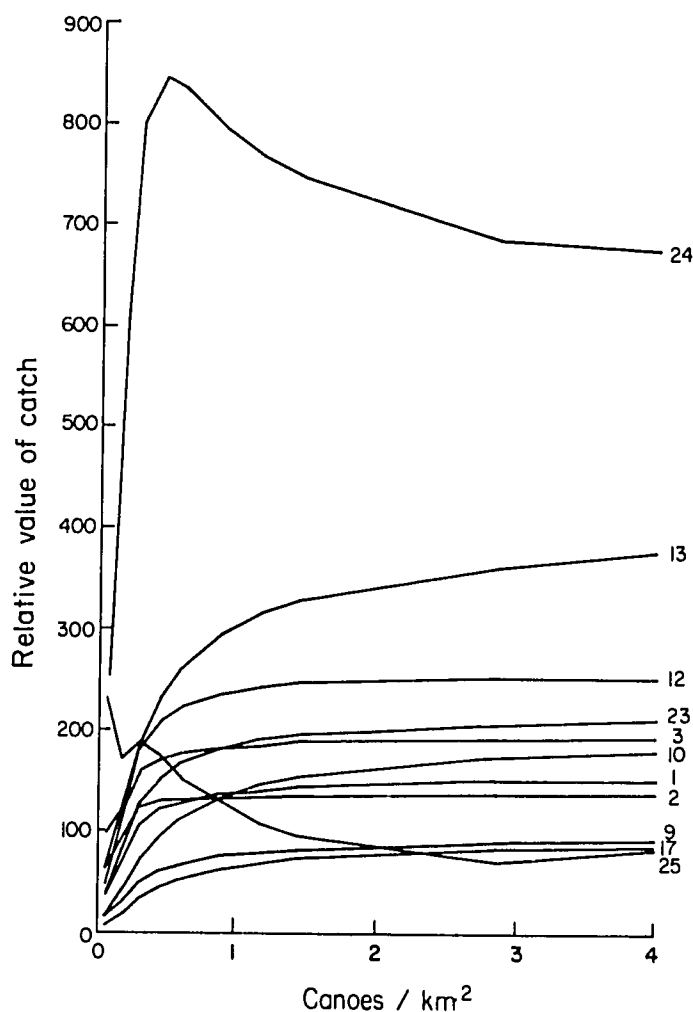


Fig. 18.6. Curves showing the relationships between fishing intensity and the calculated relative values of catches of various species at Pedro Bank when traps with 5.78 cm mesh are used. Numbers indicate the following species: 1 *Caranx ruber*, 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 9 *Mulloidichthys martinicus*, 10 *Pseudupeneus maculatus*, 12 *Haemulon plumieri*, 13 *H. flavolineatum*, 17 *Scarus taeniopterus*, 23 *Acanthurus bahianus* and 24 *Balistes vetula*. Relative yields of the remaining 11 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches in this mesh size, have been summed to give curve 25.

The Northern, Eastern and Western Shelves

The assessment of the potential harvests from the narrow shelves bounding the north, east and west coasts of Jamaica is more problematical than that for the South Jamaica Shelf. Details of the relative abundances of recruits are not available owing to the fact that the stock densities are reduced to such low levels by the fishery that statistically adequate samples of the stocks are almost impossible to obtain. Nevertheless, if it is assumed that the composition of the recruits is more or less similar to that estimated for the South Jamaica Shelf, then the yield-value curves shown in Fig. 18.4 can be applied.

The fishing effort in this area ranges between 1.5 and 5.6 canoes/km² with an average over the 660 km area of 2.95 canoes/km². Traps with a 3.30 cm mesh are used to produce about 60% of the harvest of neritic species.

Figure 18.4 shows that if 8.25 cm mesh were adopted, the value of the catch would increase by 45%, while the corresponding increase in weight would be 75%. The

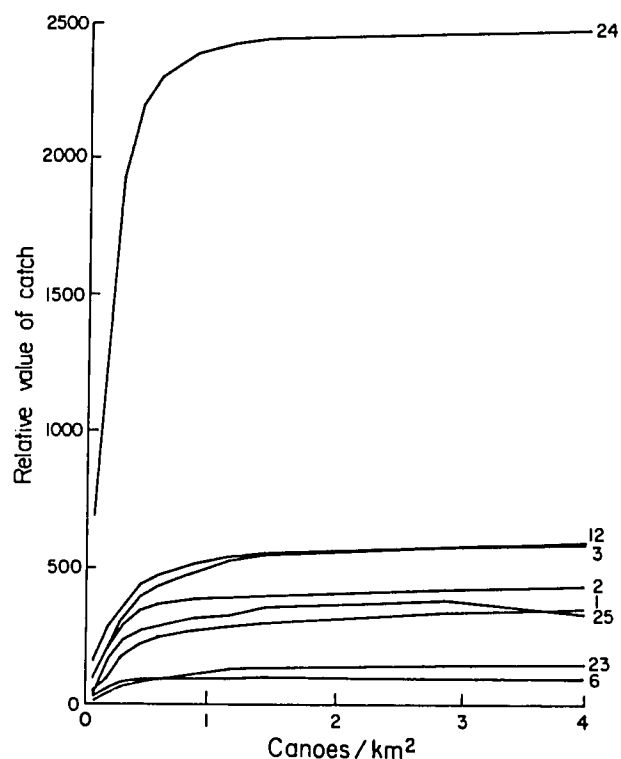


Fig. 18.7. Curves showing the relationships between fishing intensity and the calculated relative values of catches of various species at Pedro Bank when traps with 8.25 cm mesh are used. Numbers indicate the following species: 1 *Caranx ruber*, 2 *Epinephelus guttatus*, 3 *Cephalopholis fulva*, 6 *Caranx bartholomaei*, 12 *Haemulon plumieri*, 23 *Acanthurus bahianus* and 24 *Balistes vetula*. Relative yields of the remaining 14 species considered in this assessment (Table 18.1), each of which would not contribute more than 50 units of value to trap catches in this mesh size, have been summed to give curve 25.

Table 18.2. Comparison of actual and calculated composition of catches on the South Jamaica Shelf (including California Bank and the Port Royal Reefs) in traps with 4.13 cm mesh. Fishing intensity 0.4 canoes/km². Crustaceans and unmarketable fishes are excluded.

Code No.	Species	Relative value	% value	Relative weight	Percentage (calculated)	Percentage (observed)		
						Port Royal	California Bank	South Jamaica Shelf
2	<i>Epinephelus guttatus</i>	52	2.1	23.6	1.5	3.0	9.6	2.4
3	<i>Cephalopholis fulva</i>	202	8.0	91.8	5.9	0.1	8.1	3.8
9	<i>Mulloidichthys martinicus</i>	115	4.5	34.8	2.2	0.9	0.2	1.0
10	<i>Pseudupeneus maculatus</i>	231	9.1	70.0	4.5	1.0	2.5	2.4
12	<i>Haemulon plumieri</i>	172	7.2	101.2	6.5	12.8	.1	4.3
13	<i>H. flavolineatum</i>	82	3.2	48.2	3.1	1.2	2.2	5.4
16	<i>H. aurolineatum</i>	31	1.2	18.2	1.2	.1	0	2.9
18	<i>Sparisoma chrysopterygum</i>	107	4.2	107.0	6.9	6.3	0	0
19	<i>Sp. aurofrenatum</i>	37	1.5	37.0	2.4	3.0	1.3	.5
20	<i>Sp. viride</i>	77	3.0	77.0	5.0	11.1	0	0
24	<i>Balistes vetula</i>	249	9.8	249.0	16.0	1.0	28.6	22.3
11	Other spp.	164	6.5	74.5	4.8	24.7	7.9	6.7
Total (= 60% of YW)		1,519	60.3	932.3	60.0	65.2	60.5	51.7
All other spp.		-	38.7	621.5	40.0	34.8	39.5	48.3
Total catch		-	100.0	1,553.8	100.0	100.0	100.0	100.0

big difference between the increase in weight and the increase in value is because much of the increase in weight would be derived from low-priced species, particularly *Balistes vetula*.

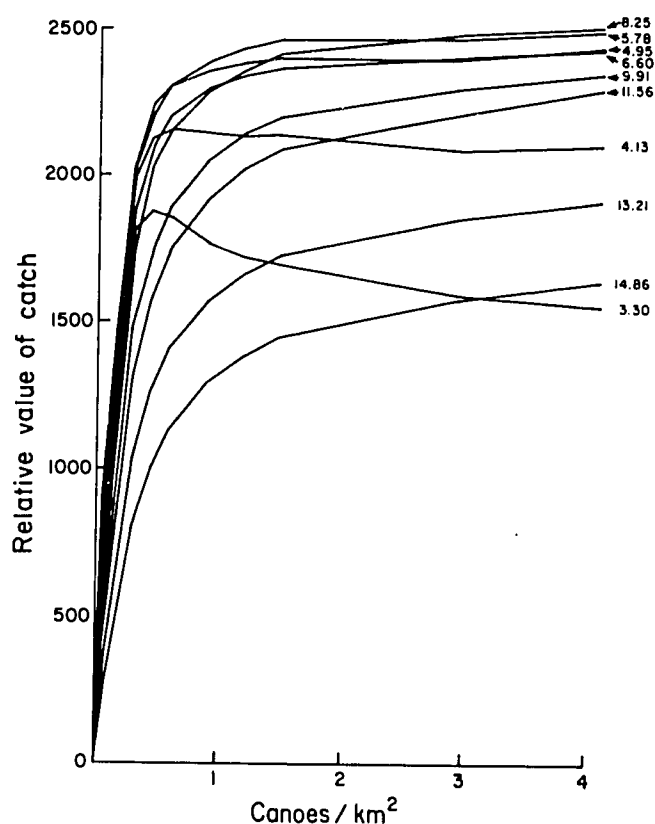


Fig. 18.8. Calculated relative total values of catches of 21 species of reef fishes (listed in Table 18.1) in various mesh sizes and at various fishing intensities at Pedro Bank.

Figure 2.4 shows that the greatest harvest per unit area of all neritic species is taken in the parish of Westmoreland on the west coast of Jamaica, where the 1968 harvest was about 4,000 kg/km². About 60% or 2,450 kg/km² was derived from trap fishing, and the remaining 1,550 kg/km² from hand-line fishing, seine nets and gill-nets. If a 75% increase in the trap catch is possible as a result of an increase in mesh size, the potential harvest is 4,300 kg/km²/yr from traps and a further 1,550 kg/km²/yr by other methods: 5,850 kg/km²/yr in total. This value is 3.3 to 4.3 times greater than that estimated for the South Jamaica Shelf. The total potential harvest from the 660 km² of this shelf is thus about 3,900 m tons to which might be added any potential increases in the harvest of species taken in gear other than traps.

The reasons for the high potential yield possibly include the greater productivity of these shelves, which are almost entirely covered by actively growing coral reefs, and greater concentrations of recruits within a given area. This also suggests that the fit of the point pertaining to the South Jamaica Shelf in the regression in Fig. 2.4 is fortuitous, and likewise suggests that the fishing effort on the South Jamaica Shelf is effectively greater than 0.4 canoes/km², owing to the high proportion of mechanized canoes.

THE PEDRO CAYS FISHERY

According to estimates made by Mr. E.L. Hamblyn (U.K. Ministry of Overseas Development Fisheries Adviser, Jamaica) an average of about 72 canoes operated from the Pedro Cays in 1974. As the area within normal range of these vessels is about 1,000 km², the average fishing intensity is 0.07 canoes/km². In the immediate vicinity of the cays the effort is estimated to be about

0.15 canoes/km². Figure 18.8 shows that substantial increases in effort are required before the maximum yields are attained. It has also been shown (Chapter 17) that the theoretical initial catch per canoe amounts to 10,824 kg/yr and this accords very well with a recent estimate by E.L. Hamblyn (pers. comm.) that the 72 canoes operating from the Pedro Cays have an annual landing of 756,000 kg, equivalent to 10,500 kg/canoe or 756 kg/km².

Figure 18.8 shows that any increases in fishing effort from the present relatively low levels will result in substantial increases in the harvest. Increasing the fishing intensity to 0.15 canoes/km² would result in a 40% increase in yield to 1,000 kg/km²/yr and if the effort were raised to 0.3 canoes/km² the harvest would be nearly doubled, and production would be 1,450 kg/km². The total annual harvest would approach 1,500 m tons. However an increase in the cay-based canoes fleet to 150 vessels, giving an effective fishing effort of only 0.15 canoes/km² would require 300 to 450 fishermen to be based on the cays. This could pose fairly difficult sociological and health problems and this appears to be the major constraint on the development of the fishery. The inhospitable living conditions at the cays and the lack of major financial incentives offered to the fishermen by the carrier vessel operators are also important factors. Nevertheless, such conditions are capable of improvement and encouragement of the development of the carrier boat fleet will lead to very large increases in landings up to the highest levels of fishing effort that could possibly be generated by cay-based canoes. The constraints on the landings from this fishery are socioeconomic and do not relate to the fish stocks.

These conclusions probably apply equally to the fishery based at the Morant Cays, and the 170 km² of banks could therefore be expected to produce a harvest of about 1,450 kg/km²/yr, or a total of 250 t/year.

THE PEDRO BANK (EXCLUDING THE PEDRO CAYS AREA) TRAP FISHERY

This area, which includes all of the area remote from the Pedro Cays and beyond the operating range of outboard-powered canoes, is presently virtually unexploited. Only one vessel (the *Lady Blythe*) fished in this 6,900-km² area during the time that investigations were in progress, and was reputed to land about 100 tonnes per year, caught mostly if not exclusively in traps. In addition, canoes from the mainland occasionally venture to the northern edge of the bank when conditions are suitable. The total harvest therefore probably does not exceed 150,000 kg/yr, or about 20 kg/km²/yr—a negligible amount by any standards.

At the present time there are no indications that more vessels intend to enter this fishery. It appears likely that the profitability of fishing the bank with traditional Z traps in the manner adopted by the *Lady Blythe* (see Chapter 2 for details) compares unfavorably

with the potential profits which can be derived from operating carrier vessels serving the cays fishery. Stackable fish traps developed during the present investigations (Chapter 2; Munro 1973) provide a solution to this, but their adoption for commercial use on Pedro Bank appears unlikely until such a time as competition within the cays fisheries induces entrepreneurs to seek greater profits in offshore areas.

It is difficult to estimate the potential harvest from this area with any precision. Figure 18.8 shows that a value close to the maximum can be attained by a fishing intensity equivalent to that exerted by 0.6 canoe/km². However, it is not known whether it would be possible to generate such a fishing effort by means of a fleet of fishing vessels utilizing stackable traps or other unconventional techniques which might be developed at some future date.

It has been shown in Chapters 5 and 17 that the relative availability of commercially important species is quite variable over the bank as a whole. The central portions of the bank in depths of 30 to 40 m, and remote from the sill reefs which fringe the edges, are comparatively sterile and produce very low trap catches. This area covers about 2,750 km². In contrast, the sill reef areas, particularly along the southern edge of the bank from Banner Reef to the southwestern tip, are highly productive, as is the entire portion of the bank lying to the east of the Pedro Cays. The northern and western edges have been shown to be rather variable, with catches at a given station ranging from spectacularly high values on occasions to negligible amounts at other times. The overall average catch rate (with effort standardized in terms of the catch of 1,000 baited hexagonal traps set for one night) at Eastern, Southern and Western Pedro Bank amounted to 2,725 kg/1,000 trap-nights. The comparable catch per unit effort at the Pedro Cays was 2,520 kg/1,000 trap-nights.

If it proves to be possible to generate a fishing intensity equivalent to 0.3 canoe/km², the theoretical catch from the areas proximal to the edges or of less than 20 m depth should be similar to, or greater than, that in the Pedro Cays area: at least 1,450 kg/km²/yr. If the central region of the bank in depths exceeding 30 m is entirely discounted as a source of any production, the remaining area within the 20 m isobath or within 9.3 km of the edge, totals 4,265 km², excluding the 1000 km² presently exploited by the fishermen based at the Pedro Cays. The maximum potential production is therefore at least 6,200 t/year. It is emphasized that this estimate is of the amount attainable using fish traps only in depths of 10 to 45 m. Additional catches might be taken on hand lines or by trap fishing in deep waters.

THE HAND-LINE FISHERIES FOR DEMERSAL SPECIES

There are extremely few data upon which to base an

evaluation of the hand-line fisheries for demersal species. The difficulty lies mostly in the absence of accurate statistics upon which estimates could be based and particularly in the poor breakdown of the contributions which different fishing gears make to the total yield in various areas. The best approximation that can be made from the 1968 catch statistics is that the total hand-line catch in the Jamaican nearshore fishery amounted to about 1,000 metric tons or about 17% of the total catch of neritic species.

Most of the species which contribute to this catch are concentrated in a narrow zone along the shelf edge on the sill reef, drop-off and deep-reef area. Details of the species comprising the catches and of the zonation have been given in Chapter 4. Various species of snappers (Lutjanidae) are of major importance, with groupers (Serranidae) and jacks (Carangidae) also contributing substantial parts of the catches. Owing to the concentration of the fishery in this extremely narrow zone along the shelf edge, the yields from the fishery are probably best expressed in terms of harvest per kilometer of edge. On this basis, the estimated nearshore catch of about 1,000 tonnes was derived from about 610 km of edge, or an average of about 1,640 kg/km.

It has previously been shown (Chapter 4 and Kawaguchi 1974) that the stocks of the important snappers, groupers and jacks are very sparse in areas currently exploited by the Jamaican fishery, and that unexploited stocks on the margins of Pedro Bank also do not produce catch rates which are sufficient to support fishing vessels which might attempt to fish exclusively for these species by means of hand-lines or powered reels. It was therefore concluded that it is likely that these stocks will only be exploited on an opportunistic basis by vessels fishing primarily by other techniques (most probably using traps). It is probably of significance that virtually no hand-line fishing is done by the fishermen based at the Pedro Cays. It has also been shown (Chapters 7, 8, 9 and 17) that the important species appear to have relatively high natural mortality rates. In particular, in the snappers *Lutjanus bucanella* and *Apsilus dentatus*, the ratio M/K

was estimated to range between 2.8 and 5.2. These are relatively high values, which suggest that stock densities and average size will rapidly decline as a result of exploitation.

Bearing in mind the limited fishing effort which is likely to be exerted on these species, the potential harvest from the margins of Pedro Bank could be guessed to lie in the region of 800 kg/km/yr. The circumference of the bank is about 590 km and the likely harvest is therefore in the region of 500 m tons/year. The catch rates determined during the present investigations and by Kawaguchi (1974) amounted to about 3.0 kg/line-hour and a harvest of 800 kg/km/year would therefore require at least 260 line-hours of fishing effort/km/year. This could, for example, be achieved by 20 vessels, exerting an average of 40 line-hours each per night for 200 nights of the year. However, the catch per line would only average $8 \times 3.0 = 24$ kg/night. This is unlikely to provide a major incentive towards effort in this direction, and underlines the belief that this fishery would only be conducted on an opportunistic basis, when conditions of wind and current appeared to be most favorable.

In contrast to Pedro Bank, Kawaguchi (1974) and others have shown that average catch rates of over 10.0 kg/line-hour can be taken on the edge of the Central American Shelf, off Nicaragua, and that similar catch rates can also be achieved quite often at Rosalind Bank and at other banks lying to the southwest of Pedro Bank. These relatively high concentrations of fish stocks have encouraged further investigations in this area, but it remains highly conjectural whether the stock densities would be sufficient to sustain the activities of specialized line fishing vessels. The results produced by an American snapper fishing vessel, the *Tiki IX*, which was chartered by the UNDP/FAO Caribbean Fishery Development Project, were not encouraging. Further investigations of this area have been made by the *MV Dolphin*, operated by the Fisheries Division of the Jamaican Ministry of Agriculture, but the results of these investigations are not known.

Management of the Fisheries

The theoretical requirements for the management of fisheries are well documented in the scientific and technical literature (e.g., Gulland 1974). Methods of effecting management requirements include adjustments of mesh sizes and hence the size at which fishes are recruited to the fishery, limitation or encouragement of fishing effort, abolition of certain types of fishing gear or introduction of new techniques and protection of stocks or of nursery areas.

All of the abovementioned methods are relevant in some degree to the management of the fisheries of Jamaica. Several points of major relevance to the trap fisheries which have emerged in the preceding pages and parts of this series of reports are worth recapitulating here.

(a) The 3.30 cm and 4.13 cm mesh sizes presently utilized by the trap fisheries capture most of the important species of reef fishes at sizes well below that at which sexual maturity is attained. The evidence presented here suggests that recruitment rates are probably adversely affected as a result. Recruitment of some species might be supplemented by juveniles originating in other parts of the Caribbean but this has not yet been established.

(b) When the fishing intensity with 3.30 cm traps exceeds 0.6 canoes/km², cohorts of most species are harvested before they have attained their maximum biomass and the total weight and value of the catch is consequently substantially less than the maximum potential harvest (Fig. 18.4).

(c) Fishing intensities in excess of 1.5 canoes/km² produce negligible increases in the total yield from traps (Fig. 18.4), although the diversification of the fishery which ensues as a result of competition for the available resources might ensure increases in yield until the fishing intensity reaches about 3 canoes/km². Thereafter the total yield declines (Fig. 2.4).

(d) Harvests of trap-caught reef fishes from the area surrounding the Pedro Cays can be increased by increasing the fishing effort, and the constraints on further development are probably of a socioeconomic nature and are not related to the abundance of fish stocks.

(e) The unexploited parts of the Pedro Bank and the other oceanic banks of the west-central Caribbean have a very great potential which is not yet realized, even in part, owing to economic and technological constraints.

The logical management procedures which follow from the foregoing are discussed below.

MESH SIZES OF TRAPS

Figures 18.4 and 18.8 show that mesh sizes of between 4.95 cm and 8.25 cm maximum aperture will give substantially greater yields, at most levels of fishing intensity, than the 3.30 cm and 4.13 cm mesh presently in use.

Within the range of sizes from 4.95 cm to 8.25 cm mesh, it is considered that a mesh size of 6.60 cm would best serve the interests of the fishery. The reasons are as follows:

(a) Within the 4.95 cm to 8.25 cm range the value of the catch will be very similar but the composition of the catch will change steadily. This is because the harvest of *Balistes vetula*, the most abundant species in the fishery, would be greatest if 9.91 cm or 11.56 cm mesh (depending upon effort) were used, but increases in the yield of *B. vetula* would be offset as a result of the smaller species never being recruited to the fishery. Figures 18.4 and 18.8 show that *B. vetula* would be predominant even in the 8.25 cm mesh, and that the goatfishes, *Pseudupeneus maculatus* and *Mulloidichthys martinicus* will be entirely eliminated from the catches. For this reason, and also because *B. vetula* is not a particularly favored species in the markets, it is considered that 8.25 cm mesh would not be best suited to the rational exploitation of the fishery.

(b) Reference to Tables 18.1 and 17.1 shows that if a 4.95 cm or 5.78 cm mesh is utilized, a substantial proportion of the larger species will still be recruited to the fishery before maturity and the possibilities of restoring recruitment rates to the original levels will not be greatly enhanced. Even in the case of the 6.60 cm mesh, 9 of the 24 species considered in this assessment, including *B. vetula*, *Caranx ruber*, *Lutjanus apodus*, *Ocyurus chrysurus* and *Haemulon plumieri*, will not have attained maturity before recruitment to the fishery. Thus, adoption of a 6.60 cm minimum mesh size would be a compromise between marketing requirements and

utilization of all available species and the protection of the greatest proportion of immature recruits.

It is important that it be noted that the suggested mesh size of 6.60 cm refers to the maximum aperture of the conventional hexagonal weave of galvanized wire mesh. The mesh size across the narrowest part of the hexagon, between the "knots", will be 5.08 cm (2 inches).

REGULATION OF FISHING INTENSITY

It is readily apparent from Fig. 2.4 that the concentration of canoes on the narrow northern shelves of Jamaica is very much in excess of the requirements for optimizing yields and probably very close to the point which allows only a negligible profit to the average fisherman. It would be desirable to reduce this fishing effort and hence increase both the total weight and value of the catch and coincidentally ensure a less tenuous livelihood for the remaining fishermen. It should also be pointed out that if adoption of an increased mesh size enhances the yields, there will be an immediate move towards an increase in fishing intensity until the average income of the individual fisherman again stabilizes at a very low level.

Introduction and enforcement of licensing restrictions to prevent this move in the most heavily fished areas might forestall the problem. Any measures to reduce the fishing intensity would raise political and administrative problems to be dealt with by the appropriate authorities. Restrictions on effort do not appear to be required in the parishes of St Thomas, Portland and those bordering the South Jamaica Shelf.

In all of the areas considered there is scope for increasing the effectiveness of the fishery, either by diversifying the techniques, by reducing costs or by employing more effective gear. Such advances would have particular relevance to the trap fisheries at the offshore cays and on the South Jamaica Shelf, where the fishing effort is limited by economic factors or by physical conditions. One of the most important possible developments in this respect is the introduction of the Cuban S trap (Fig. 5.1) which was utilized by this research program for much of the nearshore sampling. It was shown by Munro et al. (1971) that these traps capture 25% more (by weight) than traditional Z traps. The S traps cost 20% less to construct, mostly as a result of simpler construction and consequently decreased labor costs.

It should be noted that introduction of S traps on the northern shelf *without* a concurrent increase in the mesh size of the traps would result in a very short-lived increase in the trap catch followed by a decline and stabilization of the reef fish stocks at a lower biomass.

PROTECTION OF NURSERY AREAS

The nursery areas of some of the species of major

commercial importance are fairly clearly defined. The species of groupers (Serranidae), jacks (Carangidae), squirrelfishes (Holocentridae), angelfishes (Chaetodontidae), surgeonfishes (Acanthuridae) and triggerfishes (Balistidae), are all resident upon the reefs from an early age and are consequently not vulnerable to present fishing gears other than traps. The suggested increase in mesh size would add a measure of protection to the juvenile stocks which they do not presently enjoy.

In the case of other groups, particularly the grunts (Pomadasyidae), the shelf-dwelling species of snappers (Lutjanidae), the goatfishes (Mullidae) and the parrotfishes (Scaridae), the juveniles are often, but not exclusively, concentrated in shallow areas and grassy embayments between the shore and the reefs. At this stage these species are extremely vulnerable to small-meshed traps and, particularly, to beach seines with meshes which are often of less than 4.0 cm stretched mesh. Very large numbers of juveniles of species in these families are captured in seines and in many cases the major portion of fishes in the catch are of less than 10 cm length and are either discarded, or at best, needlessly harvested.

The prime use of the beach seines is for the harvest of shoaling clupeids (mainly *Harengula humeralis* and *Sardinella* spp.) and goggle-eye scad (*Selar crumenophthalmus*). There is no information concerning the mesh sizes which are required to harvest these species effectively, but it is possible that a larger mesh size might prove adequate for capturing them, consequently enhancing survival of pre-recruitment reef fishes and at the same time reducing the cost of the seine nets. Alternatively, closed seasons for seine net fishing might be stipulated, particularly in the early summer months, from April to July when the greatest concentrations of juvenile reef fishes are likely to occur in the back-reef areas (Munro et al. 1973). It is *not* suggested that seine-netting be entirely prohibited, particularly if a 6.60

cm mesh size for traps is adopted. This is because the increased size of the mesh for traps will result in under-utilization of the stocks of goatfishes which will, therefore, have to be harvested by means of seine nets (or gill-nets).

EDUCATION AND PUBLICITY

There is a need to change the attitudes of fishermen by means of educational and publicity campaigns. No plan for the management of a marine fishery has yet been fully successful in the face of opposition from the fishing community. As a corollary, no system is likely to succeed if the officers of the regulatory authority are unconvinced of the need and of the potential benefits of the regulations.

The fishermen of Jamaica and the officers of the Jamaica Cooperative Union, the parent organization of the fisheries cooperatives, have shown themselves to be well aware of the possible benefits of management in the course of several fishermen's conferences organized by the Jamaica Cooperative Union in recent years. It is the author's belief that given a positive stance by the regulatory authorities, together with a well-organized publicity and poster campaign focused on the fishing beaches, the fishermen of Jamaica will support changes in mesh sizes and licensing arrangements. The crux of the matter is that the authorities should be recognized to be acting in the interests of the fishermen and that the fishermen and the regulatory officers themselves be convinced of the merits of any legislation. Given these conditions, it is possible for the fishermen themselves to exert very great social pressures to ensure adherence to the minimum mesh sizes and non-participation in the fishery of unlicensed individuals.

Summary and Conclusions

The sizes at which maturity is attained relative to the size at recruitment to the fishery also merits the most careful consideration. It has been shown that for most areas of the Jamaican Shelf, the fishing intensity is sufficient to ensure that extremely few fishes survive for more than a year after recruitment, and the proportion of fishes which survive to spawn must be extremely small. There is no doubt that recruitment rates of many species would be enhanced if a mesh size were adopted which is sufficiently large to permit a greater proportion of fishes to spawn before becoming vulnerable to capture. The fact that initial stock densities at unexploited parts of Pedro Bank appear to be about three times greater than the theoretical initial stock densities on the Jamaican Shelf suggests that recruitment rates to the Jamaican Shelf fishery have been reduced to about one-third of their relative value as a direct result of exploitation of immature fishes, both by traps and by beach seines.

In summary, the analyses show that adoption of a mesh size, or escape gap, of 6.60 cm maximum aperture would result in substantial increases in the total value and weight of the catch. Additionally, the cost of traps constructed of larger mesh would be less and the profitability of the fishery therefore increased. The adoption of a larger mesh would, probably, enhance recruitment rates to the nearshore fisheries, although the degree of such enhancement cannot be evaluated on present data.

Yields which approach the maximum can be attained by the trap fishery by a fishing intensity of less than 1.5 canoes/km². Fishing intensities in excess of about 3 canoes/km² produce decreased yields as a result of gross disruption of the normal productive processes in the reef fish community.

The total potential harvest from the island shelf and proximal oceanic banks, and from Pedro and Morant

Banks is estimated *on a conservative basis* to amount to 15,750 to 16,950 t/year, comprised as follows:

South Jamaica Shelf and adjacent banks (traps, lines and nets)	3,400-4,600	tonnes/year
Northern, eastern and western shelves (traps, lines and nets)	3,900	tonnes/year
Pedro Bays trap fishery	1,500	tonnes/year
Morant Cays trap fishery	250	tonnes/year
Pedro Bank (areas presently unexploited)		
traps	6,200	tonnes/year
lines	500	tonnes/year
Total	15,750-16,950	tonnes/year

To this must be added landings of oceanic pelagic species (which presently total an estimated 740 t/year) for which the potential harvest is indeterminate.

The shelf areas of Nicaragua and Honduras and oceanic banks to the south and west of Pedro Bank collectively cover an area of over 130,000 km². If it is assumed that half of this area is either unproductive or inaccessible to Jamaican fishermen, the potential harvest from trap fishing alone should exceed 1,450 kg/km²/year or 95,000 t/year. The harvest taken from this area by the Jamaican fishery amounted to about 2,870 t in 1973.

The analyses described in the preceding pages must not be regarded as providing definitive answers to all problems concerning the assessment of potential yields and the management of the trap fisheries. The extreme complexity of these problems and the difficulties involved in obtaining adequate samples of the species involved and even the problem of defining which species

are of sufficient economic importance to merit consideration, have all been emphasized.

It is apparent from the analyses that, of the multiplicity of parameters involved, the estimated relative abundances of recruits to the fishery are those which are most liable to error and which cannot be improved upon until such time as a system for monitoring catch composition, landings and effort is instituted by the authorities. This does not imply that estimates of most other parameters are satisfactory. On the contrary, a continuing and intensive biological sampling program is required, directed towards the species which have been identified by this research program as being of major economic importance.

For example, the queen triggerfish, *Balistes vetula*, has been identified as the species which has, by a large margin, the greatest relative number of annual recruits. However, it is not known whether the relative abundance is always maintained at this level or whether a series of particularly abundant year-classes were recruited to the fishery during 1969-1973. Likewise, the importance of any species which was at an abnormally low level of abundance during this period would not have been recognized. Some idea of the degree by which relative abundances might vary is given by the differences in the availability of species of grunts (*Pomadasyidae*) at the Port Royal reefs in 1970 and 1971 (Chapter 10).

The details of relative contributions of various species to potential total yields should, therefore, be treated with a degree of circumspection, as any major variation in relative abundance can result in proportional shifts in the levels reached by the yield curves for that species. Emphasis has, therefore, been laid upon identifying the mesh sizes which would, if adopted, produce an increase in the yields of the greatest number of species, having due regard for their relative values.

CHAPTER 19:
EPILOGUE: PROGRESS IN CORAL REEF
FISHERIES RESEARCH, 1973-1982*

by
J.L. Munro

Introduction

Ten years have passed since the 1969-1973 phase of investigations of the ODA/UWI Fisheries Ecology Research Project in Jamaica came to an end. In that time, significant progress has been made towards an understanding of the fundamental processes governing the productivity of coral reef fisheries and substantial technical advances have been achieved which have greatly facilitated data analyses. The reprinting by ICLARM of the Project reports presents an opportunity to review this progress, reappraise some of the conclusions and analyses presented in the preceding chapters and to highlight the areas where considerable doubt or even controversy exists.

The number of recent papers which refer to fishes of coral reefs is enormous and although few relate directly to reef fisheries, they have in many cases contributed to our understanding of reef fish productivity. The early part of the past decade saw the completion of major Caribbean reef resource surveys in the Bahamas (Thompson 1978) and the completion of the FAO/UNDP Caribbean Fishery Development Project (Kawaguchi

1974; Wolf and Chislett 1974) and the, perhaps belated, recognition that coral reef fishery resources are capable of supplying a significant part of the world's fish supply (Smith 1978b; Carpenter 1977). Additionally, the presumptive causative organism responsible for ciguatera fish poisoning, *Gambierdiscus toxicus*, was isolated and identified (Yasumoto et al. 1977) giving new impetus to further investigations of this problem (Randall 1980; De Sylva and Higman 1980) and some hope of utilization of resources in areas known to harbor many ciguatoxic fish if a cheap and reliable test for ciguatoxic fish can be devised.

On taxonomic matters, the publication of the FAO Species Identification Sheets for Fishery Purposes covering the Caribbean and Indo-Pacific (Fischer 1978; Fischer and Whitehead 1974) should have reduced the major taxonomic confusions and led to some degree of uniformity on nomenclative matters for the exploited species. The publication of semi-popular manuals (e.g., Nagelkerken 1981) will also lead to a greater degree of assurance in dealing with fishermen.

Technical Advances

Several significant technical developments have paved the way for advances in coral reef fisheries research. Perhaps the most significant of these was the recognition by Pannella (1971, 1974) that certain micro-structures in otoliths were, in fact, daily rings. It is now clearly established that at least the younger stages of many coral reef fish can be aged by this technique (Brothers 1980

1982; Brothers and McFarland 1981; Ralston 1977, 1980; Ralston and Miyamoto 1981).

*Based upon a paper entitled "Some advances and developments in coral reef fisheries research: 1973-1982" presented at the 35th Annual meeting of the Gulf and Caribbean Fisheries Institute, Nassau, Bahamas, November 1982.

Secondly, the greater availability of air compressors and diving support facilities even in remote locations has extended the range of possible observations on coral reefs and their frequency and duration, leading to a better overall understanding of reef phenomena.

Thirdly, and perhaps most important of all, has been the development of length-frequency based methods of fish stock assessment. These include methods for estimation of growth rates and mortality rates from length-frequency distributions, or complete stock assessments based upon virtual population analysis and length-cohort analysis (Jones 1981).

A method for computer analysis of length-frequency data which removes the subjectivity of modal progression analyses and derives a best possible fit to any set of data has been developed by Pauly and David (1981), making consistent interpretations of modal progression data possible.

The methods for estimating mortality rates from length-frequency data have their origin in the equation developed by Beverton and Holt (1956) which states that

$$Z = K (L_{\infty} - \bar{L}) / \bar{L} - l_c$$

in which Z is the coefficient of mortality, K is the coefficient of growth, L_{∞} is the asymptotic length, l_c is the smallest length of fish which is fully represented in the catch and \bar{L} is the average length of all fishes lying between l_c and L_{∞} . Unfortunately, the usefulness of the method, whereby mortality rates can be estimated from catch length-frequency data and growth rate estimates, was not generally recognized and it remained virtually unused for many years (Munro 1980).

However, Green (1970), Ebert (1973), Ssentongo and Larkin (1973), van Sickle (1977), Powell (1979) and Jones (1981) subsequently produced a succession of papers demonstrating the estimation of growth and/or mortality rates from size distributions. Salla and Lough (1981) gave a synthesis of the above-mentioned works.

Pauly (1980a, 1980b) has demonstrated that the interrelationships which exist between temperature, growth parameters and natural mortality rates are sufficiently close that a useful degree of predictability of natural mortality rates is possible given estimates of

growth parameters and mean environmental temperatures.

Pauly and Gulland (Pauly 1982) have developed a method for deriving catch curves from length-frequency data and growth parameters and Hoenig (1982) and Hoenig and Lawing (1982) have developed equations which provide estimates of mortality rates, based only upon the age and size of the largest fishes in a sample.

Of the various methods for estimating mortality rates, the method of Pauly and Gulland is the most robust and useful as theoretical assumptions of constancy in recruitment and size-related mortality are not required. Changes in growth, recruitment or mortality will be reflected in the slopes of the catch curves. In multigear or "gauntlet" fisheries in which fishing mortality rates are strongly size-related, the method is particularly useful. The method slightly underestimates mortality rates for reasons related to the assumption that the mean age of fishes in a length group can be equated with the age of the mid-length (P. Sparre, pers. comm.). The error is small when applied to fast-growing fishes divided into small length groups.

The method of Jones (1981) is based upon the assumption that all cohorts remain catchable until they become extinct. If members of the largest size groups become progressively unavailable to the fishery or to the sampling gear the mortality rate will be underestimated. It should also be noted that the method of Ssentongo and Larkin (1973) gives erroneous results because of a logical error in derivation of their equation (P. Sparre, pers. comm.).

Microcomputer-based methods for comprehensive stock assessments based almost exclusively on length-frequency distributions have been developed by Pope and co-workers, and will soon be published.

As a result of all of the above-mentioned developments, existing sets of length-frequency data can be reappraised and improved estimates of growth and mortality rates obtained. One question that has not yet been solved is the problem of assessing what represents an adequate sample size for a length-frequency distribution and, as in any fishery, obtaining an unbiased sample of fishes.

Although new methodologies have emerged, there are still relatively few sets of data pertaining to coral reef fish to which these methods can be applied

Scientific Advances

REPRODUCTION AND RECRUITMENT

The question of the seasonality of spawning and periodicity of recruitment (which are not necessarily the same things) has received attention. In Jamaican waters, it was found that there were two main spawning periods for most of the larger species of reef fish with maxima around March-April and September-October (Chapter 17). Figures 19.1 and 19.2 show a synopsis of the Jamaican data.

Watson and Leis (1974) noted that spring and fall spawning peaks around Hawaii coincided with periods

of weakened currents and Johannes (1978) found that 13 of 18 spawning peaks listed in the literature coincided with periods when prevailing winds were weakest and suggested that reproductive strategies of tropical marine fish have evolved in part to maximize recruitment of offshore larvae to nearby inshore habitats. Data for Kenyan waters (Nzioka 1979), for the Great Barrier Reef (Russell et al. 1977) and for New Caledonia (Loubens 1980a) appear to add further weight to this hypothesis. However, data for the spawning periods of the large species of serranids (Goeden 1978; Chen et al. 1980; Nagelkerken 1979; Olsen and La

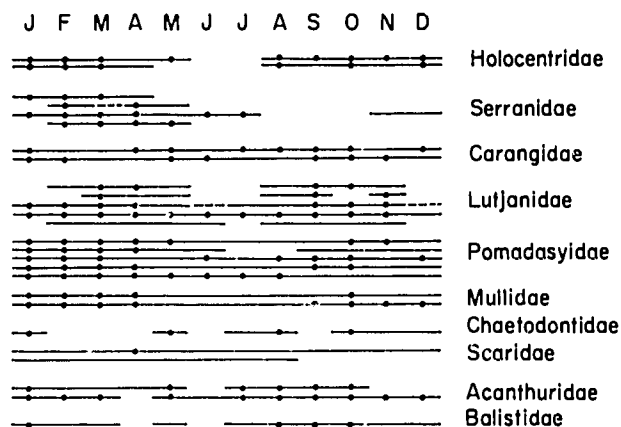


Fig. 19.1. Synopsis of data on spawning seasons of 26 commercially important species of coral reef fish in Jamaican waters. Horizontal bars indicate months in which ripe or spent fish were obtained. Dots indicate months in which more than 20% of the fish in the sample had ripe or spent gonads. Broken lines indicate months for which there were no data. (Data derived from preceding chapters)

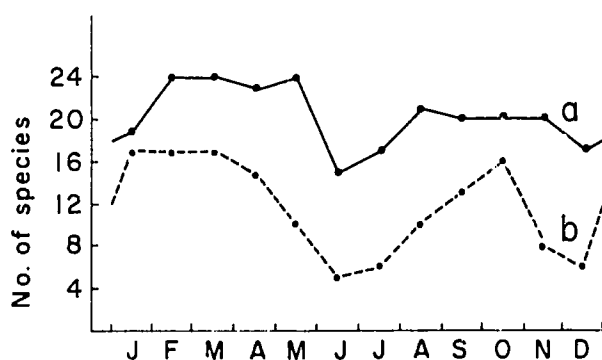


Fig. 19.2. Numbers of species in Jamaican waters, of a total of 26, in which a) some ripe fish were found in a given month and b) in which more than 20% of fish in the sample had ripe or spent gonads.

Place 1979; Loubens 1980a, and Chapter 7, this volume) do not appear to fit with any known pattern and our understanding of these phenomena is far from complete. It appears that the spring and fall peaks (Fig. 19.2) which seem to be confirmed for the Caribbean (Chapter 17, this volume; Luckhurst and Luckhurst 1977; Powles 1975), might converge in more temperate waters and be replaced by a single summer peak (e.g., Grimes and Huntsman 1980; Bradley and Bryon 1974; Futch and Bruger 1976).

Additionally, it is clear that some spawning occurs throughout the year for most tropical species (Colin 1978, 1982; Erdman 1977; Boardman and Weiler 1980) and that periodic peaks merely reflect the times of increased activity within the tropical zone. Johannes (1978) has collected ample evidence that a lunar periodicity of spawning is also most often superimposed upon whatever seasonal patterns exist.

One of the principal features of research on coral reef fish (as opposed to fisheries) in the last decade has been the enormous proliferation of ethological studies and the controversy which arose, and is perhaps not yet resolved, over whether reef fish partition the resources of the reef in some fashion or simply indulge in a scramble for space or other resources by adding new recruits to the system at the greatest possible rate. This argument appears to have been sparked off by the work of Russell et al. (1974) who, on the basis of observations on the Great Barrier Reef, suggested that colonization is essentially a random process. This was amplified by Sale (1976) and other investigators soon made contributions (e.g., Sale 1978; Luckhurst and Luckhurst 1977; Dale 1978; Smith 1978a).

Helfman (1978) summarized the then existing situation, by which time various proponents appear to have agreed that space on reefs is limiting and that recruitment from the plankton is a random process, but disagreed on whether reef fish partition the resources. The case against any sort of resource or space partitioning and in favor of a random colonization process seems to have been made by Bohnsack and Talbot (1980) who found no differences in the number of species, number of females and mean number of individuals per reef for isolated model reefs in Florida and Great Barrier Reef waters. Also, Talbot et al. (1978) and Brock et al. (1979) concluded that, at least, over small areas of reef, long-term stability of the reef fish community composition was unlikely because of the combination of high predation rates and a random process of colonization of vacant space by new recruits.

A summary of and comments on the recruitment phenomena are given by Sale (1982) and by McFarland (1982). The latter concluded "that recruitment to in-shore reefs is dependent on several factors—the individual species' capacity to prolong larval life, the effect of currents on the dispersion and settlement of recruits, the constancy or periodicity in the production of eggs and larvae through reproductive drive and the nature of the settlement site". Johannes et al. (1981) have suggested that, notwithstanding occasional long distance dispersal of larvae, postlarvae and/or juveniles, a high degree of reef fish recruitment might be derived from local spawning, that genetic interchange might be limited and discrete stocks of reef fish species might exist.

One particular feature of the reef fish debate appears to have been the tacit assumption that space on reefs is a factor which limits the population size of virtually all reef fish. However, as suggested recently by Doherty (1981), and previously by Munro et al. (1973) in a somewhat different context, there is no evidence whatever that planktonic dispersal of the larvae of reef fish regularly provides more recruitment than most reef habitats can absorb. Munro et al. (1973) observed that catch rates from virgin reef fish stocks at Pedro Bank in the West-Central Caribbean were markedly less than at Rosalind Bank (Fig. 2.1), which is proximal to the Nicaragua-Honduras shelf and suggested that the absence of any

shallow waters upstream of Pedro Bank combined with the apparent absence of any significant mechanisms for retaining larvae such as gyres, accounted for these differences.

It is here suggested that all reef-dwelling fish are normally recruitment limited. That is, it appears probable that population densities of those organisms in which the young need to settle from the plankton onto a suitable substratum are limited by the larval survival rates in the plankton, by the abundance of predators on and around the settling substratum and by the likelihood of current systems depositing the young near suitable settlement sites. The same suggestion might also apply to many other demersal organisms in which the post-larvae need to settle on a specific substratum.

Certainly, in the case of coral reef fish, if not other organisms, the factors which reduce recruitment are well known. The characteristic spawning aggregations (Colin 1982; Randall 1961b; Randall and Randall 1963) are attended by abundant egg-eating planktivores (Colin 1978) and any eggs that are not wafted away from the reefs are preyed upon by a great variety of organisms (Hobson and Chess 1978; Leis 1981). Once into the oceanic plankton, the larvae and post-larvae are also prey to a host of pelagic fishes including tuna, and are then largely dependent upon some chance current system returning them to a safe substratum. Johannes (1978), Powles (1975) and Leis and Miller (1976) have all suggested that gyres are important in retaining larvae around islands and indeed, if this were not so, islands such as Barbados, Pitcairn and Easter Island would be devoid of all neritic fish with pelagic larvae. Instead, these islands have substantial fish populations and it would be interesting to investigate whether such communities are composed predominantly of forms having short larval lives.

However, there is no evidence that the reproductive strategies proposed by Johannes (1978), which consist of spawning as far seaward as possible, preferably in the late afternoon [as predation on eggs is reduced at night (Hobson and Chess 1978)] on a strongly ebbing spring tide, combined with gyre systems at the calmest periods of the year, regularly succeed in saturating the reef environment with newly-metamorphosed postlarvae.

Rather, it now appears that the strategy of most reef dwelling fishes is to spawn over extended periods with some concentration of activity in certain favorable periods (summer or spring and fall, coinciding with calm periods with low current velocities) in the "hope" that the requisite combination of biotic and environmental factors will open the "survival window" [as proposed by G. Sharp (see Bakun et al. 1982)] and will permit significant numbers of larvae to pass through and survive to settlement. Periodic opening of the "survival window" will result in episodic recruitment. It also seems likely that the conjunction to a greater or lesser degree of all factors necessary for survival which results in the opening of the "window" might well be a local phenomenon, with only a basic relationship to the

seasons or to lunar rhythms. From the time of settlement onwards, the system will be predator-controlled, with vacant territories constantly created on the reef for those species which require a defendable territory, and heavy predation upon all small elements of the fauna.

There seems to be little doubt that very wide dispersal of larvae is achieved by those reef fish and invertebrates which have long-lived larvae and postlarvae. In many cases, favorable currents, eddy systems or geographical locations probably cause particular areas to receive abundant recruits regularly and thus support large populations of certain species, whereas different areas might be chronically short of recruits because of unfavorable geographic circumstances. Pedro Bank which lies 1,500 km downstream from the islands of the Eastern Caribbean seems a likely example of the latter condition, whereas much of the Bahamas, Cuba and the eastern coast of the USA which lie downstream of other Caribbean reef systems might be much more favorably placed to receive recruits. It is suggested that reef fisheries of most island systems which do not lie within a suitable gyre or precisely at an optimum distance downstream of another reef system are chronically recruitment limited and that even under the most favorable circumstances, there are few instances of saturation of the habitat by juveniles (e.g., Kami and Ikehara 1976).

A final point concerning reproduction which has emerged in the last decade is that many families of coral reef fish, including members of the Serranidae (Nagelkerken 1979; Jones 1980; Goeden 1978; Loubens 1980a), Lethrinidae (Lebeau and Cueff 1975; Loubens 1980a; Young and Martin 1982), Scaridae (Reinboth 1968), Sparidae, Labridae, Pomacanthinae (Smith 1975; Bruce 1980) and Amphiprioninae (Moyer and Nakazono 1978), are sequential hermaphrodites, and in some groups, also diandric or digynous (Smith 1982). We require a far better understanding of the factors triggering sex change if we are to make any rational steps towards management strategies for such species, failing which recruitment from exploited stocks might become drastically limited, if not extinguished (Smith 1982).

PARAMETER ESTIMATION

Despite the methodological advances mentioned previously, there is still no consensus on the general order of magnitude of growth rates attained by coral reef fish and of natural mortality rates which might prevail. None of the detailed studies of recruitment of small reef fish which have been conducted appear to have been accompanied by estimates of subsequent growth and mortality, such that turnover rates in the reef community could be estimated.

Age and Growth

There are still few published accounts of attempts to age commercially important coral reef fish on the basis of daily rings in otoliths, the exceptions being the works of Ralston (1977, 1980), Ralston and Miyamoto (1981)

and Moffitt (1980) on various Hawaiian reef fish and of McFarland (1980). The latter found that juvenile *Haemulon flavolineatum* could be aged at least up to 700 days, by which time they attained lengths of up to 12 cm, but that best results were for the first 100 days of life.

Pauly and Ingles (1981) have analyzed a number of sets of length-frequency data for coral reef fish using the ELEFAN I microcomputer program (Pauly and David 1981), which also can accommodate temperature-induced seasonal growth oscillations. Some of the length-frequency data reported in previous chapters have been reanalyzed using the ELEFAN I program to test whether any better interpretations of the data are obtainable. Additionally, the ELEFAN I program has been applied to length-frequency data for reef fish from the west coast of Florida published by Saloman et al. (1981). Loubens (1978, 1980b) has estimated growth rates from otoliths of 28 species of fishes from New Caledonian waters, marking a major advance in our knowledge.

All of the above-mentioned estimates plus others culled from the literature are summarized in Table 19.1, from which it is apparent that most success has attended analyses of annular marks on scales and otoliths in areas near the edge of the tropics. It is possible

that if growth checks cause discernible marks on hard parts, overall growth rates in sub-tropical regions might be lower than in equatorial regions. Also, for a given species, larger asymptotic sizes (L_{∞}) and lower growth coefficients (K) might be attained in cooler regions (Pauly 1981).

The question now arises of how the validity of the various growth estimates might be established in the absence of reliable norms or criteria. One possible approach to this problem is suggested by the work of Pauly (1980b) who showed that a plot of the logarithm of the growth coefficient, K, against the asymptotic weight, W_{∞} , for a wide variety of species yields a linear regression with a slope, very close to the theoretical value of 0.67. Thus, $\log K = a - 2/3 \log W_{\infty}$. If the slope is fixed by physiological considerations and is thus constant, differences in growth characteristics can only be reflected in the value of the y-axis intercept, a , which is the theoretical value of K which would be attained if a particular species were growing towards an asymptotic weight of 1 gram.

Calculated values of a are given in Table 19.1 and their distributions are illustrated in Fig. 19.3. Excluding the demoiselles and the haetodontids, the estimated values of a for the 59 predatory reef species or stocks

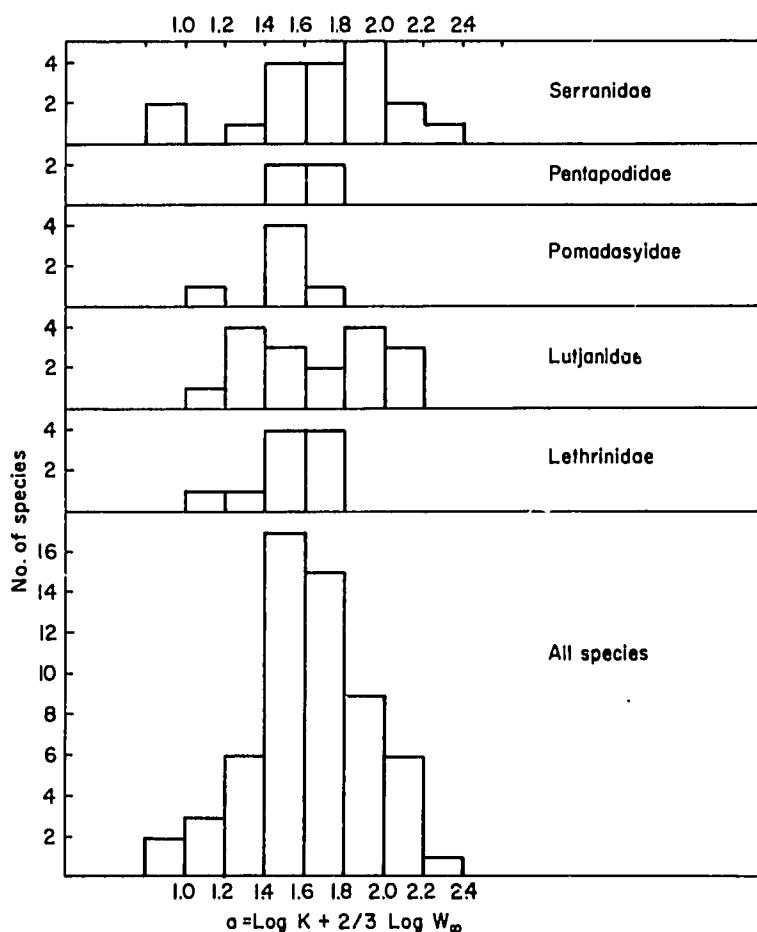


Fig. 19.3. Frequency distributions of calculated values of $a = \log K + 2/3 \log W_{\infty}$ for species of the Serranidae, Pentapodidae, Pomadasyidae, Lutjanidae and Lethrinidae and for all of the reef dwelling species

Table 19.1. Estimates of the coefficient of growth, K , and the asymptotic length L_{∞} , of the various coral reef fishes. Values marked with an asterisk (*) have been recalculated from the original data. Asymptotic lengths given in brackets are assumed values based upon the largest specimens in the sample. The value a is derived as $a = \log K + 2/3 \log W_{\infty}$ and is an index of relative growth performance of the species. See text for further details.

Species	Source	Locality	Method	K	L_{∞}	a
SERRANIDAE						
<i>Mycteroperca venenosa</i>	Chapter 7	Jamaica	Otoliths	0.17	(86) cm TL	1.92
<i>Mycteroperca microlepis</i>	Saloman et al. 1981	Florida	ELEFAN I*	0.155	129.7 cm TL*	2.26
	Manooch and Haimovica 1978	E. coast, USA	Otoliths	0.121	129.0 cm TL	2.14
<i>Plectropomus leopardus</i>	Pauly and Ingles 1981	Great Barrier Reef	ELEFAN I	0.25	64.7 cm TL	1.81
	Loubens 1980b	New Caledonia	Otoliths	0.16	50.0 cm SL	1.55
<i>Epinephelus striatus</i>	Olsen and La Place 1979	Virgin Islands	Probit analysis	0.185	97.4 cm TL	2.07
<i>Epinephelus morio</i>	Moe 1969	E. Gulf of Mexico	Otoliths	0.18	80.0 cm TL	1.88
	Melo 1976	Campeche	Otoliths	0.11	92.8 cm TL	1.80
<i>Epinephelus guttatus</i>	Chapter 7	Jamaica	Modal progression	0.24	52.0 cm TL	--
	Chapter 7	Jamaica	ELEFAN I*	0.22	54.5 cm TL*	1.60
<i>Epinephelus (Cephalopholis) fulva</i>	Chapter 7	Jamaica	Modal progression	0.63	34.0 cm TL	--
	Chapter 7	Jamaica	ELEFAN I*	0.56	35.5 cm TL*	1.63
<i>Epinephelus (Petrometopon) cruentatum</i>	Chapter 7	Jamaica	Modal progression	0.34	34.0 cm TL	1.43
<i>Epinephelus sexfasciatus</i>	Pauly and Ingles 1981	Philippines	ELEFAN I	0.51	30.9 cm SL	1.64
<i>Epinephelus (?taurina)**</i>	Loubens 1980b	New Caledonia	Otoliths	0.29	30.7 cm SL	1.45
<i>Epinephelus arcolatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.33	27.6 cm SL	1.35
<i>Epinephelus fasciatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.16	23.0 cm SL	0.94
<i>Epinephelus maculatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.28	40.2 cm SL	1.62
<i>Epinephelus hoedti</i>	Loubens 1980b	New Caledonia	Otoliths	0.28	58.1 cm SL	1.98
<i>Epinephelus merra</i>	Loubens 1980b	New Caledonia	Otoliths	0.27	17.9 cm SL	0.93
<i>Epinephelus rhyncholepis</i>	Loubens 1980b	New Caledonia	Otoliths	0.49	27.9 cm SL	1.59
PENTAPODIDAE						
<i>Gymnocranius japonicus</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.22	39.5 cm SL	1.56
	Loubens 1980b	New Caledonia	Otoliths ♀	0.24	35.1 cm SL	1.50
<i>Gymnocranius lethrinoides</i>	Loubens 1980b	New Caledonia	Otoliths	0.28	37.0 cm SL	1.60
<i>Gymnocranius rivulatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.23	46.4 cm SL	1.70
LUTJANIDAE						
<i>Lutjanus campechanus</i>	Futch and Bruger 1976	Florida	Otoliths	0.35	(60)* cm TL	2.13
	Nelson and Manooch 1982	Florida	Scales and otoliths	0.155	97 cm TL	2.00
	Saloman et al. 1981	Florida	ELEFAN I*	0.225	95.4 cm TL	2.15
<i>Lutjanus bohar</i>	Talbot 1960	Kenya	Scales*	0.27	(66) cm TL	1.89
	Wheeler and Ommanney 1953	Seychelles and Amirantes	Petersen method*	0.33	(66) cm TL	1.98
<i>Pristipomoides filamentosus</i>	Ralston 1980	Hawaiian Is.	Otolith daily rings	0.164	80.5 cm TL	1.86
<i>Rhomboplites aurorubens</i>	Grimes 1978	N and S Carolina	Scales	0.198	62.7 cm TL	1.71
<i>Ocyurus chrysurus</i>	Chapter 9	Jamaica	Modal progression	0.25	60.0 cm TL	1.78
<i>Lutjanus amabilis</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.26	33.4 cm SL	1.46
	Loubens 1980b	New Caledonia	Otoliths ♀	0.34	29.3 cm SL	1.46
<i>Lutjanus fulviflamma</i>	Loubens 1980b	New Caledonia	Otoliths	0.30	24.8 cm SL	1.28
<i>Lutjanus quinquelineatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.37	17.3 cm SL	1.08
<i>Lutjanus vitta</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.32	28.2 cm SL	1.39
	Loubens 1980b	New Caledonia	Otoliths ♀	0.30	23.8 cm SL	1.20

Continued

Table 19.1 (continued)

Species	Source	Locality	Method	K	L _∞	a
<i>Lutjanus bohar</i>	Loubens 1980b	New Caledonia	Otoliths	0.11	52.0 cm SL	1.47
<i>Lutjanus kasmira</i>	Loubens 1980b	New Caledonia	Otoliths	0.38	21.1 cm SL	1.23
<i>Aprion virescens</i>	Loubens 1980b	New Caledonia	Otoliths	0.31	65.6 cm SL	1.95
PLECTORHYNCHIDAE						
<i>Diagramma pictum</i>	Loubens 1980b	New Caledonia	Otoliths	0.28	52.2 cm SL	1.77
POMADASYIDAE (Haemulidae)						
<i>Haemulon album</i>	Chapter 10	Jamaica	Petersen method	0.20	65.0 cm FL	1.79
<i>Haemulon plumieri</i>	Manooch 1976 Chapter 10	N and S Carolina Jamaica	Scales Modal progression	0.11 0.35	64.0 cm TL 42.0 cm FL	1.50 –
<i>Haemulon sciurus</i>	Chapter 10	Jamaica Jamaica	ELEFAN I* Modal progression	0.275 0.26	39.8* cm FL 40.0 cm FL	1.49 –
<i>Haemulon aurolineatum</i>	Chapter 10 Manooch and Barans 1982	Jamaica N and S Carolina	ELEFAN I* Scales	0.24 0.22	40.2 cm FL 31.0 cm TL	1.43 1.11
LETHRINIDAE						
<i>Lethrinus enigmaticus</i>	Lebeau and Cueff 1975	Saya de Malha	Scales*	0.13	(55) cm TL	1.54
<i>Lethrinus chrysostomus</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.26	48.9 cm SL	1.77
	Loubens 1980b	New Caledonia	Otoliths ♀	0.27	45.7 cm SL	1.74
<i>Lethrinus lentjan</i>	Loubens 1980b	New Caledonia	Otoliths	0.33	29.2 cm SL	1.43
<i>Lethrinus mahsena</i>	Loubens 1980b	New Caledonia	Otoliths	0.29	32.7 cm SL	1.54
<i>Lethrinus nebulosus</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.22	50.9 cm SL	1.71
	Loubens 1980b	New Caledonia	Otoliths ♀	0.21	54.3 cm SL	1.75
<i>Lethrinus nematacanthus</i>	Loubens 1980b	New Caledonia	Otoliths ♂	0.87	16.0 cm SL	1.31
	Loubens 1980b	New Caledonia	Otoliths ♀	0.86	14.0 cm SL	1.18
<i>Lethrinus variegatus</i>	Loubens 1980b	New Caledonia	Otoliths	0.43	30.3 cm SL	1.55
CARANGIDAE						
<i>Caranx ruber</i>	Chapter 8	Jamaica	Modal progression ELEFAN I*	0.24 0.24	52.0 cm FL 56.0 cm FL	1.66 1.73
POMACENTRIDAE						
<i>Eupomacentrus planifrons</i>	Pauly and Ingles 1981	Jamaica	ELEFAN I ♀ ELEFAN I ♂	0.58 0.33	11.6 cm SL 11.6 cm SL	0.80 0.55
CHAETODONTIDAE						
<i>Chaetodon miliaris</i>	Ralston 1977	Hawaii	Otolith daily rings	1.13	12.7 cm SL	1.19
BALISTIDAE						
<i>Balistes vetula</i>	Chapter 15	Jamaica	Modal progression ELEFAN I*	0.57 0.53	45.0 cm FL 47.0 cm FL	– 2.08

***Epinephelus taurina* (Forsk.) is a large species, reported to attain up to 200 cm TL.

listed in Table 19.1 have a mean of 1.63 (s.d. 0.30). Within the families, details of the range of *a*, mean and standard deviation are as follows: Serranidae: range 1.35-2.26, mean 1.66, s.d. 0.36; Pentapodidae: range 1.50-1.70, mean 1.59, s.d. 0.08; Pomadasysidae: range 1.11-1.79, mean 1.46, s.d. 0.22; Lutjanidae: range

1.08-2.15, mean 1.65, s.d. 0.35; Lethrinidae: range 1.18-1.77, mean 1.55, s.d. 0.20. The values of *a* appear to be a possible characteristic of a family or of a species group within a particular habitat and probably represent an underlying characteristic of the energetics of that species group.

At a practical level, calculation of a serves as a check on the validity of growth estimates. For example, the values of K and L_{∞} estimated for *Epinephelus fasciatus* and *E. merra* by Loubens (1980b) yield values of a of 0.94 and 0.93, respectively, and thus lie two standard deviations below the mean for the serranids. This suggests that the growth estimates of these two species should be reviewed or that particular features of these serranids distinguish them from other members of the family.

Mortality Rates

In Chapters 6-15, the length-frequency distributions of catches of various species were used to estimate mortality rates, using the formulation of Beverton and Holt (1956). This method is now outdated by the development of the length-converted catch curve of Pauly (1982). The assumptions underlying the length-converted catch curves are that catchability is not size-related, that there have been no significant changes in recruitment or in natural mortality between years, that the samples are reasonable representations of the mean annual length-frequency distribution of the entire stock and the parameters of growth do not change over the age span covered by the catch curves. Progressive emigration or immigration will also be reflected in the shapes and slopes of catch curves.

An interesting feature of the length-converted catch curves is that the slope of the descending arm of the curve is directly proportional to the estimated value of the coefficient of growth, K , for any given estimate of L_{∞} . Thus, a constant value of the ratio Z/K emerges for a given L_{∞} and the value of K can be arbitrarily set at any value (preferably 1) in order to obtain a valid estimate of Z/K . This is of much importance if samples are available from virgin stocks in which $Z = M$, as it enables estimation of the M/K ratio, provided that L_{∞} can be approximated.

Estimates of Z derived from length-converted catch curves are sensitive to estimates of L_{∞} and very high estimates of Z/K will result from overestimates of L_{∞} . Estimates of L_{∞} set close to the size of the largest fishes normally found in an unexploited stock will provide a realistic lower boundary to Z . As an arbitrary rule, assigned values of the asymptotic length, designated $L_{(\infty)}$, have been set at $L_{\max}/0.95$ where L_{\max} is the largest fish within the contiguous annual average length-frequency distribution of the samples. The latter caveat serves to exclude outliers caused by the existence of occasional freak specimens of large size.

It should be noted that the x-axis of the length-converted catch curve is the actual age only if the value of t_0 , the theoretical time of hatching, is known. Otherwise, the values are the relative ages (calculated age (T) plus t_0). If the value of K is also unknown and is set at unity, the true age is $(T/K) + t_0$.

Length-converted catch curves for the principal species covered in Chapters 6-15 are shown in Figs. 19.4-19.25, based on the data given in those chapters and, for a few species, on more recent estimates of

growth parameters given in Table 19.1. Data points included in regressions of the natural logarithms of abundance indices against relative ages are those points which clearly lie on the descending arm of the catch curve and are based upon a length-frequency sample of not less than 0.5% of the total sample. The features of the catch curves are discussed below:

Holocentridae: The growth rates of squirrel fishes are unknown and the fully recruited length groups cover very limited length ranges. Length-converted catch curves for *Holocentrus ascensionis* and *H. rufus* at unexploited parts of Pedro Bank suggest M/K ratios of 7.3 and 7.6, respectively, sufficient to indicate that on a comparative basis the M/K ratios are probably large.

Serranidae: Catch curves for *Epinephelus guttatus* and *Cephalopholis fulva* taken at unexploited portions of Pedro Bank, at the Pedro Cays, California Bank and Serranilla Bank are shown in Figs. 19.4 and 19.5. For the exploited areas, the curves appear to descend more steeply with increasing age, thus supporting Hartsuijker's (unpublished) suggestion that catchability of groupers will increase with increasing size.

Mortality rates are as follows:

E. guttatus

Unexploited Pedro Bank	34-46 cm	$M=0.72$; $M/K=3.3$
Pedro Cays	34-46 cm	$Z=0.97$
California Bank	34-44 cm	$Z=1.06$

C. fulva

Unexploited Pedro Bank	25-31 cm	$M=2.28$; $M/K=4.1$
Pedro Cays	25-31 cm	$Z=1.79$
California Bank	25-31 cm	$Z=3.16$
Serranilla Bank	25-31 cm	$Z=2.54$

The anomalous situation in which the mortality rate in the exploited population of *C. fulva* at Pedro Cays appears to be lower than in the unexploited population is thought to be the result of decreased predation in the Pedro Cays area.

For the other grouper species, catch curves shown in Fig. 19.6 yield estimates of M/K ratios of 2.84 and 2.72 for *E. striatus* and *Mycteroperca venenosa*, respectively. Curves for *Petrometopon cruentatum* yield estimates of $Z = 1.69$ and $Z = 1.15$ for the Pedro Cays and Port Royal Reefs (Fig. 19.7).

Carangidae: The family of catch curves for *Caranx ruber* is shown in Fig. 19.8. The Port Royal Reefs population is clearly composed mostly of juveniles and the apparent mortality rate of $Z = 3.25$ undoubtedly includes a large component of offshore migration. The catch curve for Pedro Cays is highly linear and between 21.5 cm and 34.5 cm the mortality rate $Z = 1.77$. However, the curves for both the unexploited parts of Pedro Bank and for Serranilla Bank only peak at an age of 2.5 years and a length of 25.5 cm and the estimate of $Z = 1.77$ for the Pedro Cays must also contain a component of emigration. The estimates of $Z = M = 1.97$

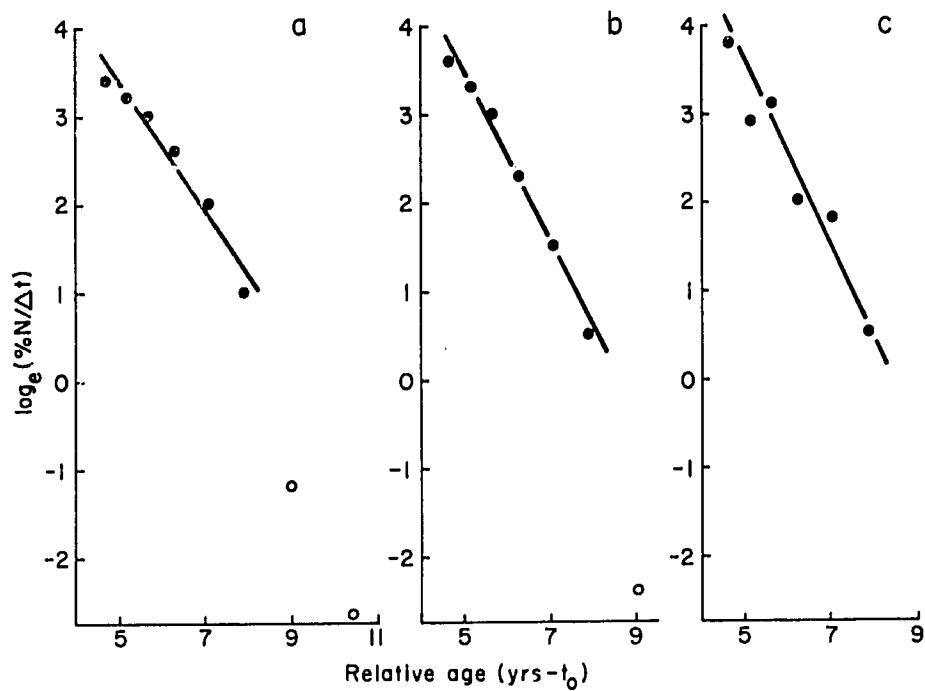


Fig. 19.4. Length-converted catch curves for *Epinephelus guttatus* at a) unexploited parts of Pedro Bank; $Z = M = 0.72$, b) Pedro Cays, $Z = 0.97$ and c) California Bank, $Z = 1.06$. Open points are not included in the regressions.

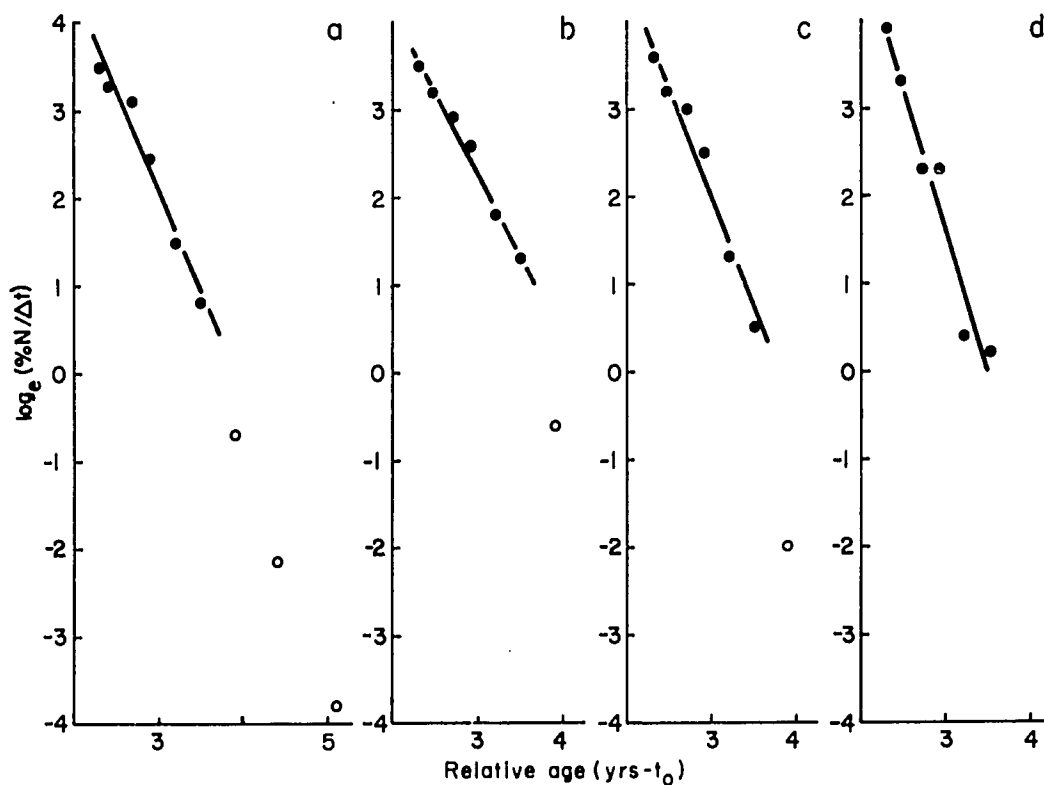


Fig. 19.5. Length-converted catch curves for *Cephalopholis fulva* at a) unexploited parts of Pedro Bank, $Z = M = 2.28$, b) Pedro Cays, $Z = 1.79$, c) Serranilla Bank, $Z = 3.16$ and d) California Bank, $Z = 2.54$. Open points are not included in the regressions.

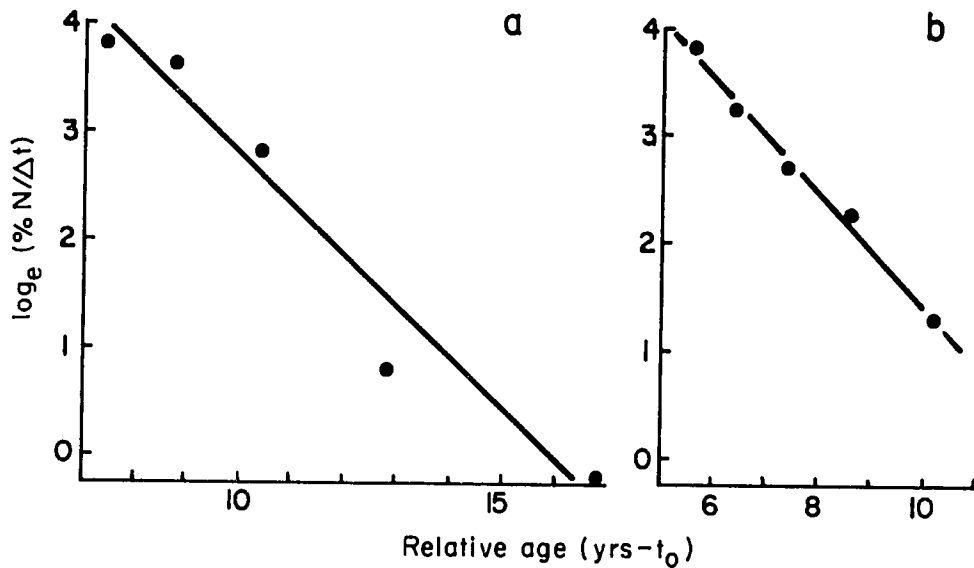


Fig. 19.6. Length-converted catch curves for a) *Mycteroperca venenosa*, $M/K = 2.84$ and b) *Epinephelus striatus*, $M/K = 2.72$ at unexploited parts of Pedro Bank.

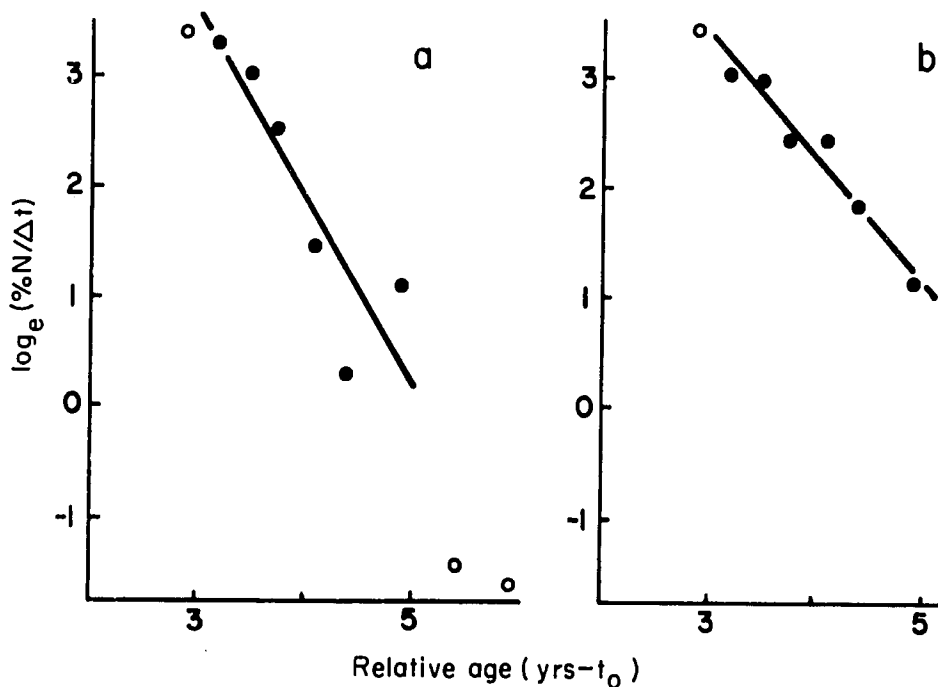


Fig. 19.7. Length-converted catch curves for *Petrometopon cruentatum* at a) Pedro Cays, $Z = 1.69$ and b) Port Royal Reefs, $Z = 1.15$. Open points are not included in the regressions.

and $Z = 2.40$ for the unexploited Pedro Bank and the Serranilla Bank fishery, respectively, imply that a fishing mortality rate of $F = 0.4$ might prevail at Serranilla Bank.

Beyond a size of 36 cm, the catches of *C. ruber* are very low both in traps and on hook-and-line. This fact, together with the observation that the ratio of M/K of 8.95 for unexploited Pedro Bank appears to be extremely high, suggests that a further change of habitat or a behavioral change might occur at around 40 cm FL.

Lutjanidae: The samples of *Ocyurus chrysurus* from Pedro Bank yield a highly linear catch curve (Fig. 19.9)

giving an estimate of $Z = M = 0.62$ between 32 and 56 cm (3.2-9.9 years), and an M/K ratio of 2.48.

For *Lutjanus buccanella* and *Apsilus dentatus* estimates of growth rates are very poorly based. Figures 19.10-19.11 show that estimates of M/K derived from unexploited stocks lie between 2.86 and 4.35.

Pomadasyidae: Catch curves for *Haemulon plumieri* at unexploited parts of Pedro Bank and at the Port Royal Reefs are shown in Fig. 19.12. The catch curve for the Port Royal Reefs shows a period of steady mortality with $Z = 0.84$ between recruitment at a

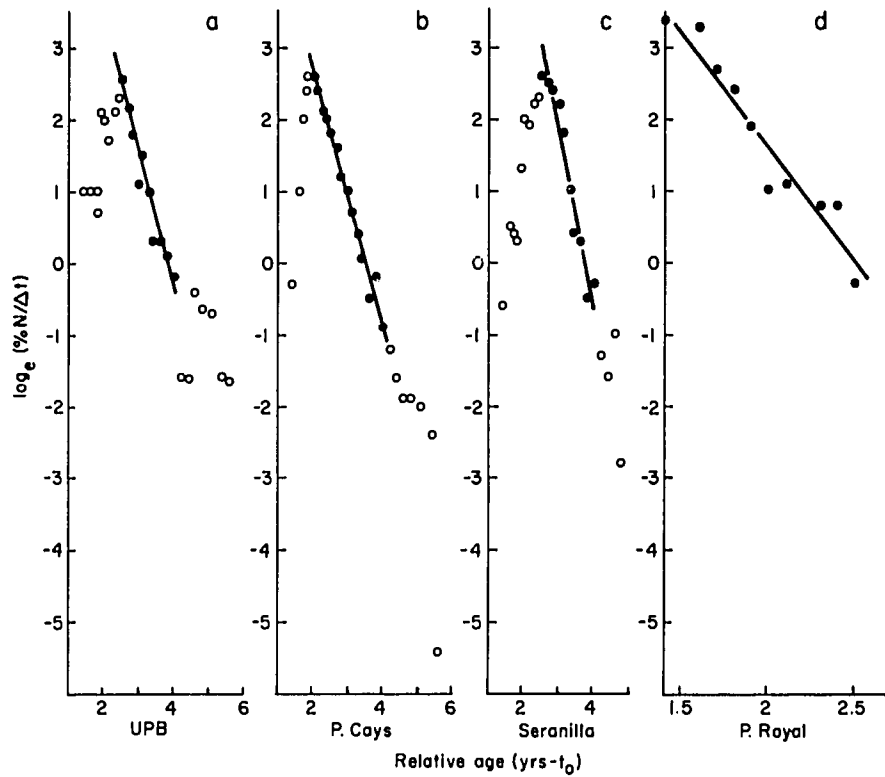


Fig. 19.8. Length-converted catch curves for *Caranx ruber* at a) unexploited parts of Pedro Bank, $Z = 1.97$, b) Pedro Cays, $Z = 1.77$, c) Serranilla Bank, $Z = 2.40$, and d) Port Royal Reefs, $Z = 3.25$. Open points are not included in the regressions.

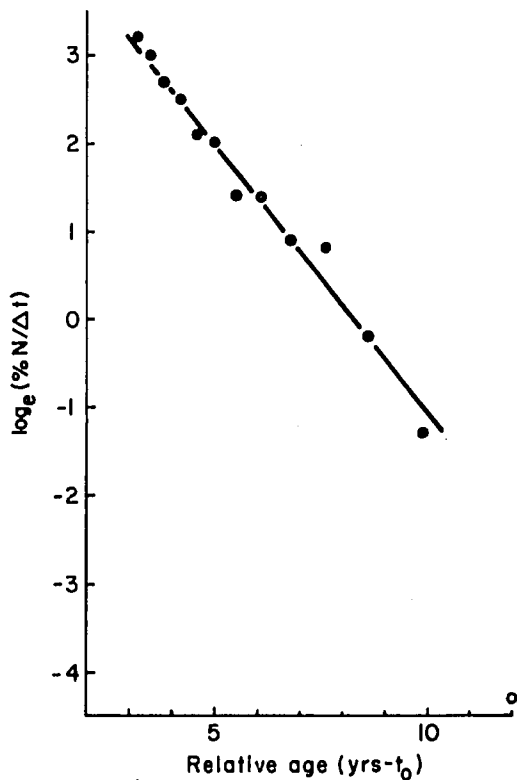


Fig. 19.9. Length-converted catch curves for *Ocyurus chrysurus* at unexploited parts of Pedro Bank. $Z = M = 0.62$. Open point is not included in the regression.

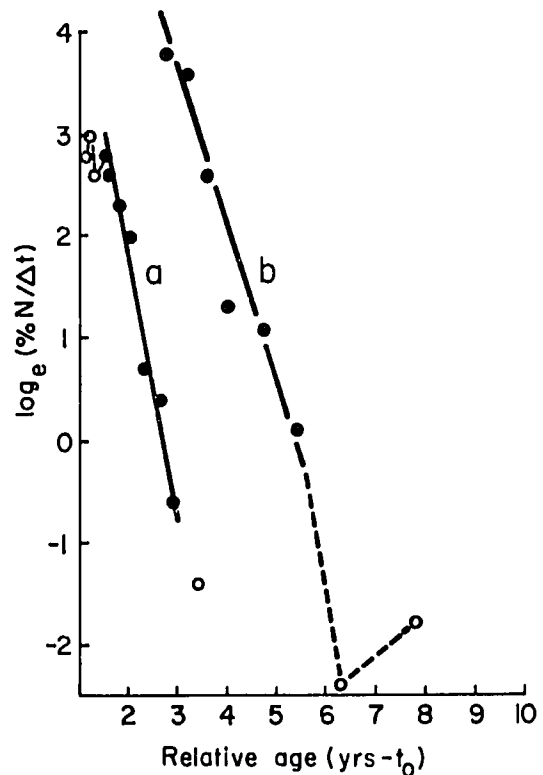


Fig. 19.10. Length-converted catch curves for *Lutjanus buccanella* at unexploited parts of Pedro Bank. a) males, $M/K = 3.60$, b) females, $M/K = 4.35$. Open points are not included in the regressions.

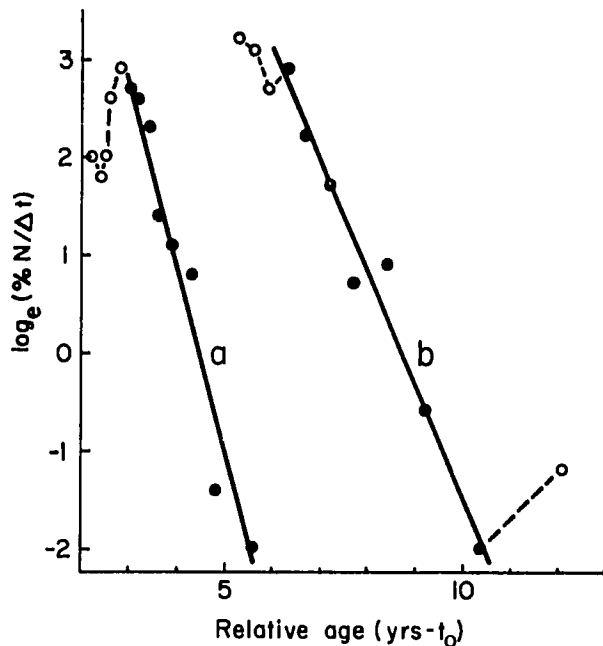


Fig. 19.11. Length-converted catch curves for *Apsilus dentatus* at unexploited parts of Pedro Bank. a) males, $M/K = 2.86$, b) females, $M/K = 3.83$. Open points are not included in the regressions.

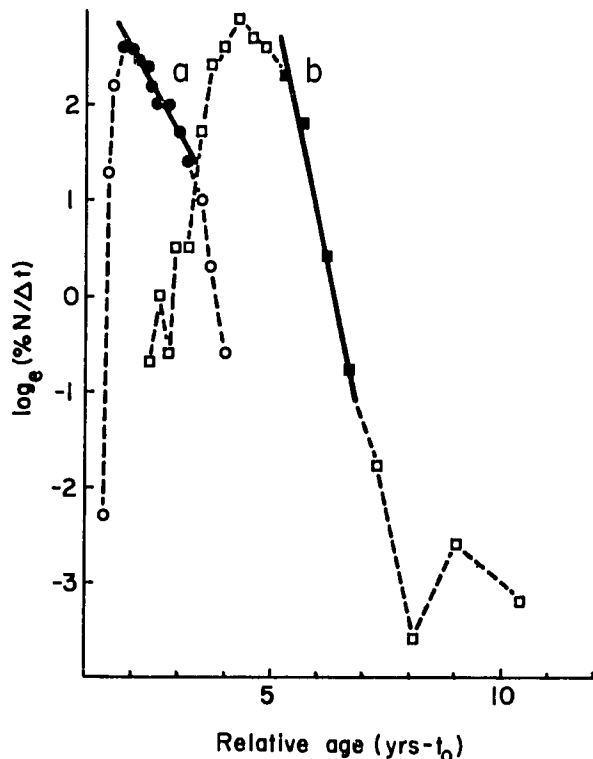


Fig. 19.12. Length-converted catch curves for *Haemulon plumieri* at a) Port Royal Reefs, $Z = 0.84$ and b) unexploited parts of Pedro Bank, $Z = 2.27$. Open points are not included in the regressions.

relative age of 2 years (15.5 cm FL.) and an offshore migration starting 1.5 years later. The catch curve for Pedro Bank shows that these fish are only fully recruited

to the catches at around 5 years of age and suffer a high apparent mortality rate ($Z = M = 2.27$; $M/K = 8.7$), which presumably can be ascribed to the high abundance of predators or to decreased catchability of large specimens.

H. album samples from Pedro Bank yield a relatively linear catch curve (Fig. 19.13) with $Z = M = 0.61$ and $M/K = 3.1$.

The catch curve for *H. sciurus* (Fig. 19.14) at the Port Royal Reefs is highly linear and yields an estimate of $Z = 1.4$.

In the cases of the other species of grunts, the growth coefficients are unknown and only ratios of M/K or Z/K can be derived from the catch curves. For *H. flavolineatum* (Fig. 19.15) the M/K ratio at Pedro Bank is 3.0, while at the Pedro Cays the Z/K ratio is 4.4 over the same size range, implying an F/K value at the Pedro Cays of 1.4. Like *H. plumieri*, apparent mortality of this species at the Port Royal Reefs undoubtedly includes a component of offshore migration and the Z/K ratio is around 7.2.

H. melanurum has a M/K ratio of 3.6 at Pedro Bank and $Z/K = 5.3$ at Serranilla Bank (Fig. 19.16) while *H. aurolineatum* appears to have an M/K ratio of 8.7 at Pedro Bank. If K is not less than the value of 0.22 estimated by Manooch and Barans (1982) for this species in Carolina waters, then M would be not less than 1.9.

Mullidae: Catch curves for male *Pseudupeneus maculatus* (Fig. 19.17) and combined male and female *Mulloidichthys martinicus* (Fig. 19.18) are highly linear. In neither case is the growth coefficient reliably known. The M/K ratio for *P. maculatus* is 2.7 at Pedro Bank and Z/K ratio is 8.1 at the Port Royal Reefs, implying an F/K ratio of 5.4.

For *M. martinicus*, the M/K ratio at Pedro Bank is estimated at 5.7, with a lower Z/K value of 4.8 at the Pedro Cays.

Chaetodontidae: The catch curve for *Pomacanthus arcuatus* at Pedro Bank is fairly irregular. The best line through the set of points (Fig. 19.19) yields an estimate of $M/K = 3.4$.

Scaridae: For *Scarus taeniopterus* at unexploited Pedro Bank, the estimated value of M/K is 3.2 between 20.5 and 25.5 cm TL (Fig. 19.20). Over the same length range at the Pedro Cays, the estimated value of Z/K is of the same general magnitude—the scatter of the points rendering the regressions not significantly different.

Acanthuridae: No growth estimates are available for the Acanthurids and only M/K or Z/K ratios can be derived from the catch curves (Figs. 19.21-19.23).

For the unexploited parts of Pedro Bank, M/K ratios are 3.2, 4.2 and 3.6 for *Acanthurus chirurgus*, *A. bahianus* and *A. coeruleus*. All species appear to undertake progressive offshore movements as they increase in size

and estimates of Z/K for the Port Royal Reefs and for Pedro Cays probably include a component of migration.

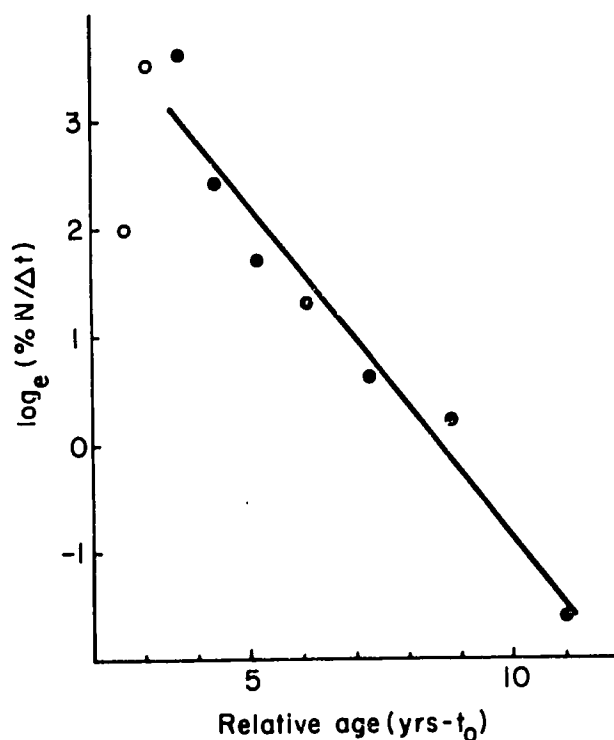


Fig. 19.13. Length-converted catch curves for *Haemulon album* at unexploited parts of Pedro Bank, $Z = 0.61$. Open points are not included in the regressions.

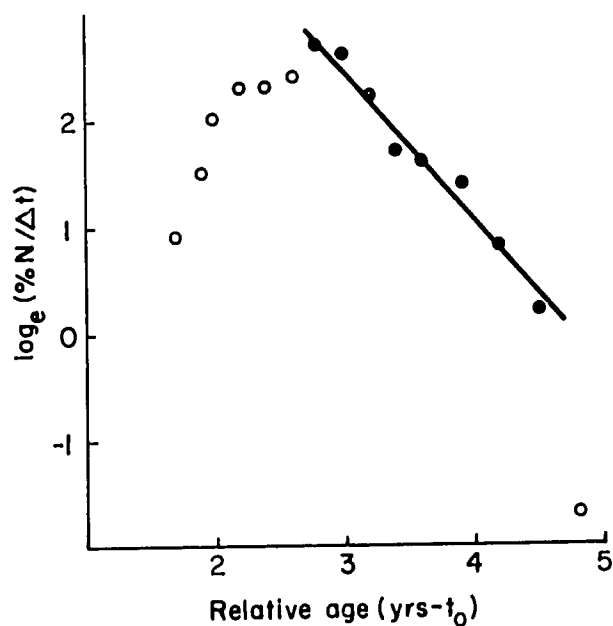


Fig. 19.14. Length-converted catch curves for *Haemulon sciurus* at the Port Royal Reefs, $Z = 1.40$. Open points are not included in the regressions.

Balistidae: The catch curve for *Balistes vetula* (Fig. 19.24) is highly linear over the range 21.5-35.5 cm FL (relative ages 1.2-2.7 years) with a coefficient of mortality $Z = M = 2.51$ and an M/K ratio of 4.7. However, the frequencies inserted into the catch curve have been compounded of catches in different depth zones (Table 15.9) and it is difficult to evaluate the validity of the estimated values of M and M/K . It is possible that larger specimens are under-represented in trap catches (Hart-suijker, unpublished).

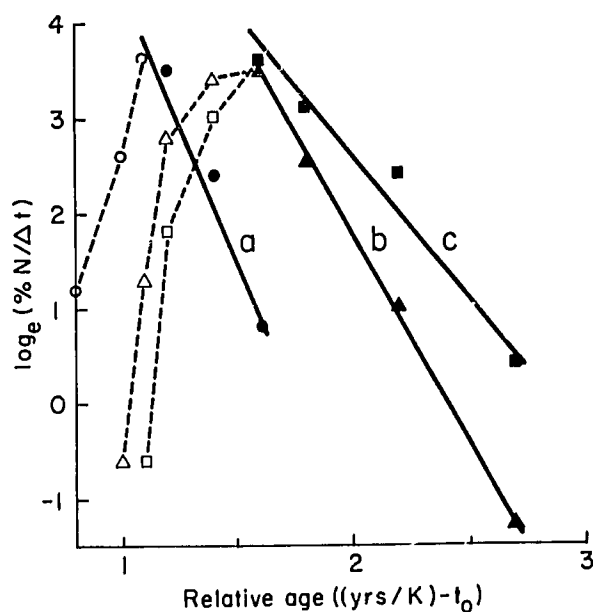


Fig. 19.15. Length-converted catch curves for *Haemulon flavolineatum* at a) the Port Royal Reefs, $Z/K = 7.2$, b) Pedro Cays, $Z/K = 4.4$ and c) unexploited parts of Pedro Bank, $M/K = 3.0$. Open points are not included in the regressions.

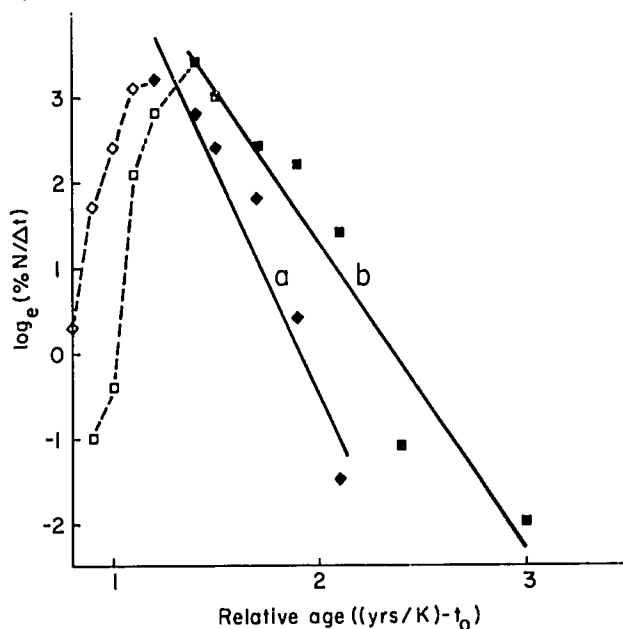


Fig. 19.16. Length-converted catch curves for *Haemulon melanurum* at a) Serranilla Bank, $Z/K = 5.3$, and b) at unexploited parts of Pedro Bank, $M/K = 3.6$. Open points are not included in the regressions.

Palinuridae: Length-converted catch curves for male and female *Panulirus argus* at the Port Royal Reefs and at Pedro Bank are shown in Fig. 19.25. The catch curves for the Port Royal Reefs are fairly linear over the carapace length range from 8.5 cm to 11.5 cm (for female) or 12.5 cm (for males) with values of Z of 1.76 and 1.35, respectively. For unexploited parts of Pedro Bank, the male and female catch curves both steepen abruptly in the last two length groups encountered, possibly as a result of a change in growth rates. Over the mid-ranges,

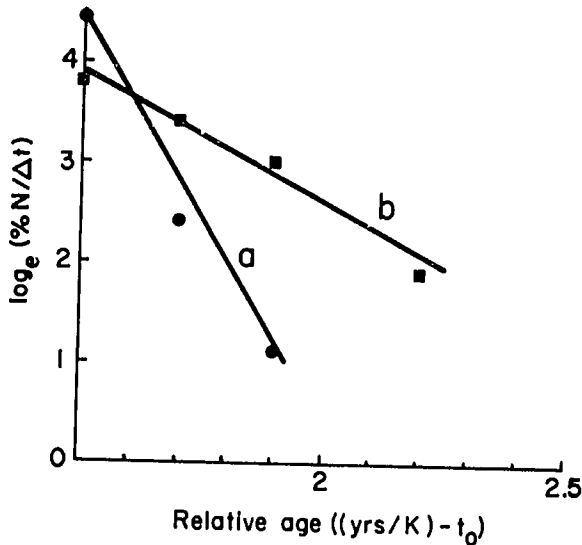


Fig. 19.17. Length-converted catch curves for male *Pseudupeneus maculatus* at a) the Port Royal Reefs, Z/K = 8.1 and b) at unexploited parts of Pedro Bank, M/K = 2.7.

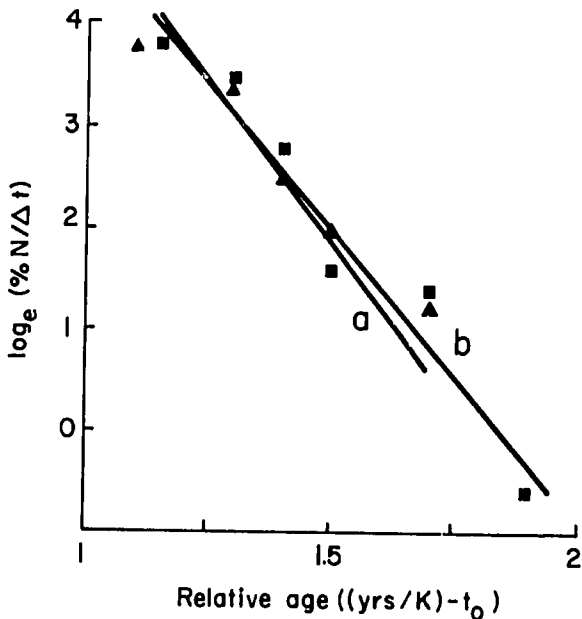


Fig. 19.18. Length-converted catch curves for *Mulloidichthys martinicus* at a) unexploited parts of Pedro Bank, M/K = 5.7, and b) at the Pedro Cays, Z/K = 4.8.

between full recruitment and the start of the decline, mortality rates appear to be modest, amounting to 0.4 and 0.6 for males and females, respectively.

Generalizations: A few generalizations appear to emerge from the foregoing. Firstly, based upon 36 comparisons, the estimates of M/K or Z/K derived from the Beverton and Holt (1956) equation average 9.7% lower than those derived from the length-converted catch curves. The difference is statistically highly significant. Secondly, estimates of M derived from the catch curves tend to be substantially higher in most cases than estimates based upon the empirical equation derived by Pauly (1980a) which states that

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$

in which M is the calculated coefficient of natural mortality, K is the coefficient of growth, L_{∞} is the asymptotic length and T is the mean water temperature.

It was argued in Chapter 17 that natural mortality rates will decrease as a result of non-selective exploitation of a multispecies fishery, primarily as a result of the decrease in the biomass of predators. Evidence of any such changes is not yet available, although for three small species (*Cephalopholis fulva*, *Mulloidichthys martinicus* and *Scarus taeniopterus*) mortality rates appeared to be lower at the exploited Pedro Cays than at unexploited parts of Pedro Bank.

STOCK ASSESSMENTS

The development of reliable scuba diving equipment has led to the development of highly sophisticated visual-

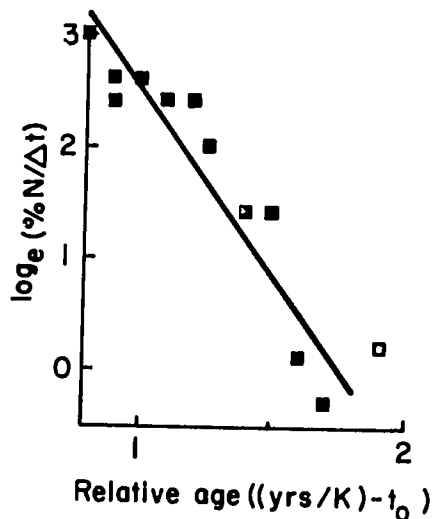


Fig. 19.19. Length-converted catch curves for *Pomacanthus arcuatus* at unexploited parts of Pedro Bank, M/K = 3.4. Open point is not included in the regression.

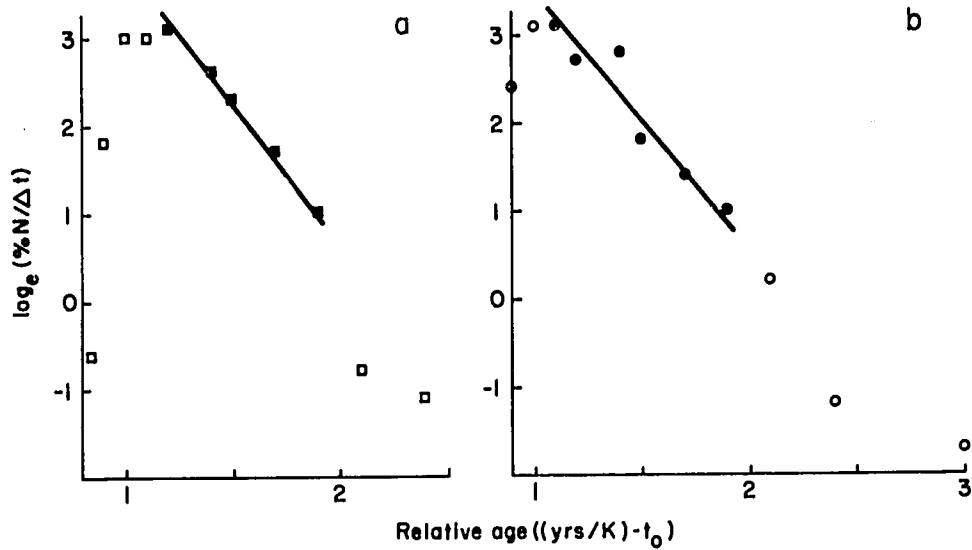


Fig. 19.20. Length-converted catch curves for *Scarus taeniopterus* at a) unexploited parts of Pedro Bank, $M/K = 3.2$ and b) at the Pedro Cays, $Z/K = 3.0$. Open points are not included in the regressions.

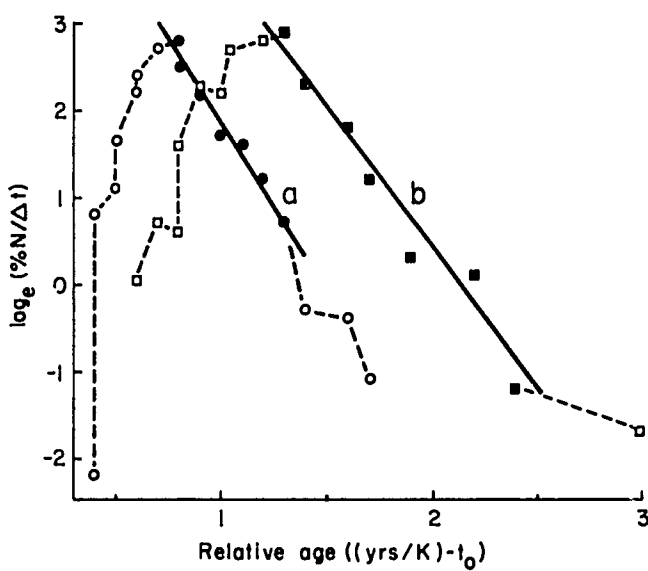


Fig. 19.21. Length-converted catch curves for *Acanthurus chirurgus* at a) the Port Royal Reefs, $Z/K = 3.9$ and b) at unexploited parts of Pedro Bank, $M/K = 3.2$. Open points are not included in the regressions.

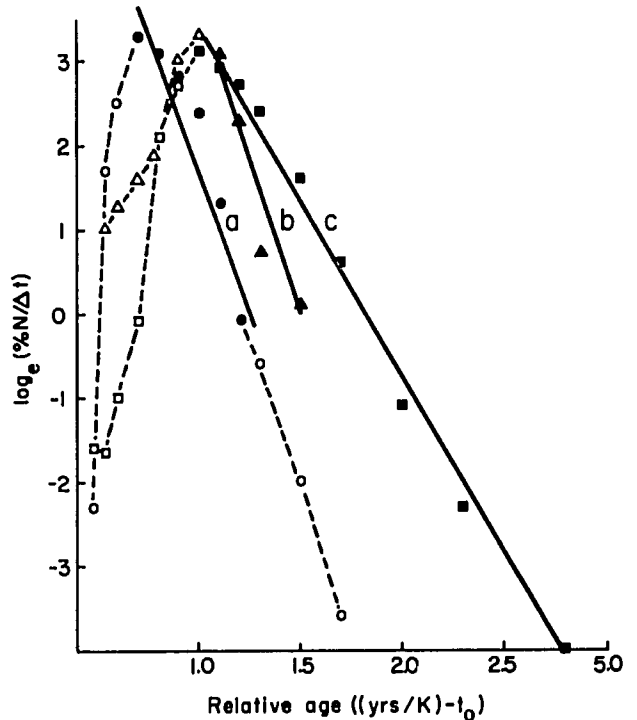


Fig. 19.22. Length-converted catch curves for *Acanthurus bahianus* at a) the Port Royal Reefs, $Z/K = 6.6$, b) at the Pedro Cays, $Z/K = 7.2$, and c) at unexploited parts of Pedro Bank, $M/K = 4.2$. Open points are not included in the regressions.

census techniques (Craik 1981; Brock 1982; Sale and Douglas 1981), giving considerable confidence in density estimates of diurnally active species when surveys are properly executed. However, with very few exceptions, such techniques have not been applied to commercially exploited species.

Additionally, Eggers et al. (1982) have presented a method whereby it is possible to estimate the average area from which a trap or other stationary fishing gear draws its catch of a particular species. The method has not yet been applied to coral reef fisheries but it appears that this, combined with the visual-census techniques and further advances in our understanding

of how traps actually function (Stevenson and Stuart-Sharkey 1980; Olsen et al. 1978; Craig 1976; Munro 1974; Munro et al. 1971) gives promise of population estimation based on trapping. If a set of definitive experiments is conducted, it might be possible to convert the results of previous trap fishery investigations (Wolf and Chislett 1974; Hartsuijker 1982) and the

results reported in Chapter 5 to estimates of population densities.

Although as demonstrated in Chapter 18 and by Munro (1977), it is possible to merely sum the results of conventional single-species assessments in a multi-species coral reef fishery, the degree of uncertainty attached to the input parameters and most especially the unknown extent to which parameters are influenced by species interactions, limit the usefulness of this approach (Munro 1980).

Total biomass-fishing intensity surplus yield curves in which the fishing intensities per unit area are regressed against catch per unit of effort from different, but ecologically similar areas (Chapter 2), have found some usefulness in making assessments in other coral reef areas (Gulland 1979), but application to coral reef fisheries remains limited by the acute lack of appropriate statistics. The methods outlined by Bazigos (1974) give some hope of correcting this situation.

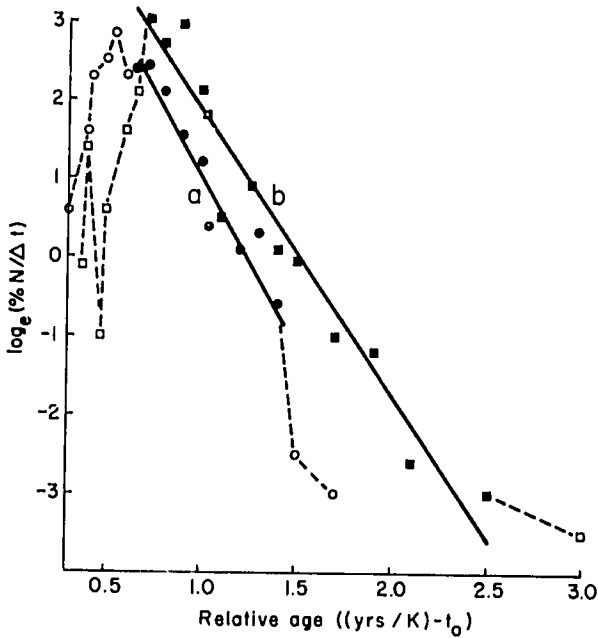


Fig. 19.23. Length-converted catch curves for *Acanthurus coeruleus* at a) the Port Royal Reefs, $Z/K = 4.3$ and b) at unexploited parts of Pedro Bank, $M/K = 3.6$. Open points are not included in the regressions.

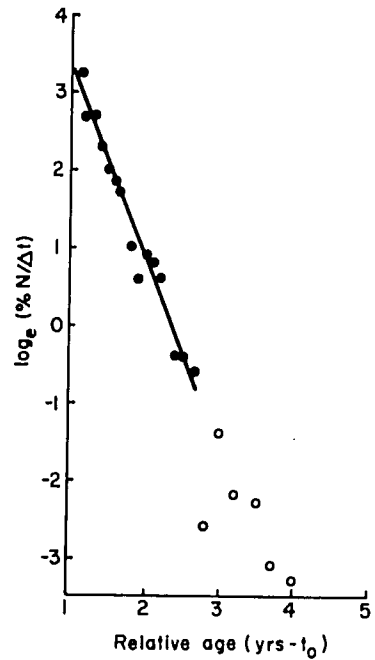


Fig. 19.24. Length-converted catch curves for *Balistes vetula* at unexploited parts of Pedro Bank, $M = 2.51$. Open points are not included in the regressions.

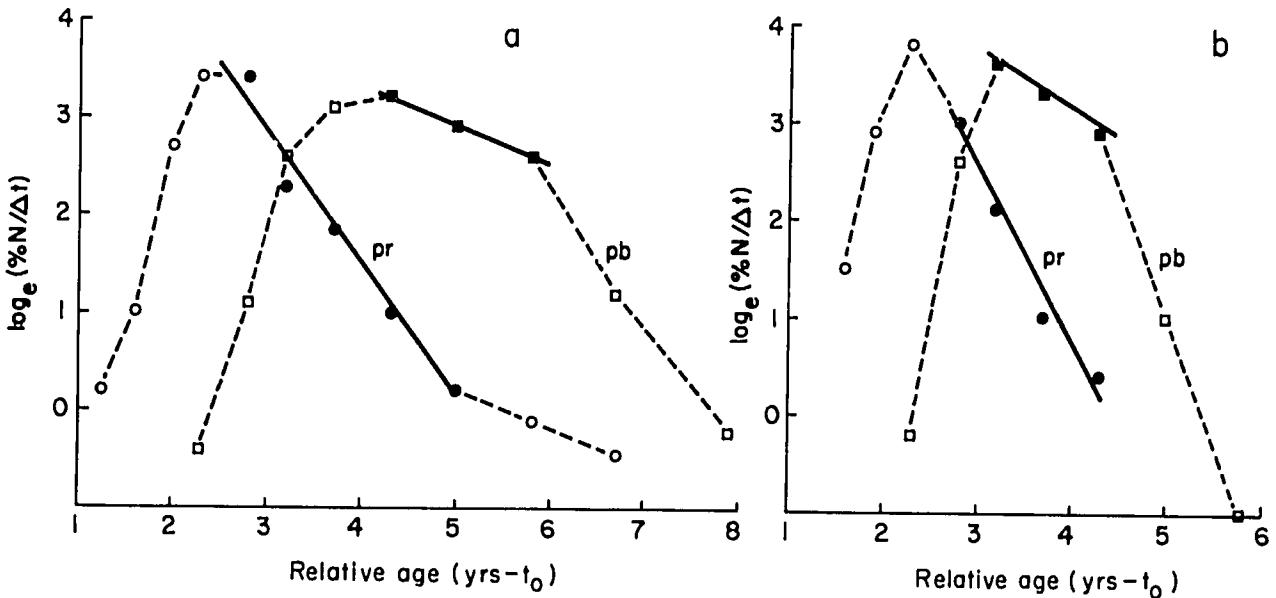


Fig. 19.25. Length-converted catch curves for a) male and b) female *Panulirus argus* at the Port Royal Reefs (pr) and at Pedro Bank (pb). See text for interpretation. Open points are not included in the regressions.

A number of multispecies models have been proposed in recent years (Andersen and Ursin 1977; Pope 1979; Saila 1982; Powers and Crow 1982) but all remain bedevilled by the problems of parameter estimation. A promising approach arising from a simplification of ecosystem models, such as that of Laevastu and Favorite (1978), has been developed by Polovina and Tagami (1980) for the French Frigate Shoals, in the northwest Hawaiian Islands, in which an ecosystem model is simply based upon estimates of biomass, production and consumption at different trophic levels. A similar approach has been developed by Larkin and Gazey (1982). Given the availability of good census techniques combined with a much improved knowledge of food and feeding of reef fish (Talbot and Goldman 1972; Ogden 1976; Ogden and Lobel 1978; Hobson and Chess 1978; Parrish et al. 1980; Randall 1980; Hay 1981) it would appear that such models have the greatest potential for giving an insight into the complex reactions wrought on a community by exploitation, which is almost invariably selective.

At a more immediate level, multispecies analyses by Stevenson (1978) of the Puerto Rican trap fishery and by Ralston (1980) demonstrate that useful results can still be generated by using fairly conventional techniques. There is clearly scope for further conventional stock assessments, particularly if length composition data are effectively utilized to conduct virtual population analysis and cohort analysis (Jones 1981).

POTENTIAL HARVESTS FROM CORAL REEF AREAS

This particular topic has generated considerable interest (Smith 1978b) and an equal amount of confusion in recent years. Most available data have been summarized by Marshall (1980) and recapitulated by Marten and Polovina (1982). Basically, it appears from the available evidence that harvests of fish of 4-6 t/km²/year are attainable from *coralline shelves* (Munro 1977; Wijkstrom 1974; Carpenter 1977; Murdy and Ferraris 1980; Bayliss-Smith, unpublished MS). Such shelves, extending from the shore to an arbitrary 200-m isobath, encompass seagrass beds, sand flats, submerged reefs and emergent reefs, and all other habitats (Marshall 1981). The fishes included in the statistics have usually comprised all neritic species.

More recent evidence from fisheries based on reef flats and almost pure stands of coral has shown that harvests of reef fish and invertebrates *per unit area of actively growing coral* are far in excess of those mentioned above. Hill (1978) and Wass (1982), respectively, estimated average yields of fish of 8 t/km²/year and 18 t/km²/year for the shoreline fishery of American

Samoa, plus very large catches of invertebrates when harvests from depths of only 0-8 m are considered. In the central Philippines, Alcalá (1981) and Alcalá and Luchavez (1981) have estimated harvests of 8.00-14.73 (mean 11.4) t/km²/year at Apo Island and a range of 9.7-23.7 (mean 16.5) t/km²/year over a five-year period at Sumilon Island. If *Elops* sp. and *Scomberomorus* sp. are excluded from the harvests at Apo Island, the yield of reef-related species averaged about 8.7 t/km²/year. The harvests in the above-mentioned instances are from depths down to 60 m and the intervening depths are substantially covered with living corals. Both island shelves have been subjected to exploitation for many years.

It is clear that questions of potential productivity of coralline shelves relate closely to the depths involved, to the areas of living coral cover and to the productivity of adjacent habitats. A recent workshop (Saila and Roedel 1980) has recommended that the possibility of relating coral reef fishing potential to a morphoedaphic index be pursued. These questions require additional field work, backed up by a solid statistical base, before they can be resolved.

In concluding, two points require emphasis. Firstly, the general confirmation of estimates of growth and mortality rates lends confidence to the assessment of theoretically optimal mesh sizes. It must nevertheless be emphasized that the results presented in this volume are based upon limited data and that we do not claim to have produced a definitive work. However, it can be claimed that the validity of length-frequency based stock assessment methodologies has now been established.

Secondly, in Chapter 18 (first published in 1975) the potential production of fisheries based upon the neritic, pelagic and demersal fish communities of the Jamaica shelf, proximal oceanic banks and Pedro and Morant Banks is estimated, on a conservative basis, to amount to about 16,000 tonnes/year. Nothing has emerged in the intervening period which indicates a need to revise this figure. However, it must also be emphasized, that the magnitude of a potential harvest is determined purely by biological and ecological factors and that the degree to which it will ever be feasible to harvest even a fraction of the potential is determined by economic and technological factors.

Only a few options are available to any fishery administrator; namely, to manage overfished nearshore resources or see harvests dwindle; to adopt more efficient fishing technologies in order to bring marginal areas into production and to diversify the industry to ensure that all resources are rationally harvested. There are no other alternatives.

References

- Albrechtsen, K. 1968. A dyeing technique for otolith age reading. *J. Cons., Cons. Int. Explor. Mer.* 32: 278-280.
- Alcala, A.C. 1981. Fish yield of coral reefs of Sumilon Island, Central Philippines. *Nat. Res. Counc. Philipp. Res. Bull.* 36: 1-7.
- Alcala, A.C. and T. Luchavez. 1981. Fish yield of the coral reef surrounding Apo Island, Negros Occidental, Central Visayas, Philippines. *Proc. 4th Int. Coral Reef Symp.* 1: 69-73.
- Alegria, C.J.R. and M.F. de Menezes. 1970. Edad y crecimiento del ariacó, *Lutjanus synagris* (Linnaeus), en el nordeste del Brasil. *Arq. Cienc. Mar.* 10(1): 65-68.
- Almeida, N.U. de M. 1965. Estudos preliminares sobre a primeira maturacao sexual, epoca de desova e sex-ratio do pargo (*Lutjanus aya*) no nordeste. *Bol. Estud. Pesca* 5: 7-17.
- Andersen, K.P. and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddr. Dan. Fisk.-Havunders. (Ny Ser.)* 7: 319-435.
- Anderson, W.D., Jr. 1967. Field guide to the snappers (*Lutjanidae*) of the western Atlantic. U.S. Fish Wildl. Serv. Circ. 252: 1-14.
- Arnov, B. 1952. A preliminary review of the western north Atlantic fishes of the genus *Haemulon*. *Bull. Mar. Sci. Gulf Caribb.* 2: 414-437.
- Austin, H. and S. Austin. 1971. The feeding habits of some juvenile marine fishes from the mangroves in western Puerto Rico. *Caribb. J. Sci.* 11: 171-178.
- Bagenal, T.B. 1968. Fecundity, p. 160-169. *In* W.E. Ricker (ed.) *Methods for assessment of fish production in fresh waters*. I.B.P. Handbook 3. Blackwell Scientific Publications, Oxford, England.
- Baisre, J.A. 1964. Sobre los estudios larvales de la langosta comun, *Panulirus argus*. *Contrib. Cent. Invest. Pesq., Havana* 19: 37 p.
- Bakun, A., J. Beyer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean sciences in relation to living resources. *Can. J. Fish. Aquat. Sci.* 39: 1059-1070.
- Bakus, G.J. 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. *Occas. Pap. Allan Hancock Found.* 27: 29 p.
- Bakus, G.J. 1966. Some relationships of fishes to benthic organisms on coral reefs. *Nature (London)* 210: 280-284.
- Bakus, G.J. 1967. The feeding habits of fishes and primary production at Enewetok, Marshall Islands. *Micronesica (J. Coll. Guam)* 3: 135-149.
- Bane, G.W. 1955a. Exploratory fishing for tunas in the Mona Passage. *Proc. Gulf Caribb. Fish. Inst.* 17: 55-60.
- Bane, G.W. 1965b. Notes on exploratory fishing and the biology of the blackfin tuna around Puerto Rico, p. 12-16. *In* D. DeSilva (ed.) *Proc. Ninth Int. Game Fish Conf., Runaway Bay, Jamaica, W.I., Nov. 1964*. International Oceanographic Foundation, Miami, Florida.
- Bardach, J.E. 1958. On the movements of certain Bermuda reef fishes. *Ecology* 39: 139-146.
- Bardach, J.E. 1959. The summer standing crop of fish on a shallow Bermuda reef. *Limnol. Oceanogr.* 4: 77-85.
- Bardach, J.E. 1961. Transport of calcareous fragments by reef fishes. *Science* 133: 98-99.
- Bardach, J.E. and D.W. Menzel. 1957. Field and laboratory observations on the growth of some Bermuda reef fishes. *Proc. Gulf Caribb. Fish. Inst.* 9: 106-112.
- Bardach, J.E., C.L. Smith and D.W. Menzel. 1958. Bermuda Fisheries Research Program Final Report. Bermuda Trade Develop. Board, Hamilton. 59 p.
- Barroso, L.M. 1965. Nota preliminar sobre a alimentacao do xareu-preto (*Caranx lugubris*, Poey 1860) no nordeste do Brasil. *Bol. Estud. Pesca* 5: 7-11.
- Bauchot, M.L. and M. Blanc. 1961. Poissons marins de l'est Atlantique tropical. I. Labroides (Teleostei; Perciformes). *Atl. Rep.* 6: 43-64.
- Bayer, F. 1969. A review of research and exploration in the Caribbean Sea and adjacent regions. *FAO Fish. Rep.* 71(1): 41-92.
- Bayliss-Smith, T. The price of protein: marine fisheries in Pacific subsistence. (Unpublished MS)
- Bazigos, G.P. 1974. The design of fisheries statistical surveys—inland waters. *FAO Fish. Tech. Pap.* 133: 122 p.
- Beardsley, G.L., Jr. 1967. Age, growth and reproduction of the dolphin, *Coryphaena hippurus* in the Straits of Florida. *Copeia* 1967: 441-451.
- Beaumariage, D.S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. *Fla. Dept. Nat. Resour. Mar. Res. Lab. Tech. Ser.* 59: 38 p.
- Beebe, W. and J. Tee Van. 1933. Field book of the shore fishes of Bermuda. G.P. Putnam & Sons, New York.
- Beers, J.R., D.M. Steven and J.B. Lewis. 1968. Primary productivity in the Caribbean Sea off Jamaica and the tropical north Atlantic off Barbados. *Bull. Mar. Sci. Gulf Caribb.* 18: 86-104.
- Bellinger, J.W. and J.W. Avault, Jr. 1970. Seasonal occurrence, growth, length-weight relationship of juvenile pompano, *Trachinotus carolinus*, in Louisiana. *Trans. Amer. Fish. Soc.* 99: 353-358.
- Berry, F.H. 1959. Young jack crevalles (*Caranx* species) off the southeastern Atlantic coast of the United States. *Fish. Bull.* 59: 417-535.
- Berry, F.H. and W.J. Baldwin. 1966. Triggerfishes (Balistidae) of the eastern Pacific. *Proc. Calif. Acad. Sci. Ser.* 4: 34: 429-474.
- Berry, F.H. and S. Drummond. 1967. Geographical index to collecting stations of the exploratory fishing vessels; Oregon, Silver Bay, Combat & Pelican. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 558. 25 p.
- Berry, F.H. and E.A. Iversen. 1956. Pompano: biology, fisheries and farming potential. *Proc. Gulf Caribb. Fish. Inst.* 19: 116-128.

- Berry, P.F. 1970. Mating behaviour, oviposition and fertilization in the spiny lobster, *Panulirus homarus* (Linnaeus). Invest. Rep. Oceanogr. Res. Inst., Durban 24. 16 p.
- Beverton, R.J.H. and S.J. Holt. 1956. A review of methods for estimating mortality rates in exploited populations, with special reference to sources of bias in catch sampling. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 140: 67-83.
- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Min. Agric. Fish Food (G.B.) Ser. II: Sea Fish. 19. 533 p.
- Beverton, R.J.H. and S.J. Holt. 1964. Tables of yield functions for fishery assessment. FAO Fish. Tech. Pap. 38. 49 p.
- Boardman, C. and D. Weiler. 1980. Aspects of the life history of three deep water snappers around Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 32: 158-172.
- Bohlike, J.E. and C.C.G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingstone Publishing Co., Wynnewood, Pennsylvania.
- Bohnsack, J.A. and F.H. Talbot. 1980. Species packing by reef fishes on Australian and Caribbean reefs; an experimental approach. Bull. Mar. Sci. 30: 710-723.
- Borges, G.A. 1966. Nota preliminar sobre a biologia e pesca do xareu preto (*Caranx lugubris*, Poey, 1860) no nordeste Brasileiro. Bol. Estud. Pesca 6: 9-20.
- Botros, G.A. 1971. Fishes of the Red Sea. Oceanogr. Mar. Biol. 9: 221-348.
- Bradley, E. and C.E. Bryon. 1974. Life history and fishery of the red snapper (*Lutjanus campechanus*) in the North-western Gulf of Mexico: 1970-1974. Proc. Gulf Caribb. Fish. Inst. 27: 77-106.
- Breder, C.M. 1949. On the taxonomy and post larval stages of the surgeon fish, *Acanthurus hepatus*. Copeia 1949: 296.
- Breder, C.M. 1962. On the significance of transparency in osteichthid fish eggs and larvae. Copeia 1962: 561-567.
- Briggs, J.C. and D.K. Caldwell. 1957. *Acanthurus randalli*, a new surgeonfish from the Gulf of Mexico. Bull. Fla. State Mus. (Biol. Sci.) 2: 43-51.
- Brock, R.E. 1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32: 269-276.
- Brock, R.E., C. Lewis and R.C. Wass. 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. Mar. Biol. 54: 281-292.
- Brock, V. 1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18: 297-308.
- Brothers, E.B. 1980. Age and growth studies in tropical fishes, p. 119-136. In S.B. Saila and P.M. Roedel (eds.) Stock assessment for tropical small-scale fisheries. Int. Cent. Mar. Res. Dev. University of Rhode Island, Kingston.
- Brothers, E.B. 1982. Aging reef fishes, p. 3-23. In G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) The biological bases for reef fishery management. NOAA Tech Memo. NMFS-SEFC-80.
- Brothers, E.B. and W.N. McFarland. 1981. Correlations between otolith microstructure, growth and life history transitions in newly-recruited French grunts (*Haemulon flavolineatum* Desmarest), Haemulidae. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 178: 369-374.
- Brownell, W.N. and W.E. Rainey. 1971. Research and development of deep-water commercial and sport fisheries around the Virgin Islands Plateau. Virgin Islands Ecol. Res. Stn. Contrib. 3. 88 p.
- Bruce, R.W. 1980. Protogynous hermaphroditism in two marine angel fish. Copeia 1980: 353-358.
- Bryne, J.E. 1970. Mucous envelope formation in two species of Hawaiian parrotfishes (Genus *Scarus*) Pac. Sci. 24: 490-493.
- Buckman, N.S. and J.C. Ogden. 1973. Territorial behaviour of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54: 1377-1382.
- Buesa Mas, R.J. 1960. Pesca exploratoria de la langosta con nasas, al sur de Camaguey, Cuba. Contrib. Cent. Invest. Pesq., Habana 11. 30 p.
- Buesa Mas, R.J. 1961. Segunda pesca exploratoria y datos biologicos de la langosta, *Panulirus argus*, en Cuba. Contrib. Cent. Invest. Pesq., Habana 12. 69 p.
- Buesa Mas, R.J. 1962. La nasa antillana. Contrib. Cent. Invest. Pesq., Habana 15. 26 p.
- Buesa Mas, R.J. 1969. Biology and fishing of spiny lobsters, *Panulirus argus* (Latreille), p. 62-78. In A. Bogdanov (ed.) Soviet-Cuban fishery research published for U.S. Dept. of Interior & N.S.F. by Isr. Prog. Sci. Transl., Jerusalem.
- Buesa Mas, R.J. and M.I. Mota Alves. 1971. Escala de colores para el estudio del ciclo reproductor de la langosta *Panulirus argus* (Latreille) en el area del mar Caribe. FAO Fish. Rep. 71(2): 9-12.
- Burdon, T.W. and M.L. Parry. 1954. Fishing methods of Singapore. J. Malay. Br. R. Asiat. Soc. 27: 24-28.
- Burgess, W.E. 1965. Larvae of the surgeonfish genus *Acanthurus* of the tropical western Atlantic. Univ. of Miami, Miami, Fla. M.S. thesis.
- Burkenroad, M.D. 1930. Sound production in the Haemulidae. Copeia 1930: 17-18.
- Caillouet, C.W., G.L. Beardsley and N. Chitty. 1971. Notes on size, sex ratio and spawning of the spiny lobster, *Panulirus guttatus* (Latreille), near Miami beach, Florida. Bull. Mar. Sci. 21: 944-951.
- Caldwell, D.K. 1959. Observations on tropical marine fishes from the north-eastern Gulf of Mexico. J. Fla. Acad. Sci. 22: 69-74.
- Caldwell, D.K. 1961. The ecology and systematics of the shore fishes of Jamaica. Yearb. Amer. Philos. Soc.: 275-277.
- Caldwell, D.K. 1966. Marine and freshwater fishes of Jamaica. Bull. Inst. Jam. Sci. Ser. 17. 120 p.
- Caldwell, D.K. and M.C. Caldwell. 1964. Fishes from the southern Caribbean—collected by Velez III in 1939. Allan Hancock Atl. Exped. Rep. 10. 61 p.
- Caldwell, M.C. 1962. Development and distribution of larval and juvenile fishes of the family Mullidae of the western north Atlantic. Fish. Bull. 62: 403-456.
- Carpenter, J.S. 1965. A review of the Gulf of Mexico red snapper fishery. U.S. Fish Wildl. Serv. Circ. 208. 35 p.
- Carpenter, J.S. and W.R. Nelson. 1969. Fishery potential for snapper and grouper in the Caribbean Sea and adjacent South American coast. FAO Fish. Rep. 71. (1): 149.
- Carpenter, K.E. 1977. Philippine coral reef fisheries resources. Philipp. J. Fish. 17: 95-125.
- Cervigon, M.F. 1966. Los peces marinos de Venezuela, Vols. I & II. Fundacion la Salle de Ciencias Naturales, Caracas.
- Chen, C-P., H-L. Hsieh and K-H. Chang. 1980. Some aspects of the sex change and reproductive biology of the grouper, *Epinephelus diaconthus* (Cuvier et Valenciennes). Bull. Inst. Zool. Acad. Sin. 19: 11-17.
- Chislett, G.R. and M. Yesaki. 1974. Spiny lobster fishing explorations in the Caribbean. Mar. Fish. Rev. 36(9): 43-49.
- Chittleborough, R.G. 1970. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21: 131-148.

- Chittleborough, R.G. and L.R. Thomas. 1969. Larval ecology of the Western Australian marine crayfish, with notes upon other Panulirid larvae from the eastern Indian Ocean. *Aust. J. Mar. Freshwater Res.* 20: 199-223.
- Chuck, L.M. 1963. 1962 sample survey of the fishing industry of Jamaica. Division of Economics and Statistics, Ministry of Agriculture and Lands, Jamaica.
- Clarke, E. 1950. Notes on the behaviour and morphology of some West Indian plectognath fishes. *Zoologica (N.Y.)* 35: 159-168.
- Cobo de Barany, T., J. Ewald and E. Cadima. 1972. La pesca de la langosta en el archipelago de Los Roques, Venezuela. *Inf. Téc. Dir. Gen. Desarr. Pesq. (Venez.)* 43. 34 p.
- Colin, P.L. 1978. Daily and summer-winter variation in mass spawning of the striped parrot fish, *Scarus croicensis*. *Fish Bull. U.S. Nat. Mar. Fish Serv.* 76: 117-124.
- Colin, P.L. 1982. Aspects of the spawning of Western Atlantic reef fishes, p. 69-78. In G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) The biological bases for reef fishery management. NOAA Tech. Memo NMFS-SEFC-80.
- Collette, B.B. and F.H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. *Nat. Hist. Mus. Los Angeles Cty. Sci. Bull.* 14: 98-124.
- Cope, C.E. 1959. Spiny lobster gear and fishing methods. U.S. Fish Wildl. Serv. Fish. Leaflet 487. 17 p.
- Cope, C.E. 1966. Equipamentos e metodos empregados na pesca da lagosta. *Bol. Estud. Pesca* 6: 7-30.
- Courtenay, W.A. 1961. Western Atlantic fishes of the genus *Haemulon* (Pomadasyidae): systematic status and juvenile pigmentation. *Bull. Mar. Sci. Gulf Caribb.* 11: 66-149.
- Courtenay, W.A. 1965. The systematic status of *Haemulon boschmae*, a grunt fish from shore waters of north eastern S. America. *Copeia* 1965: 41-45.
- Cousteau, J.Y. 1971. Life and death in a coral sea. Cassell, London.
- Craig, W. 1981. Underwater survey of coral trout *Plectropomus leopardus* (Serranidae) populations in the Capricornia section of the Great Barrier Reef Marine Park. *Proc. 4th Int. Coral Reef Symp.* 1: 53-58.
- Crawford, D.R. and W.J.J. de Smidt. 1922. The spiny lobster, *Panulirus argus*, of Southern Florida: its natural history and utilisation. *Bull. Bur. Fish.* 28(925): 281-310.
- Creaser, E.P. 1950. Repetition of egg laying and number of eggs of the Bermuda spiny lobster. *Proc. Gulf Caribb. Fish. Inst.* 2: 30-31.
- Creaser, E.P. 1952. Sexual dimorphism in weight and length relationship of the Bermuda spiny lobster. *Proc. Gulf Caribb. Fish. Inst.* 4: 64-68.
- Crocker, R.A. 1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. *Trans. Amer. Fish. Soc.* 91: 379-383.
- Cummings, W.C., B.D. Brahy and J.Y. Spires. 1966. Sound production, schooling and feeding habits of the margate, *Haemulon album* Cuvier, off North Bimini, Bahamas. *Bull. Mar. Sci. Gulf Caribb.* 16: 626-639.
- Dale, G. 1978. Money in the bank: a model for coral reef fish coexistence. *Environ. Biol. Fish.* 3: 103-108.
- Dammann, A.E. 1969. A study of the fisheries potential of the Virgin Islands. *Virgin Isl. Ecol. Res. Stn. Contrib.* 3.
- Davis, G.E. 1971. Aggregations of spiny sea urchins, *Diadema antillarum*, as shelter for young spiny lobsters, *Panulirus argus*. *Trans. Amer. Fish. Soc.* 100: 586-587.
- Dawson, C.E. 1949. Florida crawfish research. *Proc. Gulf Caribb. Fish. Inst.* 1: 21-28.
- Dawson, C.E. and C.P. Idyll. 1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). *Tech. Ser. Fla. Board Conserv.* 2. 39 p.
- Da Cruz, J.F. 1965. Contribuicao ao estudo da biologia pequeria da albacora, *Thunnus atlanticus* (Lesson) no nordeste do Brasil. *Bol. Inst. Biol. Mar. Univ. Rio Grande Norte* 2: 33-40.
- De Sylva, D.P. 1963. Preliminary report on the blue marlin sport fishery of Port Antonio, Jamaica. Unpublished Rep. Univ. Miami Inst. Mar. Sci. 15 p.
- De Sylva, D.P. and J.B. Higman. 1980. A plan to reduce ciguatera in the tropical Western Atlantic region. *Proc. Gulf Caribb. Fish. Inst.* 32: 139-153.
- Doherty, P.J. 1981. Coral reef fishes: recruitment-limited assemblages? *Proc. 4th Int. Coral Reef Symp.* 2: 465-470.
- Dragovich, A. 1969. Review of studies of tuna food in the Atlantic ocean. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 593. 21 p.
- Dragovich, A. 1970. The food of skipjack and yellowfin tunas in the Atlantic ocean. *Fish. Bull.* 68: 445-460.
- Dragovich, A. and T. Potthoff. 1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. *Fish. Bull.* 70: 1087-1110.
- Dress, J.K.W. and J. Meyer. 1965. Various aspects of the lobster and scale fishery in coastal waters (British Honduras). FAO/UNDP (Tech. Assist.) Rep. Fish. 2100. 16 p.
- Druzhinin, A.D. 1970. The range and biology of snapper (fam. Lutjanidae). *J. Ichthyol.* 10: 715-735.
- Duarte-Bello, P.B. 1959. Catalogo de peces Cubanos. Monografia 6. Universidad De Villanueva, Marianao, Cuba.
- Earle, S.A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. *Nat. Hist. Mus. Los Angeles Cty. Sci. Bull.* 14: 17-44.
- Ebert, T.A. 1973. Estimating growth and mortality rates from size data. *Oecologia (Berl.)* 11: 281-298.
- Eggers, D.M., N.A. Rickard, D.A. Chapman and R.R. Whitney. 1982. A methodology for estimating area fished for baited hooks and traps along a ground line. *Can. J. Fish. Aquat. Sci.* 39: 448-453.
- Ekman, S. 1967. Zoogeography of the sea. Sidgwick and Jackson, London.
- Eldred, B., C.R. Futch and R.M. Ingle. 1972. Studies on juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. *Fla. Dept. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep.* 35. 15 p.
- Emilsson, I. 1971. On the upper layer circulation in the Cayman Sea, p. 53-60. In Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November 1968. UNESCO, Paris. 53-60.
- Erdman, D.S. 1956. Recent fish records from Puerto Rico. *Bull. Mar. Sci. Gulf Caribb.* 6: 315-340.
- Erdman, D.S. 1977. Spawning patterns of fishes from the north-east Caribbean. *FAO Fish. Rep.* 200: 145-170.
- FAO. 1968a. Report to the Government of British Honduras (Belize) on investigations into marine fishery management, research and development policy for spiny lobster fisheries. Based on the work of W.H.L. Allsopp. FAO/UNDP (Tech. Assist.) Rep. Fish. 2481. 95 p.
- FAO. 1968b. Report to the Government of British Honduras (Belize) on investigations into marine fisheries, particularly spiny lobster and shrimp resources. Based on the work of D. Weber. FAO/UNDP (Tech. Assist.) Rep. Fish 2541. 28 p.
- FAO. 1969. Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November 1968. Report and abstracts of papers. *FAO Fish. Rep.* 71. Vol. 1. 165 p.

- FAO. 1974. Yearbook of fishery statistics: catches and landings, 1973. FAO Yearb. Fish. Stat. 37: 326 p.
- Fast, D.E. and F.A. Pagán-Font. 1973. Observations on an artificial reef of used vehicle tires. (Abstr.) 10th meeting Assoc. Island Mar. Labs. Caribb. Oct. 1973, San Juan, Puerto Rico.
- Feddern, H.A. 1968. Hybridization between the western Atlantic angelfish, *Holocanthus isabelita* and *H. ciliaris*. Bull. Mar. Sci. 18: 351-382.
- Feliciano, C. 1958. The lobster fishery of Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 10: 147-156.
- Finucane, J.H. 1969. Ecology of the pompano (*Trachinotus carolinus*) and the permit (*T. falcatus*) in Florida. Trans. Amer. Fish. Soc. 98: 478-486.
- Fischer, W., Editor. 1978. FAO species identification sheets for fishery purposes: Western Atlantic (Fishing Area 31) Vols. I-VII pag. var. FAO, Rome.
- Fischer, W. and P.J.P. Whitehead, Editors. 1974. FAO species identification sheets for fishery purposes. Eastern Indian Ocean (Fishing Area 57) and Western Central Pacific (Fishing Area 71) Vols. I-IV pag. var. FAO, Rome.
- Fishelson, L. 1970. Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. Nature (London) 227: 90-91.
- Fontaine, M., J. Deville and R. Lopez. 1973. Ecology and the regulation of calcium metabolism in coral grazer parrot-fish, p. 367-371. In R. Fraser (comp.) Oceanography of the South Pacific, 1972. Natl. Comm. UNESCO, Wellington, N.Z.
- Fonteles Filho, A.A. 1970. Estudo sobre a biologia da pesca do pargo, *Lutjanus purpureus* Poey, no nordeste Brasileiro—dados de 1969. Arq. Cienc. Mar. 10: 73-78.
- Fox, W.W. 1970. An exponential surplus-yield model for optimising exploited fish populations. Trans. Amer. Fish. Soc. 99: 80-88.
- Futch, R.B. and G.E. Bruger. 1976. Age, growth and reproduction of red snapper in Florida waters, p. 165-184. In H.R. Bullis and A.C. Jones (eds.) Proc. colloquim on snapper-grouper fishery resources of the Western Central Atlantic Ocean. Florida Sea Grant Program Report 17.
- Gibbs, R.H. and B.B. Collette. 1959. On the identification, distribution and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. Bull. Mar. Sci. Gulf Caribb. 9: 117-152.
- Ginsburg, I. 1948. The species of *Bathystoma* (Pisces, Haemulonidae). Zoologica (N.Y.) 33: 151-156.
- Ginsburg, I. 1952. Fishes of the family Carangidae of the northern Gulf of Mexico and three related species. Publ. Inst. Mar. Sci. Univ. Tex. 2: 43-117.
- Goeden, G.B. 1978. A monograph of the coral trout *Plectropomus leopardus* Lacepede. Queensland Fish. Serv. Res. Bull. 1: 1-42.
- Gonzalez Cardulis, J.R. and D. Guitart Manday. 1969. Fishery explorations and connected oceanographical research in Cuba. FAO Fish. Rep. 71(1): 163.
- Goodbody, I.M. and J.L. Munro. 1971. Biological observations off the east coast of Jamaica, p. 437-447. In Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November 1968. UNESCO, Paris
- Gordon, M.S. and H.M. Kelly. 1962. Primary productivity of a Hawaiian coral reef: a critique of flow respirometry in turbulent waters. Ecology 43: 473-480.
- Goreau, T.F. 1959. The ecology of Jamaican coral reefs. 1. Species composition and zonation. Ecology 40: 67-90.
- Goreau, T.F. 1969. Post-pleistocene urban renewal in coral reefs. Micronesica (J. Coll. Guam) 5: 323-326.
- Goreau, T.F. and K. Burke. 1966. Pleistocene and Holocene geology of the island shelf near Kingston, Jamaica. Mar. Geol. 4: 207-225.
- Goreau, T.F. and J.W. Wells. 1967. The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. Bull. Mar. Sci. 17: 442-453.
- Green, R.H. 1970. Graphical estimation of rates of mortality and growth. J. Fish. Res. Bd. Canada 27: 204-208.
- Griffiths, R.C. and J.G. Simpson. 1973. The present status of the exploitation of the fishery resources of Venezuela. Proc. Gulf Caribb. Fish. Inst. 25: 129-155.
- Grimes, C.B. 1978. Age, growth and length-weight relationship of vermillion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. Trans. Amer. Fish. Soc. 107: 454-456.
- Grimes, C.B. and G.R. Huntsman. 1980. Reproductive biology of the vermillion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. Fish. Bull. U.S. Nat. Mar. Fish. Serv. 78: 137-146.
- Guitart Manday, D. 1971. Un nuevo sistema para armas redes de ictioplancton, p. 449-459. In Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-25 November 1968. UNESCO, Paris.
- Guitart Manday, D. and M. Juarez Fernandez. 1966. Desarrollo embrionaria y primeras etapas de la cherna criolla, *Epinephelus striatus* (Bloch.) (Perciformes: Serranidae). Inst. Oceanologia, Habana. 1: 35-46.
- Gulland, J.A. 1969. Manual of methods for fish stock assessment. Part 1: Fish population analysis. FAO Man. Fish. Sci. 4: 154 p.
- Gulland, J.A., Compiler. 1971. The fish resources of the ocean. Fishing News (Books) Ltd., West Byfleet, Surrey, England.
- Gulland, J.A. 1974. The management of marine fisheries. Scientifica (Publishers) Ltd., Bristol.
- Gulland, J.A. 1979. Report of the FAO/IOP workshop on the fishery resources of the Western Indian Ocean south of the equator. Mahé, Seychelles Oct.-Nov. 1978. IOFC/DEV/79/45.
- Hamilton, W.J. and R.A. Peterman. 1971. Countershading in the colourful reef fish *Oaetodon lunula*: concealment, communication or both? Anim. Behav. 19: 357-364.
- Harrington, R.W., Jr. 1967. Environmentally controlled induction of primary male gonochorists from eggs of the self fertilizing hermaphroditic fish, *Rivulus marmoratus* Poey. Biol. Bull. (Woods Hole, Mass.) 132: 174-199.
- Harris, K.C. 1963. A brief historical review of the fishing industry in Jamaica. Division of Economics and Statistics, Ministry of Agriculture and Lands, Jamaica.
- Hartnoll, H.G. 1963. The biology of Manx spider crabs. Proc. Zool. Soc. London 141: 423-496.
- Hartnoll, H.G. 1965. The biology of spider crabs: a comparison of British and Jamaican species. Crustaceana 9: 1-16.
- Hartsuijker, L. 1982. A re-assessment of the stocks of reef fish on Pedro Bank. Fisheries Division, Min. of Agric., Jamaica Trap Fishery survey of Pedro Bank (Jamaica) 2nd phase. Tech. Rep. 4. pag. var.
- Hay, M.E. 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat. Bot. 11: 97-109.
- Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. Environ. Biol. Fish 3: 129-148.
- Herrnkind, W., P. Kanciruk, J. Halusky and R. Mclean. 1973. Descriptive characterisation of mass autumnal migrations of spiny lobster, *Panulirus argus*. Proc. Gulf Caribb. Fish. Inst. 25: 79-98.
- Hess, E. 1961. The fisheries of the Caribbean Sea, p. 213-222. In

- E. Borgstrom and A.F. Heighway (eds.) Atlantic ocean fisheries. Fishing News (Books) Ltd., Surrey, England.
- Hiatt, R.W. and D.W. Strasberg. 1960. Ecological relations of the fish fauna of the coral reefs of Marshall Islands. Ecol. Monogr. 30: 65-127.
- High, W.L. and A.J. Beardsley. 1970. Fish behaviour studies from an undersea habitat. Commer. Fish. Rev. 32: 31-37.
- Hill, R.B. 1978. The use of nearshore marine life as a food resource by American Samoans. Pacific Island Studies Program. Univ. of Hawaii. 170 p.
- Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965: 291-302.
- Hobson, E.S. 1969. Comments on certain recent generalizations regarding cleaning symbiosis in fishes. Pac. Sci. 23: 35-39.
- Hobson, E.S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70: 715-740.
- Hobson, E.S. 1973. Diel feeding migrations in tropical reef fishes. Helgol. Wiss. Meeresunters. 24: 361-370.
- Hobson, E.S. and J.R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull. U.S. Nat. Mar. Fish. Serv. 76: 133-153.
- Hoinig, J.M. 1982. Estimating mortality rate from the maximum observed age. I.C.E.S. CM 1982/D:5 Statistics Committee. 8 p.
- Hoinig, J.M. and W.D. Lawing. 1982. Estimating the total mortality rate using the maximum order statistic for age. I.C.E.S. CM 1982/D:7 Statistics Committee. 13 p.
- Holthuis, L.B. and J.S. Zaneveld. 1958. De kreeften van Nederlandse Antillen. Zool. Bijdr. 3. 26 p.
- Hornell, J. 1950. Fishing in many waters. Cambridge University Press, England.
- Hubbs, C.L. 1963. *Chaetodon aya* and related deep-living Butterfly fishes: their variations, distribution and synonymy. Bull. Mar. Sci. Gulf Caribb. 13: 133-192.
- Idyll, C.P. 1971a. The potential for fishery development in the Caribbean and adjacent seas. Univ. R.I. Mar. Bull. 1. 16 p.
- Idyll, C.P. 1971b. The spiny lobster fishery in the Caribbean. FAO Fish. Rep. 71(2): 133-148.
- Ingle, R.M. and R. Witham. 1969. Biological consideration in spiny lobster culture. Proc. Gulf Caribb. Fish. Inst. 21: 158-162.
- Itzkowitz, M. 1974. A behavioral reconnaissance of some Jamaican reef fishes. Zool. J. Linn. Soc. 55: 87-118.
- Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish 3: 65-84.
- Johannes, R.E., G.S. Helfman and J.M. Leis. 1981. Stock boundaries of reef and lagoon food fishes. (Abstr.) Proc. 4th Int. Coral Reef Symp. 1: 112.
- Jones, G.P. 1980. Contribution to the biology of the redbanded perch, *Ellerkeldia huntii* (Hector), with a discussion on hermaphroditism. J. Fish Biol. 17: 197-207.
- Jones, R. 1979. Predator-prey relationships with particular reference to vertebrates. Biol. Rev. 54: 73-97.
- Jones, R. 1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fish. Circ. 734. 55 p.
- Jones, R.S. 1963. Ecological relationships in Hawaiian and Johnson Island Acanthuridae (Surgeonfishes). Micronesica (J. Coll. Guam) 4: 309-361.
- Jordan, D.S. and B.W. Evermann. 1896-1900. The fishes of north and middle America. U.S. Natl. Mus. Bull. 47(1-4). 3313 p.
- Jordan, D.S., B.W. Evermann and H.W. Clark. 1950. Check list of the fishes and fishlike vertebrates of north and middle America, north of the northern boundary of Venezuela and Colombia. Reprint of Appendix X to the Report of the U.S. Commissioner of Fisheries for 1928; originally issued Feb. 1930. U.S. Govt. Printing Offices, Washington, D.C. 670 p.
- Juhl, R. 1971. Status and potential of the fishery in the Caribbean. Proc. Gulf Caribb. Fish Inst. 23: 175-183.
- Kami, H.I. and I.I. Ikehara. 1976. Notes on the annual juvenile siganid harvest in Guam. Micronesia 12: 323-325.
- Kawaguchi, K. 1974. Handline and longline fishing explorations for snapper and related species in the Caribbean and adjacent waters. Mar. Fish. Rev. 36(9): 8-31.
- Kipling, C. and W.E. Frost. 1970. A study of the mortality, population numbers, yearclass strengths, production and food consumption of pike, *Esox lucius* (L) in Windermere from 1944 to 1962. J. Anim. Ecol. 39: 115-157.
- Kuhlmann, D.H.H. 1970. Die Korallenriffe Kubas. I. Genese und Evolution. Int. Rev. Gesamt. Hydrobiol. 55: 729-756.
- Kuhlmann, D.H.H. 1971. Die Korallenriffe Kubas. II. Zur Ökologie der Bankriffe und ihrer Korallen. Int. Rev. Gesamt. Hydrobiol. 56: 145-199.
- Lachner, E.A. 1954. A revision of the goatfish genus *Upeneus* with descriptions of two new species. Proc. U.S. Natl. Mus. 103: 497-532.
- Laevastu, T. and F. Favorite. 1978. Numerical evaluation of marine ecosystems. Part I. Deterministic Bulk Biomass Model (BBM). Northwest and Alaska Fisheries Center, N.M.F.S. Processed Report. 22 p.
- Larkin, P.A. and W. Gazey. 1982. Applications of ecological simulation models to management of tropical multispecies fisheries, p. 123-140. In D. Pauly and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Lavenda, N. 1949. Sexual differences and normal protogynous hermaphroditism in the Atlantic sea bass, *Centropristes striatus*. Copeia 1949: 185-194.
- Lebeau, A. and J.C. Cuff. 1975. Biologie et pêche du capitaine *Lethrinus enigmaticus* (Smith) 1959 du banc Saya de Malha (Océan Indien). Rev. Trav. Inst. Pêches Mar. 39: 415-442.
- Le Guen, J.C. 1971. Dynamique des populations de *Pseudolithus (Fonticulus) elongatus* (Bowd. 1825). Poissons-Sciaenidae. Cah. O.R.S.T.O.M., Ser. Oceanogr. 9: 3-84.
- Leim, K.F. 1963. Sex reversal as a natural process in the synbranchiform fish *Monopterus albus*. Copeia 1963: 303-312.
- Leis, J.M. 1981. Distribution of fish larvae around Lizaru Island, Great Barrier Reef: coral reef lagoon as refuge? Proc. 4th Int. Coral Reef Symp. 2: 471-478.
- Leis, J.M. and J.M. Miller. 1976. Offshore distributional patterns of Hawaiian fish larvae. Mar. Biol. 36: 359-367.
- Lewis, J.B. 1951. The phyllosoma larvae of the spiny lobster, *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 1: 89-103.
- Lewis, J.B., H.B. Moore and W. Babis. 1952. Post-larval stages of the spiny lobster, *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 2: 325-337.
- Little, E.J. 1972. Tagging of spiny lobsters (*Panulirus argus*) in the Florida Keys, 1967-1969. Fla. Dept. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 31. 23 p.
- Longley, W.H. 1929. Publications based on studies at Tortugas. Carnegie Inst. Wash. Yearb. 28: 288-290.
- Longley, W.H. and S.F. Hildebrand. 1941. Systematic catalogue of fishes of Tortugas, Florida. Carnegie Inst. Wash. Publ. 535. 331 p.

- Longley, W.H. and S.F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on colour, habits and local distribution. Pap. Tortugas Lab. 34. 331 p.
- Loubens, G. 1978. Biologie de quelques espèces de poisson du lagon Néo-Calédonien I. Détermination de l'âge (otolithométrie). Cah. ORSTOM, Sér. Océanogr. 15(3-4): 263-283.
- Loubens, G. 1980a. Biologie de quelques espèces de poisson du lagon Néo-Calédonien II. Sexualité et reproduction. Cahiers de l'Indo-Pacifique 2(1): 41-72.
- Loubens, G. 1980b. Biologie de quelques espèces de poisson du lagon Néo-Calédonien III. Croissance. Cahiers de l'Indo-Pacifique 2(2): 101-153.
- Luckhurst, B. 1972. Reef fish populations on small coral heads with special reference to the territoriality of *Eupomacentrus fuscus*. McGill Univ., Montreal, Quebec. M.S. thesis.
- Luckhurst, B. and K. Luckhurst. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curaçao, Netherlands Antilles. Can. J. Zool. 55: 681-689.
- Lux, F.E. n.d. Age determination of fishes. U.S. Fish Wildl. Serv. Fish. Leaflet 488. 10 p.
- Manooch, C.S. 1976. Age, growth and mortality of the white grunt, *Haemulon plumieri* Lacepede (Pisces: Pomadasyidae), from North Carolina and South Carolina. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 30: 58-70.
- Manooch, C.S. and C.A. Barans. 1982. Distribution, abundance, age and growth of the tomtate, *Haemulon aurolineatum*, along the south-eastern United States coast. Fish. Bull. U.S. Nat. Mar. Fish. Serv. 80: 1-20.
- Manooch, C.S. and M. Halmovica. 1978. Age and growth of the gag, *Mycteroperca microlepis*, and age and size composition of the recreational catch off the south-eastern United States. Trans. Amer. Fish. Soc. 107: 234-240.
- Manter, H.W. 1930. Studies of the trematodes of Tortugas fishes. Carnegie Inst. Wash. Yearb. 29: 338-340.
- Margalef, R. 1971. The pelagic ecosystem of the Caribbean Sea, p. 477-482. In Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November 1968. UNESCO, Paris.
- Marshall, N. 1980. Fishery yield of coral reefs and adjacent shallow-water environments, p. 103-109. In S.B. Saila and P.M. Roedel (eds.) Stock assessment for tropical small-scale fisheries. Int. Cent. Mar. Res. Dev. University of Rhode Island, Kingston.
- Marshall, N. 1981. Exploring the applicability of the edaphomorphic index concept to estimating the fisheries potential of coral reef environments. (Abstr.) Proc. 4th Int. Coral Reef Symp. 1: 112.
- Marshall, T.C. 1965. Fishes of the Great Barrier Reef and coastal waters of Queensland. Angus & Robertson Ltd., Sydney.
- Marten, G.G. and J.J. Polovina. 1982. A comparative study of fish yields from various tropical ecosystems, p. 255-289. In D. Pauly and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Mattox, N.T. 1951. A preliminary report on the biology and economics of the spiny lobster in Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 4: 69-70.
- McErlean, A.J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces: Serranidae), on the west coast of Florida. Tech. Ser. Fla. Board Conserv. 41: 1-29.
- McFarland, W.N. 1982. Recruitment patterns in tropical reef fishes, p. 83-91. In G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) The biological bases for reef fishery management. NOAA Tech. Memo. NMFS-SEFC-80.
- McKenney, T.W. 1959. A contribution to the life history of the squirrelfish *Holocentrus vexillarius* Poey. Bull. Mar. Sci. Gulf Caribb. 9: 174-221.
- McKenney, T.W., E.C. Alexander and G.L. Voss. 1958. Early development and larval distribution of the carangid fish, *Caranx crysos* (Mitchill). Bull. Mar. Sci. Gulf Caribb. 8: 160-200.
- McLean, R. and W.F. Herrnkind. 1971. Compact schooling during a mass movement by grunts. Copela 1971: 328-330.
- Meek, S.E. and S.F. Hildebrand. 1925. The marine fishes of Panama. Field Mus. Nat. Hist. Publ. Zool. Ser. No. 226. 15(II): 331-707.
- Melo, A.F.M. 1976. Aspectos biológico-pesqueros de *Epinephelus morio* (Val), "mero", p. 223-266. In Memorias del Primer Simposio Nacional de Recursos Pesqueros Marinos de Mexico, Mexico. Instituto Nacional de Pesca 2.
- Menon, M.D. 1953. The determination of age and growth of fishes of tropical and subtropical waters. J. Bombay Nat. Hist. Soc. 51: 623-635.
- Moe, M.A., Jr. 1966. Tagging fishes in Florida offshore waters. Tech. Ser. Fla. Board Conserv. 49: 1-40.
- Moe, M.A., Jr. 1967. Prolonged survival and migration of three tagged reef fishes in the Gulf of Mexico. Trans. Amer. Fish. Soc. 96: 228-229.
- Moe, M.A., Jr. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser. Mar. Lab. Fla. 10. 95 p.
- Moe, M.A., Jr. 1972. Movement and migration of south Florida fishes. Tech. Ser. Fla. Board Conserv. 69. 25 p.
- Moe, M.A., Jr., R.H. Lewis and R.M. Ingle. 1968. Pompano mariculture: preliminary data and basic considerations. Tech. Ser. Fla. Board Conserv. 55. 65 p.
- Moe, M.A., Jr., D.S. Beaumariage and R.W. Topp. 1970. Return of tagged gag, *Mycteroperca microlepis* and Caribbean red snapper, *Lutjanus campechanus*, after six years of freedom. Trans. Amer. Fish. Soc. 99: 428-429.
- Moffitt, R.B. 1980. A preliminary report on bottom fishing in the North-west Hawaiian Islands, p. 216-225. In R. Grigg and R. Pfund (eds.) Proc. Symp. on status of resource investigations in the N.W. Hawaiian Islands. Univ. Hawaii Sea Grant Misc. Rept. UNIHI-SEAGRANT-MR-8004.
- Moiseev, P.A. 1971. The living resources of the world ocean. Translated from Russian by N. Kaner and W.E. Ricker. Edited by B. Golek. Israel Program for Scientific Translations Ltd., Jerusalem.
- Montalenti, G. 1937. Mullidae, p. 391-398. In S. Lo Bianco. Fauna e flora del Golfo di Napoli. Monografia 38: Uova, larve e stadi giovanili di Teleostei. Stazione Zoologica di Napoli, Italy.
- Moore, D. 1967. Triggerfishes (Balistidae) of the western Atlantic. Bull. Mar. Sci. 17: 689-722.
- Moyer, J.T. and P. Nakazono. 1978. Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. Jap. J. Ichthyol. 25: 101-106.
- Munro, J.L. 1969. The sea fisheries of Jamaica: past, present and future. Jam. J. 3: 16-22.
- Munro, J.L. 1973. Large-volume stackable fish traps for offshore fishing. Proc. Gulf Caribb. Fish. Inst. 25: 121-128.
- Munro, J.L. 1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. J. Cons., Cons. Int. Explor. Mer. 35: 337-350.

- Munro, J.L. 1977. Actual and potential fish production from the coralline shelves of the Caribbean Sea. FAO Fish. Rep. 200: 301-321.
- Munro, J.L. 1980. Stock assessment models: applicability and utility in tropical small-scale fisheries, p. 35-47. *In* S.B. Saila and P.M. Roedel (eds.) Stock assessment for tropical small-scale fisheries. Int. Cent. Mar. Res. Dev. University of Rhode Island, Kingston.
- Munro, J.L. 1982. Estimation of the parameters of the von Bertalanffy growth equation from recapture data at variable time intervals. *J. Cons., Cons. Int. Explor. Mer.* 40: 199-200.
- Munro, J.L., P.H. Reeson and V.C. Gaut. 1971. Dynamic factors affecting the performance of the Antillean fish trap. *Proc. Gulf Caribb. Fish. Inst.* 23: 184-194.
- Munro, J.L., V.C. Gaut, R. Thompson and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *J. Fish Biol.* 5: 69-84.
- Murdy, E.O. and C.J. Ferraris. 1980. The contribution of coral reef fisheries to Philippine fisheries production. *ICLARM Newsletter* 3(1): 21-22.
- Nagelkerken, W.P. 1971. A study on the occurrence of fishes in relation to coral. (Abstr) 9th Meeting Assoc. Island Mar. Labs. Caribb. Oct. 1971, Cumana, Venezuela.
- Nagelkerken, W.P. 1979. Biology of the grayby, *Epinephelus cruentatus*, of the coral reef of Curaçao. *Studies Fauna Curaçao* 60. 118 p.
- Nagelkerken, W.P. 1981. Distribution and ecology of the groupers (Serranidae) and snappers (Lutjanidae) of the Netherlands Antilles. *Publ. Found. Scient. Res. Surinam Netherlands Antilles, Nat. Hist. Ser.* 3. 71 p.
- Nahhas, F.M. and R.M. Cable. 1964. Digenetic and aspidogastroid trematodes from marine fishes of Curaçao and Jamaica. *Tulane Stud. Zool.* 11: 169-228.
- Nascimento, U.F. and C.B. Rojas. 1970. Production pesquera en Venezuela. *Inf. Téc. Dir. Gen. Desarr. Pesq. (Venez.)* 16. 52 p.
- Nelson, R.S. and C.S. Manooch. 1982. Growth and mortality of red snappers in the West-Central Atlantic Ocean and the Northern Gulf of Mexico. *Trans. Amer. Fish. Soc.* 111: 465-475.
- Nichols, J.T. 1929. The fishes of Puerto Rico and the Virgin Islands; Branchiostomidae to Sciaenidae. *Sci. Surv. P.R. Virgin Islands* 10(2): 336-338.
- Norman, J.R. 1963. A history of fishes. Ernest Benn, London.
- Nzioka, R.M. 1979. Observations on the spawning seasons of East African reef fishes. *J. Fish Biol.* 14: 329-342.
- Odum, H.T. and E.P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Enewetok Atoll. *Ecol. Monogr.* 25: 291-320.
- Odum, H.T., J.R. Burkholder and J. Rivero. 1959. Measurements of productivity of turtle grass flats, reefs and the Bahia Fosforescente of Southern Puerto Rico. *Publ. Inst. Mar. Sci. Univ. Tex.* 6: 159-170.
- Ogden, J.C. 1976. Some aspects of herbivore-plant relationships on Caribbean reef and seagrass beds. *Aquat. Bot.* 2: 103-116.
- Ogden, J.C. and N.S. Buckman. 1973. Movements, foraging groups and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54: 589-596.
- Ogden, J.C. and P.S. Lobel. 1973. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.* 3: 49-63.
- Olsen, D.A. and J.A. La Place. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. *Proc. Gulf Caribb. Fish. Inst.* 31: 130-144.
- Olsen, D.A., A.E. Dammann and J.A. La Place. 1978. Mesh selectivity of West Indian fish traps. *Mar. Fish. Rev.* 40(7): 15-16.
- Oswald, E.O. 1962. Resource appraisal project for the possible expansion of local fisheries (Puerto Rico). FAO/UNDP (Tech. Assist.) Rep. Fish. 1482. 24 p.
- Oswald, E.O. 1963. Developing an offshore fishery in Jamaica. *Proc. Gulf Caribb. Fish. Inst.* 15: 134-139.
- Ovchinnikov, V.V. 1971. Swordfishes and billfishes in the Atlantic Ocean; ecology and functional morphology. Translated from Russian. Israel Program for Scientific Translations, Jerusalem.
- Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. *Science* 173: 1124-1127.
- Pannella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes, p. 28-39. *In* T.B. Bagenal (ed.) Proceedings of an international symposium on the ageing of fish. Unwin Bros. Ltd., Surrey, England.
- Parrish, J., L. Taylor, M. De Crosta, S. Feldkamp, L. Sanderson and C. Sorden. 1980. Trophic studies of shallow water fish communities in the Northwestern Hawaiian Islands, p. 175-190. *In* R. Grigg and R. Pfund (eds.) Proc. Symp. on status of resource investigations in the N.W. Hawaiian Islands. Univ. Hawaii Sea Grant Misc. Rept. UNIH-SEA GRANT-MR-8004.
- Paul, L.J. 1968. Early growth characteristics of the New Zealand snapper, *Oryzophrys auratus* (Forster), with reference to selection of a scale-sampling site. *N.Z. J. Mar. Freshwater Res.* 2: 273-292.
- Pauly, D. 1980a. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons., Cons. Int. Explor. Mer.* 39: 175-192.
- Pauly, D. 1980b. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality and stock-recruitment relationships, p. 154-172. *In* S.B. Saila and P.M. Roedel (eds.) Stock assessment for tropical small-scale fisheries. Int. Cent. Mar. Res. Dev., University of Rhode Island, Kingston.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforsch.* 28: 251-282.
- Pauly, D. 1982. Studying single-species dynamics in a tropical multispecies context, p. 33-70. *In* D. Pauly and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Pauly, D. and N. David. 1981. ELEFAN I, a basic program for the objective extraction of growth parameters from length-frequency data. *Meeresforsch.* 28: 205-211.
- Pauly, D. and J. Ingles. 1981. Aspects of the growth and natural mortality of exploited coral reef fishes. *Proc. 4th Int. Coral Reef Symp.* 1: 89-98.
- Peacock, N.A. 1974. A study of the spiny lobster fishery of Antigua and Barbuda. *Proc. Gulf Caribb. Fish. Inst.* 26: 117-130.
- Peacock, N.A. 1976. Lesser Antilles fisheries: their management and development. Ministry of Overseas Development, London.
- Perez Farfante, I., J.I. Acosta Jimenez and M. Alemany Proenza. 1961. Datos sobre la biología pesquera del camarón (*Penaeus duorarum* Burkenroad) Ser. Estud. Sobre Trabajos Invest., ICIT, Habana. 20. 76 p.
- Perloth, I. 1971. Distribution of mass in the near surface waters of the Caribbean, p. 147-152. *In* Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November 1968. UNESCO Paris

- Pinto Paiva, M. 1960. Dimorfismo sexual observado em relacoes de peso e comprimento da lagosta, *Panulirus argus* (Latr.). Rev. Bras. Biol. 20: 51-62.
- Polovina, J.J. and D.T. Tagami. 1980. Preliminary results from ecosystem modeling at French Frigate Shoals, p. 286-298. In R. Grigg and R. Pfund (eds.) Proc. Symp. on status of resource investigations in the N.W. Hawaiian Islands. Univ. Hawaii Seagrant Misc. Rept. UNIH-SEAGRANT-MR-8004.
- Pope, J. 1979. Stock assessment in multispecies fisheries with special reference to the trawl fishery in the Gulf of Thailand. South China Sea Fisheries Development and Coordinating Programme. Fisheries Technical Papers SCS/DEV/79/19. 106 p.
- Post, J.C. 1971. The impoverishment of the fish fauna on coral reefs around Curaçao. (Abstr) 9th Meeting Assoc. Island Mar. Labs. Caribb. Oct. 1971, Cumana, Venezuela.
- Potts, G.W. 1970. The schooling ethology of *Lutjanus monostigma* (Pisces) in the shallow reef environment of Aldabra. J. Zool. 161: 223-235.
- Powell, D.G. 1979. Estimation of mortality and growth parameters from the length-frequency of a catch. Rapp. P.-v. Réunion. Cons. Int. Explor. Mer. 175: 167-169.
- Powers, J.E. and M.F. Crow. 1982. Towards models of reef fish exploitation, p. 185-201. In G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) The biological bases for reef fishery management. NOAA Tech. Memo. NMFS-SEFC-80.
- Powles, H. 1975. Abundance, seasonality, distribution and aspects of the ecology of some larval fishes off Barbados. McGill University, Montreal. Ph.D. dissertation.
- Presley, R.F. 1970. Larval snowy grouper *Epinephelus niveatus* Valenciennes, 1826, from the Florida Straits. Fla. Dept. Nat. Resour. Mar. Res. Lab. Leaflet. Ser. 4. 6 p.
- Provenzano, A.J. 1969. Recent experiments on the laboratory rearing of tropical lobster larvae. Proc. Gulf Caribb. Fish. Inst. 21: 152-157.
- Ralston, S. 1977. Age determination of a tropical butterfly fish utilizing daily growth rings of otoliths. Fish. Bull. U.S. Nat. Mar. Fish. Serv. 74: 990-994.
- Ralston, S. 1980. An analysis of the Hawaiian offshore hand-line fishery: a progress report, p. 204-215. In R. Grigg and R. Pfund (eds.) Proc. Symp. on status of resource investigations in the N.W. Hawaiian Islands. Univ. Hawaii Seagrant Misc. Rept. UNIH-SEAGRANT-MR-8004.
- Ralston, S. and G.T. Miyamoto. 1981. Estimation of the age of a tropical reef fish using the density of daily growth increments. Proc. 4th Int. Coral Reef Symp. 1: 83-88.
- Randall, J.E. 1956. A revision of the surgeon genus *Acanthurus*. Pac. Sci. 10: 159-235.
- Randall, J.E. 1961a. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus-sandvicensis*. Pac. Sci. 15: 215-272.
- Randall, J.E. 1961b. Observations on the spawning of surgeonfishes (Acanthuridae) in the Society Islands. Copeia 1961: 237-238.
- Randall, J.E. 1961c. Overgrazing of algae by herbivorous marine fishes. Ecology 42: 812.
- Randall, J.E. 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 14: 201-241.
- Randall, J.E. 1963a. Additional recoveries of tagged reef fishes from the Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 15: 155-157.
- Randall, J.E. 1963b. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3: 31-47.
- Randall, J.E. 1963c. Notes on the systematics of parrotfishes (Scaridae), with emphasis on sexual dichromatism. Copeia 1963: 225-237.
- Randall, J.E. 1964a. A revision of the file fish genera *Amanes* and *Cantherhines*. Copeia 1964: 331-361.
- Randall, J.E. 1964b. Sediment-producing fishes. Underwater Nat. 2: 30-32.
- Randall, J.E. 1965a. Food habits of the Nassau Grouper (*Epinephelus striatus*). 6th meeting Assoc. Island Mar. Labs. Caribb. 6: 13-16.
- Randall, J.E. 1965b. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46: 255-260.
- Randall, J.E. 1967. Food habits of reef fishes in the West Indies. Stud. Trop. Oceanogr., Univ. Miami 5: 655-847.
- Randall, J.E. 1968. Caribbean reef fishes. T.F.H. Publ., Neptune City, New Jersey.
- Randall, J.E. 1980. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. Fish. Bull. U.S. Nat. Mar. Fish. Serv. 78: 201-249.
- Randall, J.E. and V.E. Brock. 1960. Observations on the ecology of Epinepheline and Lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Amer. Fish. Soc. 89: 9-16.
- Randall, J.E. and W.D. Hartman. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol. 1: 216-225.
- Randall, J.E. and H.A. Randall. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bull. Mar. Sci. Gulf Caribb. 4: 444-480.
- Randall, J.E. and H.A. Randall. 1963. The spawning and early development of the Atlantic parrotfish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica (N.Y.) 48: 49-60.
- Randall, J.E., R.E. Schroeder and W.A. Starck. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Caribb. J. Sci. 4: (2/3).
- Randall, J.E. and G.L. Warmke. 1967. The food habits of the hog fish *Lachnolaimus maximus*, a labrid fish from the Western Atlantic. Caribb. J. Sci. 7: 141-144.
- Rathbun, M.J. 1902. The Brachyura and Macrura of Puerto Rico. Bull. U.S. Fish Comm. 20(2): 1-127.
- Rathbun, M.J. 1925. The spider crabs of America. U.S. Natl. Mus. Bull. 129.
- Rathbun, M.J. 1933. Brachyuran crabs of Puerto Rico and the Virgin Islands. Sci. Sur. P.R. Virgin Isl. N.Y. Acad. Sci. 15: 1-121.
- Razniewski, J. 1970. On the occurrence of spawning concentrations of some fish species over the N.W. African shelf in the summer of 1967. Rapp. P.-v. Réunion. Cons. Int. Explor. Mer. 159: 199-201.
- Reese, E.S. 1973. Duration of residence by coral reef fishes on 'home' reefs. Copeia 1973: 145-149.
- Reid, G.K. 1954. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf Caribb. 4: 1-94.
- Reinboth, R. 1968. Protogynie bei Papagei fischen (Scaridae). Z. Naturf. 23B: 852-855.
- Richards, F.A. 1960. Some chemical and hydrographic observations along the north coast of S. America. 1. Cabo Tres Puntas to Curaçao, including the Cariaco Trench and the Gulf of Cariaco. Deep-Sea Res. 7: 163-182.
- Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119. 300 p.
- Ricker, W.E. 1968. Methods of assessment of fish production in fresh waters. IBP Handbook 3. Blackwell Sci. Publ., Oxford.

- Ricker, W.E. 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.* 30: 409-434.
- Rivas, L.R. 1949. A record of the lutjanid fish (*Lutjanus cyanopterus*) for the Atlantic Coast of the United States with notes on related species of the genus. *Copeia* 1949: 150-152.
- Rivas, L.R. 1970. Snappers of the Western Atlantic. *Commer. Fish. Rev.* 32: 41-44.
- Robinson, R.K. and D.E. Dimitriou. 1963. The status of the Florida spiny lobster fishery, 1962-63. *Tech. Ser. Fla. Board Conserv.* 42. 27 p.
- Rodriguez Pino, Z. 1961. *Lutjanus ambiguus*. *Contrib. Cent. Invest. Pesq. Habana* 14. 20 p.
- Rodriguez Pino, Z. 1962. Estudios estadísticos y biológicos sobre la bajiaba (*Lutjanus synagris*). *Cent. Invest. Pesq. Habana. Nota Sobre Invest.* 4. 99 p.
- Roessler, M.A. 1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida and observations on the seasonal occurrence and life histories of selected species. *Bull. Mar. Sci.* 20: 860-893.
- Rojas, L.E. 1960. Estudios estadísticos y biológicos sobre el pargo criollo, *Lutjanus analis*. *Cent. Invest. Pesq. Habana. Nota Sobre Invest.* 2: 3-16.
- Rosa, H., Jr. 1965. Preparation of synopses on the biology of species of living aquatic organisms. *FAO Fish. Synop.* 1 (Rev. 1). 75 p.
- Rosenblatt, R.H. and E.S. Hobson. 1969. Parrotfishes (Scaridae) of the Eastern Pacific, with a generic rearrangement of the Scarinae. *Copeia* 1969: 434-453.
- Russell, B.C., G.R.V. Anderson and F.H. Talbot. 1977. Seasonality and recruitment of coral reef fishes. *Aust. J. Mar. Freshw. Res.* 28: 521-528.
- Russell, B.C., F.H. Talbot and S. Domm. 1974. Patterns of colonisation of artificial reefs by coral reef fishes. *Proc. 2nd Int. Coral Reef Symp.* 1: 193-206.
- Saila, S.B. 1982. Markov models in fish community studies—some basic concepts and suggested applications, p. 202-210. *In* G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) *The biological bases for reef fishery management*. NOAA Tech. Memo. NMFS-SEFC-80.
- Saila, S.B. and R.G. Lough. 1981. Mortality and growth estimation from size data— an application to some Atlantic herring larvae. *Proc. P.-v. Réunion. Cons. Int. Explor. Mer.* 178: 7-14.
- Saila, S.B. and P.M. Roedel, Editors. 1980. Stock assessment for tropical small-scale fisheries. *Int. Cent. Mar. Res. Dev., University of Rhode Island, Kingston.*
- Sale, P.F. 1969. Pertinent stimuli for habitat selection by the juvenile manini, *Acanthurus triostegus sandvicensis*. *Ecology* 50: 616-623.
- Sale, P.F. 1970. Distribution of larval Acanthuridae off Hawaii. *Copeia* 1970: 765-766.
- Sale, P.F. 1976. Reef fish lottery. *Nat. Hist. N.Y.* 85: 61-64.
- Sale, P.F. 1978. Coexistence of coral reef fishes—a lottery for living space. *Environ. Biol. Fish.* 3: 85-102.
- Sale, P.F. 1982. The structure and dynamics of coral reef fish communities, p. 241-253. *In* D. Pauly and G.I. Murphy (eds.) *Theory and management of tropical fisheries*. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Sale, P.F. and W.A. Douglas. 1981. Precision and accuracy of visual census techniques for fish assemblages on coral patch reef. *Environ. Biol. Fish.* 6: 333-340.
- Salmon, G.C. 1958. Report on the fisheries industry in the countries served by the Caribbean Commission. *FAO Fish. Rep.* 781. 86 p.
- Saloman, C.H. and W.A. Fable, Jr. 1981. Length-frequency distributions of recreationally caught reef fishes from Panama City, Florida in 1978 and 1979. NOAA Tech. Memo. NMFS-SEFC-61.
- Saunders, D.C. 1966a. A survey of the blood parasites of the marine fishes of Puerto Rico. *Trans. Amer. Microsc. Soc.* 85: 193-199.
- Saunders, D.C. 1966b. Differential blood cell counts of 121 species of marine fishes of Puerto Rico. *Trans. Amer. Microsc. Soc.* 85: 427-449.
- Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Bull. Inter-Amer. Trop. Tuna Comm.* 2: 247-285.
- Schroeder, R.E. 1971. Ecology of the intestinal trematodes of the gray snapper, *Lutjanus griseus*, near Lower Matecumbe Key, Florida, with a description of a new species. *Stud. Trop. Oceanogr. Univ. Miami* 10: 153-221.
- Schultz, L.P. 1958. Review of the parrotfishes, family Scaridae. *U.S. Natl. Mus. Bull.* 214. 143 p.
- Scott, J.W. 1969. A technique for producing and mounting otolith wafers for age determination. *Calif. Fish Game* 55: 86-88.
- Scotton, L.N. and D.P. De Sylva. 1972. Fish babies. *Sea Front.* 4: 194-201.
- Simpson, A.C. 1951. The fecundity of the plaice. *Fish. Invest. Min. Agric. Fish. Food (G.B.) Ser. II Sea Fish.* 17. 27 p.
- Simpson, J.G. and R.C. Griffiths. 1967. The fishery resources of Venezuela and their exploitation. *Ser. Recursos Exploit. Pesq. Of. Nac. Pesca* 1: 172-206.
- Sims, H.W. 1965. Notes on the occurrence of prenaupliosoma larvae of spiny lobsters in the plankton. *Bull. Mar. Sci.* 15: 223-227.
- Sims, H.W. 1966. An annotated bibliography of the spiny lobsters; families Palinuridae and Scyllaridae. *Tech. Ser. Fla. Board Conserv.* 48. 84 p.
- Smith, C.L. 1958. The groupers of Bermuda, p. 37-59. *In* J.E. Bardach, C.L. Smith and D.W. Menzel. *Bermuda Fisheries Research Program final report*. Bermuda Trade Development Board, Hamilton.
- Smith, C.L. 1959. Hermaphroditism in some serranid fishes from Bermuda. *Pap. Mich. Acad. Sci.* 44: 111-118.
- Smith, C.L. 1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic. *FAO Fish. Synop.* 23. 61 p.
- Smith, C.L. 1965. The patterns of sexuality and the classification of serranid fishes. *Amer. Mus. Novit.* 2207. 20 p.
- Smith, C.L. 1966. *Menophorus* Poey, a serranid genus based on two hybrids of *Cephalopholis fulva* and *Paranthias furcifer*, with comments on the systematic placement of *Paranthias*. *Amer. Mus. Novit.* 2276. 20 p.
- Smith, C.L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bull. Amer. Mus. Nat. Hist.* 146: 67-242.
- Smith, C.L. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Trans. Amer. Fish. Soc.* 101: 257-261.
- Smith, C.L. 1975. The evolution of hermaphroditism in fishes, p. 295-310. *In* R. Reinboth (ed.) *Intersexuality in the animal kingdom*. Springer-Verlag, New York.
- Smith, C.L. 1978a. Coral reef fish communities: a compromise view. *Environ. Biol. Fish.* 3: 109-128.
- Smith, C.L. 1982. Patterns of reproduction in coral reef fishes, p. 49-60. *In* G.R. Huntsman, W.R. Nicholson and W.W. Fox (eds.) *The biological bases for reef fishery management*. NOAA Tech. Memo. NMFS-SEFC-80.
- Smith, C.L. and J.C. Tyler. 1973. Population ecology of a

- Bahamian suprabenthic shore fish assemblage. Amer. Mus. Novit. 2528. 38 p.
- Smith, F.G.W. 1948. The spiny lobster industry of the Caribbean and Florida. Caribb. Res. Coun. Fish. Series 3. 49 p.
- Smith, F.G.W. 1959. The spiny lobster industry of the Caribbean. Caribbean Comm., Port of Spain.
- Smith, J.L.B. 1956. The parrotfishes of the family Callyodontidae of the western Indian Ocean. Ichthyol. Bull. 1. 23 p.
- Smith, J.L.B. 1959. The identity of *Scarus gibbus* Ruppell, 1828 and other parrotfishes of the family Callyodontidae from the Red Sea and the western Indian Ocean. Ichthyol. Bull. 16: 265-282.
- Smith, J.L.B. 1965. The sea fishes of Southern Africa. 5th ed. Central News Agency, Capetown.
- Smith, R.L. 1967. Some aspects of protein digestion in the white grunt, *Haemulon plumieri*. Comp. Biochem. Physiol. 30A: 1115-1123.
- Smith, R.L. and A.C. Paulson. 1974. Food transit times and gut pH in two Pacific parrotfishes. Copeia 1974: 796-799.
- Smith, R.L. and A.C. Paulson. 1975. Carbonic anhydrase in some coral reef fishes: adaptation to carbonate ingestion. Comp. Biochem. Physiol. 50A: 131-134.
- Smith, S.V. 1978b. Coral-reef area and contributions of reefs to processes and resources of the world's oceans. Nature 273: 225-226.
- Sogandares-Bernal, F. 1959. Digenetic trematodes of marine fishes from the Gulf of Panama and Bimini, British West Indies. Tulane Stud. Biol. 3: 71-117.
- Sogandares-Bernal, F. and L.M. Sogandares. 1961. Nine digenetic trematodes of marine fishes from the Atlantic coast of Panama. Tulane Stud. Biol. 5: 141-153.
- Springer, V.G. and A.J. McErlean. 1962. A study of the behaviour of some tagged South Florida reef fishes. Amer. Wildl. Nat. 67: 386-397.
- Ssentongo, G.W. and P.A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board Can. 30: 695-698.
- Starck, W.A. 1971. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus) in the Florida Keys. Stud. Trop. Oceanogr. Univ. Miami 10: 12-150.
- Starck, W.A. and W.P. Davis. 1966. Night habits of fishes of Alligator reef, Florida. Ichthyologica 38: 313-356.
- Steinberg, J.C., W.C. Cumming and J.Y. Macbain (Spies). 1965. Further bio-acoustic studies of the west coast of North Bimini, Bahamas. Bull. Mar. Sci. 15: 942-963.
- Stevenson, D.K. 1978. Management of a tropical pot fishery for maximum sustainable yield. Proc. Gulf Caribb. Fish. Inst. 30: 95-115.
- Stevenson, D.K. and N. Marshall. 1974. Generalisations on the fisheries potential of coral reefs and adjacent shallow-water environments, p. 147-156. In Proc. 2nd Int. Coral Reef Symp. Australia, June 1973. Great Barrier Reef Committee, Brisbane.
- Stevenson, D.K. and P. Stuart-Sharkey. 1980. Performance of wire fish traps on the Western Coast of Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 32: 173-193.
- Storey, M. 1937. The relation between normal range and mortality of fish due to cold at Sanibel Island, Florida. Ecology 18: 10-26.
- Straughan, R.P.L. 1959. The salt-water aquarium in the home. T. Yoseloff Ltd., London.
- Suarez-Caabro, J.A. 1973. Status of fisheries in Puerto Rico, 1972. Agric. Fish. Contrib. Dep. Agric. P.R. 5. 50 p.
- Suarez-Caabro, J.A. and P.P. Duarte Bello. 1961. Biología pesquera de bonito (*Katsuwonus pelamis*) y la albacora (*Thunnus atlanticus*) en Cuba 1. Ser. Estud. Sobre Trabajos de Invest. ICIT Habana. 15. 150 p.
- Sutcliffe, W.H. 1952. Some observations of the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. Proc. Gulf Caribb. Fish. Inst. 4: 64-68.
- Sutcliffe, W.H. 1953. Notes on the biology of a spiny lobster, *Panulirus guttatus* in Bermuda. Ecology 34: 794-796.
- Sutcliffe, W.H. 1957. Observations on the growth rate of the immature Bermuda spiny lobster, *Panulirus argus*. Ecology 38: 526-529.
- Swarts, W. 1969. Blood studies of some marine teleosts. Trans. Amer. Fish. Soc. 98: 328-331.
- Sweat, D.E. 1968. Growth and tagging studies on *Panulirus argus* (Latreille) in the Florida Keys. Tech. Ser. Fla. Board Conserv. 57. 30 p.
- Sylvester, J.R. and A.E. Dammann. 1972. Pot fishing in the Virgin Island. Mar. Fish. Rev. 34: 33-35.
- Tabb, D.C. and R.B. Manning. 1961. A check list of the flora and fauna of Northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July 1957 through September 1960. Bull. Mar. Sci. Gulf Caribb. 11: 552-649.
- Talbot, F.H. 1960. Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forsk.). Annals. S. Afric. Mus. 65: 549-573.
- Talbot, F.H. 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. Proc. Zool. Soc. London 145: 431-470.
- Talbot, F.H. and B. Goldman. 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef System, p. 425-444. In Proc. Symp. Coral and Coral Reefs Mar. Biol. Assoc. India.
- Talbot, F.H., B.C. Russell and G.R.V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecol. Monogr. 48: 425-440.
- Tavolga, W.N. and J. Wodinsky. 1965. Auditory capacities in fishes: threshold variability in the blue-striped grunt *Haemulon sciurus*. Anim. Behav. 13: 301-311.
- Thomas, L.P., D.R. Moore and R.C. Work. 1961. Effects of Hurricane Donna on the turtle grass beds of Bimini Bay, Florida. Bull. Mar. Sci. Gulf Caribb. 11: 191-197.
- Thompson, E.F. 1945. The fisheries of Jamaica. Bulletin 18. Development and Welfare in the West Indies, Bridgetown, Barbados.
- Thompson, R.W. 1978. Results of the UNDP/FAO Bahamas deep water fishery survey 1972-1975. Proc. Gulf Caribb. Fish. Inst. 30: 44-70.
- Ting, R.Y. 1973. Investigation of the resource potential of the spiny lobster (*Panulirus argus* Latreille) in Puerto Rico. Contrib. Agropec. Pesq. Dep. Agric. 5. 18 p.
- Topp, R.W. 1963. The tagging of fishes in Florida. 1962 programme. Prof. Pap. Ser. Fla. Board Conserv. Mar. Lab. 5. 76 p.
- Travis, D.F. 1954. The moulting cycle of the spiny lobster, *Panulirus argus* Latreille. I. Moulting and growth in laboratory-maintained individuals. Biol. Bull. (Woods Hole, Mass.) 107: 433-450.
- Ukawa, M., M. Higuchi and S. Mito. 1966. Spawning habits and early life history of a serranid fish, *Epinephelus akaara* (Temminck et Schlegel) Jap. J. Ichthyol. 13: 151-161.
- UNESCO. 1971. Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curaçao, Netherlands Antilles, 18-26 November, 1968. Papers on physical and chemical oceanography, marine geology and geophysics and marine biology. UNESCO, Paris. 545 p.

- United States Naval Oceanographic Office. 1968, 1969, 1970. Pilot charts of the North Atlantic Ocean. U.S. Naval Oceanogr. Off., Washington D.C.
- van Sickle, J. 1977. Mortality rates from size distributions. The application of a conservation law. *Oecologia* 27: 311-318.
- Vidaeus, L. 1969a. An inventory of the St. Vincent fishing industry. Rep. SF/CAR/REG 16 M5. 30 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1969b. An inventory of the Grenada fishing industry. Rep. SF/CAR/REG 16 M6. 34 p. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1969c. An inventory of the St. Lucia fishing industry. Rep. SF/CAR/REG 16 M4. 27 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1969d. An inventory of the Barbados fishing industry. Rep. SF/CAR/REG 16 M2. 34 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1970a. An inventory of the fishing industries of the Netherlands Antilles. Rep. SF/CAR/REG 189 M21. 19 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1970b. An inventory of the Jamaican fishing industry. Rep. SF/CAR/REG 180 M9. 47 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1970c. An inventory of the Antigua fishing industry. Rep. SF/CAR/REG 16 M8. 25 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1970d. An inventory of the Monserrat fishing industry. Rep. SF/CAR/REG 189 M10. 18 p. and appendix. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1970e. An inventory of the Trinidad and Tobago fishing industry. Rep. SF/CAR/REG 16 M7. 66 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1971a. An inventory of the Dominica fishing industry. Rep. SF/CAR/REG 189 M18. 14 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vidaeus, L. 1971b. Caribbean fishing industries. A summary report of a series of country studies. Rep. SF/CAR/REG 189 M24. 48 p. and appendices. UNDP/FAO Caribb. Fish. Develop. Proj., Rome.
- Vivien, M.L. 1973. Contribution a la connaissance de l'ethologie alimentaire de l'ichthyofaune du platier interne des recifs corraliens de Tulcar (Madagascar). *Tethys Suppl.* 5: 221-308.
- Wagner, D.P. and R.S. Wolf. 1974. Results of troll fishing explorations in the Caribbean. *Mar. Fish. Rev.* 36(9): 35-43.
- Wass, R.C. 1982. The shoreline fishery of American Samoa—past and present, p. 51-83. *In* J.L. Munro (ed.) Ecological aspects of coastal zone management. Proc. Seminar on Marine and Coastal Processes in the Pacific. Motupore Is. Res. Centre. July 1980. UNESCO, Jakarta.
- Watson, W. and J.M. Leis. 1974. Ichthyoplankton in Kanohe Bay, Hawaii. A one year study of fish eggs and larvae. Univ. Hawaii Sea Grant Tech. Rep. TR-75-01. 178 p.
- Weidemann-Smith, S. 1968. Otolith age reading by means of surface structure examination. *J. Cons., Cons. Int. Explor. Mer.* 32: 270-277.
- Wheeler, J.F.G. and F.D. Ommanney. 1953. Report on the Mauritius-Seychelles Fisheries Survey, 1948-49. *Fish. Publ., Lond.* 3: 1-148.
- Whiteleather, R.T. 1955. Another look at the Caribbean fisheries. *Proc. Gulf Caribb. Fish. Inst.* 7: 180-184.
- Wickham, D.A. 1971. Night lighting—a harvesting strategy for underutilised coastal pelagic school fishes. *Proc. Gulf Caribb. Fish. Inst.* 23: 84-90.
- Wicklund, R. 1969. Observation on spawning of the lane snapper. *Underwater Nat.* 4: 40.
- Wicklund, R. 1972. Feeding habits of the bar jack. *Underwater Nat.* 7: 31-32.
- Widrig, T.M. 1954. Method of estimating fish populations, with application to Pacific sardine. *Fish. Bull.* 56: 141-166.
- Wiles, D.W. 1952. Flying fish research in Barbados, p. 93-95. *In* Fisheries of the Caribbean; report of the fisheries conference, Kent House, Trinidad, March 1952. Caribbean Comm. Kent House, Port-of-Spain, Trinidad.
- Wijkstrom, V.N. 1974. Processing and marketing marine fish—possible guidelines for the 1975-1979 period, p. 55-67. *In* A.S. Msangi and J.J. Griffin (eds.) International Conference on Marine Resources Development in Eastern Africa. University of Dar es Salaam and International Center for Marine Resources Development, University of Rhode Island, Kingston.
- Willimovsky, N.J. and E.C. Wicklund. 1963. Tables of the incomplete Beta function for the calculation of fish population yield. Institute of Fisheries, Univ. British Columbia, Vancouver, Canada.
- Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. *Fish. Bull.* 65: 1-298.
- Winn, H.E. 1955. Formation of a mucous envelope at night by parrotfishes. *Zoologica (N.Y.)* 40: 145-148.
- Winn, H.E. and J.E. Bardach. 1957. Behaviour, sexual dichromatism and species of parrotfishes. *Science* 125: 885-886.
- Winn, H.E. and J.E. Bardach. 1960. Some aspects of the comparative biology of parrotfishes at Bermuda. *Zoologica (N.Y.)* 45: 29-34.
- Winn, H.E., J.A. Marshall and B. Hazlett. 1964. Behaviour, diel activities and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. *Copeia* 1964: 413-425.
- Winn, H.E., M. Salmon and N. Roberts. 1964. Sun-compass orientation by parrotfishes. *Z. Tierpsychol.* 21: 798-812.
- Witham, R., R.M. Ingle and E.A. Joyce, Jr. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. *Tech. Ser. Fla. Board Conserv.* 53. 31 p.
- Witham, R., R.M. Ingle and H.W. Sims, Jr. 1964. Notes on post-larvae of *Panulirus argus*. *J. Fla. Acad. Sci.* 27: 289-297.
- Wolf, R.S. and G.R. Chislett. 1974. Trap fishing explorations for snapper and related species in the Caribbean and adjacent waters. *Mar. Fish. Rev.* 36(9): 49-61.
- Wolf, R.S. and W.F. Rathjen. 1974. Exploratory fishing activities of the UNDP/FAO Caribbean Fishery Development Project, 1965-1971: a summary. *Mar. Fish. Rev.* 36(9): 1-8.
- Wood, E.J.F. 1971. Phytoplankton distribution in the Caribbean region, p. 399-410. *In* Symposium on investigations and resources of the Caribbean Sea and adjacent regions, Willemstad, Curacao, Netherlands Antilles, 18-26 November 1968. UNESCO, Paris.
- Woods, L.P. 1955. Western Atlantic species of the genus *Ithlo-centrus*. *Ithelidiana Zool.* 37: 91-119.
- Wust, G. 1964. Stratification and circulation in the Antillean-Caribbean basins I. Columbia Univ. Press, New York and London.
- Yasumoto, T., I. Nakajima, R. Bagnis and R. Adachi. 1977. Finding of a dinoflagellate as a likely culprit of ciguatera. *Bull. Jap. Soc. Sci. Fish.* 43: 1021-1026.
- Young, P.C. and R.B. Martin. 1982. Evidence for protogynous hermaphroditism in some lethrinid fishes. *J. Fish. Biol.* 21: 475-484.
- Zans, V.A. 1958. The Pedro Cays and Pedro Bank. Report on the survey of the cays, 1955-57. *Bull. No. 3. Geol. Surv. Dep., Jamaica.* 47 p.