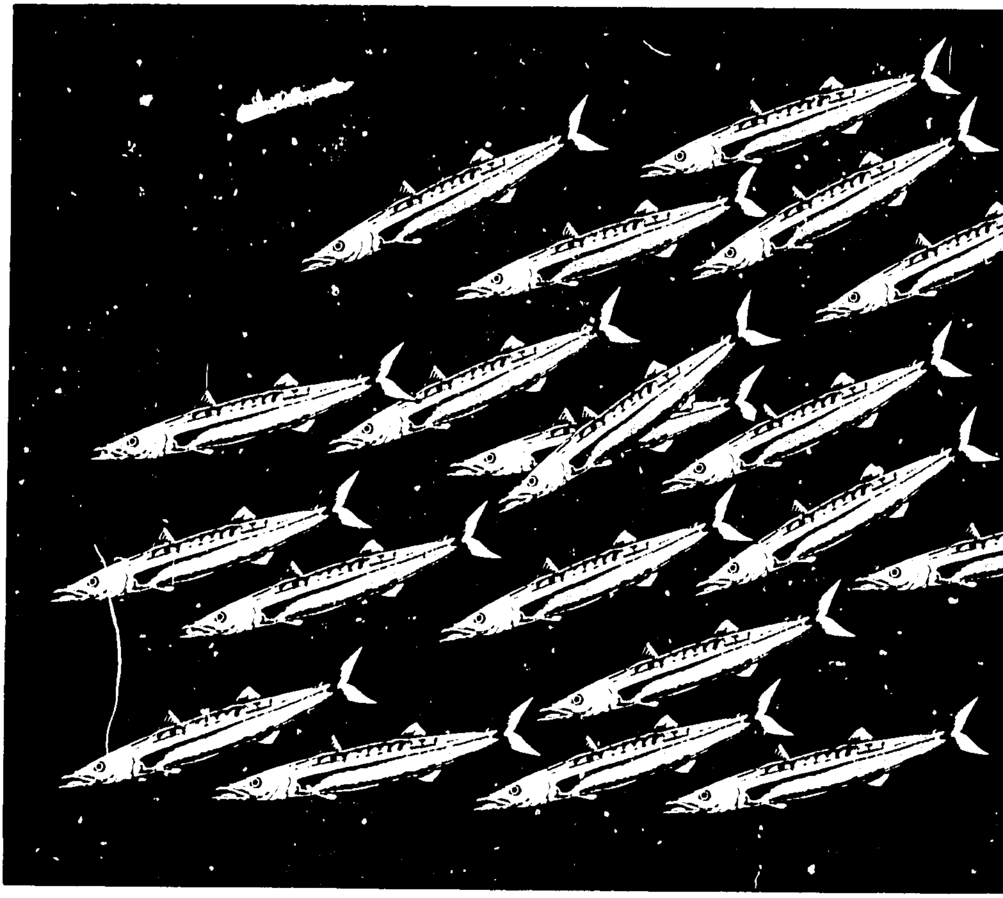
PN-AAK-976

FISH BEHAVIOR
AND ITS USE IN THE CAPTURE AND CULTURE OF FISHES

John E. Bardach, John J. Magnuson, Robert C. May
and Johanna M. Reinhart, Editors



INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT

ICLARM CONFERENCE PROCEEDINGS 5

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Proceedings of the Conference on the
Physiological and Behavioral Manipulation
of Food Fish as Production and Management
Tools, Beliagio, Italy, 3-8 November 1977
held jointly by the Hawaii Institute of Marine
Biology and the International Center for
Living Aquatic Resources Management, Manila

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Printed in Manila, Philippines

Published by ICLARM, MCC P.O. Box 1501, Makati,
Metro Manila, Philippines

Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart, Editors. 1980. Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

ISSN 0115-4389 ISBN 971-02-0003-8

Preface

This book had its origins in the recommendations of the World Food and Nutrition Study of the U.S. National Academy of Sciences. The Aquatic Food Sources Panel of that study which I chaired recommended bio-technical research for gear development as one of the areas that would help augment the world-wide availability of high grade animal protein. Aquaculture was another area for research emphasis with the same goal. The Rockefeller Foundation and ICLARM, the International Center for Living Aquatic Resources Management, were receptive to my suggestion that a conference on fish behavior and fisheries management would be a logical sequel to the just mentioned recommendations. The Rockefeller Foundation then offered its Bellagio Study and Conference Center for a conference on fish behavior and fisheries management and bore, together with ICLARM, travel and other conference costs. In furthering the plans for the conference, the Hawaii Institute of Marine Biology at the University of Hawaii became the third cosponsor.

Bio-technical gear development and yet other facets of capture fisheries, as well as aquaculture, rely to a substantial extent on the knowledge and understanding of fish behavior. Attempts to devise certain new management methods and to improve certain old ones are difficult, if not futile, without a thorough background on how and why fish behave in response to manipulations of various kinds.

With this rationale, I organized the program and asked the Foundation to invite the participants, each of whom presented a paper; these papers comprise most of this book. Dr. John J. Magnuson edited the papers and assisted me substantially in writing the first chapter on Perspectives. It both briefs the reader on the thrust and the implications of the contributions and provides a summary for those who need an overview without much technical detail. To highlight application possibilities, the first chapter is arranged simply into sections on capture, culture, and ranching. The main part of the book provides documentation for the Perspectives in the form of individual "state of the art" papers, each followed by a discussion that often emphasizes application, with attention to the efficiency and simplicity of certain operations and measures. The discussions were recorded and edited by Dr. Robert C. May who also helped organize the conference. The fourth editor, Johanna M. Reinhart, edited all written material into a final, consistent text.

Inasmuch as many individual contributions deal with topics that do not permit an easy separation into what might apply to hunting and what else to farming (e.g., chemoreception and feeding, sex inversion, artificial imprinting), the papers in the book proper are grouped into three broad categories: (1) those that apply to the manipulation of fish behavior essentially through the animals' senses, i.e., to attract or repel them, to enhance their feeding, etc., (2) those that apply to controlling or predicting the reproduction or recruitment of fishes, and (3) those that apply to predicting the distribution of fishes and their responses to fishing gear.

There are several ways to use this book: specialists may wish to read thoroughly only one or several chapters and the discussions pertaining to them, and perhaps browse through the rest of the book. Managers and decision makers may elect to begin with the Perspectives and if they desire amplification and technical detail, they would consult one or the other specific contribution. Students and persons with a general interest in fisheries and aquaculture would read the whole book, realizing that some repetition can hardly be avoided in the organization we have chosen. We are sure, though, that this very organization gives the book a special flavor that makes it suitable for a wide audience.

Several persons were prominently involved in making the conference a success as well as in the preparation of this volume. Thanks go to Dr. John A. Pino and his staff at the Rockefeller Foundation, Dr. John C. Marr at ICLARM and Dr. and Mrs. William C. Olson and their staff at Bellagio. I also thank Mrs. Mary Kalaiwaa and Mrs. Linda Hamada for helping with voluminous pre- and post-conference correspondence. Dr. Roy Harden Jones prepared the excellent indexes to the book.

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SENSORY CAPABILITIES AND MANIPULATION OF FISH BEHAVIOR

REPRODUCTION AND RECRUITMENT

BEHAVIOR AND DISTRIBUTION

Introduction and Perspectives

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BARDACH, J E., AND J.J. MAGNUSON. 1980. Introduction and perspectives, p. 1-31. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Men have traditionally interacted directly with fishes, first as hunters and more recently as farmers. Methods used by the hunters and farmers of fishes were developed slowly, by experience, over hundreds of generations. Hunting methods were effective enough that fishery management and science developed largely around problems of overexploitation. Inefficiency often has been encouraged to preserve stocks or for social reasons. Aquaculture developed in some regions and overcame some of the uncertainties confronted in capture fisheries. Problems dealing directly with methods of capture and culture of fishes were left largely to the hunters and farmers of fishes, while fishery science and management concentrated primarily on population dynamics of fishes and occasionally attempted to supplement reproduction of exploited stocks.

Increased efficiency of capture and culture was for the most part a matter of individual responsibility and benefits rather than of societal responsibility and values. After the Second World War, fishery production increased greatly but by the late 1960s, world yields began to level off, problems of overcapitalization and overexploitation of important stocks became more pervasive, and at the same time, energy and material shortages developed for society. As a consequence, efficiency has become identified as a solution of benefit not only to an individual, but also to society as a whole.

This book deals with the utility of information on behavior and physiology in the management of fisheries. Our concern is with the control and prediction of behavior and physiology in such a way as to increase efficiency of use of energy, material, direct monetary inputs, and even time associated with capture and culture of fishes. In this connection, one should note that many fisheries are inefficient and overcapitalized, even in the developed nations.

Manipulations of obvious interest are to attract and repel fishes, control their reproduction in captivity, and to optimize rate of body growth. Predictions of value include being able to determine a priori their location in space and time, and their behavioral response to fishing gear. Manipulations of fish behavior, as envisaged, apply to both capture and culture fisheries, while the predictive capabilities seem more relevant to capture than culture fisheries. In open systems, control of behavior is more difficult and has higher payoffs than in small enclosures.

Ours is not the first conference or book to highlight the utility of information on fish behavior in fisheries. Those major conferences we know of occurred over a 10-yr span from 1957 to 1968 (Table 1).

The two FAO fishing gear conferences in 1957 and 1963 treated behavior in a minor way in respect to locating, detecting, and attracting fishes in capture fisheries. Kesteven's treatment in the Symposium on Fish Behavior in 1958 was more comprehensive and had behavior as the focus. Evidence was reviewed on the influence of fish behavior on liability to capture, fish distribution, reproduction,

TABLE 1. Major conferences from 1957-1968 noting application of fish behavior to fisheries.

Date of conference	Date of English publication	Title	Editor(s)
1957	1959	1st FAO World Fishing Gear Congress	Kristjonsson
1958	1960	Symposium on Fish Behavior IPFC	Kesteven
1963	1964	2nd FAO World Fishing Gear Congress	Finn
1967	1969 1969a,b	FAO Conference on Fish Behavior in Relation to Fishing Techniques and Tactics	Ben-Tuvia and W. Dickson
1968	1971	All-Union Conference on Fish Behavior and Fishing Techniques	Alekseev
1977	1980	ICLARM Bellagio Conference	Bardach, Magnuson, May, and Reinhart

growth, and natural mortality. At a time when population dynamics dominated fishery science, Kesteven pointed out that behavioral data were important to help estimate vital statistics of fish populations. These three early conferences also attempted to stimulate additional behavioral research in relation to capture fisheries and to set some priorities for fisheries-oriented behavioral research and its applications.

By 1967 an entire FAO conference was devoted to fish behavior in relation to capture fisheries. Its objectives were primarily to systematically review fish behavior in relation to fishing gear and operations and to stimulate further work. The number and variety of papers at this conference indicated that behavioral studies had become an integral part of fishery research. The All-Union Conference (USSR) at about the same date (Alekseev 1968) also emphasized the importance of behavior in capture fisheries. In particular, stress was laid on how behavior studies might help to develop new methods to capture underexploited stocks on the high seas and perhaps to intervene in some way to increase ocean fish productivity.

These events that occurred 10 to 20 yr before our conference at Bellagio did stimulate considerably behavioral research based on the hope and the promise that new techniques and applications of behavioral data would increase the yield of capture fisheries around the world, but we could find no quantitative evaluation(s) of the application of these efforts.

Yet we believe, like others before us, that capture fisheries intimately depend on the knowledge which hunters of fishes have of fish behavior. Our conference and earlier conferences had this assumption in common but the treatment at Bellagio differed from the previous ones in two important aspects: (1) we placed behavioral data in culture fisheries in a position of equal importance to their previously identified role in capture fisheries, and (2) we attempted to examine in our discussions how information on fish behavior could be related to increases in efficiency of fishing and fish farming operations. In earlier conferences, an important goal was to further the increase in yields from underexploited stocks. Though these latter still exist today in places, worldwide energy and material shortages suggest that efficiency of direct and indirect energy use be given equal, if not greater, weight than the amount as such of catch or pond production. All participants agreed on the importance of this subtheme, but we would remind the reader that the stress on it will vary in individual contributions depending on the nature and the state of the art of various subjects, as well as on the approach to them taken by individual authors.

When fisheries are considered today as one component in food systems, with decisions to be made by planners on the various modes of protein supply that may best satisfy a country's nutritional and economic needs, one question relating to efficiency stands out: which mode of animal protein production—fisheries, fish farming, or animal husbandry—uses energy inputs to best advantage? Fishing operations have been subjected to energy accounting (Slesser 1974; Rawitscher and Mayer 1977) and when one compares the amounts of energy required to produce 1 g of protein (in unprocessed foods) from fisheries, aquaculture, and animal husbandry (Table 2), it becomes apparent that certain water-based operations compare favorably with most, if not all, modes of rearing avian or mammalian livestock. Some of the reasons for such favorable comparisons in the case of fisheries lie in the need only to gather rather than produce massive aggregations of animal protein. Knowledge of fish

TABLE 2. Energy used to produce one gram of protein in unprocessed foods (U.S.); values in Kcal (rounded to nearest integer) from Rawitscher and Mayer (1977) and from Bardach (unpublished data).

Carbohydrate staples	
Wheat	14
Rice	40
Fisheries	
Herring (Atlantic)	7
Ocean perch (Atlantic)	17
Blue crab (Chesapeake)	28
Pink salmon (Pacific)	30
Cod, haddock, halibut (trawl fishery)	79-93
Tuna (high seas)	81
Shrimp (Gulf of Mexico)	600
Lobster (Maine)	770
Aquaculture	
Polyculture (Israel)	65
Catfish (Southern USA)	139
Catfish (Idaho, copious free water)[a]	83
Carp (in cages, sewage-fed stream)[a]	10
Malaysian prawn (Hawaii)	200 (328, tails only)
Oysters (Hawaii, cement raceways, pilot, likely potential)	400
Animal husbandry	
Eggs	132
Broilers	149
Pork	186
Milk	263
Range-land beef	685
Feed-lot beef	800

[a] Unique conditions.

whereabouts, and/or modern detection devices for them applied to take advantage of certain aspects of their behavior such as schooling further explain the relative effectiveness of some fishing processes. Also of note is the striking difference illustrated in Nomura's Table 1 detailing severalfold increases in energy expenditures with fishing distance while also pointing to the energy-saving characteristics of large setnets. This advantage is also illustrated by the low energy input into setnet-caught herring in Table 2. In aquaculture, energy expenditures in production have been reduced by seizing ecological advantages, for instance, through nutrient recycling in polyculture or even by integrating agriculture and aquaculture. Behavior can be used in both fisheries and aquaculture to reduce energy inputs and thus to reduce production costs per unit of protein; this is amplified in the remainder of the Perspectives.

When efficiency is applied to labor rather than to the use of energy and materials, the question of equity, in this case the right and opportunity to earn a livelihood, inevitably arises. It does so with urgency in the case of artisanal fisheries that undergo mechanization.

Though the questions of equity in fisheries and aquaculture were discussed, conference participants disclaimed competence to offer suggestions for dealing with these sensitive socioeconomic issues. They could not help but observe that they will become more pressing as we reach in capture fisheries the limits of biologically sustainable production of conventional stocks, as the physical bases for aquaculture become subjected to increasingly competitive pressures for alternative uses and as inputs into fish farming become increasingly costly. Even though the conference did not consider postharvest events, it may be germane to stress that processing of fish may take as much, if not more, energy than capturing them (Rawitscher and Mayer 1977). Naturally much attention will be devoted to the use of renewable energy sources in aquaculture and even in fishing, especially in the tropics.

Whatever the nature and intensity of inputs into fish capture and culture, it was agreed that socioeconomic and ecological balances ought to be sought which would optimize energy, labor and hence monetary costs of fisheries and aquaculture while giving satisfying and remunerative employment to many. If this balance is the goal while not depleting wild stocks and while lowering the cost of cultured fishes, knowledge of fish behavior can contribute much to the armentarium of the fisherman and the fish farmer; the few examples given here with their strong emphasis on efficiencies in the use of inputs point the way to further necessary background investigations and ensuing applied and adaptive research.

Capture Fisheries

Behavioral information developed at our conference is important in locating concentrations of fishes and capturing them. In addition, behavioral information is also significant in establishing management policies for fishes because their behavior influences their susceptibility to overfishing and how one must go about assessing their stocks.

Locating Fishes: Kemmerer illustrated how identification from aircraft and/or satellite of a certain water color, reflecting amount and kind of phytoplankton, permitted surprisingly accurate prediction of the whereabouts of Gulf menhaden. The implication for shortening search time and thus saving energy and money in the fisheries for other schooling species was very clear from this example of relating ecological and hydrographic variables to schooling behavior. A fairly massive deployment of vessels was necessary for ground truthing, a costly operation, but it must be remembered that the research effort was exerted only once to benefit the management of a renewable and thus perpetually exploitable resource.

Satellites will acquire greater resolution, and multispectral sensing will be refined still further, but even today the Gulf of Mexico menhaden study points the way to future cost-effective assessment methods of capture-facilitating behavior of schooling fishes in other parts of the world.

Distributional responses of fishes to physical and chemical gradients were considered by Magnuson from the point of view of predicting, a priori, the concentrations of particular fish species so as to minimize search time as well as maximize the catch per unit of effort. The easily measured variable, water temperature, can sometimes be used to locate the concentrations (Dietrich et al. 1959). In regions of very sharp fronts it may be useful to monitor bottom temperature with a towed thermister and to fish bottom trawls at particular temperatures or temperature gradients by the use of remotely sensed temperature from the trawl. Since distribution of species susceptible to capture by bottom trawls is usually not detectable from surface water temperature, satellites cannot be used routinely for locating these concentrations. To apply this technology, fishermen themselves would need to base their fishing activities on continuously monitored environmental variables. With temperature this is not difficult. In addition, evidence is accumulating that individual species prefer a particular temperature and that knowledge of this could be of use in attempts to fish more selectively for desired species. Oceanic fronts occur at the boundaries between major water masses such as the Gulf Stream but are found worldwide when it is recognized that the thermocline at the bottom of the mixed layer is analogous to a horizontal front.

Another example for the prediction of whereabouts of a species for fisheries exploitation came from Harden Jones who spoke largely about plaice migrations. These migratory fish follow defined routes in regular movements within areas occupied by particular stocks. This is well known to fishermen who pursue seasonal fisheries along these migration routes. The area covered by the migration circuit of a particular stock often appears to be contained within a specific regional hydrographic regime. Thus, it is clearly important for management to know how the behavior of the animals is related to hydrographic conditions along the migration routes. Observations from Lowestoft suggest that flatfish use tidal transport when migrating.

The initial "lock on" mechanism to the tidal stream used by the fish appears to rely on their capacity at certain stages of maturity to distinguish the various stages of the tides, i.e., to "tell' high water from low water slack. Best times for passive transport are thus perceived and "hitchhiking" off the bottom, where they rest at other times, is accomplished by the fish with least energy expenditure. Experimental catches during various parts of the tidal cycle bear out this part of the hypothesis. In addition, the fish have been shown to maintain a semi-diurnal pattern of vertical movement so that they repeatedly join and leave the appropriate tide when on migration. Eventually, they must "know" when they have reached their spawning grounds, that is, they must perceive an essential feature of that particular area. In the case of the plaice, Harden Jones advances the hypothesis that these fishes tell their spawning grounds by perceiving groundwater seepage.

If simple methods provide evidence for "homing" to groundwater seepages, one may entertain the further hypothesis that various groundwaters differ in their chemical characteristics and that olfactory imprinting may occur. This, in turn, would point to the existence of numerous substocks with profound implications for fishery management. It is possible that the phenomenon extends to other species, which share with the plaice close evolutionary relations to fishes that once upon a time spawned in fresh water.

Attraction and Repulsion: As man gained knowledge about the variety of the senses of fishes and the manner in which the various stimuli (especially sound) are propagated in the water, speculations, experiments, and observations were made on how to use these stimuli to guide fishes. Here subsumed would be attracting fishes, containing them, or excluding them from certain areas.

An earlier study on selective biological barriers (Huguenin 1968) summarizes some important aspects of fish reactions to visual, electrical, acoustical, and chemical stimuli and advocates that further research and development work be done with them. Table 3 taken from this feasibility study summarizes what sensory stimuli are thought to be most promising for influencing fish behavior.

TABLE 3. Summary of barrier elements to contain fishes (from Huguenin 1968).

Type of barrier	Previous use as repellent or barrier	Effectiveness	Effective with respect to	Mechanisms involved	Selectivity	Potential as a barrier element	Remarks
Light (white)	Yes	Good	Species	Not understood	Fair	Fair	Usually used as attractant
Color effects	Not intentionally	Fair	Species	Not understood	Fair	Fair/good	Distinct color effects, so more repellent than others; Contradictory results on which colors produce which effects and reasons for these effects
Electric barrier	Yes	Excellent	Length Species	Understood	Good	Excellent	Best suited to barring large predators Fright reaction may be exploitable, with the use of very little electric power

continued next page

TABLE 3 (con't.)

Acoustic barriers (biological sound)	Yes	Excellent	Species	Possibly understood	Good	Excellent	Boundaries likely to be indistinct
Bubble curtain	Yes	Very good	Size Species	Possibly understood	Unknown	Very good	Effectiveness is limited in currents, turbid water, and at night
Physical restraint	Yes	Excellent	Size Species	Understood	Very good	Excellent	Best known; May be limited by sea, wind, current, and ship damage
Chemical (olfactory)	Yes	Good	Species Age Sex	Possibly understood	Good/ excellent	Good/ excellent	Potential largely unknown; May prove the most selective

While the study deals mainly with containment or creating barriers, one ought to remember that barriers can also lead fish and are therefore potentially valuable for capture. The prominent treatment of sensory stimuli at this conference and their influence on behavior led to an appraisal of potential use of sensory clues in management, given the state of present knowledge. Smell and sound are prime candidates as instruments for manipulating fish behavior. Behavioral correlates of both are still only slightly known; for instance, few fish species in general, and even fewer commercial ones still can be identified by sound (Tavolga, this volume). Yet in some cases it may be possible to locate fishes by underwater listening. Inasmuch as several species produce sounds especially at spawning, the onset of reproduction may be ascertained by listening; it is, however, difficult to isolate the sounds of individuals, if not species, in the often uncommonly noisy underwater environment.

Playing back sounds, especially feeding sounds, to attract fish appears tantalizingly possible, but requires both greater knowledge of the role of sound communication among fishes and the development of better and cheaper equipment for underwater projection of low frequency sounds (Tavolga). It was agreed that certain aspects of sound, especially artificially produced biological sounds, would be worthy of further exploration so as to better guide the movement of certain species of fish and to do so more easily and efficiently than is now possible.

In hook and line fisheries attraction culminates in a strike usually oriented by visual stimuli. Blaxter dealt with vision and related adaptations of the eye of fishes to various environmental conditions, especially turbidity. He emphasized differences in visual reaction depending on hunger and fright. Contrast enhancement in fishes occurs through anatomical mechanisms such as polarizing and other filters as well as head movement in relation to still objects that should be perceived, e.g., sessile prey. Vision is important in feeding in many fishes, but acts together with other senses in peculiar sequences of dominance so that certain sensory modalities are more important at certain stages of the feeding act than others. For instance, hearing or chemical senses may be activated before an animal is able to sight a prey. It is therefore important to obtain information on the role of each sense in feeding behavior when fashioning attracting devices. Vision also counts in recognition of mates, especially their state of sexual maturity, in social recognition (schooling, space sharing with other species) and the recognition of predators. All existing hook-related lures (except for baited hooks) are based on empirical understanding of fish vision. Much scope exists for refining these devices with the help of research into the visual sense of fishes.

Recent research into the chemical senses of fishes has established that smell and taste play a substantial role in reproductive and social behavior of fishes and that feeding relies more, and in more complex fashion, on chemosensory stimulation than is commonly assumed (Atema, Hasler, Iwai, and Myrberg, this volume). Chemical stimuli can aggregate fish or guide them into traps, create barriers, and act as feeding enhancers. Chemoreception is also the basis of imprinting of migratory fishes and the use of pheromones in aquaculture. The last two promising subjects will be discussed under Culture and Ranching later in this chapter.

From the standpoint of commercial fisheries, attractants would have most value for stationary gear such as treated by Nomura. But the attraction or retention of schooling predators in any one area also seems interesting. Another possible use of chemical attractants might be to "shorten the time between bites" through inducing predators to strike more readily. Even less is known about chemical stimuli aversive to fishes than about those that might attract them. Perhaps compounds of potential value for excluding fishes from an area would be cheaper than attractants and that such methods should be investigated further. Even so they are likely to be effective on small to moderate scales and in closed or semi-enclosed environments.

Natural chemical attractants are used in a number of artisanal fisheries where traps are baited or areas are chummed, even with offal, and bait on the hook does, of course, also function as a chemical lure. When bait is used for schooling predators as it is for skipjack tuna, the attractant value of the bait lies in providing visual stimulation though there is also a strong olfactory component to tuna feeding as will be explained below.

It is not surprising that artificial chemical attractants in commercial fisheries have not been developed systematically. One reason is that knowledge about certain components of the natural attractants is recent and far from complete (Bardach 1975). Even if one could safely prescribe effective fish attractants, large amounts of substances would be necessary to be effective on a commercial scale and that therefore the species for which one would employ them would be preferably those that fetch a high cash return. (It is to be noted that artificial attractants of unknown composition are on the market in the U.S.A.; these are used for recreational fishing where a low unit cost of the compound or compounds is not of overriding importance.)

Reports exist on reactions of fishes to single amino acids (Sutterlin 1975) and to mixtures of compounds prominently including amino acids (Bardach 1975). Research concerning chemosensory reactions of tuna (Atema, this volume) reveals that the animals react with searching behavior even to the exhibition of feeding bars when they smell a rinse of their customary prey. Amino compounds singly and in combination, as well as the non-amino fraction of this same prey rinse (after volatile compounds have been evaporated from it), elicited feeding reactions, though weaker than when both were released together. Thus, olfactory stimuli for feeding are likely to be complex, at least for certain fishes. Inasmuch as rinses of different species have different chemical composition, somewhat like different fingerprints, chemical feeding stimuli likely vary by species and by prey, if not by location. Even aside from using chemicals in managing anadromous fishes, chemical lures appear to have enough potential of selectivity to enable their use in management over and beyond their use in facilitating commercial capture as mentioned speculatively by Huguenin (1968).

Alverson and Wilimovsky (1964) proposed to guide pelagic fishes by scent trails deployed from the air. The suggestion was imaginative but made when less was known about fish chemoreception and behavior than is known now. The practicability of such large-scale applications can be questioned if one remembers that the best recipe for attractants is a mix in which amino acids figure prominently. However, the amino acids that now appear likely as prominent components of such a mix are still so expensive that one kilogram or liter of concentrate of scent would likely cost several thousand dollars; in the open ocean, one liter does not go very far. On the other hand, it is easily stored and takes little space, far less than live or even frozen bait.

In addition, the attention span of pelagic fishes to chemical stimuli seems relatively short, a behavioral trait that appears to be adaptive since the ultimate stimulus for ingestion is visual. The fish would expend a great deal of energy in rapid swimming if they were to follow the scents of schools of prey for longer than a few minutes before they encounter them.

There are two possible uses of scent attractants for pelagic fishes, which appear a little more promising than those above. One is to fashion large floating traps equipped at the bag or pound end with intermittent scent-releasing devices. The other is to use a scent of favorite prey or an artificial substitute thereof together with bait that is either unfamiliar or not as attractive as the favorite food. For instance, one might spray anchovy scent in the sea while chumming tuna with shad or other cultured bait fishes. Reduction in the occurrence of natural bait makes the scheme interesting in some locations. It has not yet been tried, however, at a pilot level which could lead to a decision concerning prototype research.

As opposed to food scents which are composites of several chemicals with the potential to attract several species, pheromones appear to be highly selective on congeners, implying that both species segregation together with attraction may be possible through them (Solomon 1977). For instance, Timms and Kleerekoper (1972) reported the use of caged female catfish (emitting a pheromone) to capture large numbers of males in setnets. Obviously such practices are effective only during the reproductive season. Finally, we would cite again the hypothesis that plaice recognize their spawning grounds on the basis of smelling or tasting freshwater seepages (Harden Jones, this volume). Chemical signals, including pheromones, can safely be assumed to play a greater role in fish behavior than is now known; learning more about them so that this information can be used in capture and culture fisheries presents a challenge to fishermen and fishery scientists alike.

Responses to gear: Fishing gear can be grouped into passive and active gear depending upon whether the fish simply encounter the gear (set lines, traps, and gillnets) or the gear is used to actively pursue or enclose the fishes (purse seine, trawl) or to make them strike (trolling). Large energy savings are possible if passive rather than active gear can be used. This potential was developed by Nomura (this volume) and should receive serious attention in our future fisheries. The susceptibility of a fish to capture by passive gear can be readily assessed with data on its basal swimming activity. Skipjack tuna, for example, continuously swim several body lengths per second (Magnuson 1978). They would be expected to be captured efficiently by the appropriately designed passive gear.

Passive gear should be large so that the fish have a high probability of encountering it, and then have a means of retaining the fish at the gear. Leading the fishes into a bag as described by Nomura (this volume) for setnets or attracting them to the baited hooks of a longline are cases in point. Large setnets and floating traps, perhaps in connection with floating logs or branches and scent releases, should be effective. Alverson and Wilimovsky (1964) even suggested that such structures might be equipped with electronic fish detectors that alert a collector vessel to the presence of an accumulation of fishes. Research directed towards developing devices of this kind that rely on behavior and combine facets of various technologies in an innovative fashion has been advocated by the Aquatic Food Sources Panel of the World Food and Nutrition Study of the U.S. National Academy of Sciences (1977).

Nomura (this volume) detailed how net design in the Japanese setnet fishery takes into account the behavior of the species to be captured so as to obtain more fish per set, possibly at lower overall costs. For instance, enclosed spaces leading into the pound proper vary according to the milling behavior of different species, as do angles and lengths of wings. Here fishermen have important inputs into new adaptations of net design as they are being tested by Japanese fisheries research organizations.

With active fishing gear such as trawls and purse seines, the escape behavior of fishes is very important, but it was not treated by any of the contributors. The design and use of towed nets depends greatly upon the swimming abilities of the fish being sought. Accurate equations have been developed that predict "burst" or escape speeds of fishes. An understanding of difference in speed owing to shape and size of the fish is emerging. To demonstrate the role of this knowledge in gear design, it is instructive to contrast the requirements of a towed net to capture the large, sleek and powerful tuna (burst speeds faster than 16 km/h and the small pudgy flatfish (burst speeds no greater than 0.8 km/h. Since towing speeds are usually considerably less than 8 km/h, a very large net would be needed to engulf and retain a tuna. How large? A theoretical study by Barkley (1964) relevant to towed nets provides a basis for such computations and relates escape speeds to the required net diameter and towing speed. Another behavioral consideration included in these equations is the distance from which the fish first senses and reacts to the net. Differences in abilities to see and hear and thus escape or avoid a net, along with maximum swimming speed, spell success or failure for a fishing attempt.

Population Assessment and Prediction: The management of capture fisheries, in essence, involves matching the abundance of fish with the abundance of fishermen, taking biological, economic, and social factors into account. The prerequisite for successful management in capture fisheries is to know and/or predict abundance of fish over as long a time span in advance as is feasible since the management measures are likely to involve restrictive manipulations of ships and gear. They affect invested capital and deployment of fishermen, that is, labor, and as already stated, capture fisheries management has strong social and economic implications.

A particularly important segment of the world fish catch, namely around 30% but fluctuating from year to year, consists of schooling fishes. Most of these are small fishes, but they occur in very great numbers at certain times and places. The most important families of schooling fishes are the herrings and sardines (Clupeidae) and the anchovies (Engraulidae); large predatory fishes of the high seas, tunas and their relatives, also school.

Murphy (this volume) began his presentation on Schooling and the Ecology and Management of Marine Fishes by pointing out that schooling is not a phenomenon entirely peculiar to fishes. Birds flock and ungulates form herds. The origin of schooling is clouded in speculation but in the case of fishes one can well advance the tenet that originally schooling may have been an adaptation to the featureless environment of the open water realm. Its advantages to the individual lie in enhancing the chances of feeding and in reducing the chance of the individual's being preyed upon. Observations and theoretical calculations seem to bear out the latter, but probably also the former assumptions of the survival values of schooling. Schooling has a number of effects on the dynamics of the populations, which are by and large of the same species to which Hunter (see below) addressed himself, namely the herrings, anchovies, and tunas and their relatives. Schooling behavior is "good" for fish, as just stated, and it evolved during a long portion of the total history of life on the planet; long before man arrived on the evolutionary scene. As he perfected ships and gear, he became the prime predator on schooling fish, subjecting them to stronger predation pressure than they had experienced before.

A historical look at schooling fish populations reveals that a number of schooling species have collapsed since the early 1900s, apparently as a result of heavy fishing pressure. In other words, predictive capabilities were not good enough to provide early warning signals that the collapse in those fisheries was impending. One should note that schooling fish are easily overfished, to the point of no return, because they are captured not as individuals but as schools, and critical levels can be reached before declines in catches per unit of effort become apparent throughout the fishery. In addition, schooling fishes apparently have low survival rates and few age classes of spawners. These attributes and the efficient capture techniques which man developed for them further reduce chances to reproduce. Several chances to spawn might be essential when resilience to spawning failures is required.

How then should we manage schooling species on a sustainable basis? It appears that management must be in a position to impose Draconian reductions on the level of exploitation at the appropriate time. But to do so, measures of abundance must be developed that are independent of catch per unit of effort. Importantly, organizations responsible for research on schooling fish must support more studies aimed at understanding the schooling strategy of a population under exploitation and the ecological role of their schooling. This would enable the development of indicators and models in connection with early life history stages with recruitment, that is, their entry into or availability for a fishery.

As Hunter (this volume) stated, "natural fluctuations in the size of fish populations may vary from about 0.3 to 2 orders of magnitude." They are caused primarily by annual variability in the strength of incoming year-classes which usually has no obvious relation to the size of parent stock and is generally unpredictable. Lack of understanding of the relation between stock and recruitment has hindered effective management of marine fish stocks. Many experts believe that studies of mortality of early life history stages, particularly those of eggs and larvae, hold the key to elucidating the stock and recruitment relation. Thus, studies of the behavior and ecology of larval stages in relation to the sources of mortality and stock size may provide much of the needed information.

The offshore marine environment in which most of the schooling species are found is characterized by relatively stable environmental conditions. However, there occur catastrophic events (e.g., el niño in the case of the Peruvian anchovy) which could not be predicted in the past. Prediction of such events would be important in addition to establishing routine relations between larval abundance and that of later life history stages. The two main causes of larval mortality—starvation and predation—are difficult to assess simultaneously; they have therefore been approached separately. Starvation has received more attention as it is probably the more important determinant of larval abundance. Laboratory experiments indicate that the incidence of starvation can be identified by chemical, morphological and histological criteria, with the latter at present the most commonly ascertained.

It appeared from Hunter's presentation and interaction with other invited schooling fish experts (Blaxter, United Kingdom—herring; Murphy, Australia—Peruvian anchovy, tuna stocks) as if safe predictions on impending recruitment cannot be derived from our knowledge of the relation between the various aspects of larval behavioral ecology and future harvestable stock. Laboratory data will have to be evaluated continuously against sea conditions and cause-and-effect models will have to be refined over the next few years so as to have them adequately relate recruitment to stock density at various life history stages. It has to be added to these observations, while stressing the large percentage of the world fish harvest involved, that such research demands high biotechnical skills and would benefit from international collaboration. Such collaboration would include the training of scientists from developing countries in laboratories on temperate seashores where the main schooling fishes occur. At the same time, such training will help form much needed cadres of fish managers with high technical competence.

Fisheries for schooling species exploit one species at a time. In contrast, the bulk of artisanal and semi-industrialized fisheries in the tropics exploit a large number of species simultaneously. These include fisheries of coral reefs, sea grass beds, and those associated with mangrove swamps, incidentally providing a substantial contribution to the animal protein fare of tropical regions. The most important of these environments are coral reefs, characterized by high diversity; furthermore, the fish species on them exhibit extremely varied behavior patterns as a result of living together in a complex habitat. Management of these species is beset with difficulties as we lack life history information for many of them. In addition, in most countries where fishing prevails for these communities of reef and lagoon fishes, there is not enough money nor enough adequately trained people to mount sophisticated fisheries management programs. Under such conditions, practical management schemes must be simple and inexpensive. In fact, Johannes (this volume) proposes such schemes. He bases one of them on the fact that there occur among shallow water marine fishes of the tropics collective multiple species spawning peaks and also, more importantly, single species spawning aggregations of important food fishes such as the groupers (see also Reinboth, this volume). At other than spawning times, these fishes are relatively dispersed and their populations are fragmented. Once local spawning sites and times of various species are known, as they seem to be to artisanal fishermen, fishery biologists can monitor spawning populations year by year. As local fisheries concentrate around them, management strategies of limiting fishing efforts there become possible.

Another management-related observation of Johannes deals with spawning times and sites of these species which have pelagic larvae. Spawning appears to be geared to wind and currents in such a fashion that offshore transport of larvae would be minimized, assuring adequate recruitment into the juvenile, more sessile, shallow-water phases of their life cycles. It would follow intuitively that year-to-year variations in wind and current would influence the numbers of larvae that settle annually and eventually also the quality of fishing. He suggests that systematic investigations of the relations of wind and current to recruitment of several selected species be made over several years in various locations. If the former two variables are well correlated to the latter, wind and current measurements may become good predictors for recruitment. The simpler the nearshore hydrography, as for instance around isolated tropical islands, the clearer this relation may be.

It should be noted though that the pelagic larvae of some species regularly arrive inshore en masse during specific lunar periods. Such fishes are obviously not entirely at the mercy of offshore currents, but how they detect and move toward shallow water and how they time their arrival there is not known. Research on the behavior and general biology of reef fish larvae has been very limited and much valuable information awaits discovery.

Culture Fisheries

Conference participants reaffirmed that aquaculture has great promise to contribute selectively to the supply of animal protein for a hungry world. Better understanding and use of behavioral observations and ecological principles present advantages to aquafarmers which will ultimately be expressed in economic terms. Two important constraints to the development of aquaculture, especially in the sea, still are control over reproduction and the rearing of the offspring through highly vulnerable and delicate larval or juvenile stages; in short, seed production.

Reproduction: Controlled reproduction has been achieved on a commercial scale with only a few freshwater species, enabling aquafarmers to capitalize on all advantages of selective breeding such as better growth characteristics, disease resistance, and fitting the strain to special environmental and market conditions (Kinne and Rosenthal 1977; Kinne 1977). In this connection, the conference attendants reaffirmed the unquestionable value of treatment with pituitary hormones of fishes that are ready to spawn (see Liley, this volume) but noted and elaborated on certain relations among environmental, behavioral, and physiological variables that act on spawning readiness, in addition to the hormonal influences.

It is well known that certain fishes held under culture conditions begin to develop sexually but do not reach the final stages of maturity, whereas their wild congeners have no problems of reproducing normally. Oocytes may mature but ovulation and oviposition does not follow. Hormone injection may lead to spawning, but it also happens that the final stages of gonad maturation are not reached (Fontaine 1976). One must then embark on a rather lengthy hormone treatment which sometimes is not even effective. True, the purification of fish gonadotropins had led to further facilitation of spawning but purified fish gonadotropins are still costly and rely on a highly sophisticated technical base not easily obtained in many developing countries.

While purified fish gonadotropins have often given good results in facilitating spawning of the recalcitrant species, there are other biochemical manipulations which invite attention. They rely on compounds that appear to influence physiological pathways that affect hormone balances as a whole. Reference is made here to facilitators of mammalian ovulation such as clomiphene citrate (Jindra-Runac and Fijan 1975) and prostaglandins (Jalabert and Szöllösi 1975; Fontaine 1976). The results of these experiments have not been applied but they point the way to further research which may yield techniques less costly than some of those presently used.

Of equal promise for the armentarium of the commercial fish breeder are substances that finalize the spawning act, as it were (Liley, this volume). These are sex pheromones and chemicals released from the soil. Their importance has been demonstrated in a sufficient number of species, mostly freshwater, to have prompted a consensus at this conference towards urging vigorous pursuit of research on sex pheromones, that is, into the nature and action of chemical messengers, acting through smell, emanating from one or the other sex, that play an important role in facilitating or enabling the spawning act. Sex pheromones can also aid in fish capture as is described in the section of Attraction and Repulsion. Likewise, it was agreed that chemical substances emanating from the environment with a mode of action similar to that of sex pheromones should be investigated.

Little is yet known about pheromones in reproductive processes of fish except that they do exist and play a role in certain species. Fontaine (1976) states that pheromones have been implied to lead to increased activity by the male in some species, and to recognition of spawning partners in others. Several of these species are not used in commercial aquaculture but they illustrate a mechanism that bears further scrutiny among many more species than the relatively few for which pheromone action has been proved or is strongly implied (e.g., catfishes, salmon, and trout; Fontaine 1976). It is important to note also that there is strong interaction between reproductive maturity and the endocrine state associated with it and pheromone secretion and action.

Fontaine (1976) surmises that there are not only pheromones that facilitate the spawning act but others that may inhibit it. The latter may well be produced under stress, and as stress always operates under conditions of captivity, it follows that here is a fruitful area for research, probably one that will not be very costly to pursue. However, it does require more pronounced cooperation of biochemists, physiologists, and biologists than could be observed hitherto in research related to the development of aquaculture.

Soil chemicals, which like pheromones, act through chemosensory channels, play their role under certain peculiar climatic conditions. In Australia and Africa and by implication also in Asia where annual changes of drought and high water prevail, the spawning periods of many species coincide with the first rains and the onset of inundation. In a number of instances several Australian species would spawn only when dry soil was bathed by the first flood waters that lead into basins or reservoirs where spawning takes place (Lake 1967). Similar observations were made with a South African catfish of known aquaculture potential (van der Waal 1974), where oily compounds were found on the surface of the freshly inundated reservoir or ponds where spawning took place. The name given to this substance is "petrichor." Its chemical nature is unknown but investigations into the detailed chemistry of such a spawning facilitator may pay off handsomely as it is in the tropics and subtropics where the most substantial advances in aquaculture can be expected.

Finally though, one should also note the conference consensus that ecological, physiological, and behavioral studies into fish reproduction must be pursued simultaneously. This [illegible]ld permit emphasis on the interaction among the variable[illegible]sses, and substances that influence such a highly complex ph[illegible]on as the spawning of fishes and would be likely to lead to advances in understanding and therefore in the control of fish reproduction.

One aspect of this complex subject treated at the conference was the phenomenon of sex change. Steroid hormones, especially testosterone compounds, may elicit an actual change from female to male or suppress egg development. For instance, having mixed sexes in *Tilapia* and *Sarotherodon* ponds easily leads to crowding since the fishes mature early and have efficient parental care. While there are other ways to produce unisexual populations in these species, such as hybridization or early sexing by looking at the vent (Bardach et al. 1972), they may be less efficacious than hormone treatment (Tayamen and Shelton 1978). The rearing of all male populations in these fast growing tropical species is advantageous because the testes require less food energy and materials for their maturity than do the ovaries (Shul'man 1974).

The situation is different in the slower growing, later maturing salmonids of the temperate zone where culture of all female populations may be desirable because females generally mature 1 yr later than males (Hoar 1957). It may thus be possible to rear them to commercial harvesting size before they divert any of their feed into the maturing of gonads. Johnstone et al. (1978) report on the production of such all female populations by placing oestradiol in the rations of early juvenile rainbow trout and Atlantic salmon.

As to the ambisexual fishes treated by Reinboth (this volume), isolation of males from females in time and sometimes in space facilitates the rearing of one sex only, especially when sex change is elicited by the previously mentioned hormone techniques. In one ambisexual fish, the grouper *Epinephelus tauvina*, the onset of the male sex phase has been hastened experimentally (Reinboth) to take advantage of the edge in growth which males are reported to have over females. Likewise relevant, especially for establishing inbred lines, is the possibility of sperm storage for later self-fertilization in a protandrous (male first) ambisexual species.

The physiological mechanism underlying sex reversal, a feature common to several hundred species of teleosts, is poorly understood. It should be studied further because of its potential contribution to the physiology of reproduction among vertebrates and because of the direct and indirect applications the phenomenon may have in capture fisheries and aquaculture (Reinboth).

Rearing of Larvae: At the end of the larval or juvenile period through which hatchlings are cultured, stock is often transferred to different waters or actually released (see also Ranching). Observations of the behavior of such hatchlings revealed that management could be improved by training or preparing the stock for new conditions to be encountered in a new environment (Henderson, this volume). For instance, there will be noises to which they are not accustomed, light conditions with which they are unfamiliar, and shapes on the horizon or near them such as people, birds, or planes. One can train the stock to be released to become accustomed to these factors and thus effectuate better survival and hence savings. Another example of seizing on the knowledge of behavior in this phase of aquaculture management has to do with schooling patterns of young fishes. Juveniles of several species show pronounced schooling tendencies which may, however, abate with age. Juvenile schooling is thought to have protective value against predation. It does not take place at high light intensities; thus knowledge of proper light level for schooling is important. While certain acclimatization techniques are now being practiced in fish culture, such as the gradual mixing of resident with new water, the conference participants agreed that more sophisticated inputs by animal behavior experts to aquaculture management research teams have every chance of being highly fruitful.

In view of the massive literature on the rearing of fish larvae and of the fact that the problems of larval rearing were treated selectively by contributions to the conference (Hunter, Iwai), no useful purpose can be served in reviewing the main problems here, beyond a very few remarks. Kinne (1977) and Kinne and Rosenthal (1977) have given the latest and complete resume of the rearing of fish larvae. They treat the subject under the headings of fertilization, incubation and hatching, critical period, environmental requirements, nutritional requirements, size and structure of food items, concentration of food items, food selectivity, starvation, insufficient or abnormal stimuli, schooling, prey catching, and antibiotic treatment. Each of these areas require attention with problems to be solved almost on the species level. But it is especially in the interactions of factors and processes that now influence rearing success where advances may be expected. Such interactions will differ for various species but as their ranges of distribution are regional rather than national (with the subcontinent of India being somewhat of an exception here); and with few rather than many kinds eventually to emerge as the most suitable ones for aquaculture, one cannot but reiterate the need for broad interaction among aquaculture research and development institutions (U.S. Nat. Acad. Sci. 1977).

Feeding Enhancers: Simply put, it is problems of breed, seed, feed and weed (read diseases and parasites) that bedevil aquafarmers all over the world. To alleviate one of them, manipulation of feeding behavior through chemical stimuli has been proposed for aquaculture where the skills of the food chemist could be brought to play on larval feeding and on fashioning feeding enhancers. The rearing of larvae, especially feeding them adequately, is listed as one of the prime problems yet to be overcome in successful mariculture of finfishes (Kinne and Rosenthal 1977). Food particles have to be present at a high density to rear larvae of a number of choice potential aquaculture species. The first few days after the onset of feeding one aims at having at least five food particles per cubic centimeter, each often less than 100 *u*m in diameter, a size imposed by the small mouth sizes of the larvae of some marine species (de Mendiola 1974).

It would be of obvious advantage to the culturist to have micro-encapsulated larval feeds. Such feed is not (yet) available, in part because of the estimated high costs of micro-encapsulated food compared to laboratory-reared live food such as copepods and rotifers, even though sanitation of the larval rearing installations would be easier with micro-encapsulated food. Storage would also be easier. For details of the manufacture of such minute food particles that represent a complete diet, see Kinne and Rosenthal 1977, p. 1373. One notes that the wall material of such micro-encapsulated food might be so fashioned that a controlled slow release of water soluble attractants would occur. This provision would take account of the fact that a number of fish larvae have been shown to develop olfactory epithelia at the onset of feeding (Iwai, this volume). Concomitant with this information one should note that a mixture of amino acids especially proline, alanine, and methionine promotes the feeding activities of juvenile yellowtail and that true feeding enhancers for fishes appear to exist; inosine monophosphate (IMP) is one (Takeda, personal communication in Iwai). It may be surmised, given the early development of chemical senses in many larval fishes (Iwai), that a good purpose would be served if amino acids or other feeding enhancers could indeed be incorporated in the shell of minute food pellets so that they are released very slowly.

Compounds other than IMP that enhance feeding and/or growth have been incorporated into experimental diets for juveniles (Sen and Chatterjee 1976). The most notable success here has been achieved with micronutrients (e.g., cobalt) as growth enhancers but without involvement of the chemical senses. Still, before one were to consider the practice on some scale, one would have to evaluate carefully the potential gains as several such chemicals appear to be relatively costly. It should be ascertained if enhanced appetite by fishes and consequently more frequent feeding or ingestion of larger amounts at one feeding lead to faster growth, better assimilation, or both. One would further have to establish whether or not such advantages as are demonstrated in trials, and hence could lead to economic gains, do indeed warrant the increased cost of culture operations on a substantial scale.

Other Chemical Interventions in Aquaculture: Cultured fishes are often kept at far higher densities than prevail in nature. Deleterious chemical crowding factors, in part representing excess metabolites, in part pheromones (Bardach and Todd 1970), are then generally eliminated by flushing with water at high flow-through rates. As water saving in future aquaculture is likely to be of paramount importance, Solomon (1977) suggests, the question of metabolites aside, that chemical intervention or selective breeding of strains which produce less of such pheromones, possibly related to alarm substances, may be promising. He also speculates that better knowledge of pheromones and pheromone-induced behavior could help in "beneficial conditioning" (not explained) in the sorting of mixed species populations and, of course, in the control of reproductive behavior. (see also section on Reproduction)

Polyculture: Just as multiple cropping on land permits highly rational and effective use of a given piece of ground, so does the growing together of several compatible species (polyculture) increase the yield per unit volume of water in a pond. Species complexes presently used in polyculture are few but their choice has been based on feeding habits as well as other behavior traits.

A recent assessment based on data from 80 polyculture fish farms in Israel (B. Hepher, Fish and Aquaculture Research Station, Dor, personal communication), which grow common carp, silver carp, tilapia, and mullet and employ, in part, chicken manure for fertilizer stated that this type of fish culture is energy-efficient while it also makes effective use of land and water. It needs about half the energy inputs (expressed in kilocalories) per gram of unprocessed protein produced than are expended to produce catfish or broiler chickens in the United States (Table 2). Such polyculture produces protein more cheaply from an energy accounting vantage point, which reflects, to a large extent, real costs than do several marine fisheries which require much fuel for fish capture (Rawitscher and Mayer 1977). It appears that labor aside (labor costs vary widely in different nations), artificial fertilizer, extraneous feed, and the pumping of water are the most cost-sensitive inputs. The lessons are clear here for developing ecologically sound polyculture schemes, using behaviorally compatible species, recycling, and organic fertilizers.

Fishelson (this volume) points out that new and different associations ought to be tried involving, for instance, several more species of the genus *Sarotherodon* (tilapia). Similarly, the future of freshwater aquaculture in Latin America may well rely on suitable species selections from the ranks of the characins and the cichlids. Their behavior is still very incompletely known, but several of the former appear to have good growth and excellent taste characteristics; some have been spawned in captivity, albeit only experimentally so far (FAO 1977). Fishelson also suggests that one try to incorporate into polyculture not only fishes with different feeding habits, but also with different innate feeding times, especially for extraneous feeding.

Polyculture can also be the growing together of aquatic and avian or mammalian stock where behavior and habits of all members of the complex are compatible. While this is not the place for presenting a manual on fish cum pig or poultry culture, a few remarks about it are in order. Experimentation at the Fish and Aquaculture Research Station at Dor, Israel (R. Moav, personal communication) suggests that common carp, silver carp, some grass carp, and *Sarotherodon* (tilapia) *aurea* x *niloticus* hybrids thrive in ponds on which there is a small platform for ducks. The ponds are fenced in such a manner that the ducks must spend their entire time on the water or on their roosts which are provided with facilities for entry into the water. The composition of fish species intends to prevent reproduction in the ponds, and thus the preying on small fishes by the ducks. It is also interesting to note that the ducks so reared are very clean at duck-harvesting time, a decided economic advantage, and that having them roost on a platform above the water points the way to dealing with chickens in a similar fashion. In a warm climate the evaporative cooling from the pond's surface seems to provide the birds with considerable comfort, possibly even favorably affecting their growth efficiencies. These trials as well as others in other countries (Woynarovich 1976) indicate that such polyculture enchances the energy efficiency of the entire system and raises the yields of both the poultry and the fish compared to growing them separately.

Fishelson (this volume) also dealt with some behavioral aspects of mariculture; in several environments (coral reefs, rocky coasts) carrying capacities appear limited by shelter rather than food, and the predators are often nocturnal. If one were to afford shelter at night, especially to young fishes, and perhaps also practice some extraneous feeding during the day, one could substantially increase the production of certain valuable species. By doing so one would, in turn, raise the earnings of fishermen, albeit with substantial inputs of labor. This has been one of the aims of planting certain fish such as sea bream in the Seto Inland Sea of Japan (Fujiya, this volume).

Ranching

Aquacultural animals need for their rearing more procedural attention than has to be lavished on most domestic stock. For instance, many species are carnivores with complicated food requirements; the control of diseases and parasites still based on insufficient knowledge appears to be more complex in the water than among animals that live on land; and environmental control of water volumes and water management is beset with high costs and is technically complex. It is not surprising, therefore, that those who speculate about the future of aquaculture base substantial expectations on the ranching of certain marine or freshwater species. Such speculations about ranching appear particularly justified by virtue of peculiar histories of some aquacultural species, e.g., the migratory salmon. These anadromous fishes can be reared for the early part of their life cycle, sent out to pasture, and harvested when they have reached a certain size, either by intercepting them on a known path or by directing their movements to facilitate capture. Thus, ranching combines components of capture and culture fisheries.

There are limits as well as facilitating conditions to ranching, and they may well bear stressing before a more detailed discussion: (1) the life history of the species must be known in detail, especially its spawning behavior; requirements during its larval and juvenile period must be well understood; and seed production must be well in hand; (2) the natural limits to ranching depend on the total production, in an ecological sense, in the ocean area or lake in which the species spends the unconfined portion of its life cycle. Ranching works especially well or promises to do so when predators or grazers can be introduced into an environment where either productivity has increased or former predators or grazers have diminished. Two cases in point are the introduction of coho salmon in Lake Michigan where the fish were capable of feeding on a large supply of alewives *(Alosa pseudoharengus)* for which the original potential predators, the lake trout, had been eliminated by the sea lamprey (Christie 1974; Tody and Tanner 1966). The other example of a substantial potential for ranching may well lie in the introduction of salmon stock into Antarctic waters from bases in the southern part of South America (Joyner 1975). One expects the salmon to pasture on krill that are insufficiently grazed because of the near demise of Antarctic whales, though one has to be mindful of potential disturbances in portions of the Antarctic marine ecosystem that may follow from such an introduction. The management of man-made lakes presents comparable challenges of introducing forage species and others that feed upon them and that can be managed in a ranching mode.

Introduction of a new species for ranching is not a matter to be taken lightly or without a thorough evaluation of potential negative impacts. Ranching with non-native species will often turn out to be imprudent. In freshwater systems, the introduction of new (exotic) species has had a serious and costly impact on the ecosystems and their use by man (Zaret and Paine 1973; Magnuson 1976). This results because animals through their actions as consumers play an important role in maintaining the structure of aquatic communities (Paine 1966). When combinations of species that have not coevolved are put together, it is common that useful native species become locally extinct and the species structure becomes unstable and changes unpredictably over time (Magnuson 1976).

It is theoretically possible to increase the carrying capacity of a range. It has been done by range management on land and it has been attempted in certain situations in the sea. However, with a complex food web from first primary producer, i.e., floating algae, to the species finally harvested, i.e., fish that are very likely secondary or tertiary carnivores, the success of fertilization has been equivocal. Ranching is likely to pay off handsomely under ecological circumstances that seem favorable without manipulation of the substrate.

Another prerequisite for ranching lies in the capability in producing the fry or juveniles of the species in question. This entails rearing them through stages to a size at which they are far less vulnerable to predation than earlier in life. Thus, migratory, anadromous species appear eminently suited for ranching. Not only are practices for rearing freshwater fishes more advanced, the fishery for them is also more easily managed. Since ranching relies on massive stocking, we emphasize certain proposals made at this conference (Henderson, this volume) to improve the chances of survival of the stock released (see also Rearing of Larvae, this chapter).

As one looks at fishes worldwide, one is struck by the fact that the anadromous habit has developed mainly in the temperate zone. This may well be related to the lower fertility of most tropical seas compared to the temperate ones, but one must also note that the biology of temperate zone species is better known than that of those in the tropics. A more attenuated search for ranchable species in the tropics, then, may well reveal more of them than appear amenable to this management practice at present, such as the river-running herring *Hilsa canagurta* of the Indian subcontinent.

It has been stated that species may be amenable to ranching if their migratory behavior and routes are known; thus, one may think of ranching also fish species which spawn in restricted locations in the sea and grow to near maturity in fresh water. However, pressures on presently unused or unmanaged freshwater areas, such as the swamps of New Guinea or certain inundation regions of Africa, are likely to increase in the future at a far greater rate than those we are likely to observe in a more intensive use of the marine realm. If one adds to this consideration that greater difficulties are experienced with the forced reproduction and larval rearing of ocean spawners, e.g., eels, it appears more promising to look for ranchable species among those with freshwater rather than saltwater spawning habits.

Among both terrestrial and aquatic animals it is difficult to draw a hard and fast line between extensive ranching and more intensive management modes. By and large, land animals are more easily controlled while the peculiar nature of the aquatic environment and the long distances over which aquatic ranching stock may forage make it potentially important to direct or recall the animals being ranched. Two promising techniques have been developed and discussed at this conference: imprinting with chemicals for later return to a site where this same chemical will be deployed (Hasler), and training to sound by conditioned reflex techniques so that fish can be "recalled" later to a feeding station where they may be captured (Fujiya, this volume). The latter can be practiced on any species that has a moderate feeding range; it is not particularly applicable to fishes that have spawning migrations.

The use of specific chemicals to imprint salmon juveniles to return to a later release site of that same chemical, relies on the fact that salmon recognize their home streams by specific odors. Were one to use the method on species other than those belonging to the family Salmonidae one would first have to ascertain whether or not they also recognize their spawning sites by odor. It is possible, perhaps likely, that Hasler's theory of home stream recognition by odor applies to species in other families as well.

To manage anadromous stocks by imprinting with specific chemicals, one should study various aspects of the imprinting process: for instance, what is the earliest and latest larval or juvenile period at which successful imprinting is accomplished? Is there a peak period in the early life history of the species at which imprinting is most effective and how long does it last? What are the most suitable substances for imprinting, given the substantial volumes necessary in the practice and a possibly far more widespread use of it? Clearly there are also implications in ranching of national or subnational ownership of certain stocks through new ocean regimes. Another question of interest might be to ascertain whether or not the fish respond to the odor of their imprinting compound sometime before they return to mouths of their rivers, and whether or not techniques based on chemical recall could be used in high seas fisheries for them.

The other mode of recall, by sound rather than by scent, has been practiced in ranching fishes over a much more restricted range. It is based on a training process (Fujiya, this volume) which requires substantial biotechnical skills and technical infrastructure. It also appears that the range of such recall is limited. A radius of 1 to 2 km appears the farthest distance over which sound can be deployed in the bays where the ranched fishes are released. The limitations to such recall are predicated upon difficulties of projecting sound nondirectionally over a large distance through the water while successfully competing with ambient underwater noises. To do so requires substantial sound pressure and hence expensive equipment. Thus one will have to consider a trade-off between the distance from which fish are recalled and the cost of achieving this (Tavolga, this volume).

Our experience to date with the genetic improvement of organisms used in aquaculture is limited and circumstantial, and some hard evidence suggests that similar if not greater genetic gains can be expected that have been obtained in land animal husbandry (Calaprice 1976). If one has control over the reproductive phase of the species, genetic manipulations in ranching appear to hold particular promise; by genetic selection one may choose the time of return, greater fecundity, and other desirable traits (as summarized in Calaprice 1976; Bardach et al. 1972, p. 495-498). These gains, so far achieved mostly with salmonid fishes, rely on releasing successively improved batches of juveniles. The release of selected progenitors with heritable traits that would improve wild populations has also been proposed (Moav et al. 1978). Of course it presupposes mastery over seed production, and it appears better suited to fish in lakes and reservoirs than to marine species. Yet it is certainly a specific variant of ranching particularly applicable to species which do not return to specific sites to spawn and on which fishing may have long-term deleterious effects through inadvertent fishing out of the most desirable (e.g., fast-growing) genotypes (Gwahaba 1973; Silliman 1975).

The "improvement" of wild stock through incorporation of desirable traits such as improved growth, body conformation, i.e., a smaller head or a higher and more fleshy back than in the wild type, or even altered taste of the flesh, has obvious appeal. However, phenotypic changes in the population so produced may well be an improvement only in the human eye; wild populations are undoubtedly optimally adapted to their environment viewed from the vantage point of evolution and incorporation of certain traits into them may even do them harm. For instance, the Chinese race of the common carp avoids net better than the European one, a commercially undesirable trait (Wolfarth et al. 1975), as net avoidance may be fully or partly synonymous with predator avoidance. Thus, one must recognize that genetic manipulation to affect inherited behavior traits of wild populations, if and when attempted even with sterile hybrids, may have deleterious ecological side effects; clearly trade-offs are involved and a running account must be kept of ecologic and economic costs and benefits.

Implementation

The need for efficient use of energy, materials and monies in capture and culture fisheries seems self-evident. Likewise, the potential application of behavioral information in these industries seems high even though documented evidence of planned application in past years is not extensive. For applications to occur after problems have been systematically identified, the role of behavioral information in their solution must be evaluated and adaptive research tasks must be identified and executed. Direct inquiries of fishermen and fish farmers were judged by the participants to be the most important initial step in both identifying problems and in delineating the potential role of behavior in solving problems. In fact, one participant in charge of research on a developed fishery (plaice; Harden Jones) has begun such inquiries as a result of the conference. Also, as artisanal tropical fisheries change, primarily through mechanization, it will be valuable to incorporate tenets derived from the age-old practical experience of fishermen whose conduct of the hunt was more conservation-oriented than is commonly assumed (Johannes, this volume). Synthesis of existing knowledge and planning of strategic research are the next elements. We hope that the publication of the Bellagio Conference proceedings is a phase in implementation, but even more importantly, we hope that it will stimulate applications of existing knowledge in a discipline that we believe can occupy an important place in fishery science.

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Vision and the Feeding of Fishes

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Blaxter, J.H.S. 1980. Vision and the feeding of fishes, p. 32-56. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Vision is vital for feeding of many near-surface teleosts. The visual threshold for feeding of about 0.1 lux is similar to the light intensity at which dark-adaptations of the retina takes place. The time available for feeding per 24-h day depends greatly on the seasonal changes of day length in high latitudes. In light-adapted fish, feeding efficiency depends on the shape and size of the visual field, the distance covered during searching, the feeding drive, and on characteristics of the prey such as its size, conspicuousness, and density. The visual axis, acuity, and contrast perception of predators are discussed together with camouflage of prey and the reaction distances for prey perception and volumes searched while feeding. Information on volumes searched per unit time and visual thresholds allows an estimate to be made of volume of water searched for food per 24-h day. This gives some insight into whether available prey biomass is adequate to support the predator population.

Introduction

Vision seems to be the dominant sense in feeding and other activities of many near-surface teleosts. Deep-water teleosts and elasmobranchs often depend on other senses, especially olfaction, or olfaction in combination with mechanoreception. There is recent evidence, however, that some elasmobranchs have a more elaborate retina than was previously thought (Gruber 1975). This chapter concerns the "visual" teleosts which locate their food and seize it using sight as the dominant sense. They have well developed eyes often with a specialized duplex retina and a large optic tectum. Teleosts which depend on other senses, especially olfaction, have an elaborate system of taste buds on the head, body, and barbels and well developed olfactory mucosae (see Atema, this volume; Tesch 1975). The location of food by mechanical disturbance of the ear or lateral line is not well documented, although there is some evidence that fish orientate to such sources of stimuli (e.g., Schwartz and Hasler 1966; Myrberg et al. 1976; Nelson and Johnson 1976; Maniwa 1976).

Dark/Light Adaptation

The structure of the teleost eye is too well known to redescribe here (see Walls 1963; Brett 1957; Ali 1975). What is of importance is the process of dark-and light-adaptation, during which vision is transferred between the rods and cones. As the eye dark-adapts, various anatomical changes, the retinomotor responses, take place in the retina. These enable light to reach the rods easily in poor illumination without any masking effect by the cones. The reverse of these movements occurs as the eye light-adapts.

Histological examination of the eye after fixing the retina or behavioral and psychophysical tests during changes of light intensity allow a threshold for light/dark adaptation to be determined. This threshold for 27 teleost species ranged from 10^{-3} to 10^{1} lux (Blaxter 1970a). The change usually takes place near 10^{-1} lux (equivalent to late dusk or early dawn or 0.4 μW cm^{-2}sec^{-1} at the surface).

Visual abilities also change during adaptation (Table 1). The transfer from rod to cone vision influences acuity, sensitivity, and color vision.

TABLE 1. Scheme for dark/light adaptation changes.

Dark-adapted	⟵⟶	Light-adapted
Rod vision (scotopic)		Cone vision (photopic)
High sensitivity to light		Low sensitivity to light
Low acuity (much summation)		High acuity (less summation)
More sensitive to blue	⟵ Purkinjie ⟶ Shift	More sensitive to yellow-green
No color vision		Color vision
Low frequency for flicker fusion		High frequency for flicker fusion
Decrease	Feeding, schooling and other "visual" responses.	Increase

Visual Feeding Thresholds

In experiments to test the feeding of fish at different light intensities, the ability to feed falls progressively during dusk or as the illumination is artificially reduced (Fig. 1). The threshold for feeding averages about 10^{-1} lux, suggesting that the eyes of "visual" teleosts need to be light adapted for feeding to occur.

The implications of these results are considerable. Visual feeders will have greatly differing times available for feeding in each 24-h day depending on latitude and season (Fig. 2). The figure is based on surface light readings; at greater depths the time available for feeding will usually be less. Diel vertical migration may be, in part, a response to prolong the visual day especially keeping the fish in rather critical light intensities at dusk and dawn. In high latitudes during the polar summer "visual" species may be able to feed throughout the 24-h day; in the polar winter they may not be able to feed at all. Such seasonal changes are much less near the equator.

This is, of course, a simplistic approach to the problem; in the polar winter the temperatures will be low and food requirements probably at a minimum. The rather short visual day in the tropics may be linked to higher demand for food. Many fish exhibit diel rhythms of feeding during the day, suggesting intense feeding at dawn after a period of nocturnal non-availability of food, followed by a period of satiation and a later bout of feeding towards dusk. This implies an abundance of food without the need for continual visual searching by day which may apply in some but not all circumstances.

The application of the threshold concept to aquaculture suggests that in some carnivorous species additional artificial light after dusk or before dawn would prolong the feeding day with possibly beneficial results on growth, though not necessarily on food conversion rates. Such changes of day length might also influence reproductive rhythms or temperature tolerance with undesirable effects.

Feeding Efficiency

Feeding efficiency is dependent on light intensity which influences the performance of the eye, and on other factors intrinsic to the predator, the prey, and the interaction between them. Predator factors consist of (1) shape and size of visual field which is determined by the scanning ability of the eye, its visual axis, range determination, visual acuity, and contrast sensitivity, (2) distance covered during searching, and (3) feeding drive, which may be influenced by the degree of satiation, presence of competitors, and temperature. Prey factors consist of (1) size and conspicuousness, (2)

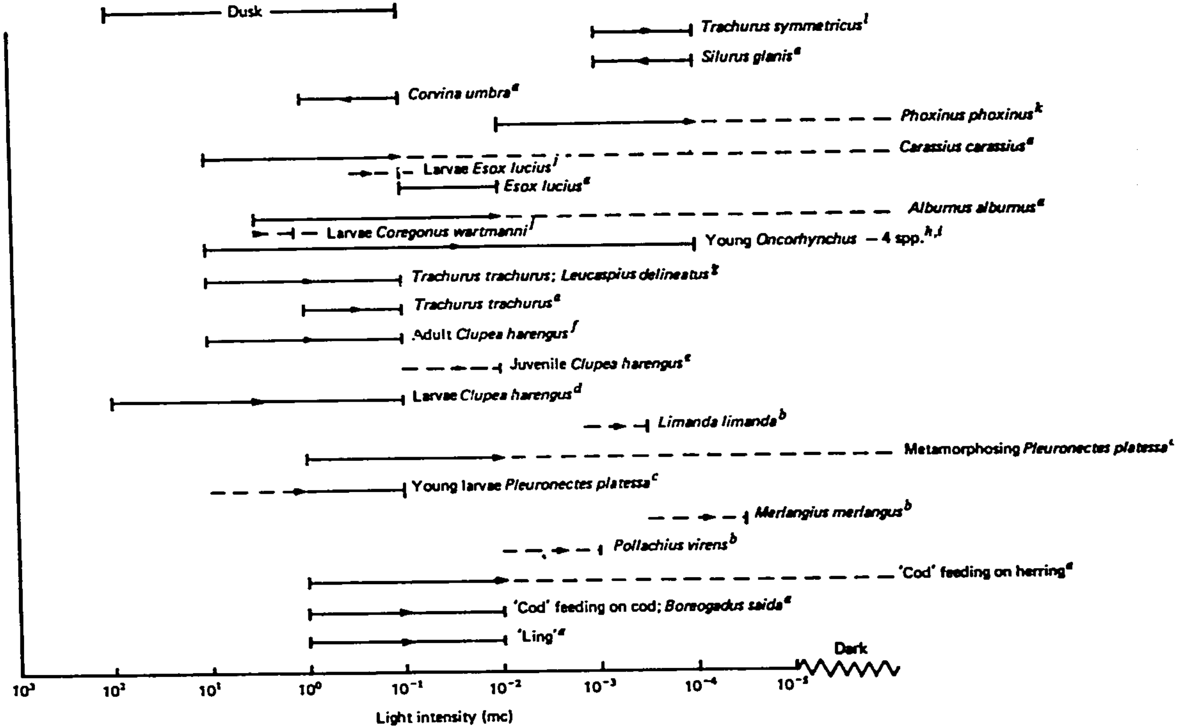

FIG. 1. Range of light intensities over which feeding declines. Broken lines indicate that complete range is not determined or that feeding continues into dark. Arrows indicate direction of decrease of feeding intensity. mc equivalent to lux. (Superscripts refer to different authors; see Blaxter 1970a).

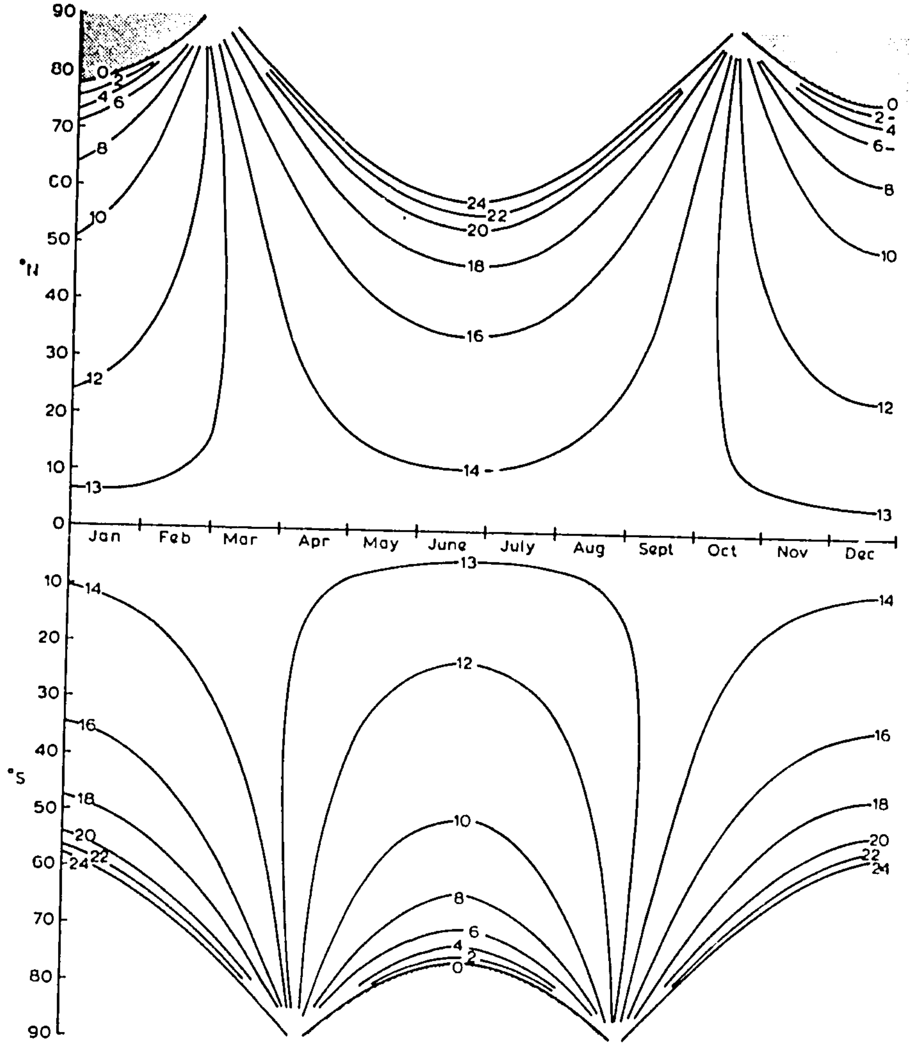

Fig. 2. Hours per 24-h day at which surface light intensity is 0.1 lux or above, related to season and latitude. (From Blaxter 1970a; reprinted from Marine Ecology by permission of the publisher, John Wiley and Sons, Ltd.).

movement, and (3) density. Predator/prey interactions consist of (1) swimming ability of predator, (2) mouth size of predator, and (3) escape ability of prey. The visual aspects of these factors will be considered in the rest of this chapter.

Detection of Prey

In visual conditions the ability of fish to search for prey (optic "filtration") will depend on the cross-sectional shape of the visual field and on sighting distance. The visual field depends on such factors as the axis of accommodation of the eye, specialized regions of the retina and on head movements. The shape of the visual field in clupeoid larvae has been shown by Blaxter (1966), Rosenthal and Hempel (1970), and Hunter (1972). The sighting distance depends on overall sensitivity of the eye and its ability to accommodate, and on its acuity and contrast sensitivity, as well as on the existing level of illumination, and turbidity and color of the water.

VISUAL AXIS

The nature of the visual axis in fish is probably best known from the works of Tamura (1957) and Tamura and Wisby (1963). Accommodation takes place along an axis which, if projected outwards from the head, represents the direction along which fish sight prey or other objects; if projected inwards to the retina it often meets a specialized region of high cone density (Table 2). High cone density is likely to confer a high acuity along the visual axis.

Although Walls (1963) considered fish to be myopic with the "resting" eye focused at the near point and accommodating for distance vision by moving the lens towards the retina (Fig. 3), other workers (see Schwassmann 1975) have disagreed, considering that the fish eye is often hyperopic or emmetropic. The near point depends, nevertheless, on the size of the lens and size of the fish but in general small fish should be able to see objects nearer the eye than large fish. Whether they can see objects farther away will depend not only on the extent of accommodation but on other factors which control the sensitivity of the eye to distant objects such as acuity and contrast perception. The fish, however, will have its greatest versatility for focusing along its visual axis.

Many species have overlapping visual fields between the two eyes (Table 3). This may assist fish in judging distance both from improved stereoscopy and from the extent of convergence of the visual axes.

The lateral movements of the head described by Bainbridge (1963) as a reaction to the lateral swimming movements of the tail may also tend to increase the scanning ability of the eyes by sweeping the

TABLE 2. Direction of visual axis (after Tamura 1957).

Species	Retinal region of highest cone density (no. per 0.1 mm^2)	Direction of greatest myopia (refraction in diopters)	Visual axis	Axis of maximum binocular overlap[a]
Pagrosomus major	Dorso - temporal (303)	Lower - fore (—16.5)	Lower - fore	—20°
Erynnis japonicus	Dorso - temporal (570)	Lower - fore (—13.0)	Lower - fore	—20°
Sparus hasta	Dorso - temporal (400)	Lower - fore (—13.0)	Lower - fore	—20°
Leiognathus argenteus	Dorso - temporal (236)	Lower - fore (—14.0)	Lower - fore	—20°
Xesurus scalprum	Dorso - temporal (252)	Lower - fore (—10.5)	Lower - fore	−20° to 0°
Epinephelus septemfasciatus	Temporal (1050)	Fore (—14.0)	Fore	0°
Sebasticus marmoratus	Temporal (380)	Fore (—12.3)	Fore	0°
Therapon oxyrhynchus	Temporal (133)	Fore (—14)	Fore	0°
Lateolabrax japonicus	Temporal (259)	Upper - fore (—13.6)	Fore - upper-fore	+ 30°
Trachurus japonicus	Ventro - temporal (288)	Upper - fore (—20)	Upper - fore	+30°

[a] 0° is horizontal plane, negative angles below, positive angles above.

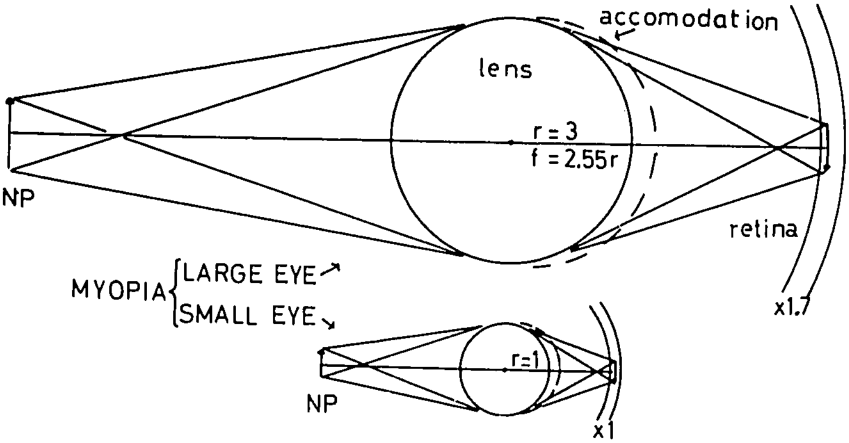

FIG. 3. Diagram showing the effect of eye and lens size on the position of the near point. Dotted line gives position of lens when accommodated for distance vision. Lens radii (r) are 1 and 3 units, focal length obtained using Matthiessen's ratio f = 2.55 r.

visual axis from side to side. Rosenthal and Hempel (1970) also considered this movement to have a role in the feeding of herring larvae.

ACUITY

The discrimination or resolution of detail is often determined by testing the ability to distinguish two parallel lines closely adjacent to each other. Acuity is defined as the angle in minutes of arc which two such lines subtend at the eye at their threshold separation for resolution. Acuity or minimum separable angle is thus independent of distance. Acuity is enhanced by a high density of retinal receptors and by a long focal length (which will give a larger image on the retina). Tamura and Wisby (1963) give a useful formula to calculate acuity from histological information:

$$\operatorname{Sin} \alpha = \frac{1}{F} \quad \frac{0.1\,(1 + 0.25)}{n} \quad \times\ 2$$

where α is the minimum separable angle, F is the focal length of the lens, 0.25 is the estimated degree of shrinkage during fixation, and n is the number of cones in an area of 0.01 mm^2. The focal length of the lens can be obtained by Matthiessen's ratio where $F = 2.55\ r$, r being the radius of the lens.

Histological calculations of acuity agreed fairly well with the much scarcer data obtained by psychophysical experiments (Table 3).

Table 3. Visual acuity of fish (Minimum separable angle in minutes).

Anatomically			Behaviorally		
Species	Acuity	Body length (cm)	Species	Acuity	Test object and light intensity
Seriola dumerili[b] (greater amberjack)	3.0-3.2	85-95	*Microcanthus*[f] *strigatus* (convict fish)	4.9	Grating 282 1x
Coryphaena hippurus[b] (dolphin)	2.0-3.0	75-105	*Phoxinus laevis*[f] (minnow)	10.8	Grating 170 1x
Acanthocybium[b] *solanderi* (wahoo)	2.4	155	*Euthynnus*[e] *pelamis* (skipjack tuna)	5.5	Grating 170 1x
Euthynnus pelamis[b] (skipjack tuna)	2.3	52	*Euthynnus affinis*[e] (kawakawa)	7.4	Grating 170 1x
			Thunnus albacares[e] (Yellowfin tuna)	3.6	Grating 170 1x
Euthynnus[b] *alletteratus* (little tunny)	3.0	52	*Aequidens*[f] *portalegrensis* (cichlid)	5.8	Grating

Scomberomorus[b] *cavalla* (king mackerel)	4.0-4.2	75	*Astronotus*[f]	5.3	Dots
Thunnus atlanticus[b] (blackfin tuna)	2.2-2.4	62-67	*Carassius*[d] *auratus* (goldfish)	20.0	Disc Light adapted
Istiophorus albicans[b] (sailfish)	1.9-2.3	130-170			
Tetrapturus albidus[b] (white marlin)	1.8	—			
Sphyraena barracuda[b] (great barracuda)	3.1-3.5	95-120			
27 species[a]	4.2-15.4	7-30			
Clupea harengus[c]	7.0-50	2.5-30			

Data from [a]Tamura (1957), [b]Tamura and Wisby (1963), [c]Blaxter and Jones (1967) [d]Hester (1968), [e]Nakamura (1969), [f]listed by Muntz (1974).

Acuity improves with size of fish (i.e., the minimum separable angle becomes smaller) (Fig. 4). This implies that the increased image size in the larger eye has a greater influence on acuity than the reduction in density of the retinal mosaic which is also found with growth (see for example Blaxter and Jones 1967). Muntz (1974) discusses further the reasons for acuity being better in large eyes, and it appears that diffraction and spherical and chromatic aberration will all have constraining effects with small lenses. With their higher acuity larger fish should be able to see detail further away which should certainly give them longer sighting distances than small fish.

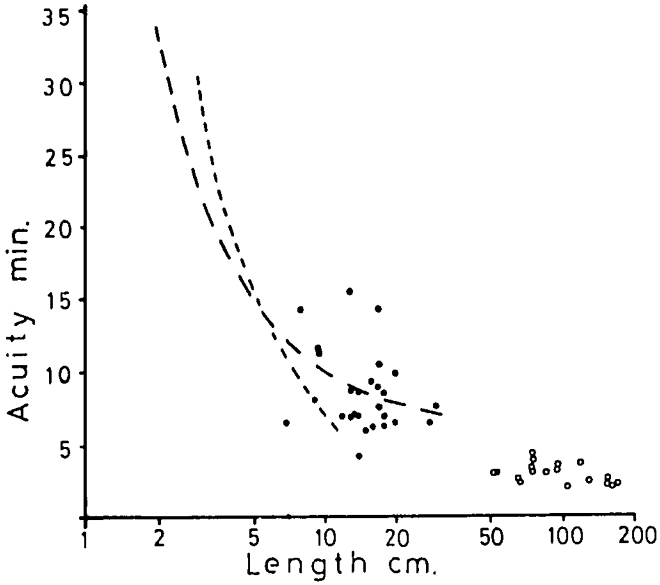

Fig. 4. Change in acuity (minimal separable angle in minutes) with length. Short dashes indicate *Aequidens portalegrensis* (Baerends et al. 1960); long dashes *Clupea harengus* (Blaxter and Jones 1967); black dots, 27 marine teleosts (Tamura 1957); open dots, 10 large pelagic marine teleosts (Tamura and Wisby 1963).

CONTRAST PERCEPTION

Whether or not potential prey is visible at a distance depends on the acuity of the eye, almost certainly whether the prey is moving or stationary, but most of all on the contrast between the prey and its background. This contrast will be determined partly by the conditions of illumination and turbidity of the water. The brightness discrimination of the eye will determine whether a given contrast is visible to the fish. Some data are given in Table 4 and further information is in Blaxter (1970a). Brightness discrimination varies from species to species but Kobayashi (1962) among others showed that it also depends on the general level of illumination which

TABLE 4. Brightness discrimination; increment of light intensity discriminated (Δ) as a percentage of the light intensity of adaptation (I) as shown by electroretinogram (from Protasov 1964). $\Delta I/I$ is known as the Weber Fraction.

Species	$\Delta I/I$ as %
Gadus morhua (Atlantic cod)	1
Pollachius virens (pollock)	1
Mallotus villosus (capelin)	0.01
Pleuronectes platessa (plaice)	7–10
Hippoglossoides platessoides (American plaice)	7–10
Anarhichas lupus (Atlantic wolffish)	10–12
Myoxocephalus quadricornis (fourhorn sculpin)	3
Raja radiata (thorny skate)	7–10

presumably determines the number of visual receptors which can be deployed by the fish. In brightness discrimination trials dark objects on light backgrounds may give different results from bright objects on dark backgrounds. In water, prey are more likely to be seen as light objects against a darker background.

The contrast of an object (Duntley 1962) is defined as:

$$C = \frac{T - B}{B} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{Equation 1}$$

where T and B are the brightness of the target and background, respectively. The rate at which contrast falls off with distance is given by:

$$C_r = C_0 e^{-ar} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{Equation 2}$$

where C_r and C_0 are contrast at distance r and zero, respectively, and a is the beam attenuation coefficient.

For example, if the brightness ratio between target and background is 1.5, $C = 0.5$ (Eqn. 1). If it is assumed that the prey disappears when the contrast reaches 0.1 (equivalent to a Weber Fraction of 10%; see Table 4) and assuming $a = 0.1$ for clear water and 0.4 for turbid water, then the sighting distance $r = 16$ m for clear water and 4 m for turbid water (Eqn. 2). If brightness discrimination is assumed to be about 10% for a light intensity of 1-10 lux but falls to 20% at 0.1lux and improves to 5% at 100lux, it is possible to calculate the effect of this on sighting distances (Table 5).

The effect of light intensity on brightness discrimination is not well established in teleosts so these results can only give an impression of the possible effects. One of the few detailed studies of brightness discrimination in fish was that of Hester (1968) who used

TABLE 5. Estimated sighting distances at different light intensities in water of different turbidity, assuming brightness ratio of 1.5 between prey and background at zero distance.

Light intensity lux	Contrast threshold Weber Fraction	Turbidity, beam attenuation coefficient (a)	Sighting distance (m)
0.1	20%	0.1	9.2
		0.4	2.3
1.0-10.0	10%	0.1	16
		0.4	4
100	5%	0.1	23
		0.4	5.8

a classical conditioning technique to determine whether goldfish could detect a target (a bright spot) against a darker background. The contrast threshold was better (lower) in large fish, for large targets and for bright light (Fig. 5) all of which was predictable though not quantifiable a priori. Of interest, also, was his finding that the binocular threshold was 0.67 that of the monocular threshold, showing that interaction of the eyes in the binocular field has advantages other than giving range or stereoscopy.

Contrast sensitivity may be enhanced in various ways:

a) Many species of fish feed looking partly upwards (with an upper-fore visual axis—Table 2). Deep-sea fish often have eyes pointing directly upwards. The so-called tubular structure or telescopic nature of the eyes also improves their light-gathering ability (e.g., see Munk 1966).

b) Some fish such as sand gobies have iridescent corneas which probably help to reduce the glare from downwelling light (Lythgoe 1975).

c) It is possible that some fish have polarizing filters in the eye which would reduce the backscatter of light from particles in the water. This could be inferred from the work of Lythgoe and Hemmings (1967) who measured the sighting distance of gray targets for human divers with and without polarizing screens in front of the face mask. They found that the sighting distance was improved by about 10% using the polarizing screen.

d) The characteristics of the visual pigments may enhance contrast perception. It has often been thought that the wavelength of maximum absorption (λ_{max}) of visual pigments in fish is similar to the wavelength of maximum transmission of light by the water. Sometimes the λ_{max} of the visual pigments is offset. This will have the effect of reducing the sensitivity of the eye but

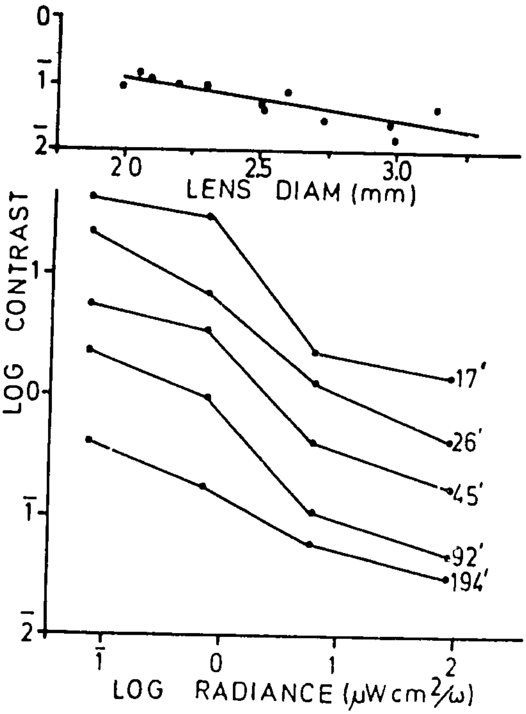

FIG. 5: Upper. Effect of lens diameter (fish size) on the contrast threshold for 14 goldfish. Lower. Effect of general level of radiance and target "diameter" (the size of a white spot in minutes of arc subtended at the eye) on contrast threshold. Points are mean for 2-5 goldfish. Both figures are redrawn from Hester (1968).

increasing contrast perception (Lythgoe 1968).

e) Most teleosts are thought to have color vision (Muntz 1974). Walls (1963) discussed the pitfalls which beset many earlier workers, many of whom failed to control their experiments. Some earlier work by v. Frisch and co-workers (see Herter 1953) where fish were given an elaborate system of choices of colored and gray feeding containers almost certainly proved the existence of color vision. Later experiments (e.g., Muntz and Cronly-Dillon 1966) on goldfish, where brightness cues were eliminated, confirm the better of the earlier work. Although no experimental evidence is available, it seems likely that contrast perception is enhanced by color vision.

Camouflage

It is worth considering at this point the defense mechanisms of the prey of "visual" feeders. These mechanisms almost all depend on reducing contrast with the background. The role of countershading (dark dorsal surface, light ventral surface) and of camouflage by chromatophore changes is too well known to reiterate here. There are other more recent discoveries worth mentioning. Silvery-sided fish are now known to have a special orientation of their guanine crystals (Denton and Nicol 1966). The sides of the body are then equivalent to a vertical mirror which makes them difficult to see from any angle as long as the distribution of downwelling light is symmetrical in azimuth. This adaptation of surface-schooling species has the direct effect of reducing contrasts, especially when the sun is near the zenith. At dusk and dawn the light from the surface will be less symmetrically distributed. Since schooling is often visually mediated like feeding (see Blaxter 1970a) and the schools break up at night, the fish are more likely to locate each other and so aggregate at dawn when they are most visible to each other (and to potential predators).

Another prey adaptation is the ventrally located photophores of many deep-sea teleosts. These have evolved in such a way that the pattern of light emitted matches the distribution of the downwelling light and almost certainly reduces the silhouette for the upward-looking predators (Denton et al. 1972). Some predators such as *Scopelarchus* have yellow lenses (Fig. 6). These seem to have the function of detecting the yellow "tail" of the bioluminescence spectrum at the expense of reducing the overall sensitivity of the eye (Muntz 1976).

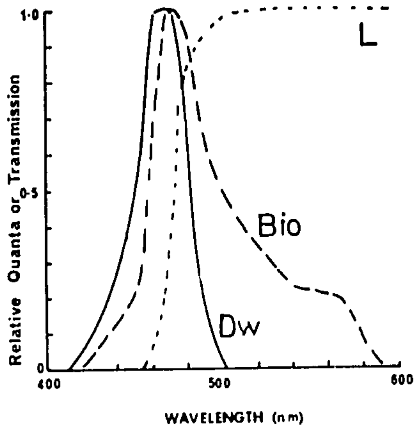

FIG. 6. Function of yellow filters. Spectral characteristics of downwelling light at 500 m (Dw) and of the bioluminescence of *Myctophum punctatum* (Bio). Transmission characteristics of lens of *Scopelarchus analis* is shown by the line L (partly redrawn from Muntz 1976).

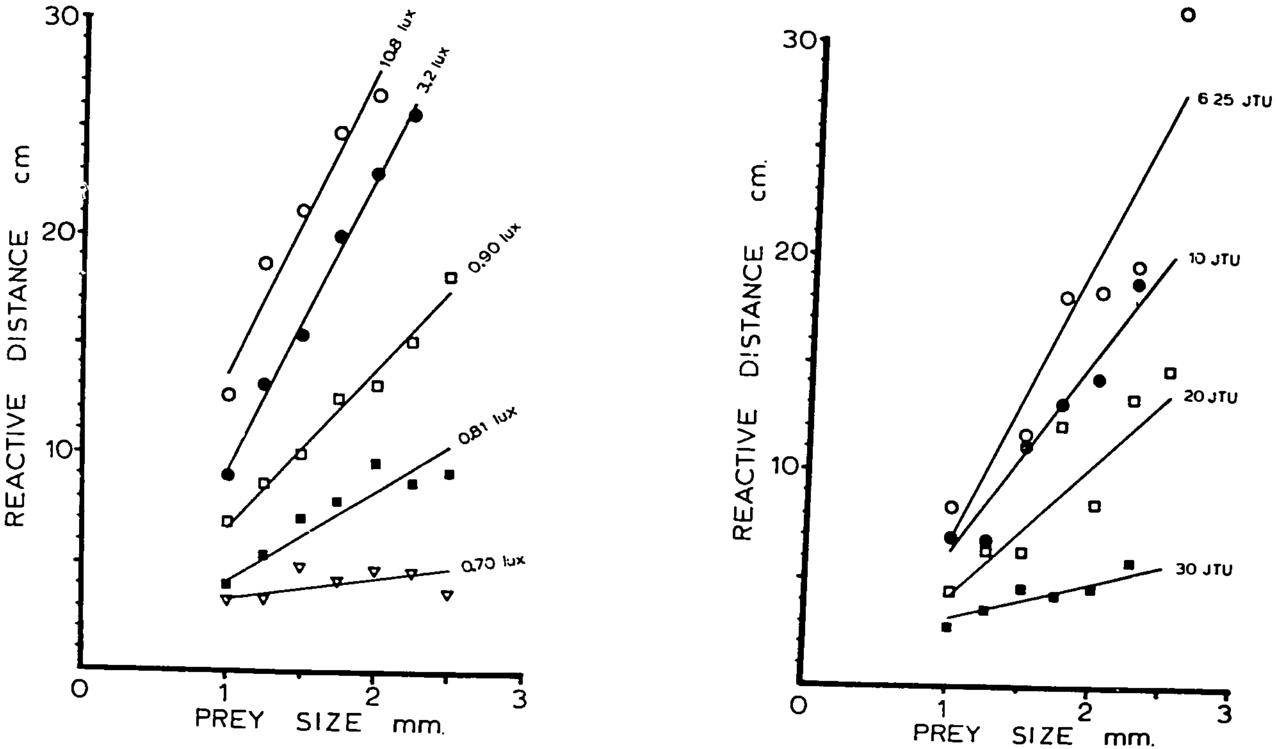

FIG. 7. Reactive (sighting) distance in *Lepomis macrochirus* depending on prey size and illuminance (in lux) at a low turbidity of 1 JTU (lefthand figure) and on prey size and turbidity (in JTU) at a constant illuminance of 34.9 lux (righthand figure). (From Vinyard and O'Brien 1976; reprinted from the Journal of the Fisheries Research Board of Canada by permission of the publisher. Scientific Information and Publications Branch, Fisheries and Environment Canada.

Reaction Distances

Fish will sight prey somewhere near maximum range along the visual axis, but perhaps nearer to the eye if the peripheral retina is in use. Fish will seize their prey between the maximum sighting distance and the near point. In general small fish will have shorter sighting distances, because of the constraints of the smaller eye with poorer acuity and contrast perception, but they can take food nearer to the head because the near point is closer to the lens. Presumably the success of capture is higher if a fish commences to attack prey from as near as possible.

Sighting distances have been measured mainly by subjective observation of change of behavior or locomotion of a fish while searching for food. No objective training experiments have been done. Even the subjective data are limited and largely confined to fish larvae for which studies of feeding ecology and behavior have been in vogue over the past few years (see Hunter, this volume). Vinyard and O'Brien (1976) have recently made a more thorough study in bluegill showing that the reactive (sighting) distance depends on the size of the target, on the turbidity of the water, and on light intensity (Fig. 7). A brief summary of the other information available is given in Table 6.

TABLE 6. Sighting distances and searching power of selected species of fishes.

Species	Size (cm)	Sighting Distance (cm)	Volume Searched liters/hour
Coregonus spp.[a] (whitefish)	1	0.05 - 0.3	14.6
Sardina pilchardus[d] (pilchard)	0.5 - 0.7	0.1 - 0.3	0.1 - 0.2
Pleuronectes platessa[d] (plaice)	0.6 - 1	0.3 - 0.5	0.1 -2.2
Clupea harengus[c] (Atlantic herring)	1 -1.9	1 - 2.6	1.5 - 8
Clupea harengus[d] (Atlantic herring)	0.8 - 1.6	0.3 - 0.5	0.2 - 2
Lepomis macrochirus[e] (bluegill)	6.5	3 -28	?
Clupea harengus[b] (Atlantic herring)	15	30	150,000

From [a]Braum (1964), [b]Blaxter (1966), [c]Rosenthal and Hempel (1970), [d]Blaxter and Staines (1971), [e]Vinyard and O'Brien (1976).

Searching Power

Once the sighting distance has been measured and some idea gained of the shape of the visual field and swimming speed of the fish, it is possible to calculate the volume searched per hour (Table 6), and by applying a visual threshold for feeding of 0.1 lux, the time available for feeding per 24-h day can be determined. There have been very few calculations made along these lines. Blaxter (1966) compared the searching power of larval and young adult herring (Fig. 8) and found that as a result of enhanced sighting distances and swimming ability a young adult searched about 100,000 times more water than a larva per day. This approach is, of course, an oversimplification; adult herring feed in schools so there will be an interaction between fish on a small scale. There will also be the problem of the leading fish first picking off the prey in the path of the school and the problem of rapid utilization of the food available. Fish may become satiated with a resultant drop in activity (the original school leaders may thus fall back). A discussion of the relative merits of searching for food as a school or as a single fish is, however, beyond the scope of this chapter.

Applications

Even in visual feeders, which stop feeding in the dark, other senses may be involved during daytime. Mechano- and chemoreceptors may enhance awareness or a feeding drive; chemoreceptors may be involved in secondary selection within the mouth. It is likely that there are more potential applications with these other senses, for example, the use of recording of feeding sounds or of artificial bait to attract fish to food or fishing gear. The role of vision in fish capture was, however, shown neatly by Murphy (1959) who found that catches by gillnet were higher in turbid water and by trolling with live bait in clear water. Evaluations might be made about the efficiency of certain fishing methods at different times of day at different depths or turbidities on the basis of studies of the interaction of vision and feeding.

Evaluations of the adequacy of biomass concentrations of prey for maintenance or growth of a fish stock also require knowledge of the searching power of the predators. Almost all the work on fish larvae to date (see Hunter, this volume) suggests that prey numbers in a particular region are adequate only if the prey is contagiously distributed. Blaxter (1966) found a similar result for herring larvae but concluded that the biomass of prey in the North Sea on the nursery grounds was adequate to support the older fish.

In aquaculture many species are herbivores or feed in captivity by the use of a number of senses (e.g., salmonids). The larval stages of

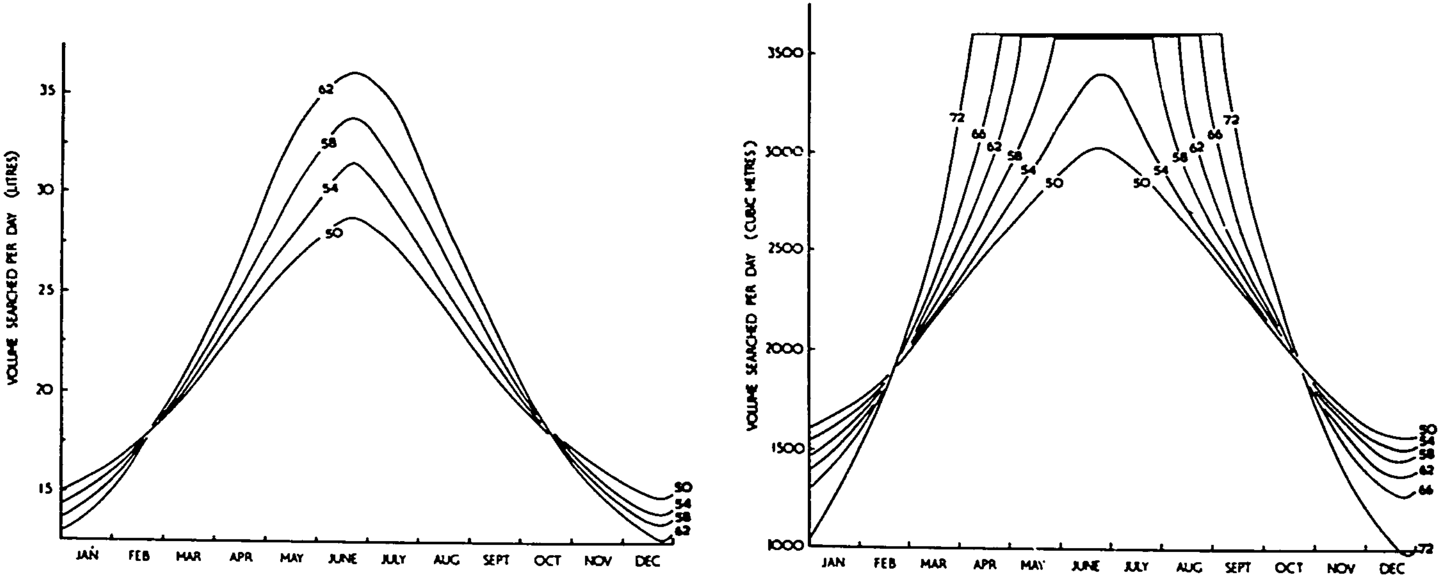

FIG. 8. Maximum volumes searched by herring per 24-h day in different latitudes and seasons. Lefthand figure, larvae, volume searched in liters; righthand figure, juveniles, volume searched in cubic meters. Figures on graph show degrees of latitude North and represent the likely range of the different herring stages (From Blaxter 1966; reprinted from the British Ecological Society Symposium 6 by permission of the publisher, Blackwell Scientific Publications Limited.)

young marine farmed species may depend much more on vision, however, and it is in this field that the determination of optimum light intensity, color, distribution and daylength might be rewarding. The tendency is to give larval fish homogenous conditions with rapid changes of light at "dusk" and "dawn" by switching artificial lights. It is possible that larval fish suffer a degree of sensory deprivation as a result (Blaxter 1970b). Training and leading fish by lights may be less rewarding than by sound (see Fujiya, this volume) because of the poor penetration of light even in quite clear water.

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Discussion

REINBOTH

Are you talking about feeding activity or about uptake of food? These are different things.

BLAXTER

Investigations have recorded food actually taken; for example, the number of prey items taken per hour would be a measure of feeding intensity. In very bright light, larvae might take 100 *Balanus* nauplii per hour, and at low light intensity, they might take no food.

LILEY

You ignored the question of hunger, and yet it's known that this has a marked effect upon reaction distance, and at least in trout it can affect reaction distance quite considerably. It could have a considerable influence upon the volume searched.

BLAXTER

I don't think this would be true of marine fish larvae. There's really very little work on reaction distance described in the literature. A snapping action by midwater larval predators is the best situation to look at. I can't believe that a feeding drive affects the actual sighting distance for a carnivore. Why should it?

LILEY

Yes, but your only measure of the sighting distance is when the animal reacts. It may have seen the object 20 m away but only reacted when it is 50 cm away.

BLAXTER

That's possible.

LILEY

That is always a problem. Beukema (Behavior 31; 1-26, 1968) found that the reaction distance of the stickleback was determined by the palatability of the food and to some extent the hunger level. For example, the stickleback would only react to *Drosophila* larvae when it was quite close and yet it would react to *Tubifex* at a much greater distance. This indicates that the fish can probably see the *Drosophila* larvae at that greater distance but it just doesn't react.

BLAXTER

I think you're taking the model one stage further. We originally used a situation where food was limited and fairly large volumes were being searched, a situation where satiation was unlikely. Now you're taking it a stage further and probably looking at a situation where searching isn't of any importance at all. The whole consideration of feeding may be really meaningless if fish can survive a long time without food. For example, adult herring can survive without food for 129 d at 6-12°C, and even the larvae survive 2-3 wk without food. I think you've got to keep this in the back of your mind when discussing feeding, food densities, predation rates, and so on.

HASLER

Several years ago Grinnel published an interesting paper on the feeding characteristics of birds. The robin cocks its head and looks and watches for the worm to move and grabs it. The nuthatch keeps bobbing around, and by using that mannerism makes the still object move. I was wondering if there was something about vision that measured movement. All these examples you have seem to involve staring at an object and grabbing it if the object moves. If the fish made some sort of movement to make the prey appear to move, that would give it an advantage.

BLAXTER

Of course as fish are swimming along their heads are moving from side to side, aren't they?

HASLER

Yes, they tend to be a little bit like the nuthatch.

BLAXTER

It's a reaction to the movement of the tail in fish. If their heads are moving it may give the eye the ability to scan.

HASLER

I was just wondering if anyone had looked at that experimentally or analytically to see the movability of the object and the ability of the animals to make the object more apparent. It seems like it might give it quite an advantage.

MAGNUSON

If you watch yellowtail swimming, their eyes move in opposition to the side-to-side movement of their head so that they point laterally rather than scan with the head movement.

ATEMA

The eye stays fixed on the object?

MAGNUSON

It's not staying fixed on the object because the tuna is moving forward too, but the eye points in a fixed direction perpendicular to the fish's path of progression.

BLAXTER

A lot of fish have binocular vision which is probably involved in range detection. Tamura also looked at the overlap of vision fields.

HASLER

Sumner, many years ago, found that camouflaged fishes adapted to a dark background had greater survival when exposed to a predator such as heron. I was wondering if you had any information on the role of contrast in prey perception in fishes.

BLAXTER

Contrast is basically the appearance of an object against its background. Many prey organisms are very transparent in the sea, but I think fish have developed means of improving contrast perception. I have not mentioned all the methods. Some deep-sea fish have yellow lenses, and these are probably involved in improving contrast as well. Other fish have iridescent corneas which may prevent intraocular glare from downwelling light. A diver can increase the sighting distance of grey targets by using a polaroid filter over his face mask. This seems to prevent backscatter of polarized light. Fish may use this trick as well. Good contrast perception is probably more important to fish than high sensitivity.

MURPHY

That curve (of Vinyard and O'Brien) you showed of size of object on the horizontal axis and reaction rate or sighting distance on the vertical axis had several lines and different illumination levels, and they were more or less straight but they would have to fall off if you kept increasing size and distance, wouldn't they? They'd lose their linearity, just because of the scattering.

BLAXTER

Yes, you would come to a point where the light intensity would be such that the object would disappear. You're probably looking at the middle of a reasonable visual range. This is Hester's work on training a goldfish using cardiac conditioning. The fish was trying to pick out flat discs against a background.

FISHELSON

Some years ago we started working with silver carps in Israel, and after very few experiments with injections of hypophysis we got millions of eggs, millions of larvae. In 5 d they all died in spite of the feeding and other measures. So the fishermen came over and asked me what to do to prevent mortality. They were growing the fish in tanks with a lot of illumination. We could see each larva swimming around trying to escape from the lights. The larvae were not feeding, so I told them to switch off the lights and let only diffuse light come in. Now we're exporting silver carps to Iran.

KEMMERER

Do you believe that adult herring and other fishes avoid predators through adaptive mechanisms involving diurnal vertical movement patterns in water columns? Some fish seem to prefer waters of specific turbidities while others prefer just reduced light levels.

BLAXTER

Vertical migration is very common in the oceans and it's very difficult to explain its adaptive value in all its forms. A general explanation might concern feeding. The euphotic zone is at the surface and the herbivores are filter-feeding there, so at some stage the other predatory fish must come up to feed on them. Now it seems that the herbivores come up at night themselves to filter-feed when they are safest, but they go down during the day because they are very vulnerable in brighter light. What is difficult to explain is why some of the carnivores just don't stay at the surface all the time and wait for the herbivores to come up at dusk. They may have their own predators and so be safe themselves in the lower illumination deeper in the water.

ATEMA

I wanted to ask you about the information you gave concerning the polar regions, that there are long periods during the year when it's too dark to feed. Is it reflected any way in the anatomy or the behavior of the fishes that you find there?

BLAXTER

I can't really answer that question. There are probably not many fish in the highest southern latitudes, but near the North Pole in winter, it may be so cold that feeding ceases or is not required anyway.

HARDEN JONES

Cod feed very heavily when there is virtually total darkness at Bear Island.

BLAXTER

And there would be a very large number of species which are browsing over the bottom. My data apply to visual feeders as shown by experimental work.

HENDERSON

From a practical standpoint, this question of turbidity and its effect is a bit complicated too, because if the feeding of a species is affected, that of its predator is affected in much the same direction. I am interested in the increase in visual acuity and contrast sense with size. The larger fish would tend to have the advantage under turbid conditions.

Chemical Senses, Chemical Signals, and Feeding Behavior in Fishes

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ATEMA, J. 1980. Chemical senses, chemical signals, and feeding behavior in fishes, p. 57-101. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Appreciation of the role chemical senses play in fish feeding behavior is ancient and widespread, and the resulting fishing techniques are based on each fish's natural feeding. Bait fishing and "chumming" to attract and excite fish are common practices usually based on centuries of trial and error. The process of choosing the most effective bait or chum may be accelerated when chemical signals and the senses of smell and taste are properly understood in the context of each individual species.

Chemical stimuli in the aquatic environment require solubility. Therefore macromolecules, including proteins, can be part of the chemical stimulus environment of fishes. Most chemical signals turn out to be mixtures of compounds which can carry specific information. Distribution of chemical signals in the aquatic environment is usually unpredictable and patchy due to turbulence and currents. Thus, locating the stimulus source is difficult, unless special conditions such as trails or steep gradients exist. As a result many fish use chemical signals to detect and identify their food at a distance, but then use other senses to locate the source. The olfactory sense organ with its complex neuroanatomy appears to be used for the detection phase of feeding behavior.

Food quality, including the presence of poisons, can best be tested during food chewing. Almost all fish seem to use internal (mouth) taste for this purpose. In several groups of fishes an external sense of taste exists as well, often on lips and barbels, sometimes over the entire body surface. This specialization is used to detect distant bait and, in some cases, to guide search behavior.

Several molecules stimulate both smell and taste organs, but behavioral responses to these stimuli can be very different. In general, amino acids and related compounds are important in eliciting both neurophysiological and behavioral responses.

Sensitivity of olfactory and gustatory receptors to specific chemical compounds can not be predicted and is highly variable among species and even individuals. Each animal is finely tuned to its ecological niche and it is likely that chemoreceptive potential reflects the biological significance of specific chemical environments. Innate food odor preferences can be modified by experience, including the effects of "ingestive conditioning," "specific appetite," and "bait shyness." Various physiological states, particularly hunger, have profound effects on food acceptance thresholds. These general considerations should be kept in mind in practical applications of chemical stimuli for fisheries and aquaculture.

Introduction

Age-old fishing practices of chumming, trapping, and bait fishing have taken advantage of the chemical senses of fishes. Understanding how fish use chemical senses in feeding behavior, however, requires an understanding of the properties of chemical stimuli and the distribution of these stimuli in the environment. Once these general principles are understood, it may be possible to evaluate more effectively the potential use of chemical lures and other techniques in fisheries where no historical fishing experience exists, or perhaps to improve on existing techniques.

The first section of this paper will describe properties of chemical stimuli, the anatomy and biological function of chemical senses which evolved to extract information from the chemical environment, and the extent to which one can expect these senses to control the major phases of feeding behavior. In this context some new terms will be introduced and defined. The second section reviews the literature to illustrate the principles discussed in the first section. Because of recent developments in the field and the existence of several older reviews, major emphasis is placed on the most recent literature. The third section briefly speculates on possible applications of our rapidly expanding knowledge of chemical senses and chemical signals in the aquatic environment to fish capture and culture.

CHEMICAL STIMULI IN THE AQUATIC ENVIRONMENT

Chemical stimuli have three important properties which determine their value for behavior and survival: they contain endless possibilities for specificity; their presence lasts beyond the moment of production; and they are in themselves usually nondirectional. The latter two properties are specific for chemical stimuli only and have important consequences for their biological use. This section will describe the molecular composition of chemical signals and their distribution in the aquatic environment.

Solubility: size of molecules

With respect to chemoreception the aquatic environment is different from the terrestrial environment only in the ways in which chemical compounds can be distributed: (a) molecules need to be in solution rather than in the gaseous phase to be transported; (b) water is a slower carrier medium both for diffusion and for currents. Thus, solubility rather than volatility determines the type of compounds that can be found and utilized as chemical signals. Consequently, macromolecules such as polypeptides and proteins with molecular weights as high as 100,000 are part of the aquatic stimulus environment of molluscs (Gurin and Carr 1971; Carr et al. 1974; Atema and Stenzler 1977) and Crustacea (Derby and Atema 1978). For fish, heat-stable, nonvolatile compounds with molecular weights of 500-1,000 have been implicated in conspecific recognition (Hara and MacDonald 1976) and in homestream recognition (Atema et al. 1973). However, amino acids and related compounds of comparable size are prominent components of the odors and tastes of the food of fishes (see next two paragraphs and Bardach 1975).

Specificity of mixture: identification

Specificity of a chemical signal is contained in its molecular structure, including its stereo-isomeric configuration. For instance, among the well studied insects, there are examples in which mixtures of cis and trans isomers of the same compound carry species-specific information (Borden et al. 1976). There is no reason to believe that such extreme specificity does not exist in the aquatic environment. Even for one-compound chemical signals organisms can choose from thousands of different molecules with potential for signal specificity. This potential increases with molecular size. Since macromolecules are used in aquatic chemical signals, the extent of single molecule specificity seems nearly unlimited.

Most environmental chemical stimuli, however, are mixtures of compounds. Acoustic and visual stimuli usually contain complex mixtures of wavelength patterns creating a sound picture or a visual picture. In analogy, we might call complex mixtures of chemical compounds chemical pictures. Mixtures of compounds can convey specificity with great accuracy, particularly if the mixture ratio is important. Fish are probably not different from man in that their natural environment contains a great number of chemical pictures which identify particular items of interest. We may think of the complex mixtures we call coffee or wine, versus the complex mixtures which to fish identify their natural prey or home stream.

Distribution: gradient, trail, and nondirectional active space

To understand the distribution of chemical stimuli in the medium we can consider the following three major situations which I will call gradient, trail, and nondirectional active space. The term "active space" describes any area where a chemical stimulus is present in superthreshold quantities (Wilson and Bossert 1963) and applies to all of the stimulus situations. I have chosen to use the terms "gradient" and "trail" as special cases of active space for practical purposes, involving an animal's frequent need to locate a chemical source. Steep gradients and trails, especially polarized trails, contain sufficient information for localization. However, the gradient in an active space is generally so small and distorted that other nonchemical stimuli are necessary to achieve localization (Kleerekoper et al. 1975).

The most commonly encountered situation is probably created by the intermittent release of chemical compounds from an irregularly moving animal in a moving, turbulent environment. Here, a three-dimensional area is "activated," i.e., a large area in space contains the distribution, the exact location of the source cannot be determined from chemical cues alone. Only by searching the prey's entire active space can a predator hope to encounter its prey. Usually other sensory information, such as current direction and acoustic-mechanical signals will help long-range localization. Exaggerated lateral extensions of chemosensory organs, such as the barbels of catfish taste, the nares of hammerhead shark, or moray eel olfactory organs, can aid in the detection of a gradient vector necessary for true tropotactic orientation. However, their normal function may well be to increase the search area within an active space.

Theoretically, when both source and medium are not moving with respect to each other, a chemical diffusion gradient will result, the steepness of which depends essentially on concentration and molecular size. Molecular diffusion in water is very slow (10^{-6}m per sec at most). In practice, however, wind, thermal- or density-driven currents and turbulence always exist even in apparently still water. They distribute a chemical signal significantly faster (10^{-2}m per sec). Major currents and rivers may run at speeds of meters per second. Molecular diffusion is thus negligible for distribution of a chemical signal. Turbulence and currents, including those created by the animals themselves, cause a typically patchy distribution of the chemical signal. Relatively steep chemical gradients may still exist, for instance where a carcass is rotting on the botton of a still pond. Even here, signal distribution cannot be expected to be smooth, and determination of the gradient vector will depend on the averaging of a number of patches with different signal strength.

When an evenly producing source moves in a still medium, a narrow odor corridor or a trail is laid, which may be two- or three-dimensional, but under conditions of limited turbulence its width or diameter will be small compared to its length. The deposition of a trail is pictured most easily as an ink line drawn on paper, or, for a three-dimensional trail, the smoke writing of aerobatic airplanes or jet exhausts. The speed of movement and the rate of production determine odor dilution. Under conditions of an evenly and constantly producing source, the gradient along the trail will be small due to dilution by diffusion, convection, and changes in chemical composition. Two-dimensional aquatic trails with polarity exist in molluscs (Crisp 1969; Wells and Buckley 1972; Hall 1973; Cook and Cook 1975; Trott and Dimock 1978). Three-dimensional trails (or odor corridors) may be laid down by swimming fish or fish schools. A still source in a moving medium presents the same stimulus situation as a trail, as does the case where both the source and the medium move along the same path in the same or opposite directions.

Trail following in molluscs (see refs. above) and worms (Ressler et al. 1968) is used in conspecific "communication." Conspecific use of trails is not known in fish. However, catfish follow food trails by taste (Bardach, Todd, and Crickmer 1967), and eels follow trails by smell, even in three-dimensional space (Teichmann 1959). However, both for catfish and eels, trail following is not a gradient search but appears to involve sequential comparison of concentrations on and off the trail. Their normal mode of search is by exploring an active space in rather haphazard fashion.

Persistence

Chemical pictures may not be essentially different from visual, mechanical, sound, or electrical pictures in containing specific information, but only chemical pictures last beyond the moment of production. A chemical picture can be left behind. This is actively used in territorial and shelter marking, which has been observed recently in fish (P. J. Rubec, Biology Department, Texas A & M University, College Station, Texas, pers. comm.; Müller-Schwartze and Atema 1978, pers. obs.). It can also be used in trail laying and following. The stability of trails is often enhanced by adsorption to a substrate. Persistence of a chemical signal in the aquatic environment has been demonstrated for alarm substances released from wounded conspecifics. In snails this may be as long as 1 d (Atema and Burd 1975; Atema and Stenzler 1977; Snyder 1967). Although fish alarm substances are equally well known (see Myrberg and Liley's chapters in this volume), the fish's days-long avoidance of natural areas where alarm substance was released (von Frisch 1938) is probably due to associative learning of geographic features of such areas rather than to long-lasting presence of odor. Persistence of chemical identity could theoretically be used to form decoys to sidetrack predators, but I am not familiar with examples of this use of chemical pictures.

Summary

The aquatic environment is not different from the terrestial environment in that it contains a multitude of chemical pictures. These are made up either of ordinary compounds, such as the ones entering the environment from animal metabolism in the form of feces, urine, and mucus or other skin products, or of exotic compounds, such as some specific pheromones, or poisons. Substrates, each with their own ecosystems of plants, microorganisms, and decomposition products, form another rich source of chemical pictures. Aquatic organisms, including fish, use these pictures to gain information about their environment. Although chemical pictures are excellent aids in identification of the source, they only rarely contain clues to permit direct localization. The resulting unpredictability of chemical stimuli may, in turn, have led to the greater amount of plasticity found in the behavior of fish that are dominated by chemical senses compared with visually dominated fish (Atema et al. 1969). This may be true for all vertebrates (Herrick 1924).

CHEMICAL SENSES

Distinctions between smell and taste

The meaning of the terms "smell" and "taste" is historically based on human experience. The validity of applying these terms to aquatic animals has been questioned in the scientific literature for nearly a century (Nagel 1894; Bardach 1975) and it has been suggested that the neutral term "chemoreceptors" be used for all organs of chemical sensing in the aquatic environment (Bardach 1975). Indeed, several putative characteristics of human smell and taste cannot be used to distinguish these senses in fish. Smell and taste extract information from the same carrier medium—water; in several fish, "taste" is as sensitive to certain compounds as "smell"; the number of different compounds distinguished by "taste" is not restricted to the classical four of human taste; "taste" in some specialized fish can act as a long-distance receptor system.

It has long been recognized, however, that distinguishing features of smell and taste neuroanatomy appear to be very similar in all vertebrates (Herrick 1908). Both the peripheral receptor cells and the central connections of smell are as distinct from those of taste in fish as they are in man. Briefly, smell receptor cells are primary ciliated neurons whose axons form the olfactory nerve (I), which enters a complex glomerular neural network in the olfactory bulb; bulbar connections in the telencephalic brain areas are complex and many. Taste receptor cells are microvillar epithelial cells. They are innervated by the facial (VII) nerve and glossopharyngeal (IX) and vagal (X) nerves, all of which enter the medulla area of the brain; their secondary connections are relatively few and simple. Many investigators have used the terms smell and taste for fish based on these solid anatomical distinctions.

Anatomical differences most likely reflect functional differences. Behavioral evidence for distinct smell and taste functions has already been given by von Uexküll (1895) for sharks. Thus, the distinction may be fundamental, if all vertebrates including the aquatic ones share the same anatomical plan for smell and taste. An attempt at formulating a functional distinction between smell and taste in fish (Atema 1977) can be briefly summarized as follows:

Smell is capable of recognizing complex chemical mixtures for which it has flexible "chemical search images." These search images are thought to be neural filters at the level of the olfactory bulb; their function is thought to preferentially enhance the reception of important chemical mixtures, such as prey odors (Atema 1977). Thus, smell is involved in various appetitive behaviors, including prey detection, social recognition, and home area recognition. Taste guards the intake of food, determines its palatability, and detects food poisons. Thus, it serves a role in the consummatory phases of feeding behavior. Although taste receptor systems are capable of rapid (one time) learning as is evident in the bait-shyness effect (see section on bait shyness), the olfactory system may be designed more specifically to adapt to a changing chemical environment.

Experimental evidence for this generalized concept has been presented elsewhere (Atema 1977) and aspects of it will be discussed later. Let it suffice here to state that both on morphological and functional grounds the distinction between smell and taste is as clear for aquatic vertebrates as it is for terrestrial vertebrates. In fact, the distinction between these two major chemosensory receptor systems may be so fundamental that it transcends the vertebrate-invertebrate barrier (Atema 1977).

Response spectrum of smell and taste

In the aquatic environment there is no physical or chemical reason why certain compounds should be smelled or tasted, or both. Receptor sites, the chemical substrates for biological recognition of molecules, could be located in olfactory receptor cells as well as in taste receptor cells. One assumes that their presence is based on biological need, i.e., survival value. Certain compounds such as amino acids may be needed as much for the detection of distant prey as for the decision to swallow or reject food. Neurophysiological experiments on fish taste receptors showed that they respond to many more "classes" of compounds than the four basic human tastes (Konishi and Zotterman 1963; Bardach and Case 1965; Hidaka et al. 1975). Thus, the response spectra (= the different compounds that can cause a neurophysiological response in a primary receptor cell) for smell and taste organs can have varying degrees of overlap. A good example is presently under investigation independently by Caprio, Little, and Atema, each using different techniques with catfish. Caprio (1977) has clearly shown that smell and taste nerves in catfish have different, widely overlapping response spectra for amino acids and certain alcohols. Little (1977a) using heart rate conditioning and Atema (1977) and Herbert and Atema (1977) using behavioral training have shown that the same chemical stimulus causes different responses when smell or taste organs are blocked. Thus, the same stimulus appears to have a different behavioral "meaning" depending on whether it is received by smell or by taste organs. This illustrates that the distinction between the chemical senses is based on biological function and neural interpretation.

Response spectra may vary within a species, within a population, and probably even within a litter. Since receptor sites are probably genetically fixed, they set absolute limits on the animal's capabilities to respond to chemical compounds. Subsequent behavioral responses to compounds and mixtures within the spectrum may be learned.

FEEDING BEHAVIOR: MAJOR PHASES

Generally, feeding behavior has been divided into an appetitive and a consummatory phase. The appetitive phase can be further divided into a detection and identification phase (alert) and a locating phase (search). The consummatory phase can be subdivided into a bite or pick-up phase, a chew and test phase, and a swallow or ingest phase. It will be helpful to discuss briefly the chemosensory aspects of these phases to point out the different control mechanisms involved. Smell often plays a role in the alert phase and taste nearly always in the test phase.

To identify food an animal must have an image of it. This image can match one compound of the chemical picture emitted by the food source or many of its compounds in specific ratios. I have called this a chemical search image. In water, where visibility is often limited, chemical identification is common, and widely different species take advantage of the specificity found in chemical pictures to be alerted to the presence of food.

In the subsequent locating phase, the animal has to cope with frequent nondirectionality of the chemical stimulus and with the possibility that the source of stimulation no longer exists. Live prey may have moved beyond the range of capture and dead bait may have been eaten by another animal. Only in cases of chemical gradient vectors or trails can the animal locate the source solely with the help of chemical senses. In common situations where odor is carried by the current, rheotactic orientation is often employed to locate the chemical source. Generally, animals identify an important odor and become activated to do something specific about it (i.e., search, attack, flee), but ensuing search behavior is guided by directional stimuli such as sounds, currents, and visual stimuli. Of the three major phases in feeding behavior, the greatest differences among animals are to be found in the locating phase.

Both appetitive and consummatory phases of feeding behavior are subject to environmental and endocrine stimuli and particularly to hunger state.

Finally, once the food has been located, a decision must be made whether to accept or reject it. Some fish use visual (tuna) or electrical (shark) properties of the food to elicit bite or pick-up behavior; others (catfish) use external taste or texture. Most fish, however, briefly chew their food, making it possible for internal taste to judge palatability. Some fish ("gulpers") may not taste their food before ingestion; others ("mouth tasters") use taste and texture to sort edible material from a mouthful of debris and mud. Where there are two distinct senses of taste (catfish, carp), internal taste has a higher acceptance threshold than external taste (Atema 1971). Thus, the consummatory phase nearly always involves taste.

Review of Literature

CHEMICAL PROPERTIES OF ATTRACTANTS

Scientific curiosity and the potential for practical application has prompted several studies to identify the active ingredients in prey odor. Such odors have generally been found to be complex mixtures of species-specific composition constituting a typical "chemical picture" as discussed in the introduction. Furthermore, different species appear to respond differently to identical mixtures, i.e., each species has a specific set of receptors and its own characteristic "search image." To date only a few studies have been published with a detailed account of behaviorally active compounds and only these will be reviewed below.

The first study of this kind measured the responses of the lamprey, *Petromyzon marinus*, to the "body odor" of the two trout species, *Salvelinus fontinalis* and *Salmo trutta*, its common hosts. Reconstitution of the complete body odor with 9 constituent amino acids and 11 amines, singly or in combination, showed that two amines were largely responsible for the entire activity, particularly amine 'F' (Kleerekoper and Mogensen 1963), possibly identified as isoleucine methylester (Kleerekoper 1971, pers. comm., in Bardach 1975). The authors raised the question whether this substance would be part of the chemical stimulus picture for predators in general, since they found it present in the body odor of 32 other fish species examined. More recent investigations, however, have shown that each predator species recognizes a different mixture of compounds, of which amino acids and amines often form an important part. For instance, several aquatic invertebrates were shown to release specific ratios of free amino acids into the environment (Johannes and Webb

1970).

The most complete studies of identification were not done on naturally released odors but on tissue extracts. Extracts from the clam, *Tapes japonica*, contain seven amino acids, mostly glycine, but also alanine, taurine, glutamic acid and aspartic acid, with traces of serine and threonine. A synthetic mixture evoked feeding responses in eels *(Anguilla japonica)* but not as strongly as the original clam extract (Konosu et al. 1968). This indicates that the eels responded to a particular selection of amino acids. Furthermore, their sensitivity to each did not correspond to the strength of their concentration in the whole extract. They were most sensitive to arginine, which is only a minor constituent of the clam amino acids. Such differential sensitivity would "distort" their perception of the clam's chemical picture, corresponding to a species-specific chemical search image: the eel's "view" of a clam.

Similar results were obtained in the most exhaustive study on this subject to date. In a series of four papers, Carr and his associates determined the fractions of mullet, crab, shrimp, oyster, and sea urchin extracts which were active for two species of fish, the pinfish *Lagodon rhomboides* and the pigfish *Orthopristis chrysopterus*. Betaine proved to be the major single compound to induce feeding behavior in these fish. However, amino acids in specific concentrations needed to be added to reconstitute complete behavioral effectiveness, and in some instances non-amino acids were apparently needed as well. For oyster extract, betaine alone when presented in its original extract concentration accounted for about 70% of total activity. For shrimp extract, betaine gave only 40% activity and amino acids in original extract concentration were necessary to reconstitute full activity. For blue crab and mullet, both betaine alone and amino acid mixture alone were only 2-9% active; when the two parts were added in original strengths, activity was partially (60%) restored, other non-amino acids playing a further part. Finally, in sea urchin extract, unknown compound(s) of low molecular weight seemed required to recreate the complete chemical picture of urchin as seen by the fish (Carr et al. 1976, 1977). These important results are summarized in Table 1.

As was found in other studies, not all amino acids played a role in the stimulatory activity. A mixture of betaine plus aspartic acid, glycine, glutamine, isoleucine, and phenylalanine was virtually as effective as mixtures containing betaine plus all 21 amino acids present in the extract (Carr et al. 1977; Carr and Chaney 1976). Thus, as did eels, these fish responded to a selection of compounds. It is important to note that *L. rhomboides* and *O. chrysopterus* responded to different chemical mixtures of the same food extract, shrimp. In *L. rhomboides* (family Sparidae), a synthetic mixture of betaine plus 20 amino acids accounted for only about 25% of the potency of shrimp extract, whereas in *O. chrysopterus* (family

TABLE 1. Amounts of various extracts and fractions (µL/mL) required to elicit a standardized feeding response from a group of pigfish *Orthopristis chrysopterus.* Values are rounded to first decimal whenever possible. Betaine and amino acids were presented in the quantities in which they naturally occurred in the various extracts. This value expressed as µM/mL is given in parentheses in the table. The ultrafiltrate contained compounds with molecular weights less than ca. 1,000. Shrimps, *Penaeus duorarum*; crab, *Callinectes sapidus*; oyster, *Crassostrea virginica*; sea urchin, *Arbacia punctulata*; fish, *Mugil cephalus.* (Adapted from Carr 1976; Carr et al. 1977).

	Shrimp	Crab	Oyster	Sea urchin	Fish
Betaine	0.9 (8.4)	1.1 (3.7)	1.4 (3.4)	—	26.5 (1.1)
Amino acids	1.3 (31.6)	1.7 (29.2)	5.1 (5.5)	—	104.7 (3.2)
Betaine plus amino acids	0.4	0.06	1.3	2:2	4.5
Filtrate	0.4	0.04	1:0	0.16	2.4

Pomadasyidae) a similar synthetic mixture elicited 100% activity. Also, in shrimp extract, betaine alone represented nearly 40% activity for pigfish, but only 10% in pinfish (Carr 1976). Apparently different species have different chemical images of the same food extract.

Such species differences were also noted by Pawson (1977a), who found that a synthetic mixture of amino acids which had been shown to be attractive to eels (Konosu et al. 1968) had little or no effect on whiting (*Merlangius merlangus*). In his study, glycine appeared as the single most effective substance for whiting and Atlantic cod (*Gadus morhua*). Interestingly, the glycine response threshold was at least 10 times lower than other amino acid thresholds, and both glycine and alanine were present in amounts about 100 times greater than the other five prominent amino acids in *Arenicola* extract. Together, these facts lead to the conclusion that cod and whiting have a highly restricted image of *Arenicola* extract, focusing narrowly on glycine. However, here also, non-amino compounds are required to reconstitute full potency. Both whiting and cod responded equally strongly to aqueous extracts from *Nereis, Arenicola, Mytilus,* and *Loligo;* unfortunately only *Arenicola* extract was analyzed chemically. A selective filter focusing on the prey's most common amino acid constituents has also been suggested for goatfish (*Parupeneus porphyreus*) which are excited by the dominant, but not by other, amino acids of their crustacean prey (Holland 1978).

Glycine again was found most active for winter flounders (*Pseudopleuronectes americanus*) and mummichogs (*Fundulus heteroclitus*) during field attraction tests (Sutterlin 1975). These field experiments confirm the laboratory results discussed above in the major two accounts:

1) mixtures are more effective than single compounds;

2) each species selectively responds to a specific mixture of compounds.

A dramatic example of the latter is the Atlantic hagfish *Myxine glutinosa),* which could not be attracted by any single compound or partial combination of amino acids and other substances from otherwise attractive extracts (Sutterlin 1975). The hagfish apparently depends on other compounds for its chemical identification of food.

With the exception of the lamprey work, these studies employed tissue extracts as the chemical stimulus. For hunting predators, this must be an unnatural situation, which tells us little about their chemical identification of live prey, such as seen in various sharks (Sheldon 1911; Parker 1913; Tester 1963; Hobson 1963). One other study was done on the body odor chemistry of natural prey. Yellowfin tuna *Thunnus albacare* responded to prey school odor, the odor of fresh dead prey, and prey tissue extract. Responses diminished with further chemical separation of amino acids, but a slight response was still obtained when tryptophan, the single most prevalent amino acid in one of the prey odors, was introduced. It was calculated that in these tests the tuna responded to a stimulus concentration of 10^{-11} M tryptophan (Atema 1977; Atema et al. 1979).

The reported studies on the active ingredients of natural attractant mixtures point to the possibility that some substances, which in themselves do not elicit behavioral responses, may still play an important role in the stimulatory properties of the whole mixture. Some of these odor enhancers may still stimulate chemoreceptors. Combined neurophysiological and behavioral studies could identify such compounds, which, only in combination with other substances, result in overt behavior and increase the responses to full activity. Their practical importance is obvious.

Neurophysiological studies on peripheral chemoreceptors for the identification of behaviorally active compounds must be interpreted with caution, since, as discussed above, species-specific selective filters in more central parts of the olfactory pathway modify peripheral reception to form a search image. It is through matching a search image with a chemical picture that behavioral responses are elicited. The search image is not (yet) accessible to direct electrophysiological monitoring. Despite this word of caution, both multifiber and single-fiber recordings from fish taste receptors have consistently shown that whole extracts, already in these peripheral neurons, evoke greater responses than single compounds or partial mixtures (Bardach and Case 1965; Fujiya and Bardach 1966; Konishi et al. 1966; Zippel and Breipohl 1975; Hidaka and Kiyohara 1975). Since single taste fibers innervate many different receptor cells, it remains unknown whether this increased activity is caused by the summation of individual receptor cell responses or by the interaction of different compounds on each responding cell. Only single cell recordings can answer some of these questions, but their discussion falls beyond the scope of this paper.

The increased effectiveness of whole natural extracts over partial mixtures and single compounds has been demonstrated both for olfactory (Atema 1977) and gustatory detection (Zippel and Breipohl 1975). In attempts to identify active fractions, similar conclusions have been obtained (van Weel 1952; Tester et al. 1954, 1955; Hsiao and Tester 1955; Haynes et al. 1967; Hodgson and Mathewson 1971; Bardach 1975). Although not specifically investigated, one can assume that the olfactory system was involved in these studies.

Variations in the effectiveness of certain mixtures on taste reception exist even between different strains of a species, as shown by the different sensitivities to silkworm pupae extract in Swedish and Japanese carp (Konishi and Zotterman 1963). Such differences in peripheral response spectrum also exist between species (Hidaka et al. 1975; Bardach and Case 1965) and support the idea of "tuned prey reception" (Holland 1978).

The importance of highly specific mixtures received via olfaction is further implied in studies of homestream recognition (see Hasler, this volume), social recognition (see Myrberg, this volume) and prey detection (Tester 1963). The latter study shows one other important fact, that some sharks detect and become far more excited by the odor of distressed or damaged fish than of quietly cruising individuals. Similar results have been seen in catfish intraspecific odor detection (Elgin and Atema 1978), and chemical analysis of the mucus of stressed catfish has shown a change in the normal chemical picture emitted by the fish (Bryant and Atema unpubl.). Stress odors may be useful in the manipulation of fish behavior, both in capture and in culture.

These studies as well as many other less detailed observations have made it clear that species-specific mixtures cause the greatest behavioral responses. Among the single compounds that represent major effectiveness in these mixtures a few can be identified: betaine (Hodgson et al. 1967; Carr 1976; Carr et al. 1977), glycine (Hashimoto et al. 1968; Sutterlin 1975; Pawson 1977a), alanine (Sutterlin 1975), and perhaps taurine (Hashimoto et al. 1968) and amine F (Kleerekoper and Mogensen 1963).

Field testing of chemically isolated fractions of attractants has been conspicuously lacking, with the exception of Sutterlin's (1975) work. It has been indicated that laboratory tests cannot be expected to yield equal results in the field (Pawson 1977a).

CHEMICAL SENSES IN FEEDING BEHAVIOR

The literature on the role of olfaction and taste in fish behavior, including feeding behavior, has been reviewed on several occasions (von Frisch 1942; Teichman 1962; Kleerekoper 1969; Bardach and Atema 1971; Bardach and Villars 1974; Hara 1975), eliminating the need for another survey. The most complete review of the older literature was done by Kleerekoper (1969), where many important, sometimes inaccessible, German papers can be found. However, none have systematically approached the role of chemoreception in fish behavior from the logical point of view of the chemical stimulus environment in which chemoreceptors evolved to contribute to adaptive behavior. Therefore, it seems most useful to illustrate the model presented in the introduction with experimental evidence. First, two extreme examples will be discussed: the use of chemical senses in the feeding behavior of bottom-dwelling, slow-moving, nocturnal catfish and in oceanic, fast-swimming, diurnal tuna. These may serve as a background for reference. Then, the three major phases of feeding behavior will be discussed to show that chemical senses are almost always involved in the alert and testing phases. The locating phase is under the control of a number of different senses, including chemical senses, depending on the ecological niche of the animals involved. By far the most research effort has been spent on this latter phase. It will be treated in two parts: olfactory-guided search and taste-guided search.

Catfish and tuna: two extreme examples

Yellow bullhead *Ictalurus natalis* and brown bullhead *I. nebulosus* populate the bottoms of freshwater ponds, lakes, and rather stagnant parts of rivers. Their habitat is often covered with vegetation in sand and mud, in which they dig small burrows or use natural shelters under logs and rocks. Generally, visibility is low. These catfish have small eyes, which in one isolated lake, have become reduced to near blindness (Weisel and McLaury 1964), indicating a limited importance for vision. Their nocturnal activity peaks around dusk and dawn (Rubec 1975). They lead a slow-moving existence. Bullheads feed mostly at night, largely on benthic invertebrates and plants (Rubec 1975), but also on live fish (Moore 1972). They readily eat dead bait. It is not surprising that under such environmental conditions chemoreception, both smell and taste, has become well developed, together with slow search behavior.

Catfish (Siluridae) have specialized in their sense of taste, which together with touch, directs most of their feeding behavior, at least with respect to dead bait. Bullheads have eight barbels. The four mandibular and two maxillary barbels are often trailed along substrates, or the two nasal and two maxillary barbels along the water surface, in search of food. Taste buds cover their entire body and are particularly dense on the barbels (Atema 1971). Taste projection areas in the brain have become visibly enlarged to form the paired facial and vagal lobes (Herrick 1905). Two senses of taste can be distinguished morphologically and functionally. External taste buds found on the lips, barbels and the entire body are innervated by the facial nerve (VII) and project in the facial lobes; pharyngeal or internal taste buds are found inside the mouth, pharynx, and gill arches and project via the glossopharyngeal (IX) and vagal (X) nerves in the vagal lobes (Herrick 1905; Atema 1971; Finger 1976). Lesions of the facial lobes showed that the locating and pick-up phases of feeding behavior were severely affected or abolished entirely; vagal lobe removal resulted in a blocking of swallowing behavior (Atema 1971). It was concluded that in catfish external taste serves to locate dead bait at a distance and to trigger the pick-up reflex, whereas internal taste serves as a second, more restrictive screen for food intake controlling swallowing. The more restrictive function of internal taste is easily observed in cases where less palatable food is accepted by external taste (pick-up behavior) and then rejected by internal taste (spitting behavior). When dummy pellets of various textures—rubber, polyethylene, glass, and ceramic—were presented mixed in with food pellets of the same size and shape, the dummies were only picked up when they had been in contact with food materials (or human hand). Clean dummies were never picked up, even when touched with the barbels, demonstrating that chemical stimulation of external taste is necessary to trigger pick-up behavior. After some "chewing" the dummies were invariably rejected and the real food pellets eaten, taste and touch acting in concert to sort out food items in the mouth (Atema 1971).

Dead bait and body tissue extracts contain among many other compounds large amounts of free amino acids (see section on Chemical Properties of Attractants), which stimulate the bullhead's sense of taste (Bardach, Fujiya, and Holl 1967). Taste thresholds for amino acids were determined electrophysiologically (Caprio 1977) and with conditioned heart rate responses (Little 1977a) for the closely related channel catfish, *I. punctatus*. Threshold values of 10^{-12} M are not uncommon. Bait localization, including the moment of first alerting, is not detectably altered by removal or blocking of the sense of smell (Bardach, Todd, and Crickmer 1967; Atema 1969, 1971). Thus, it has become clear that in these catfishes the two senses of taste control the entire feeding behavior sequence from alert to swallowing, when dead bait is involved.

However, ictalurid catfish are not only scavengers of dead bait, they are also efficient predators of snails, worms, insect larvae, and fish. Detection of live prey (concealed worms) was abolished when olfaction was blocked, but not when barbels were removed (Parker 1910). Although barbel removal is only a partial block of taste capabilities, these tests indicated that the sense of smell is involved in live prey detection. Indeed, catfish have well developed olfactory organs and brains (Atema et al. 1969; Atema 1969; Finger 1975) with which they can detect amino acids in great dilution (Caprio 1977) and discriminate between the odor of male and female conspecifics (Herbert and Atema 1977) as well as individuals (Todd et al. 1967). Earlier experiments on the minnow *Phoxinus laevis* had shown already that these fish are capable of learning to discriminate between many species through olfaction (Wrede 1932; von Frisch 1941; Göz 1941). Finally, discrimination of the tank water (body odor) of different prey fish species, which were readily hunted down and eaten in the laboratory, was abolished by plugging the catfish's nose (Wier and Atema, unpublished). Thus, smell plays an important role in the detection and location of live prey. Based on experiments with bluntnose minnows *(Pimephales notatus)* which demonstrated the ability to distinguish between various plant odors by smell (Walker and Hasler 1949), we may guess that in catfish, feeding on plants also involves smell for detection and discrimination, and taste for final testing.

Laboratory tests on the location and capture of live prey fish have shown that brown bullhead use electrical detection of their prey at short range, about 15 cm (Kalmijn 1974). We can thus far only guess that other senses, such as lateral line and vision, may also be involved in prey detection. Internal taste probably retains its final checking function in the consummatory phase of feeding on live prey as it does for dead bait.

Thus, there is a role division between the senses of smell and taste, which together almost entirely dominate the feeding behavior of catfish. Smell is used for detection, discrimination, and location of plants and the body odors of live prey. External taste is used to detect and locate dead bait, and internal taste screens for palatability and controls swallowing. The catfish represents one end of the chemosensory spectrum of feeding strategies in fish.

At the other end of the spectrum are such fish as tuna. Yellowfin tuna are large, diurnal, highly visual predators. Their habitat is the open ocean and they are found in all but the arctic regions of the world. They constantly cruise in large schools in the upper water layers in search of usually fast prey, such as anchovy and squid. When a prey school has been encountered, hungry tuna go into a feeding frenzy. Tuna are capable of great speed. They hunt by day, consuming large amounts of food and growing fast. Their large eyes are important in the nearby localization of prey and in directing the final attack and strike. Visual discrimination appears acute (Nakamura 1968; van Weel 1952). However, visibility even in the clearest tropical waters is limited, and it is unlikely that in distant-prey detection tuna can rely on vision. A role for olfaction is indicated by their large olfactory organs (Gooding 1962; Iwai and Nakamura

1964). Indeed, experiments in large tanks (van Weel 1952; Magnuson 1969; Atema 1977; Atema et al. 1979) showed that tuna responded to prey extracts with increased swimming speed, changing swimming patterns, head thrusts and occasional snapping. Even "feeding bars" (dark vertical stripes on their body associated with feeding excitement) were occasionally noticed when the extract of their favorite prey was introduced. Not only prey extract, but also the water collected from a live prey school elicited responses. It could be shown that amino acids are part of their prey odor image and that the olfactory threshold of detection lies at about 10^{-11}M (Atema 1977; Atema et al. 1979). With respect to the detection of live prey at a distance, tuna may not be so different from catfish.

Although Hawaiian fishermen slap their poles on the water surface to attract and excite tuna, there are no studies available to show that acoustic prey detection occurs. Electroreception likewise has never been studied. Once the prey has been sighted, visual behavior apparently takes over. During their final high speed strike, tuna make split-second decisions on food acceptance. This also appears visually guided. However, after food has been struck it can still be rejected (van Weel 1952; Atema, pers. obs. 1976). This may be a decision based on texture and taste. No information is available on the presence or the biological function of taste in tuna, but it seems likely that internal taste keeps its general biological function also in these fish.

Thus, despite their obvious differences in niche, behavior, and anatomy, both catfish and tuna probably rely on smell for distant prey detection, and on internal taste for final food intake screening. These functional similarities were predicted from the physical properties of chemical stimuli, as discussed in the introduction. It was also expected that the greatest differences among fish would be found in the search and locating phase. The following sections will review a number of other studies on fish to illustrate their use of chemical senses in the three major phases of feeding behavior.

The detection phase

Not only catfish and tuna use smell for distant prey detection and identification; nearly all other fish studied are alerted to prey by olfaction as well. Exceptions to the use of smell in prey detection may be found in the most visual fish, such as the nearly anosmic sticklebacks (Atema et al. 1969) and lunging predators such as the pikes (Wunder 1927; Pipping 1926, 1927), which appear never to be alerted by chemical stimuli alone; see also von Frisch (1941). Also, the sand eel *Ammodytes marinus*, in contrast to true eels, ignores live prey odor (Winslade 1974). Exceptions at the other extreme are the catfish (Atema 1971) and the goatfish (Holland 1978) which do not need olfaction to become alerted to dead bait and can use external taste information.

The locating phase: olfaction

Olfactory alert is most often followed by a rheotactic orientation and locating phase. In a few species, olfactory location of an odor source in still water is possible. Experiments on sharks illustrate this phenomenon most clearly. In precisely monitored laboratory tests on the capabilities of nurse sharks *Ginglymostoma cirratum* to locate a point source of shrimp extract, flowing water provided the direction vector for locating, which "is very precise in flowing water and is dependent on the gradient of the stimulus in the medium. Downstream sites of stimulation are better localized than upstream. In stagnant water only generalized localization occurs" (Kleerekoper et al. 1975). Similar results were obtained by Hodgson and Mathewson (1971), who compared nurse sharks and lemon sharks (*Negaprion brevirostris*) in their chemical locating capabilities in a hydrodynamic tunnel. Here the visual, pelagic lemon sharks reacted to chemical stimulation by orienting against the current until close to the source. Other pelagic sharks showed similar behavior and did not locate odor sources precisely: blacktip shark (*Carcharhinus melanopterus*), grey shark (*C. menisorrah*) (Tester 1963), whitetip shark (*Triaenodon obesus*) (Hobson 1963), lemon shark, and bonnethead (*Sphyrna tiburo*) (Hodgson et al. 1967). These fish require other stimuli for the final phase of food location.

The slower, benthic nurse shark, however, oriented "toward a chemical source by true gradient searching and exhibited circus movements following unilateral chemosensory deprivation" (Hodgson and Mathewson 1971). The deprivation in these experiments consisted of nose plugs. Dogfish species also showed apparent gradient localization of dead bait (*Scyliorhinus canicula* and *S. stellare*) (Teichmann and Teichmann 1959: Dijkgraaf 1975). Circus movements (i.e., predominant circling toward the intact side after unilateral deprivation) were not observed in *Scyliorhinus* sp. (Teichmann and Teichmann 1959) but did occur in the more active and visual smooth dogfish *Mustelus canis* and *M. laevis* (resp. Parker 1913; Teichmann and Teichmann 1959).

However, according to Dijkgraaf (1975) and Kleerekoper et al. (1975), even in the ecologically "catfish-like" sharks, true gradient search, i.e., following a chemical concentration vector, probably did not occur. The typical behavior of such fish is response to chemical (olfactory) alert, subsequent upstream swimming, and rather haphazard checking of the general area around the odor source until it is located. When present, directional near-field orientation cues such as electric fields or mechanical water disturbances are used, both by these sharks and by catfishes, and they override chemical gradient cues (Kalmijn 1974; Dijkgraaf 1975). This observation is important because it underscores the fact that through evolution these fish have ignored chemical localization, nondirectional as it often is, and use directional information from electric fields whenever possible. Although hammerhead sharks, *Sphyrna spp.*, appear eminently built for true olfactory gradient search, it has never been proven that in fact they use their laterally extended nares to determine the gradient vector.

Chemically stimulated upstream orientation has been demonstrated in number of other fish which can be attracted by a chemical source (Pawson 1977b; Sutterlin 1975; Bardach et al. 1959; Teichmann 1962). In some cases odor sources can be located by trial and error using olfaction alone (see Kleerekoper 1969 for review). For ultimate olfactory performance, in the laboratory at least, eels (*Anguilla anguilla*) can follow scent trails by smell by successive comparison of odor intensities across the trail (Teichmann 1959).

The general rule appears to be that in the locating phase, eels and other "catfish-like" species, either by smell or by external taste, can follow a chemical trail or odor space, whereas "tuna-like" species increase their swimming speed after chemical detection, often in an up-current direction.

In nearly all cases precise food location is accomplished with the help of other more directional sensory systems. Even in animals that are not capable of locating a chemical source, olfactory stimulation appears to be one of the most powerful means of exciting an animal and then keeping it motivated to pursue its visually guided locating behavior (van Weel 1952).

The locating phase: external taste

The search and locating phase of feeding behavior can utilize chemical stimuli without relying on olfaction. In several species the function of the sense of taste has been extended to locate or even becoming alerted to food. In most cases this extension involves innervation by branches of the facial (VII) nerve and true taste buds. Most prominent in this respect are, of course, the catfishes, an example of which was discussed previously. But there are other groups of fish with special appendages serving a taste function. Cod (Gadidae) have one chin barbel, carp and suckers (Cyprinidae), mullets (Mullidae) such as goatfish *(Parupeneus porphyreus)*, and nurse sharks have two barbels, and sturgeon (Acipenseridae) have four barbels. All of these fish typically search the substrate for food, trailing their barbels over the ground. When they touch a chemical stimulus source, a reflex pick-up movement follows and the material is taken into the mouth, often mixed with sand, pebbles and mud which are sorted out and later rejected. Detailed discrimination of taste and texture is accomplished in this process (Atema 1971).

Other taste appendages are found in the extended pelvic fin rays of gouramis (Anabantidae) and red hake *Urophycis chuss* (Gadidae). The latter species requires olfaction to locate food at some distance (Bardach and Case 1965). An interesting case is presented by the northern searobin *Prionotus carolinus* and striped searobin *P. evolans*, which also need olfaction to elicit search behavior. Here, bait location is accomplished via the extended first three pairs of pectoral fin rays, with which these fish "walk" over the substrate (Bardach and Case 1965). These fin rays are not cranially (VII) innervated but spinally, and taste buds are absent. When the fin rays are stimulated with food extracts or amino acids, reflex digging behavior results. Taste buds are present on the lips of the sea robin. When these are stimulated, gulping and swallowing reflexes are elicited (Bardach and Case 1965). Apparently these fish are alerted by olfaction to a chemical source and begin to explore the up-current environment. When the pectoral fin rays then hit a concentrated chemical stimulus, digging behavior is released and the mouth is brought to the same spot (Bardach and Case 1965). Gulping follows lip stimulation. Presumably the internal taste does the final checking, although this was never tested. The most interesting aspect of this specialization is that an anatomically different taste system is used for a typical external taste function. The chemically sensitive tips of the fin rays are provided with small skin lobes which are densely innervated by a spinal nerve plexus (Bardach and Case 1965; Bardach 1967). The corresponding areas in the first three ganglia of the spinal cord are greatly enlarged (Morrill 1895) similar to the facial and vagal lobes of catfishes. Another example of a chemosensory appendage is found in *Blennius antennarius*, which carries a pair of supraorbital tentacles on its head. These tentacles have small tastebud-like cell clusters which appear different from the regular tastebuds on this animal's lips and mouth (Schulte and Holl 1972). Since neither behavior nor neuroanatomical connections were described, the identity of these buds cannot be determined.

Extended appendages are not always present; facial skin (carp, Evans 1952; Marui 1977; and blind cave fish, Schemmel 1967) and even the whole body surface (catfishes, Atema 1971) can be sensitive to chemical stimulation with food substances. Whether or not these chemically sensitive areas aid in distant food location is not known. It is more probable that the taste sense here works entirely in conjunction with the tactile sense as demonstrated in simple and elegant experiments on catfish where well-directed responses can be obtained even after tactile adaptation (Herrick 1904). In most fish, lips are organs of external taste, innervated by facial nerves and provided with tastebuds, for instance in puffer fish (Hidaka et al. 1975).

In support of the notion that anatomical differences reflect physiological-behavioral needs, feeding habits can be correlated with the distribution of tastebuds and the size of sensory brain areas for a number of fish species (Evans 1931; Evans 1952; Davis and Miller 1967; Miller and Evans 1965; Singh 1972). Generally the bottom feeders have extensive external taste development on lips or barbels, which seem to have evolved several times independently. Taste projection areas in the brain change accordingly: large vagal lobes are found in mouth tasters such as carp and suckers where a palatal organ—a taste bud-packed lobe in the roof of the mouth—exists; large facial lobes exist in the brains of skin, lip and barbel tasters such as catfish.

Thus, we see a wide spectrum of taste adaptations to assist in the locating phase of fish feeding behavior. External taste innervated by the facial nerve can be restricted to lips or spread over the face and whole body surface; or it can involve special appendages, such as barbels or extended fin rays. Generally, the more extensively external taste has developed, the more likely it is that it serves to locate food at a distance. In the most extreme case of catfishes and goatfish, taste has replaced olfaction even for detection of distant bait.

The testing phase: internal taste

The role of internal taste seems predictable and self-evident, but has not been well studied. Apart from observations that fish reject quinine-treated, poisoned, or denatured foods after first taking them in their mouth (moray eel, Bardach et al. 1959; shark, von Uexküll 1895; Tester 1963; tuna, van Weel 1952), the only other experimental observations on the role of internal taste were made on catfish (Atema 1971) as discussed previously. Internal taste further plays a role in "bait shyness" effects and perhaps in "ingestive conditioning" (see section on Food Odor Preference). Internal, vagal (X) and glossopharyngeal (IX) innervated taste is assumed to serve as a final checking gate for palatability for all fish. The role of taste in fish feeding behavior has been reviewed more completely elsewhere (Bardach and Atema 1971).

Summary

Nearly all fish appear to rely on olfaction for distant prey detection. Some fish with prolific external taste development use that sense to alert themselves to the presence of distant bait. Once alerted, the subsequent locating phase is sometimes under chemosensory control, and both smell and taste can aid in the location of a chemical source. Most often, however, other more directional stimuli are used. Internal taste appears always to control food intake.

FOOD ODOR PREFERENCE

Feeding behavior and food intake are regulated by a number of mechanisms which regulate both the detection and the acceptance threshold for different foods. These mechanisms include innate and acquired food odor preferences, biological rhythms, and hunger. As discussed in the section on chemical properties of attractants, restrictions on chemical food detection are placed on the animal first by its chemoreceptor sites, then by its neural filters, such as the search image.

Differences in response to food odors are ultimately determined by the receptor sites available for interaction with various odor molecules that constitute the chemical picture of food. Such differences are probably genetically fixed and expressed at the level of the chemoreceptor cells. Indeed, species and even race differences in neurophysiological responses to various substances have been well documented (Konishi and Zotterman 1963; Bardach, Fujiya, and Holl 1967; Fujiya and Bardach 1966). However, neural filters are important in the determination of what an animal will respond to behaviorally. These filters are thought to be constantly modified by experience, e.g. "ingestive conditioning," "specific appetite," and "bait shyness." The filters may also change in response to animal age and size, food abundance, and season, and in circadian or tidal rhythms. Ecologists have long recognized the importance of changing feeding behavior with food accessibility for population stability (Murdoch and Oaten 1975).

Although little is known about most of these mechanisms in fish, a brief discussion of each may serve to focus attention on our lack of knowledge of such important modifiers of fish feeding behavior. Examples from animals other than fish are used to illustrate the potential existence of these mechanisms in fish.

Innate and acquired food odor preferences ("ingestive conditioning")

Innate food preferences have been established for naive garter snakes, which show preferential responses for different food odors immediately after hatching. Differences exist between populations of different geographic areas (Burghardt 1970) and polymorphism exists even within the same litter (Burghardt 1974). These differences are probably genetically determined and not based on the mother's diet (Burghardt 1971). Such elegant examples of innate food odor preferences do not exist in the fish literature. Similar phenomena are shown by sea lampreys which increase their activity when presented with the odor of trout, a common prey. This response was also obtained from naive young lampreys (Kleerekoper and Mogensen 1963). Strong evidence for innate preferences was obtained in the predatory gastropod snail *Urosalpinx cinerea.* Piotrowski and Cole (in prep.) presented barnacles and mussels (biomass ratio 1:30) to *U. cinerea* which had been born in the laboratory and raised on mussels. Even with the available biomass strongly in favor of mussels, the snails exhibited a strong preference for barnacles, the naturally preferred food for this population.

On the basis of experiments with field-collected populations of *U. cinerea,* Wood (1968) proposed the mechanism of "ingestive conditioning" in which "the predator's tendency to respond to effluents from a given prey species is increased after it has ingested living tissues from that species." While possible explanations for the contradictory results of these two studies on *U. cinerea* do not belong in this paper, these studies do point to the need for careful genetic control to demonstrate the mechanism of ingestive conditioning. Some control existed in the study of garter snake food odor preferences, where it was shown that innate preferences could be easily and quickly modified by subsequent feeding experience (Burghardt 1974). Evidence for ingestive conditioning was further found in sea stars *Asterias rubens*, which would not move in a Y-maze towards a bait of oyster spat unless they had been previously conditioned to eat oysters for about a month (Castilla 1972). Similarly, sockeye salmon smolts *(Oncorhynchus nerka)* ". . . did not respond to any of the food extracts tested except when they had previously eaten the foods" (McBride et al. 1962). Yellowfin tuna increased their feeding excitement behavior to previously unknown prey odor after being fed on it for a few weeks (Atema 1977; Atema et al. 1979). Little (1977b) found that the channel catfish, which accepted L-cysteine flavored foods naturally, could learn to accept foods flavored with 4 x10^{-3}M quantities of other amino acids. In the marine catfish *Plotosus anguillaris* conspecific body odor appears to be important in schooling behavior. Here also, "the attractive response is not innate, but acquired by constant learning" (Kinosita 1975). While this is not feeding behavior, it is not unreasonable to assume that similar "constant learning" of body odors may also take place in predatory-prey relationships. Specialized sensory detection may also be involved in the individual food specialization found in trout, where fish from the same area had significantly different stomach contents. By repeatedly pumping the fishes' stomachs, Bryan and Larkin (1972) showed that individual fish specialized in different foods.

Examples from such diverse animals lead one to the preliminary conclusion that innate food odor preferences are probably common, fish being no exception. Further, it appears that in some cases such preferences may persist regardless of food actually eaten, and that in other cases feeding experience modifies innate preferences. Some of the advantages that innate and modifiable preferences may have for resource partitioning have been discussed by Burghardt (1974). It should be mentioned that not only preferences can change, but also response thresholds and reactive distances (Ware 1971). The implications are important for potential application in fisheries, management, and fish culture.

Predictable and pre-programmed changes in food odor preference

Perhaps other factors can change an animal's food preference. In many instances during growth and development animals utilize different food resources. This is particularly evident in animals that go through metamorphosis. In the extreme case, larval fish may not even have chemoreceptors in their early days of life and must rely on vision and tactile information to find food (see Iwai, this volume). In all cases the animal's size and speed set limits on what it can find and eat. It seems logical that with changing food resources there is a need to adopt new odor preferences so as not to waste energy locating unmanageable or low-calorie food. Such teleological arguments are fruitful in directing future research, but to date experiments are lacking to show that fish are programmed to develop different odor preferences as they grow, independent of the effects of "ingestive conditioning."

Similarly, there are many instances known where animals change their diet according to food abundance. Generally, such animals become increasingly effective in finding the newly developed resource. It was as a result of these observations that the concept of a search image was first formulated (Tinbergen 1960) and further discussed (Krebs 1973). However, no studies exist which demonstrate that a change in food odor preference, such as described for tuna (Atema 1977), is actually correlated with prey abundance in the field. In instances of predictably changing food resources, it may even be effective for an animal to have a pre-programmed, seasonally-changing search image for these resources. Long-term seasonal changes are often correlated with hormonal levels, which in some cases do influence olfactory performance (see below).

Following the same reasoning of hunting cost-effectiveness, it can be expected that short-term biological rhythms may also be correlated with food preferences. I have found only one example in the aquatic environment where a regular short-term (tidal) change in food preference has been demonstrated. The marine snail *Acanthina punctulata* appears to search for snail prey *Littorina* sp. during the early low tide and for barnacles later in the low tide cycle. This behavior is advantageous because the predator gets more calories from a snail that from a barnacle, but it takes longer to drill a hole in the snail than in the barnacle. The job of finding the prey needs to be finished before incoming high tides pose dangers to the predator. Thus, when snail prey is not found in time, it "pays" to look for smaller, but easier barnacle prey. This may constitute the optimal compromise between "maximum energy obtained and minimizing risk for mortality" (Menge 1974). Prey detection and locating in this species are probably chemically mediated. It may be expected that other short-term cycles, such as circadian rhythms, also modify food preferences in some species.

"*Specific Appetite*"

The role of olfaction in feeding behavior is detecting odors associated with food, since nutritive substances are not necessarily transported or detected. The separation of odor and diet requires a feedback system, which in fish is probably partially fixed and otherwise subject to experience. Feedback through experience means that animals must monitor their nutritional needs and select food rich in the essential nutrients. This was first shown in rats (Harris et al. 1933). The phenomenon is based on odors associated with good food and has become known as "specific appetite." Thiamine-deficient rats associated the odor of a thiamine-rich food with their subsequent well-being. It was shown that they selected on the basis of odor and not nutrient when the associated odor was added to a poor diet. The rats then chose the non-nutritious, flavored food until they relearned a preference for unflavored food. Experimental evidence for this mechanism is reviewed by le Magnen (1971).

Specific appetite represents a functional analog to the reversed effect of bait shyness to be discussed next. Both mechanisms lead the animal to associate odor or other characteristics of food with subsequent health. I am not aware of examples of specific appetite in fish, but it seems due to a lack of experiments rather than absence of this important mechanism. Practical applications could be made in the area of food development for fish culture. The association of an (artificial) odor with a good diet may well result in enhancing the feeding and growth of fish stock.

"Bait shyness'

Garcia et al. (1974) clearly established that vertebrates have a mechanism by which the last food eaten before sickness is subsequently avoided. The sickness need not be caused by the food itself. This type of avoidance (i.e., "bait shyness") is mediated by the senses normally involved in food detection and testing and nearly always involves internal taste as one of the filters for rejection. The earliest report of this effect in fish was by Pipping (1927) for cod, *Gadus morhua* and *G. merlangus*, and a labrid *Labrus rupestris*.

Bait shyness, mediated by chemical senses, has been shown in Atlantic cod *Gadus morhua* (Mackay 1977) and channel catfish (Little 1977b). These fish would learn to avoid food which was associated with a single instance of lithium chloride toxicosis. Mackay (1977) found that both visual and chemical cues were involved in forming the aversion and that the aversion was specific to the food which had been consumed just prior to toxicosis. Little (1977b) found a similar situation in aversive conditioning experiments with catfish. Fish conditioned to associate LiCl toxicosis with a particular amino acid flavor (methionine, serine, or cysteine) would avoid only the amino acid to which they were conditioned, i.e. cysteine and structurally similar methionine. Serine-flavored food was not associated, indicating specificity of the aversion.

Behavioral observations indicated that both facial and vagal taste systems were involved. Initially, conditioned food was picked up but immediately rejected when it came in contact with the internal taste receptors. At this stage, vagal and facial taste would give conflicting assessments of the quality of a given food, resulting in a repetitive pick-up spit-out sequence (see also section on chemical senses in feeding behavior). Three or four days after toxicosis, however, food would be rejected when contacted by the barbels (facial taste). Similar effects were found for the brown bullhead (Bryant and Atema, pers. obs.).

Repellents

Repellents are odors that cause avoidance behavior in general. Two examples of this type of avoidance are downstream swimming responses of sharks presented with holothurin (Hodgson et al. 1967) and of salmon encountering human hand rinse or L-serine (Idler et al. 1956). In neither case is it known if these are innate or learned responses. Contrary to bait shyness, avoidance of repellents is not specific for feeding behavior. It does, however, seriously affect the animal's feeding motivation and is thus briefly mentioned here.

For practical application it is important to know that such repellent chemical substances exist, so that they can be avoided in situations where attraction is desired. Some repellents may well be specific: for instance, in contrast to salmon, yellow bullhead are attracted to L-serine (pers. obs.) Thus, one could perhaps take advantage of this specificity in the sorting of species for harvest in polyculture systems.

EFFECTS OF PHYSIOLOGICAL STATE ON CHEMORECEPTION AND FEEDING BEHAVIOR

Feeding behavior is affected by the physiological state of the animal, most notably hunger. In some instances the internal physiological state of the animal may exert effects on chemoreception involved in feeding, perhaps through efferent nerves or the endocrine system. These effects are most likely exerted first on central (i.e., telencephalic) areas related to chemoreception, and perhaps as far peripherally as the olfactory bulb. Even the receptor cells themselves may be affected. In other instances hunger and other physiological states may change feeding behavior thresholds, but not affect the first and second order processes of chemoreception. In the following section only the former will be considered.

Effects of hormones on olfaction

In the context of hormone effects on fish sexual behavior, Liley (this volume) discussed the influence of sex hormones and reproductive state on olfaction in general. In male gobies *Bathygobius soporator* (Tavolga 1955) and in male goldfish (Hara 1967; Oshima and Gorbman 1968, 1969; Partridge et al. 1976; Goff 1978) elevated levels of sex hormones associated with the spermiated, prespawning state increase olfactory sensitivity to female sex pheromones but also to food odors (Partridge et al. 1976). It is not known if this increased olfactory acuity is actually used in feeding behavior.

Godet and Dupé (1965) suggested that thyroid hormones in the lungfish *Protopterus annectens* act via telencephalic brain centers to increase olfactory sensitivity, which, in turn, would evoke normal feeding behavior. During the dry season, when these fish are in a dormant state inside a mud cocoon, general metabolism and olfaction are shut down by low thyroid hormone levels, thus conserving energy (Dupé and Godet 1969). With the onset of the wet season these animals show an "awakening reaction of olfactory origin" (Dupé 1973). It may be an illustration of the arousal function that has been ascribed to the olfactory system in general.

In both examples, hormone effects on olfaction regulate seasonal changes. A similar seasonal regulation of olfactory (and other sensory) acuity may well serve an energy conserving role for fish that hibernate in temperate climates. In such cases chemosensory thresholds would be affected nonspecifically as suggested by the results of some of the studies mentioned in this section. It is also possible that hormones set specific thresholds to allow for maximal perception of seasonally important odors, such as sex pheromones. No examples of this have been found, however.

Biological rhythms

In addition to long-term seasonal rhythms, short-term circadian and tidal rhythms can regulate fish activities. Circadian rhythms activating diurnal and nocturnal animals to start their daily activity period are common in fish (for instance, Winslade 1974, for diurnally active sand eels; Bardach et al. 1959, for nocturnally active moray eels). These activity cycles probably prepare animals for their optimal food gathering period, as shown in the laboratory for bluegill *Lepomis macrochirus* and largemouth bass *Micropterus salmoides* Davis 1964). Recently a number of studies have shown physiological and anatomical changes on a circadian cycle in the visual system of aquatic invertebrates, *Limulus* (Barlow et al. 1977), crayfish (Sanchez and Fuentes-Pardo 1977), and *Aplysia* (Benson and Jacklet 1977). There are no studies showing circadian changes in chemosensory acuity, but the existence of such changes can be expected. In the section on Food Odor Preference, tidal changes in food preference were mentioned, but no examples of tidal changes in chemosensory acuity are known in fish. Natural biological rhythms can be modified under conditions of captivity and fish easily learn a new circadian rhythm based on an imposed feeding schedule (Davis 1964). It is not known if during inactive periods olfaction and taste are actually "shut off" at the receptor level or that their signals are not transmitted to more central brain areas.

Hunger

It is our common experience that hunger has a profound influence on the food we eat, making less palatable foods acceptable. The same is true for fish. Food selectivity ("finickiness") increases during a feeding bout (carp, Ivlev 1961; tuna, Nakamura 1962; stickleback, Beukema 1963; bluefish, Olla et al. 1970). Highly preferred food may be eaten in large amounts before satiation occurs (Ishiwata 1968; Stanford 1974). With increasing food deprivation (16-88 h) three-spine sticklebacks *Gasterosteus aculeatus* showed an increase in both food searching and the probability that encountered prey would release a feeding response (de Ruiter and Beukema 1963).

In some studies chemical senses were shown to be involved. Satiated tuna do not respond to food odors that evoke feeding frenzy in hungry conspecifics (van Weel 1952; Atema et al. 1979). Hungry goldfish start active searching behavior when they perceive food odor; this response ceases when the nares are blocked (Grimm 1960). It is clear that olfactory signals are involved since electrical stimulation of the olfactory tracts and of certain forebrain areas evoked normal searching behavior, whereas stimulation of the vagal taste lobes in the medulla did not (Grimm 1960). It is not known how the effects of hunger are transmitted to the olfactory system, or at what neural level olfactory responses are blocked by satiation.

The gustatory system is also subject to hunger effects as evidenced by catfish. When not very hungry, *Ictalurus* spp. will go through a repeated sequence of picking up and spitting out normally acceptable food. This is similar to the situation when rather unpalatable food is presented to a hungry catfish. Completely satiated catfish do not respond to the presence of food (Atema 1971). Apparently hunger state and food palatability form a balanced system guided by taste.

Practical application of hunger effects on feeding is self-evident. Under natural conditions hunger is probably associated with circadian or tidal rhythms.

OLFACTORY MODIFICATION OF OTHER SENSORY INPUTS

Perception of an odor has been shown to modify responses to visual and other stimuli. Minnows *Phoxinus laevis* exposed to alarm substance released from the skin of injured conspecifics become easily disturbed by sight and sound stimuli they normally ignore. Adding the odor of their natural predator, the northern pike *Esox lucius* can further enhance the response (von Frisch 1941). Goldfish *Carassius auratus* begin to respond to visual and tactile stimuli and pick up pebbles and debris when they are stimulated with food odors. They also do this when their olfactory tracts or certain telencephalic areas are electrically stimulated by implanted electrodes (Grimm 1960). Catfish *Ictalurus* spp. exhibit similar behavior

(Atema 1971). Yellowfin tuna begin to focus their attention on visual targets such as drain pipes when even very dilute food odor is added to the tank (Atema et al. 1979). Numerous examples could be added to this list. Indeed, nearly all fish seem to exhibit such "olfactory arousal" of other senses.

A neural mechanism is not implied for this behavior. However, this phenomenon is important for practical applications and has been employed successfully in many fisheries. In general, the proper chemical stimulus can enhance fish responses to otherwise ignored objects such as lures.

Potential for Practical Application

In many cases the capture and management of fish stand to benefit from the ability to capture the right fish at the right time. This applies to fishing wild stock as well as to harvesting fish from culture ponds. Selective fishing would reduce catch effort and avoid unnecessary killing or sorting of undesirable species or size classes. When selective fishing is properly used, overfishing may be avoided, thus aiding in the management of both wild stock capture and mixed species polyculture.

Application of chemical signals may be an effective method to selectively excite, attract, and catch fish. As shown in the previous sections, fish use species-specific chemical signals to detect food, induce searching behavior, and elicit actual food intake. The signals involved in these two phases of feeding behavior can be different. They can also be different from the nutritional elements in that food. The projected applications of chemical stimuli in fish culture, capture, and management make use of the two major roles of chemical senses in feeding behavior: arousal to search (usually through olfaction) and stimulation to swallow (through taste). A particularly attractive aspect of chemical food signals is that they are effective in small amounts and that some of them may be easily and cheaply available, for instance as by-products of food processing.

This section will not deal with the commonly known applications of chemical signals for fish capture, such as bait fishing and chumming. Also, interference with feeding behavior by chemical pollutants acting on chemical senses will not be discussed.

CHEMICAL LURES IN FISH CAPTURE

Common fishing experience shows that some fish can be attracted to a chemical source, as noted previously. Chemical attraction can also be highly specific, so that some species are not attracted by a chemical mixture that is effective for other species. Thus, a general, broad-spectrum "fish attractant" can not be expected, although some amino acids or related compounds (i.e. glycine, alanine, taurine, and betaine) are capable of attracting a rather wide range of species. There are some efforts to develop broad-spectrum fish attractants to be used in time-release capsules for fish traps. Only field testing can prove their effectiveness.

Perhaps the greatest benefit of chemical signals is their potential for specificity, which would make selective fishing possible. Chemical signals can be potent stimuli in arousal, resulting in some cases in "feeding frenzy," in other cases making visual lures acceptable, and, in general, lowering the fish's threshold for "danger" such as nets. Some fish show general excitement when they perceive food odors (for instance tuna), whereas other fish can actually be attracted to a source of chemical stimuli, which may be placed in a net (for instance, several catfish and shark species). Attractants could possibly be made species-specific, but again, actual field research is required to demonstrate this. Selective fishing is of obvious benefit to conservation, leaving undesired species and perhaps year classes untouched until their harvest time.

Many fish learn odor-food associations readily and naturally. Thus, in "ocean ranching", fish may be attracted to the feeding-capturing area by specific (even synthetic) odors to which they were imprinted during hatchery raising. Afterwards, this odor would probably need to be presented at regular intervals to avoid extinction. Depending on geographical features such as currents, bays, etc., this may work better than sound conditioning and attraction (see Fujiya, this volume). It is possible that wild stock could be quickly conditioned by odor to a feeding-capturing station.

The existence of cyclic changes in food preference, either short-term daily changes, long-term seasonal change, or changes with growth and development, point to the possibility that the same chemical attractant may not always be optimal. It also points out, once again, that to derive maximal benefit from chemical attractants, one must know the habits and life history of the animal to be captured. For instance, fishermen adapt their lures to the time of day, the visual environment and the appearance of the prey that their fish are hunting. Similarly, for optimal success, chemical lures need to be adjusted to the particular situation.

FEEDING ENHANCERS IN FISH CULTURE

In fish culture, the obvious use of chemical signals is in olfactory and gustatory enhancement of feeding. Olfactory arousal could be used to enhance the feeding motivation of fish in culture ponds. The addition of attractive odors may enhance the acceptability of food, even in visual feeders, causing "feeding frenzy." Proper flavoring would further enhance feeding and food intake through taste, the "sweet pill" effect. Both odors and food flavor can be potent long-term feeding enhancers through association with a healthy diet (see section on specific appetite). The opposite effect of "bait shyness" in which food is associated with ill effects, should be avoided. If, for any reason a food does become associated with sickness, it may be possible to start the fish feeding again by switching to a new odor and/or flavor, even if it is added to the same food.

In fish culture, selectivity may be the second most important application. In mixed species culture there may be need for selective harvesting, which might be accomplished by attracting different species with either natural food attractants or by artificial odors associated with their food. For the latter, the different species need to be fed different diets with different odor properties, so that each learns to associate food with only one odor. Repellents may be used similarly by temporarily repelling the undesirable species during harvest. Outside harvest time the specificity of chemical signals may be used to feed different diets to different species in polyculture, leading to resource partitioning. Establishing food odor preferences for different species by early feeding experience may be used.

In culture-pond species, as in wild stock, possible cyclic changes in feeding behavior need to be appreciated.

SPECIES SELECTION FOR POLYCULTURE

Efficient resource partitioning in mixed-cultured fish ponds has been achieved by selecting fish with different feeding habits, such as midwater visual feeders, midwater filter feeders, and chemosensory bottom feeders. Where new species of potential pondfish with poorly known feeding habits are considered for polyculture systems, species selection may benefit from a casual look at the development of the animal's sensory brain areas and sense organs (see section on Chemical Senses in Feeding Behavior; The locating phase: external taste).

Acknowledgments

I thank Linda Ashkenas, Bruce Bryant, Chuck Derby, Elisa Karnofshy and Susan Oleszko-Szuts for stimulating discussions and help with editing the manuscript, and John Bardach for his continued encouragement.

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Discussion

HASLER

When an animal is following a chemical gradient, it seems to me that there could be a problem with the animal's becoming fatigued or habituated to the chemical; then the gradient wouldn't make any difference. It seems to me that a gradient works only if the animal can get completely out of it and can crisscross it like a dog does.

HARDEN JONES

Habituation could be avoided if the fish took serial samples of the water, that is, if they sniffed.

ATEMA

They have a ciliary flow mechanism which is under neural control. The ciliary beat can be manipulated by the animal and can enhance the contrast between right and left. Pumping is another mechanism which tuna have: if they open and close their mouth, they pump and ventilate the olfactory epithelium.

BLAXTER

Do we have to assume that fish habituate?

ATEMA

Yes. I think at a theoretical level, the olfactory system habituates as much as the visual system. If your eyeball is fixed, you don't see anything. But I think that water is probably turbulent enough so that in the active space there are different concentrations—they're not directional, they're haphazard.

BARDACH

Harden Jones is right. There are contrast enhancing mechanisms, there are central mechanisms that turn on and off, there are antidromic impulses. I think contrast enhancement by the animal is used in the olfactory system as it is in other sensory systems.

LILEY

We're too often misled by what happens in a physiological preparation. It tends to exaggerate this habituation and adaptation process.

ATEMA

Yes, especially in electrophysiology where you have to standardize all your conditions, but I think it remains a point to be proven.

FISHELSON

I think some experiments argue against this. If you observe fishes in large aquaria swimming toward the food source you will see the type of klinokinesis that the planaria is making.

BLAXTER

The problem with most sensory systems is that they fatigue. Proprioceptors, like muscle spindles, don't necessarily fatigue.

MAGNUSON

When Reg Gooding and I anchored a raft with underwater viewing enclosure in deep water off Hawaii we had a 55-gal drum full of squid juice which we released into the current through a Tygon tube. Many mahimahi, *Coryphaena hippurus*, swam from the downcurrent side directly to the end of this tubing when the odors were being released. The fish appeared at the limit of our visibility swimming in the odor trail toward the raft.

ATEMA

I'm familiar with that experiment. I believe that up to a certain point it's chemical but with this tube trailing behind they have a visual target also. Don't you believe this might be the case? I'm not excluding chemical orientation, because of course you cannot in this experiment.

MAGNUSON

Well, at the time I didn't think that they were attracted to the visual image of the tubing.

ATEMA

But you didn't have dead tubing hanging next to it that did not produce odor.

MAGNUSON

The only control we used was turning on and off the release of squid juice. Mahimahi did not approach the raft or the tubing when the flow was turned off.

ATEMA

Odor may be giving them the necessary excitement, so it still doesn't tell you whether that animal really locates by olfaction. I don't think the crucial experiment has been done.

HASLER

I would like to comment on electrophysiological data obtained from anesthetized fish. In our work, salmon seemed not to respond well after being anesthetized. We now use a physical restraining device so as not to use anesthetics. We're skeptical about their effect.

ATEMA

I agree.

HASLER

Anesthetics have to be making some other neurological disturbances you aren't able to control for.

ATEMA

In Professor Dijkgraaf's laboratory in Utrecht we operated on sharks. When we restrained sharks physically without anesthetics, we had several cases of the sharks' dying within a few hours. After anesthesia there was no problem.

HASLER

Well, different types of anesthetics give different results.

BLAXTER

We've used cardiac conditioning for measuring pressure threshold in gadoids. We find that trained fish after recovery from MS222 anesthesia retain the conditioned response. This suggests MS222 is harmless.

LILEY

Another point is that it's well known that any form of stress may cause an increase in secretion of corticosteroids (Mazeaud et al. 1977). In addition there is work with mammals that shows that ACTH and corticosteroids affect avoidance conditioning. It appears that you cannot win: you stress the animal by holding it unanesthetized and alter corticosteroid levels and therefore possibly affect the readiness to be conditioned shortly afterwards, or you anesthetize it and perhaps introduce behavioral effects which confound your experimental results!

HASLER

We need to do research on better anesthetics for fish.

HARDEN JONES

The problem of artificial baits is relevant to the United Kingdom inshore fisheries, where the smaller vessels land up to 45% of the annual value of the UK catch. Longliners have low fuel cost but bait is expensive; and there are domestic problems with regard to baiting, which used to be carried out by the womenfolk. An artificial bait compatible with an automatic line-hauling system could have a revolutionary effect on even a developed country's fisheries. There is scope for an ethological approach to the whole cycle of events that involve the fish being attracted to the bait; examining, snapping, mouthing and swallowing the bait; and finally being hooked. The problem has engineering, biochemical, physiological, and behavioral aspects in addition to those of practical fishing. I think that the level at which such work is supported is far below that which could be justified by the potential benefits.

BLAXTER

Concerning the point about appetite enhancers—as you say, it's been a very neglected field, but I think there is a danger if you apply in a culture situation something that will enhance the appetite. It may have an undesirable effect on the conversion rate. You may find if you enhance the appetite that food will just be pushed through the gut and be defecated with a lot of waste.

ATEMA

If you have the perfectly nutritious food that is absolutely tasteless or even revolting to the poor animal that's supposed to swallow it, all you may have to do is coat it with something very attractive.

HENDERSON

As reported in my paper, Main et al. (1976) have used cobalamin as an appetite stimulant. They were able to get bluegills to take trout pellets in larger quantity with cobalamin than without.

REINBOTH

Is there any biological basis for the use of amino acids as attractants? I have difficulty accepting the idea that there are no free amino acids in the waters.

JOHANNES

Marine invertebrates contain very high levels of free amino acids in their tissues which they are continually releasing into the water.

ATEMA

If you know enough about the animal to utilize just the combination of compounds that elicits the optimum response, you may have it made. But people at the moment are just taking any type of juice from an animal's natural prey. It may be detected because the animal has receptors for it, but it may not release the optimum response. I believe that for different animals there are optimum combinations of compounds.

HASLER

How would you test your theory?

ATEMA

I think Freeman's study on rabbit olfactory bulbs demonstrated the response specificity of each compound. You might next use the same experimental approach with mixtures of compounds, particularly those that are behaviorally very powerful.

HASLER

Yes, I think that's very essential. I think the weakness of the EEG is that it takes a small amount, so there's a big difference between the EEG and the behavioral result.

HUNTER

By mapping can you tell how compounds might be affiliated with each other? It seems like a logical step and useful background if one is going to try to design a synthetic attractant.

ATEMA

Exactly. No, as far as I know this is where it is. The electrical picture that you get from the olfactory bulb is totally different. One theory holds that particular areas in the bulb are particularly sensitive to one type of compound, so that the decoding of the message of the environment is partially spatial. That is a very interesting idea to follow up, and one way of measuring it is what you're suggesting. But in terms of application, I don't see it going in the direction of EEG analysis. I think we should utilize behavioral work there entirely and just find a powerful chemical stimulus. With some animals you already get quite close just with one compound, betaine. Another point is that you might be able, just on neuroanatomical grounds, to select the right species for chemical luring because there have been very good studies correlating neuroanatomical development with feeding habits, for instance, or with the general olfactory/chemosensory dominance.

BARDACH

How interested are chemical companies in working with us?

ATEMA

I think they're interested to the point that if anybody comes up with something that has promise for profit, they'll go right away, obviously, like any company. I would like to quote Pawson from Harden Jones' laboratory, who says it is significant that most artificial chemical fish and crustacean baits developed to date have not upheld their apparent effectiveness when tested in the field. And that, of course, is the whole problem, although I think with Sutterlin's work, which is concerned with natural attraction in the field without conditioning or learning, theory and practice can already be put together. I think there is more than Pawson said. Also, Bill Carr of the University of Florida is field testing fish attractants.

HARDEN JONES

As an exercise, I've gone through all the patents since 1854, looking at the artificial lures to see all the rubbish that's been put in them. People have been doing this since the 1860s.

JOHANNES

I haven't heard of any attempt so far to relate experiments with different olfactory stimulants to compounds marine animals are known to excrete into the water. You mentioned glycine as being particularly effective. Glycine appears to be by far the most important free amino acid in the release products of marine invertebrates (e.g., Johannes and Webb 1970; see references after Atema's paper for full citation).

ATEMA

I agree. That is the way to go, to look at what the natural prey excretes and then start from there. That is essentially what we were after with our tuna work, where we found that tryptophan is the main constituent. But tuna is not a fish you can lure in with even a complex mixture of amino acids; you need other compounds, perhaps very complex compounds, and perhaps it's useless even to explore this commercially. But there may be species for which that is the way to go.

BLAXTER

You mentioned the point of polarity of trails. It seems to me that could be very important, but I don't quite understand how a trail could have polarity.

ATEMA

The only example to my knowledge is a special case: the trails laid on rocks by snails. There is a polarity to the trail, and there are two theoretical explanations. One is that there is a compound that decays over time, so that by comparing left and right over a short distance there is a slight difference and the snail knows which way it goes. That to me is rather unlikely. The other explanation is that there is a mechanical aspect to the trail that can be picked up with a mechanoreceptor, but this hasn't been shown.

BLAXTER

Then it's very unlikely there would be an application of this to our concerns in fisheries.

ATEMA

I don't think so. For instance, the way I picture tuna schools hunting for anchovy schools is that the anchovies activate a huge space which is far beyond visual range. When tunas or part of the tunas go into that active space they get excited, thereby exciting the rest of the school and covering a much larger distance by swimming fast.

MAGNUSON

I didn't see you present any data on that.

ATEMA

There aren't any data.

MAGNUSON

So I don't see why the tuna was singled out as being so different from the catfish in terms of following a trail. It seems to me that it's purely a hypothesis at this time. A tuna 1 m long traveling 10 body lengths per second in a feeding bout traverses the range of its visibility in about 3 sec. I would be very surprised if it hadn't evolved locating devices on the high seas other than vision.

ATEMA

I think what you are saying is an argument for not needing such devices, because they are so fast and so efficient that it makes no difference whether part of the school spends time to go right and the other part to go left and explore the visual space very quickly.

MAGNUSON

They are seeking food in oligotrophic seas with very contagiously distributed organisms in patches. To make sensory contact with prey could require a much longer search if there is no ability to follow an odor trail. I think if I were going to frame a hypothesis, I would frame the hypothesis that there is an odor trail. The alternative is that there is not, but I don't think we're at a point where we can say.

BARDACH

The tanks in which we experimented are spaces in which one cannot demonstrate this; they're too small. However, we may be able this year to go to sea to lay odor trails, and we hope to be able to tell you more about it by the end of next year.

HASLER

To what extent is ammonia an active component? It's a very strong component in urine. If one just tried straight urine from other species of fish, it might be useful way to start.

ATEMA

In my literature search I have not been able to find any convincing data in that direction.

BARDACH

Trimethylamine does not appear to be important.

BLAXTER

You're also looking for specific amino acids, and these are more likely to say come from mucus than from urine.

FISHELSON

Are there any infrared pictures of moving schools of anchovies and tuna? Because if a school of anchovies moves close to the water surface, they must change the temperature regime and leave traces behind them. Maybe tuna are sensitive to those changes of temperature.

KEMMERER

There has beeen some work done involving infrared sensing of tuna, but I do not believe that it was very successful. Joseph and Stevenson (1974) reported that thermal gradients between skin temperatures of tunas and porpoises was sufficiently small so that direct thermal detection of these species was not feasible, at least in the foreseeable future. However, I recall from conversations with Dr. Stevenson that he was able to detect the presence of some fish through slight changes in surface water temperatures. (Joseph, J., and M.R. Stevenson. 1974. A review of some possible uses of remote sensing techniques in fishery research and commercial fisheries. 16th COSPAR Survey Problems Symposium, 1973, p. 75-100). The temperature change was due to fishes' disturbing temperature gradients in the upper millimeter or two of the water column, not because of the temperature of the fish.

Several years ago there was considerable interest in indirect sensing of fish through detection of fish oils. Fortunately, Dr. Donald W. Strasburg, formerly with the National Marine Fisheries Service, Fisheries Engineering Laboratory and now with the Naval Research Laboratory, Washington, D.C., did some aquarium studies and found that fish such as menhaden did not extrude detectable quantities of oil. Apparently oils are produced only when the fish are being lacerated by predators.

MURPHY

I'd like to refer back to what was said earlier with respect to skipjack tuna, and this discussion about chemical homing and the fact that skipjack are important predators on their own species. I don't see how they could use chemical homing on themselves.

ATEMA

That's not necessarily true, because there's a good possibility that big fish smell different from small fish.

MAGNUSON

Especially if they're sexually mature.

MURPHY

We're talking about sexually immature skipjack in some of these cases, in the Marquesas for example.

LILEY

Can I push it one step further? What do you think about the possibility of imprinting young fish on certain food odors, or chemicals associated with a particular food, so that you can rearouse a response to that odor at a later date? It may be much easier to condition fish to odors rather than sounds, and by using water currents and trails it may be possible to draw in fish from a large area if they can be conditioned to associate a particular odor with desirable food early in life.

ATEMA

I think that's certainly a good possibility that ought to be investigated. The only problem I can see is habituation. If these fish are away from it, it may not have that much meaning for them anymore. They forget these images, too. They create different ones if they need to.

LILEY

There are a fair number of examples of imprinting on food. I don't think that this type of work has been done with fish, but I think it would be worthwhile examining the possibility that exposure to a food odor early in life may have more important or longer lasting effects than food experiences it acquires later in life.

ATEMA

The only evidence that I know of is Burghardt's work on snakes, where the young snakes start out with a food odor preference as soon as they come out of the egg, without any training. But this can be overridden by later experiences if they encounter different food: their odor preference can either be reversed or changed.

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Hearing and Sound Production in Fishes in Relation to Fisheries Management

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TAVOLGA, WILLIAM N. 1980. Hearing and sound production in fishes in relation to fisheries management, p. 102-123. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Fish can be detected through sounds that they produce, and their behavior can be significantly affected by artificially projected underwater sounds. The current state of our knowledge on the hearing capacities of fishes is adequate to permit some generalization. Sound production by fishes, although known to exist in many species, is rarely distinctive enough for species recognition, at least according to the state of our present knowledge. Behavioral correlates for sound production and details of sonic communication are adequately known for only a few species. The playback of sounds to affect the behavior of fishes has had limited success, and the few available results are still equivocal. Although the potential for the use of acoustics in fisheries seems to be enormous, its successful utilization is thus far surprisingly small. There is need for a considerably expanded research effort directly toward obtaining basic information on audition, sound production, and acoustic communication in species of importance to fisheries. With an adequate foundation of such information, the application process will follow inevitably and effectively.

Introduction

The importance of acoustics in underwater communication resides in the fact that it is the most effective long-range energy channel available. Photic and electrical energy are relatively limited in range, and chemical dispersion is slow and possesses no direction information. If we need to interact with aquatic organisms, fishes in particular, acoustic energy becomes the best choice. For purposes of fisheries management, fish can be detected through acoustics, and potentially, at least, their behavior can be affected by sound.

Before any serious attempt is made to use acoustics in any such manner, there are some basic data that are necessary. We must be aware of the acoustic receptive capacities and limitations in fishes. We must also know the kinds of species-typical sounds fishes produce, and most significantly, the kinds of behavior patterns associated with the sounds.

Detailed reviews of this material are available in recent publications (Hawkins 1973; Myrberg 1972a; Popper and Fay 1973; Schuijf and Hawkins 1976; Tavolga 1971, 1976a, 1977a). The following will be a brief survey of the state of our current knowledge in the field of hearing and sound production in fishes. This survey will serve as a basis for the generation of ideas and speculations on the course of future research, particularly as regards the application of acoustics to fisheries management.

Hearing in Fishes: A Survey

We have come a long way since the days at the turn of the century when scientists were arguing as to whether fish could hear at all. Over the past two decades, the progress in the field has been extremely rapid, due in large measure to the application of psychophysical techniques and principles to the study of hearing in fishes. We are now beginning to realize that the fish's acoustic sensory system, especially in teleosts, is capable of much finer discriminatory capacities than had ever been suspected.

THRESHOLDS

A fundamental question in the study of a sensory capacity is its sensitivity and the limits of the sensitivity. In audition, these data are expressed quantitatively in the form of audiograms, i.e., graphs of frequency vs. threshold. Threshold is commonly accepted as being the stimulus level at which there is a 50% probability of a positive response, and frequency is expressed in Hz (Hertz = cycles per second). Stimulus level in audition is given in dB (decibels) in reference to a standard sound pressure, and in underwater acoustics, this reference value is 1 μb (microbar = dyne per cm^2). Table 1 compares some common acoustic phenomena in and out of water.

Over the past several years, data have accumulated on hearing capacities in many species of fishes, representing several major families. Although the total number of species studied (about two dozen) is miniscule in relation to the total number of known species (over 20,000), a pattern is beginning to emerge that can permit some broad conclusions. Audiograms of the species studied are given in graphic form by Popper and Fay (1973) (reprinted in Tavolga 1976b), so that

TABLE 1. Comparative chart of approximate acoustic pressure levels of common sounds in air and in water[a] (from Tavolga 1971[b]).

	Acoustic pressure (dB)	
Jet aircraft takeoff (at 75 m)	60	Underwater dynamite explosion (at 100 m)
Threshold for human aural discomfort (discomfort at 1000 Hz)	50	25 hp outboard motor (at 15 m)
Loud auto horn (at 1 m)	40	Toadfish boat-whistle sound (at 1m
Small propeller aircraft (at 5 m)	30	Rough sea (state 6)
New York subway train (at 10 m)	20	Large chorus of marine catfish
Noisy business office	10	Noise of ships in busy harbor
Home high fidelity set	0	Large chorus of snapping shrimp at 100 m)
Average conversation (at 1 m)	—10	Calm sea (state 0)
Private business office	—20	Squirrelfish hearing theshold (at 800Hz)
Average residence	—30	
	—40	Threshold of hearing of ostariophysine fishes
Quiet country residence	—50	
Quiet whisper	—60	
Human hearing threshold (at 1000 Hz)	—70	
	—80	

[a] The reference point is set at 0 dB = 1 ub (= 1 dyne/cm^2). To convert to a reference point of 0.0002μb add 74 dB.

[b] Reprinted from Fish Physiology by permission from the publisher, Academic Press.

the summary graphs presented here (Fig.1) represent generalizations drawn from the data. It is immediately clear that fishes fall into two major and unequal groups with respect to hearing sensitivity. The "hearing specialists" are members of the Order Ostariophysi, an order of mainly freshwater and estuarine species comprising several rather diverse families, including such forms as characins, goldfish, milkfish, electric eels, catfish, and carps. The principal unifying characteristic of all these groups is the presence of the Weberian apparatus, a chain of small bones that links the swim bladder with the inner ear. In 1820, Weber proposed that these bones operate like middle ear bones in mammals, and couple sound vibrations from the swim bladder to the inner ear. Proof of Weber's contention has finally been established (see papers in Tavolga 1976b). The ostariophysine fishes, on the average, have a sensitivity 30 to 40 dB better than other species.

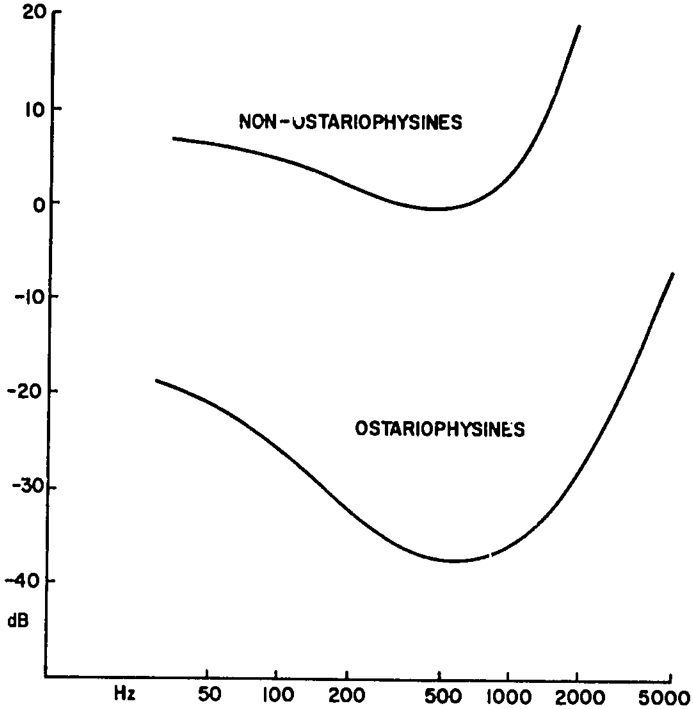

Fig. 1. Comparison of audiograms of ostariophysine and non-ostariophysine fishes, the latter group covering several families of widely divergent fishes. Derived from data summarized by Popper and Fay (1973) and Tavolga (1971).

The upper frequency sensitivity in the ostariophysines is significantly greater than that of non-ostariophysines, with some species able to detect frequencies of 5 kHz or more, while non-ostariophysines are virtually deaf above 2 kHz (Fig. 1). These graphs conceal a great deal of variability, and audiograms of different species can be as much as 20 dB higher (as in the sea robin, for example) or 20 dB lower (as in squirrelfish).

The majority of studies have been made with species that are amenable to captive conditions, and these are, more often than not, species with little or no importance in fisheries. The few audiograms available for species of significant commercial value fall generally within the range depicted in Fig. 1 for non-ostariophysines. Fig. 2 (curves A, B, and C) are based on thresholds determined under captive conditions for Atlantic cod *Gadus morhua* (Buerkle 1967), the yellowfin tuna *Thunnus albacares* (Iversen 1967), and the kawakawa *Euthynnus affinis* (Iversen 1969).

Also shown on Fig. 2 (curve D) is a summary of data derived from audiograms obtained under essentially open water conditions. Three species were shown to have similar audiograms: the Atlantic cod *Gadus morhua* (Chapman and Hawkins 1973), the haddock *Melanogrammus aeglefinus*, and the pollack *Pollachius pollachius* (Chapman 1973). These data, obtained without the severe acoustic

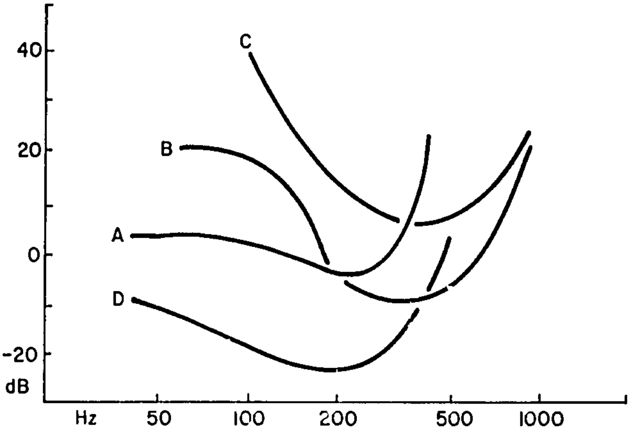

FIG. 2. Comparison of audiograms of several teleost species of importance to fisheries. A. Atlantic cod *Gadus morhua* (Buerkle 1967); B. yellowfin tuna *Thunnus albacares* Iverson 1967; C. kawakawa *Euthynnus affinis* (Iversen 1969); D. combines data from three species, based on open water experiments (Chapman 1973; Chapman and Hawkins 1973).

problems of aquarium tanks, gave thresholds that are significantly lower than those from many other non-ostariophysines, but still not within the range of the forms equipped with the Weberian apparatus.

DIFFERENCE LIMENS

Data on the capacity of fishes to discriminate between sounds of different intensities or different frequencies are limited to a few experimental, psychophysical reports. For a "hearing specialist," the goldfish, the ability to discriminate intensity appears to be in order of 3 to 6 dB, as compared to the human difference limen of 0.5 dB or less (Jacobs and Tavolga 1967). The only quantitative study done with non-ostariophysines was that of Chapman and Johnstone (1974) who obtained an average difference limen of 7 dB for the Atlantic cod and haddock. However, it seems likely that fishes in general would have a poor capacity to discriminate intensities. This is a speculative conclusion based upon the fact that their dynamic range of audition is narrow. Most non-ostariophysines have a range of only about 30 dB from threshold to the peak level of biologically tolerable sounds compared to the human dynamic range of almost 130 dB from threshold to pain level.

The data on the capacity of fishes to discriminate frequencies are a little more extensive. The "hearing specialist" goldfish can discriminate a 3.5% frequency difference at 500 Hz (equivalent human performance would be better than 0.3%). Non-ostariophysines show significantly poorer discriminative capacities, and the available data give values of from 12 to 50%; indeed, there are many species that may not have any frequency discriminative ability at all. The problems of frequency discrimination are closely linked to the theoretical problems of hearing mechanisms in fishes, and these aspects have been covered in more detail elsewhere (Tavolga 1974, 1976c).

From the point of view of potential uses of sound in fisheries management it would be helpful to have data available on the ability of fish to detect a signal with ambient noise present. As summarized elsewhere (Tavolga 1974, 1976a), most fish tested against broad-band background noise are capable of detecting a signal when the power ratio of signal to noise is about at unity or more. If the broad-band noise is measured in terms of spectrum level (in dB per Hz), then the minimum signal/noise ratio at which detection is possible is about 20 to 25 dB. This is the so-called "critical ratio." Since ambient sea noise is generally broad-band, such data may be of value in the application of sound to affecting the behavior of fishes.

SOUND SOURCE LOCALIZATION

Before any consideration is given to the use of sound in directing movements of fishes, it is essential to have some data on the capacity of fishes to detect sound source position, i.e., range and bearing. The study of sound localization in water, especially, is confounded by the fact that acoustic energy actually exists in two forms: pressure and displacement.

Sound pressure is what a hydrophone normally receives and measures. It consists of a series of alternate compressions and rarefactions propagated by the sound source, and it may be periodic or non-periodic, or both. At a given reception point, this form of acoustic energy is measured in pressure units, e.g., microbars (μb), dynes/cm^2, or newtons/m^2. Most often the values are given in decibels (dB) with reference to some standard, such as 0 dB = 1μb. A single measurement, at a single point provides no directional information as to the sound source position, since pressure is a scalar quantity. In air, with two separated ears, we can obtain directional information by detecting phase differences as the pressure waves arrive at the two ears. In water, since the velocity of sound is almost five times that in air (1500 m/sec in water; 330 m/sec in air), the ears would have to be five times farther apart to obtain the same phase difference. Fishes, however, have essentially a single ear. Although it is theoretically possible for the inner ears to receive some pressure energy directly, all the evidence thus far points to the swim bladder as being the only adequate acoustical discontinuity in the body of a fish, and the swim bladder then transmits the vibrations to the inner ears. In effect then, fishes should not be capable of detecting sound source direction from pressure information alone.

The second component of acoustic energy is displacement, and often the term used for this is near-field energy, as contrasted with far-field for pressure. Displacement comprises the actual movement of water particles, and this movement has three essential parameters: amplitude, velocity, and direction. Amplitude and velocity are related in direct proportion, but direction is an independent vector quantity. The mathematical and theoretical relationships between pressure and displacement were described in detail by Harris (1964), but a commonly used approximation is given by the formula:

$$d = \frac{p \times 10^7}{2\pi f \rho c} \left(1 + \left(\frac{\lambda}{2\pi r}\right)^2 \right)^{1/2}$$

The variables are: p = pressure in μb
f = frequency in Hz
λ = wavelength in cm (= c/f with c = 150000 cm/sec velocity)
r = sound source distance in cm
ρc = acoustic impedance (see later)
d = displacement in nanometers

The formula shows that there is a complex relationship between pressure and displacement. As f and r decrease, the displacement component increases. This is especially noted by the term in parentheses, the so-called near-field component. As wavelength decreases, the near-field term approaches unity. In practice, the near-field effect becomes negligible as the sound source distance goes beyond about one-sixth of a wavelength. Unfortunately, many workers have the impression that near- and far-field are mutually exclusive. This is far from true, as a close look at the above formula shows. If the pressure energy is high enough, there will be a significant displacement energy effect at distances far beyond that of a wavelength. Conversely, even at close range, with displacement energy dominant, there is also a strong pressure energy component. An understanding of these theoretical relationships of near- and far-fields of acoustic energy can be of enormous importance in design of acoustic equipment to be used in directing the movements of fishes.

Another factor in the above equation that can affect the entire pressure-displacement relationship, is the ρc term. Normally, this is the product of the density of the medium and the velocity of sound propagation in that medium. Expressed in acoustic ohms, this term equals 42 in air, and 150000 in water. In actual practice, when aquaria are used or observations made in enclosed bodies of shallow water, the acoustic impedance of the water can be much less. In a small aquarium tank, the acoustic impedance can approach that of air, and the displacement amplitude becomes much greater than in a large tank or in the open sea, even though sound source pressure output and frequency remain the same. Conceivably, inequalities in water density, as from a thermocline, can affect the empirical value of acoustic impedance.

Returning to the question of localization of a sound source by a fish, it is evident that directional information would be available only from the vector component, i.e., the displacement energy generated by a sound source. Equally evident is the fact that localization would be most efficient at low frequencies and at close range to the source. Detection of displacement energy by a fish can occur through two modalities. Both of these depend essentially on the oscillations of the medium that bend certain specialized sensory hairs. The prime target of displacement energy would be the lateral line system. This consists of an array of displacement detectors on the body and head of most fishes. For details on the structure and function of this system, see the volume edited by Cahn (1967).

A second concentrated area of displacement detectors can be found in the inner ears of fishes (as well as all other vertebrates). Some of these are associated with detection of angular acceleration and other movements, i.e., the equilibrium sense, and some are associated with detection of sound. The latter depends primarily on the swim bladder as their acoustic energy source. Conventionally, it has been assumed that the inner ear-swim bladder complex is primarily the far-field, pressure detector, while the lateral line system is the near-field, displacement detector. The detection of sound source position, then, must fall entirely within the province of the lateral line system. Recent studies, particularly those reported by Schuijf and Hawkins (1976), have shown that this conventional wisdom is not entirely correct. At the present time, there is considerable controversy as to the mechanisms by which fish can detect sound source position, and this is not the place to review the topic (but see Tavolga 1976a,c).

However they do it, fishes are evidently capable of detecting sound direction, at least within a short range. To date, however, there are few quantitative data on this capacity. Chapman and Johnstone (1974) have given us about the only available numbers. They reported a difference limen of about 20° in Atlantic cod and haddock. Significantly, the fish performed best at low frequencies, high intensities, and short range. Predictably, the directional sense was effective within the near-field where displacement energy was strong.

Sound Production in Fishes :A Survey

The following is a summary of material that is reviewed in detail elsewhere (Tavolga 1971, 1977a).

Three general types of sounds are emitted by fish: (1) stridulatory (rubbing or rasping), (2) swim bladder vibrations, and (3) hydrodynamic sounds.

(1) The stridulatory sounds would be roughly comparable to the sounds produced by crickets rubbing their wings. The movement of

any rough surface against another would produce a noise which consists of a number of short noise pulses. Many species of fish produce such sounds by gnashing their teeth, moving fin spines, or rubbing patches of denticles in the pharynx. Often these sounds are produced during the course of feeding, but in some cases, are emitted during fright or when the fish is captured. In some groups, notably the grunts, the rasping sounds take on a resonant quality with a predominant frequency at about 100 Hz. This is thought to be caused by the resonance of the tooth-scraping sounds within the nearby swim bladder. By and large, these stridulatory sounds are not specific for any particular species of fish, and identification of sound sources is extremely difficult or, more often, impossible.

(2) Many species of fish are equipped with a set of specialized muscles attached to or surrounding the swim bladder. These drumming muscles are capable of vibrating, and the swim bladder with its enclosed air acts as an underwater loudspeaker of considerable efficiency. Prominent in this group are the members of the drumfish family (Sciaenidae), including croakers, sea trout, and sea drum. Important sound producers of this type are also the groupers (and some of the other sea bass), marine catfish, toadfish, squirrelfish, and others. The sounds are basically harmonic, with a fundamental frequency (or pulse repetition rate) varying from about 100 to 500 Hz, depending upon the species. Some of the sounds are short gruntlike pulses of a duration of about 0.1 sec, and these can be rapidly repeated in groups of five or ten to produce a rattling or hammering effect. Often a particular species can be recognized by the patterning of these pulse groups. This is particularly characteristic of the drumfish and croakers. The toadfish, on the other hand, produces a long call (up to 0.5 sec in duration) with a fundamental frequency of 200 or 300 Hz. This sound is quite characteristic and recognizable and has often been called the "boat-whistle" sound.

(3) The physical movement of a fish through the water produces a displacement and a pressure wave. Although this may not be periodic, it does have the properties of sound and can be detected on hydrophones. This hydrodynamic noise is generally low in frequency, ranging down to the subsonic, and often sounds like an earthquake or some other seismic disturbance but may be explosion-like in character. Sounds of this sort are particularly evident when the fish changes speed or direction abruptly.

SPECIES-TYPICAL "SIGNATURES"

A recurrent and important problem is the potential recognition or discrimination of sounds from different species of fishes. It was with this in mind that Marie P. Fish and her co-workers (M.P. Fish and Mowbray 1970) provided a catalogue of recorded sounds of identified species, a compilation that was initiated almost 20 yr earlier (M.

P. Fish 1954). With a few notable exceptions, it is remarkable to see that the differences between species are small indeed. In fact, considering the variability among individuals, it is virtually impossible to define species "signatures" in most cases. The sounds produced are monotonous low frequency pulses. Besides, many of the recordings were made under conditions of captivity with unspecified acoustic reflections and reverberations. Furthermore, the stimulus to sound production in most cases was unspecified "distress" or "alarm," often induced by administration of an electric shock.

A few species are known to produce some specific, recognizable sounds, e.g., the toadfish *(Opsanus)*, some of the members of the Sciaenidae (drumfish, croakers, etc.), and possibly others. The majority of species "auditioned" cannot be reliably identified from field contacts. One approach that may become more fruitful was suggested by Winn (1964, and reprinted in Tavolga 1977b). Although the individual sound pulses produced by many species may be virtually identical, the temporal patterning of the pulses is not. Some species, squirrelfish, for example, produce sounds in groups, usually 15 or 20 pulses per group, like bursts from a machine gun. Others show little or no patterning, while some species exhibit variability with respect to the behavioral situation of the moment. Unfortunately, much of our data where the species has been identified as the sound source comes from aquaria in which fish are captive and normal behavioral routines are disrupted. Combined video and acoustic observations such as those reported by Cummings et al. (1964) show some promise, but even there the specific sound-producing animal cannot always be identified.

BEHAVIORAL CORRELATES OF SOUND PRODUCTION

Correlation between sound production and behavior in fishes has been described in a number of groups and within at least five major behavioral categories. The detailed references will not be repeated here, and these can be found in articles by Tavolga (1971; 1977a), and Winn (1964).

1. *Alarm Sounds:* Virtually any species that is sufficiently distressed will emit some form of sound. An electric shock can often elicit a body musculature contraction so as to produce a detectable "sound." Since most of our data on this type of sound is derived from highly artificial laboratory situations, it would not be useful to detail such reports. In some cases, however, territorial sounds (see below) may actually function as alarm signals.

2. *Territorial Sounds:* Such sound outputs are so defined when it appears that the animal is in the process of defending an area, usually from intrusion by conspecifics. Such behavior would be characteristic of bottom dwelling species and, especially, those that inhabit reefs or similar rocky habitats. Among marine fishes, the

following groups contain species where territorial acoustic behavior has been observed and verified: groupers (Serranidae), squirrelfish (Holocentridae), toadfish (Batrachoididae), triggerfish (Balistidae), and demoiselles (Pomacentridae). Among freshwater forms, territorial acoustic behavior has been verified for the following: cichlids (Cichlidae), characins (Characidae), and sunfish (Centrarchidae). Many other species are suspected of producing territorial sounds, and often, territorial sounds are not distinguishable from courtship sounds (see below). Thus, the preceding list is probably conservatively short. Species characterization of territorial sounds is extremely difficult, since most of these consists of short low-frequency pulses or bursts of pulses.

3. *Spawning Sounds:* Probably the best known group in which sound production, mostly by males, is associated with spawning behavior is the family Sciaenidae, including drumfish and croakers. Also well known are the loud foghorn-like sounds of toadfish *(Opsanus)*. Codfish and haddock (family Gadidae) have been found to produce low pitched sound pulses during pre-spawning behavior. Several small reef and benthic species also emit specific sounds during courtship: demoiselles (Pomacentridae), gobies (Gobiidae) and blennies (Blenniidae). Specific identification of courtship sounds in freshwater species is limited to the croaking gourami (Macropodidae) and sunfish (Centrarchidae).

4. *Schooling Sounds:* Sounds associated with schooling behavior, especially at night or in turbid waters, have been described for searobins (Triglidae) and marine catfishes (Ariidae). Some sounds have been ascribed to schools of pelagic species, such as mackerel and tuna, but these are more likely to be vibrations of hydrodynamic origin, detected at close range.

5. *Feeding Sounds*: The actual stridulatory sounds of jaws and teeth during feeding are often readily detectable, as, for example, the scraping of a coral by a parrotfish. Swimming sounds, i.e., hydrodynamic vibrations, can also be associated with feeding. In most cases, however, such sounds cannot be characterized as to species, and there is no evidence that fishes utilize them in any form of communication.

6. *Echolocating Sounds:* Thus far, only one species, the sea catfish (*Arius felis*), has been shown to use its own sounds in obstacle detection (Tavolga 1976c, 1977a). The system appears to be primitive and usable over a very short range (a few cm). Whether other species are capable of using low frequency sound pulses for acoustic orientation has yet to be investigated.

Acoustics and Fisheries Management :The Questions

Ever since the development of ASDIC and Sonar, the effectiveness of echo-ranging equipment in detecting marine life has shown a steady increase. Although not directly related to sound production and detection by fishes, the utilization of these techniques for detection of fishes has moved to increasing degrees of precision (Hester 1967; Cushing 1967, 1973; Weston 1967) and deserves mention here. Sonar has already proved its value in assisting the commercial fisherman, and it promises to be an excellent tool for the study of fish locomotion and the behavior of fish schools. This aspect of acoustics will not be treated here further.

For fisheries management, acoustics (aside from Sonar techniques) potentially can provide answers to several basic questions about fish behavior.

WHERE?

Through passive listening, the location of sound-producing fishes can be determined. With directional hydrophones or directional arrays, the locations can be determined with considerable precision. The fundamental design of a good listening system was presented by Tyrrell (1964), and with a minimum of three hydrophones, properly spaced, the sound source location can be accurately placed in terms of range, bearing and depth. The design outlined at that time is still a theoretically effective one.

Simpler systems can even be utilized. Breder (1968) was able to track schools of sonic sea catfish *(Arius felis)* with a pair of inexpensive hydrophones mounted about 120 cm apart. This was the basis for a "audiogoniometer" that used a pair of matched amplifiers and stereophonic earphones. The principle actually used the excellent directional hearing capacities of the human auditory system, but simply set the "ears" farther apart to compensate for the almost fivefold increase in sound velocity under water. The phase difference detection was accomplished by the human listener and the apparatus could be turned to the point toward the sound source at distances of over 20 m with remarkable accuracy. It is curious that this simple technique has not been utilized, to my knowledge, in any other studies on fish behavior. Breder's report could well be a model of what information can be obtained through directional listening techniques.

Another excellent example of acoustical location of sonic fishes was the hydrophone installation at the Lerner Marine Laboratory, Bimini, Bahamas (see several chapters in Tavolga 1964). This was a shore-based station, with hydrophones on cables extending a few kilometers into the Gulf Stream nearby. Eventually, a bottom-mounted television camera was added to the installation, and this, of course, permitted the identification of many hitherto unrecognized sonic species. Unfortunately, this project has been discontinued, but here too is a model of what can be done with modern electronic techniques to far surpass the fish-listeners of Ceylon (Moulton 1963).

WHEN?

Although through the accretion of information over a long time, the seasonal and diurnal occurrence of sonic fishes has become known, the major part of this information is crude and sporadic, being derived from fishermen's lore. The seasonal spawning choruses of many sciaenids serve as a good example. The accumulation of reliable data of this sort can come only from long-term monitoring stations, such as the Bimini installation or an individual effort such as that of C.M. Breder. Acoustical data also need to be supported by catch figures and visual observation, as by divers or television cameras.

WHITHER?

If directional listening equipment is available, then the determination of movement of the fish becomes relatively easy. However, even without directional equipment, the presence of several listening stations, shore-based or floating, can provide this information through comparison of sound intensities of the moving fish.

HOW MANY?

Even with the most primitive forms of equipment, estimates of abundance can be made by listening to sonic fishes. However, such estimates can be made more accurate with the addition of some basic information on the sonic characteristics (pitch, pulse repetition rate, etc.) and sound source power.

WHO?

For a small number of species, identification of the sound source is a simple matter. The foghorn-like hoots of toadfish and the sob-like cries of the gafftopsail catfish *(Bagre marinus)* are among the easily recognizable sounds. By themselves, the bubbling sounds of sea catfish (*Arius felis*) may appear distinctive, but in an average estuarine locality in Florida during spring spawning, the total cacophony of croakers, drumfish, searobins, catfish, and others becomes just a blur of sound. The individual sounds of all these species are short duration pulses with a fundamental frequency range of from 50 to 150 Hz, and any temporal characteristics, e.g., pulse groupings and repetition rates, are masked out. It is possible, however, that with the application of computer techniques for signal enhancement, the species characteristics could be sorted out.

WHY?

Probably one of the most crucial pieces of information that we could obtain from listening to sonic fishes would be the function of the sounds in their behavior. Armed with such information, we could not only determine what the fish were doing, but predict their next moves and locations. We could also determine something of their size, reproductive state, degrees of aggregation, and other conditions that could be highly pertinent to fisheries management.

Acoustics and Fisheries Management :The Applications

Here we can pose the question of application. How can information about fish hearing and fish sound production be used to advantage in commercial fisheries, aquaculture, ecological impact studies, and other problems within the general area of fisheries management?

PASSIVE LISTENING

Given appropriate equipment and background information, it should be possible to answer many if not all of the questions posed above just by passive listening. These are the things we should like to do, and these are potentially possible with acoustical techniques. However, such plans must be tempered with the realization that the basic data available cannot permit us to do much more than to speculate.

For example, an essential problem mentioned earlier is that of species identification. In spite of all efforts, we can now recognize perhaps a dozen species on the basis of sound alone. By deductive reasoning and elimination through the use of additional data on habitat, season, and other environmental factors, we can increase the number to 25 or 30 species. The following list, with pertinent references, includes those marine species whose sounds can usually be used to identify the species or, at least, group of related species:

Gafftopsail catfish *(Bagre marinus)* - Tavolga 1960
Sea catfish *(Arius felis)* - Tavolga 1960, 1977c; Breder 1968
Atlantic cod *(Gadus morhua)* - Brawn 1961
Haddock *(Melanogrammus aeglefinus)* - Hawkins and Chapman 1966
Squirrelfish *(Holocentrus and Myripristis* spp.) - Winn, Marshall and Hazlett 1964; Horch and Salmon 1973; Winn and Marshall 1963
Spotted sea trout *(Cynoscion nebulosus)* - J.F. Fish and Cummings 1972; M.P. Fish 1954; M.P. Fish and Mowbray 1970
Atlantic croaker *(Micropogon undulatus)* - Dobrin 1947; M.P. Fish 1954; M.P. Fish and Mowbray 1970
Black drum *(Pogonias cromis)* - M.P. Fish 1954; M.P. Fish and Mowbray 1970

Bigeye *(Priacanthus* sp.) - Salmon and Winn 1966

Beaugregory and other demoiselles *(Eupomacentrus leucostictus* and other Pomacentridae) - Bright and Sartori 1972; Myrberg 1972b; Myrberg and Spires 1972

Longhorn sculpin *(Myoxocephalus octodecimspinosus)* - Barber and Mowbray, 1956

Margate *(Haemulon album)* - Cummings, Brahy, and Spires 1966

Tigerfish *(Therapon jarbua)* - Dorai Raj 1960; Schneider 1964

Searobin *(Prionotus* sp.) - Moulton 1956

Oyster toadfish *(Opsanus tau)* and Gulf toadfish *(O. beta)* - Gray and Winn 1961; Tavolga 1958a

Midshipman *(Porichthys* sp.) - Greene 1924

Triggerfish *(Balistes* sp. and related forms) - Salmon, Winn, and Sorgente 1968

It is possible that with a bit of luck and some visual data, other species can be added to the list, but it is also possible that some listed could not be identified with any certainty under many conditions. In addition, the practical value of the above list is reduced because of the few species of much commercial interest that are included.

Partially as a result of our difficulties with identification, our available data on the specific functions of fish sounds are pitifully small. A few species have been amenable to laboratory studies, as in the case of the frillfin goby *(Bathygobius soporator,* Tavolga 1956, 1958b), for example, and some freshwater species of cichlids (Myrberg, Kramer, and Heinecke 1965). Beyond the broad correlation of sound production with reproductive behavior, the specific use of sounds as courtship or territorial signals has been demonstrated through field studies in the oyster toadfish *(Opsanus tau,* J.F. Fish 1972) and the bicolor damselfish *(Eupomacentrus partitus,* Myrberg 1972b). The latter study was aided immeasurably by the presence of a shore-based video-acoustic system, so that the animals could be observed both visually and acoustically. Several additional studies of behavioral correlates to sound production have been reported recently (see review by Tavolga 1977a), so that the state of our knowledge is improving.

BEHAVIORAL CONTROL THROUGH SOUND PLAYBACK

Given the appropriate equipment and information, it should be possible to influence the behavior and movements of fishes by the appropriate choice of playback sounds. Sounds characteristic of feeding, courtship, and schooling, for example, could attract some species, while sounds of predators or alarm could repel. Repellent sounds could be used to guide fishes into traps or nets or away from obstacles and noxious conditions.

The utilization of sound to guide fish has only recently been applied commercially. The bibliography compiled by Moulton and Backus (1955) showed that these techniques for guiding or attracting fishes have been utilized by fishermen in many parts of the world. Some of the techniques are primitive and of ancient origin (Busnel 1959; Wolff 1966). Recent attempts have been made with modern electronic equipment to attract fishes by playback of their feeding sounds, and some success in this area has been reported (Hashimoto and Maniwa 1967; Maniwa 1976). Preliminary studies on guiding migrating salmon by acoustic stimuli have also shown promise for the future (Vanderwalker 1967). The observations by Richard (1968) demonstrated the feasibility of attracting a variety of predatory fishes by low frequency sound. For the successful development of these techniques, it is clear that more basic information is still required on the hearing range of many of the commercially important species, as well as more information on the behavioral significance of sounds produced by these fishes.

Although the technique of listening for sounds produced by fishes is known as an art among fishermen in several areas of the world (Moulton 1963), the use of this method in major commercial fisheries has yet to be tested. Some preliminary studies have been attempted, using a combination of sonobuoy and telemetry equipment (Hashimoto et al. 1960).

A list of the principal investigations of the effects of sound playback in the open water appears on the next page.

At first glance, the list seems to indicate that the feasibility of using sound to control fish behavior has been adequately demonstrated. There are several cautions to observe, however. For example, the report by Steinberg et al. (1965) was based on a few observations on occasional individuals seen at close range through the aid of a video-acoustic installation which, in itself, proved attractive to many local coral reef species. Fright or startle responses are often difficult to replicate, since the fishes become quickly habituated to the stimulus. The shark attraction experiments, although clearly effective at close range, are equivocal in the results at distances beyond 50 to 100 m. The attractive effects reported by Maniwa (1976) were to previously recorded "feeding" sounds. As presented, these data are only suggestive and far from conclusive. Control periods or signals were not clearly defined, and the general attractive effects of drifting vessels were not eliminated.

Theoretically, we should be in a good position to estimate the optimal frequencies and intensities to use in any playback experiments. As reviewed earlier, the available data on auditory sensitivity in fishes are now sufficient for some generalizations. It is curious indeed that even with such information available, experimental designs and equipment are still used that clearly do not match the hearing capabilities of most f[illegible] Recently, a system

	General Response	**Reference**
Searobin (*Prionotus*)	Change in sound production	Moulton 1956
Anchovy (*Anchoviella*)	Startle response	Moulton 1960
Goby (*Bathygobius*)	Attraction to courtship sounds	Tavolga 1958b
Mullet (*Mugil*)	Fright and dispersal	Shishkova 1958
Toadfish (*Opsanus*)	Change in sound production	Winn 1967; J.F. Fish 1972
Yellowtail (*Seriola*)	Fright response	Hashimoto and Maniwa 1967
Yellowtail (*Seriola*)	Attraction	Maniwa 1976
Mackerel (*Scomber* and *Trachurus*)	Attraction	Maniwa 1976
Sea bream (*Pagrus*)	Attraction	Maniwa 1976
Slippery dick (*Halichoeres bivittatus*)	Fright response	Steinberg et al. 1965
Yellowtail (*Ocyurus*)	Attraction	Steinberg et al. 1965
Snapper (*Lutjanus*)	Attraction	Steinberg et al. 1965
Margate (*Haemulon album*)	Startle response	Steinberg et al. 1965
Demoiselle (*Eupomacentrus*)	Effect on territorial behavior	Myrberg 1972b
Cod and Pollack (*Gadus* and *Pollachius*)	Both attraction and repulsion	Chapman 1976
Sharks (several species)	Attraction	Myrberg et al. 1976; Nelson and Johnson 1976

was demonstrated to me in which the sound projector used was obviously incapable of producing any significant energy under water below a frequency of about 1000 Hz. In this instance, I am not free to be specific, but in the case of the studies described by Maniwa (1976), their sound projector attenuated severely below 200 Hz. As described earlier, most fish sounds are in the neighborhood of 100 Hz or lower, and for the non-ostariophysines, the auditory sensitivity is best in the 100-200 Hz range with a rapid deterioration above about 500 Hz. If one is to design sonic gear for playback purposes, the low frequencies are clearly the most important, and this was amply demonstrated by the studies on sharks (reviewed by Myrberg et al. 1976).

In my own experience, I have been approached on several occasions by manufacturers of fishing lures with the question: "We are producing a lure that makes noises. What noises should it make to attract trout (or bass, or barracuda, etc.)?" It would be nice to be able to pull out a table of pertinent data and give an answer. Unfortunately, we are not in a position to do this. First of all, we are still quite ignorant as to the exact role of acoustic communication in the vast majority of fish species, especially those of any commercial value. In addition, the equipment required to project 50 to 100 Hz sounds at significant levels is not cheap and not readily available.

Problems and Prospects for the Future

From a comparison between the data we have and the things we should be able to do with acoustics, it is evident that a serious gap in our knowledge still exists. With a view toward the application of acoustics to fisheries management, I should propose the following major areas of research that, I think, would be ultimately productive:

AUDITORY CAPACITIES OF FISHES

As noted before, the number of species for which accurate data on auditory thresholds are available is quite small, and among these, fewer still are the species that have any commercial or food value. The techniques are available and have been successful as evidenced especially by the work of Chapman and others (Chapman 1973; Iversen 1967; and see chapters in Schuijf and Hawkins 1976). Without this kind of fundamental quantitative information, any further work on acoustic effects would be unlikely, at best, to be productive. The recommendation, therefore, would be that both laboratory and field studies be initiated to determine the hearing capacities of fish species important to commerce.

ACOUSTIC COMMUNICATION IN FISHES

Before designing and implementing playback experiments, it is necessary to have some understanding of the role of sounds in the behavior of the species in question. Such information is presently available for only a few species, and again, fewer still that are of any potential or actual commercial value. Field experiments are, of course, difficult to manage, since we do not have the same degree of control over the conditions as we do in the laboratory. This is no reason, however, to ignore basic experimental design and the use of controls. For a general and theoretical treatment of the problems of field vs. laboratory experimentation, I suggest a careful reading of a paper by one of the foremost behavioral scientists, T.C. Schneirla (1950, and reprinted 1972).

What will be the practical value of such research effort? At this point, our total information is still too meager to predict. Here one can begin to see the heavy dependence of "applied science" on "basic science," if indeed there is a difference.

"No, a thousand times no; there does not exist a category of science to which one can give the name applied science. There is science and there is the application of science, bound together as the fruit to the tree that bears it," — Louis Pasteur, 1871.

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Sensory Anatomy and Feeding of Fish Larvae

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IWAI, TAMOTSU. 1980. Sensory anatomy and feeding of fish larvae, p. 124-145. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Developmental patterns of sensory organs in teleost larvae differ from species to species. Newly hatched larvae from demersal eggs are provided with rather developed eyes as well as other sensory organs. On the other hand, in larvae from pelagic eggs, sensory organs are not well differentiated at hatching, except for naked neuromasts. Differentiation of taste buds is generally delayed, especially in marine species. The taste buds are usually found in the oro-pharyngeal cavity of larvae after onset of feeding. Teleost larvae search for food mainly by sight, but they rely partly on the mechanoreceptors and chemoreceptors in feeding. Preliminary behavioral experiments revealed that *Tilapia* larvae can detect the source of chemical stimulants. The results are discussed in relation to the role of chemoreceptors in feeding behavior of fish larvae.

Introduction

In recent years, aquacultural techniques have advanced surprisingly, and various kinds of fishes are cultivated in sea water and fresh water on a commercial basis. One principal requirement in fish culture is to succeed in mass-production of fry as seed stock. Heavy mortality usually occurs early in the life history of fish if suitable food is scarce, especially when the yolk is exhausted and the larvae must begin active feeding. Since culturing techniques for food organisms have improved, it is now possible to produce millions of fry of some marine teleosts. Further investigations of food preparation techniques for larvae are still required before the nutritional manipulation of fish larvae will be feasible.

Vision plays an important role in the life of growing teleost larvae, especially in detection and capture of prey (e.g., Dambach 1963; Braum 1964; Blaxter 1965, 1968, 1969, 1975; Schwassmann 1965; Rosenthal and Hempel 1970; Hunter 1972). But mechanoreceptors and chemoreceptors probably play a considerable role in certain aspects of their feeding behavior. The main purpose of my paper is to draw attention to (1) developmental patterns of these sensory organs in correspondence with the feeding behavior of teleost larvae, and (2) the role of chemical senses in the feeding behavior of teleost larvae with special reference to effective diets containing attractants.

In speculating about functions of receptors in larval stages, I attempted to obtain histological evidence on the sensory equipment and behavioral evidence.

Newly Hatched Larvae

When they hatch, teleost larvae are usually transparent with some pigment spots which we often use for species identification. Developmental patterns of the various organs differ from species to species. The period of embryonic life is relatively long in species with demersal eggs compared to those with pelagic eggs. Larvae hatch from demersal eggs with rather well developed eyes and other organs (Table 1). Usually, their mouths are open, and they can swim and catch prey shortly after hatching. On the other hand, most pelagic eggs hatch relatively soon after fertilization, though the incubation period varies of course with temperature. Newly hatched larvae from pelagic eggs generally are not advanced in development, and their sensory organs are not well differentiated except for the naked neuromasts. There is no indication of a pigmented retina, and the mouth and gut lumen are not yet open. The voluminous subdermal space is one of the peculiar characteristics of pelagic larvae believed to be related to the pelagic life (Shelbourne 1956). Even for larvae hatching without a functional mouth, rapid development of the digestive system enables them to take external foods before the yolk is exhausted.

Lateral Line System

The lateral line system in teleost larvae is serially arranged naked neuromasts on the head and body. Naked neuromasts, onion-like in shape, lie in the epidermal layer and protrude slightly beyond the surface. They are composed of apically arranged sensory hair cells, tall supporting cells surrounding the hair cells, and a slender cupula

TABLE 1. Comparison of digestive tract and sensory equipment in teleost larvae from different types of eggs.

			Digestive tract and sensory equipment in newly hatched larvae					
Species	Common name	Type of egg	Mouth[a]	Anus[a]	Gut lumen[a]	Pigmented retina	Naked neuromasts with cupula	Development of taste bud
Hypomesus transpacificus	pond smelt	FD	open	open	+	+	—	xo
Carassius auratus	goldfish	FD	open	closed	+	+	+	xo
Hemiramphus sajori	halfbeak	MD	open	open	+	+	—	xo
Fugu niphobles	puffer	MD	open	open	+	+	—	x
Tilapia mossambica	Mozambique mouth brooder	FMB	closed	closed	+	+	?	o
Lateolabrax japonicus	sea bass	MP	closed	open	+	—	+	xo
Acanthopagrus schlegeli	black porgy	MP	closed	closed	—	—	+	x
Pagrus major	porgy	MP	closed	closed	—	—	+	x
Kareius bicoloratus	right eye flounder	MP	closed	closed	+	- -	+	x

[a] Information from Tanaka (1973).

FD freshwater demersal; FMB freshwater mouth brooder; MD marine demersal; MP marine pelagic; + present; —absent; o before commencement of feeding, x after commencement of feeding.

(Fig. 1). Each hair cell has sensory hairs, an asymmetrically placed kinocilium, and some 30-40 stereocilia on the apical border. The arrangement of kinocilia alternately on opposite sides in adjacent hair cells is the same as that found in the lateral line canal organs of adult fish (Flock 1965; Yamada and Hama 1972). Nerve endings are present along the basal border of the hair cells. A rod-like cupula bending in response to water flow is peculiar to the naked neuromasts of teleost larvae.

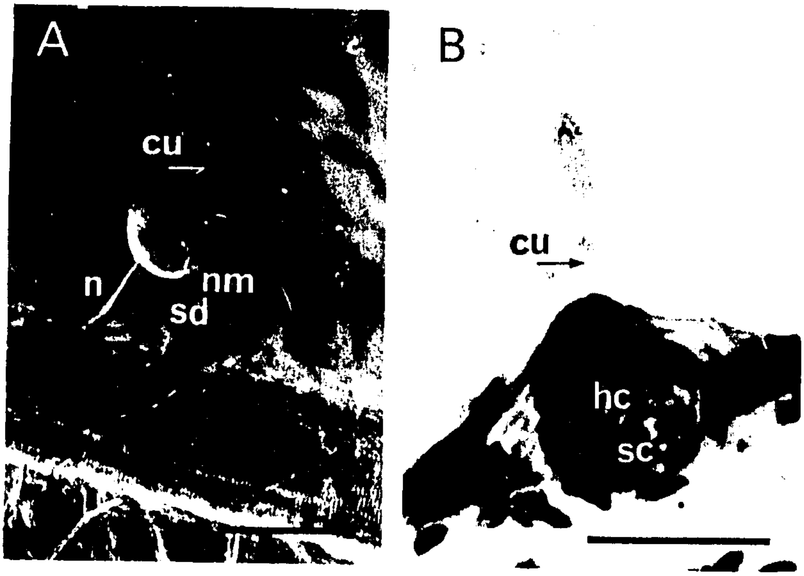

FIG. 1. Naked neuromasts in teleost larvae. A, Phase contrast photomicrograph of trunk neuromast in 2-day-old larva of *Acanthopagrus schlegeli*. Note the neuromast separated from muscle layer by subdermal space. B, Longitudinal section of head neuromast in 4-day-old larva of goldfish. cu, cupula; hc, hair cell; n, nerve; nm, neuromast; sc, supporting cell; sd. subdermal space. Calibration bars: 30 μm for A and 20 μm for B.

Species differences are recognizable in the number of neuromasts and particularly in the stage of development at which cupulae are formed (Iwai 1967, 1972). In larvae of the sea bass *Lateolabrax japonicus*, the black porgy *Acanthopagrus schlegeli*, the porgy *Pagrus major*, an oplegnathid fish *Oplegnathus fasciatus*, a pleuronectid fish *Kareius bicoloratus*, the blenny *Blennius yatabei*, and the puffer *Fugu niphobles*, including both pelagic and demersal types of eggs, the neuromasts are provided with well developed cupulae at hatching. In contrast, in larvae of the goldfish *Carassius auratus*, the carp *Cyprinus carpio*, a cyprinid fish *Zacco platypus*, the pond smelt, *Hypomesus transpacificus* and the halfbeak *Hemiramphus sajori*, all from freshwater or marine demersal eggs, the cupulae on the neuromasts do not become slender until age 1 d or a few days after hatching. The basic pattern of arrangement of naked neuromasts is common in early stages of many teleost larvae (Fig. 2). For example, neuromasts on the head lie near the olfactory cup, near the eye, and just in front of the auditory capsule. Five to seven neuromasts are spaced along each side of the body. The subdermal space is conspicuous in pelagic larvae, and neuromasts on the body are separated from underlying muscle layer (Figs. 1A and 2A). In some pelagic larvae without pigmented retinas, naked neuromasts are well developed. In these larvae, a pair of neuromasts lying between the eye and auditory capsule are larger than the others and have a longer cupula.

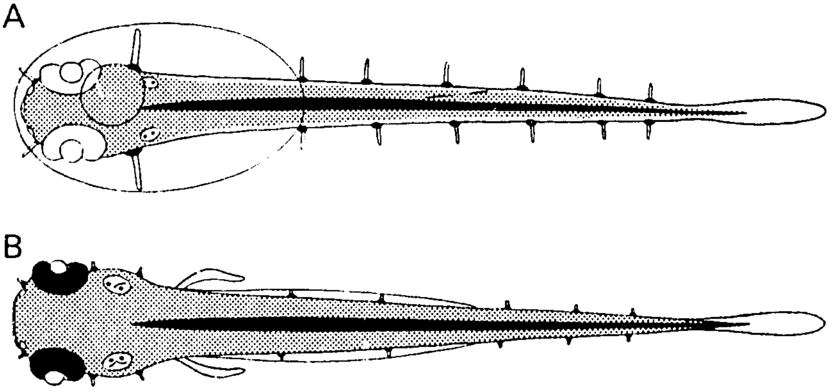

FIG. 2. Schematic drawings of arrangement of naked neuromasts in teleost larvae. A, Ventral view of 1-day-old larva of *Lateolabrax japonicus* from pelagic egg. Note the eyes without pigment. B, Dorsal view of 1-day-old larva of goldfish from demersal egg. Note well developed eyes.

The cupulae on the naked neuromasts are gelatinous, fragile structures. They cover the kinocilia and stereocilia of hair cells, and directly contact the surrounding water. When larvae are in the posture of repose in still water, the cupulae project perpendicular to the longitudinal body axis. If the larvae are exposed to flowing water the cupulae continuously oscillate and are sensitive to the water flow. Cupular oscillation or bending is believed to produce a lateral line microphonic potential. Cahn et al. (1968) denied the role of naked neuromasts in larval fish, and stated that mature neuromasts in the lateral line groove are more important than early naked neuromasts in the formation of schools of *Menidia* fry. But innervated naked neuromasts in early larvae possibly function as mechanoreceptors. In some species hatching without functional eyes, naked neuromasts are said to be an important receptor in relation to avoidance of predation during early larval stages (Blaxter 1975). In some pelagic larvae such as *Acanthopagrus* and *Pagrus*, the larvae are at first inactive. They float upside down with the yolk sac, containing an oil globule, uppermost and head directed slightly downwards. The larvae frequently sink head first to a considerable depth, and then turn upright to the surface. They repeat this pattern of movements for a couple of days. In connection with such vertical movements, ambient pressure changes probably directly stimulate the cupulae and naked neuromasts. It is conceivable that naked neuromasts with long cupulae not only perceive the direction of the current but contribute to the perception of pressure changes.

Generally, newly hatched larvae from freshwater demersal eggs rest on the substrate or vegetation. After hatching, slender cupulae rapidly develop on the naked neuromasts. In due course those larvae begin to swim up and become sensitive to movement of objects in the water. Apparently, naked neuromasts are adaptations for life in the water column.

Adult fishes use the lateral line sense in feeding. The panchax *Aplocheilus lineatus* perceives surface waves with the lateral line system on the head and uses wave formation to detect prey (Schwartz 1965). The blackstripe topminnow *Fundulus notatus,* having a well arranged lateral line on the head, is sensitive to surface waves and is thus able to find prey at the water surface (Schwartz and Hasler 1966). In pelagic fish, sometimes vision at the water surface is practically impossible, and these fish seem to use a highly specialized lateral line system in detecting prey (Schwartz 1967).

Mechanoreceptors of fish larvae have received little attention in relation to feeding behavior. Experimentally, frequent cupular bending can be seen in larvae placed in a glass tube, where swimming movements of *Artemia* nauplii cause water currents. With this system larvae may perceive the water displacement by the movements of objects around them. No experimental data are available concerning whether or not fish larvae use the naked neuromasts in detecting prey. One interesting suggestion is Disler's (1971) hypothesis that the lateral line system in teleost larvae plays a secondary role in food searching. Neuromasts of some cyprinid larvae which hunt for prey on the bottom are concentrated primarily on the lower and lateral surfaces of the head, while in others which pursue prey through the water column, the neuromasts are more uniformly distributed on both the lower and upper surfaces of the head. Thus, neuromasts in the larvae of species from different ecological groups are not arranged in the same way.

Chemoreceptors

Many larvae from demersal eggs have distinct olfactory receptors at hatching in contrast to some larvae from pelagic eggs. In newly hatched larvae of *Tilapia,* the olfactory epithelium is already developed along the basal surface of the olfactory cups. The epithelium of 2-day-old larvae is well differentiated (Fig. 3A) and it is composed of sensory cells, supporting cells, and ciliated cells. The olfactory nerve is detectable at the base of the epithelium. The sensory epithelium increases in size as larvae grow. The nasal cavity is well developed by 6 days after hatching, but olfactory rosettes are not yet visible (Fig. 3B). Major bundles of nerves run between the olfactory epithelium and the brain (Fig. 3C). The basal part of the epithelium is well vascularized.

In newly hatched pelagic larvae of *Pagrus*, only a few sensory epithelial cells are differentiating along the shallow olfactory cups, and the olfactory nerve is indiscernible. In 8-day-old larvae, the epithelium is obvious (Fig. 3D), and the sensory cells, supporting cells, and ciliated cells can be recognized in the epithelium. The olfactory nerve is now present in the basal part of the epithelium and extends to the brain. The olfactory epithelium and related nerve develop gradually, and in 12-day-old, larvae the apical border of the epithelium is lined by clusters of cilia. Nerve bundles leave the posterior medial portion of the olfactory epithelium. Olfactory rosettes are not formed even in the 20-day-old larvae (Fig. 3E).

The general developmental patterns of the olfactory epithelium and related nerves in both pelagic and demersal larvae are similar to those of salmonoid fishes described by Gawrilenko (1910), Watling

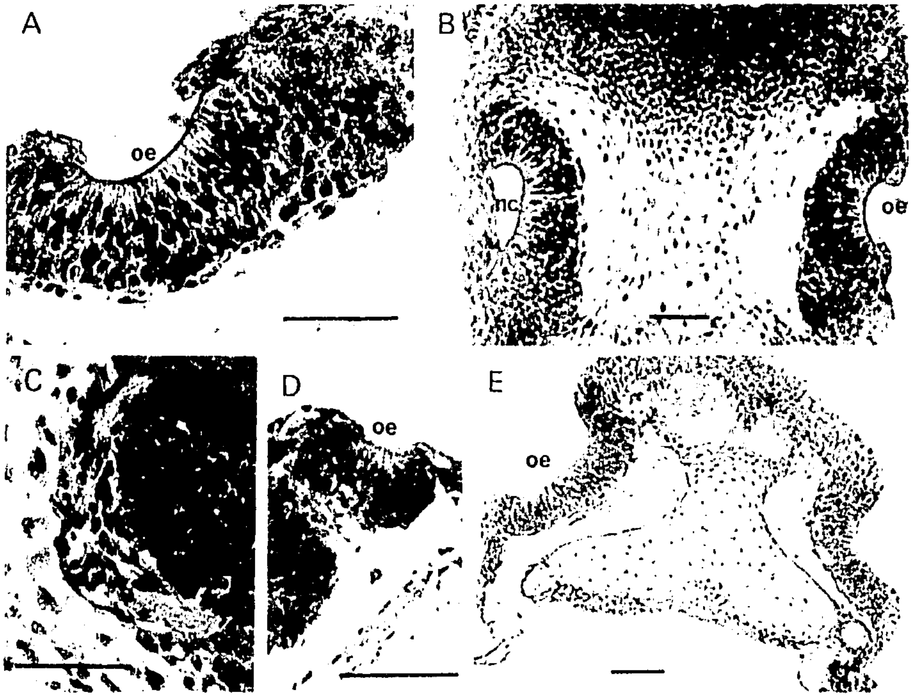

FIG. 3. Photomicrographs of olfactory epithelia of teleost larvae. A-C, Cross sections of snout of 2-day-old larva (A) and 6-day-old larva (B and C) of *Tilapia mossambica*, showing olfactory epithelia and olfactory nerve running along the lower border of olfactory epithelium. D and E, Cross sections of snout of 8-day-old larva (D) and 20-day-old larva (E) of *Pagrus major*, showing olfactory epithelia. nc, nasal cavity; oe, olfactory epithelium; on, olfactory nerve. Calibration bars: 40 μm.

and Hillemann (1964) and Jahn (1972), though the first indication of a fully differentiated olfactory epithelium differs from species to species.

If the olfactory receptors of larvae are to play a role in detecting potential food, the olfactory epithelium has to receive the surrounding water continuously. Although the water circulation in the nasal cavity of larvae is not as highly evolved as in adults, water with olfactory stimulants washes over the head with the respiratory movements. Watling and Hillemann (1964) working with grayling fry stated that the movement of water is dependent solely on respiratory movement and not even in part on the action of cilia present in the nasal cavity. Verraes (1976) considered that ventilative effects of ciliary currents in the nasal cavity are not to be neglected during postembryonic development. In some species, for example larval *Plecoglossus altivelis*, the ciliated epithelium of the olfactory cups serves to circulate water. In this case ciliary currents directed partly towards the olfactory cups and directed partly towards the gape are clearly seen, and these carry olfactory stimulants as well as minute food particles to the snout region (Iwai 1964). Based on the structural evidence it is plausible that 2-day-old larvae of *Tilapia* and 8-day-old larvae of *Pagrus* are capable of perceiving olfactory stimuli.

Gustatory receptors appear as pear-shaped taste buds in the oropharyngeal cavity of the larvae after hatching (Fig. 4). They lie in the epithelial layer on a stalk of connective tissue, and protrude a little beyond the superficial flattened epithelium. Typical taste buds are composed of a few horizontally placed basal cells and some vertically placed elongated cells closely packed together. According to Reutter (1971), light cells with prominent processes at the apical edge are sensory cells, and dark cells with a cluster of microvilli at the apical edge may serve as an aminoenergic mode of transmission of impulses through the basal cells. An intensive reaction indicating cholinesterase activity can be seen by histochemical techniques in the areas of the nervous plexus located around the basal cells. Hirata (1966) suggested that basal cells function as accessory receptor cells. The basal cells probably play some role in the transmission of impulses.

The first appearance of immature taste buds is observed in 1-day-old larvae of *Tilapia*, 2-day-old larvae of *Hypomesus*, 2-day-old larvae of *Carassius*, 5-day-old larvae of *Lateolabrax*, 8-day-old larvae of *Fugu*, 14-day-old larvae of *Kareius* and 16-day-old larvae of *Pagrus*. Thereafter, the taste buds increase not only in number but also in size, and those in the pharyngeal region are more numerous than those in the oral cavity in early stages. Descriptions of developmental patterns of taste buds in fish are essentially similar. In *Catostomus* and *Coregonus*, taste buds first arise in the endodermal lining of the pharynx and spread to ectodermal regions (Johnston

1905). Edwards (1930) made a similar observation in the carp. In catfish, taste buds appear simultaneously on the anterior ectodermal lining of the oral cavity and on the endodermal lining of the pharyngeal region (Landacre 1907). Fishelson (1966) described the development of taste buds in the oro-pharyngeal region of *Tilapia.* Campos (1969) presented a detailed table of distributional patterns of taste buds on the lip, oro-pharyngeal cavity and esophagus of some freshwater fishes.

Differentiation of taste buds seems slower in marine species than in freshwater species. Since taste buds are fully developed after the onset of feeding during the early stages, there seems to be little role for the gustatory sense in feeding during the early stages. Taste buds are densely arranged in the oro-pharyngeal cavity by the postlarval stage. Therefore, they may help in determining the palatability of food in the later stages of larval development. Blaxter (1965) reported that herring larvae first take almost any kind of floating object, but secondary selection by taste and texture then takes place within the mouth.

Chemosensory Behavior

Larvae of *Tilapia* begin swimming in laboratory aquaria 5 days after hatching. Periods of swimming become longer than those of resting on the bottom. Swimming larvae are randomly oriented and the fish-to-fish distances are not constant. Larvae still have a reduced yolk sac in the abdominal cavity but attempt to feed on *Artemia* nauplii or *Tubifex* chips when these foods are offered near the snout. Once larvae are successful in feeding, they become more proficient in capturing prey. Those fed with *Tubifex* chips as an initial food, later also prefer *Tubifex*. As with other teleosts, visual perception is the key sensory system in detecting food in early larval stages. When larvae see moving particles or *Tubifex* chips nearby, they dart and strike at them.

The stage at which feeding begins differs among fishes. In sardines, the feeding reflex does not appear immediately after the yolk sac is absorbed. Schumann (1965) presumed that adjustment is necessary in the visual organ and some other organs in relation to feeding. Searching initially appears in sardines when larvae show an S-shaped posture and keep a moving prey in focus.

According to Atema (1971), feeding behavior in fish is divided into the following four steps: (1) alert, (2) orientation and search, (3) food pick-up, and (4) food ingestion, and chemical senses are involved in some or all of these steps. In larval and juvenile stages, chemical senses may be effective in perceiving the presence of food, because of the limited visual field in those fish.

To determine the role of chemical receptors in feeding, preliminary experiments were conducted. Larvae of *Tilapia* were fed with *Tubifex* chips, and their searching movement in a Y maze was examined. By 14 d they were sensitive to water introduced from a tank containing living *Tubifex*. At first, water from the *Tubifex* tank was released into the left arm of the Y maze, in the next into the right arm, and so on alternately throughout the series of experiments.

In tests with groups of larvae, when stimulant water was introduced from the *Tubifex* tank to the waiting chamber through the Y maze, 14-day-old larvae became excited and actively moved in various directions. Within a few minutes almost all entered the stem, and swam toward the point-of-choice of the Y maze. There, about 72% of the larvae distinguished between the *Tubifex* water and control water and entered the arm containing *Tubifex* water. Once they entered the arm of *Tubifex* water, they were able to locate the source of the stimulus at the upper end and often bit at the tip of the glass capillary through which the *Tubifex* water was released. If they could not find the living *Tubifex* there by vision, they often left in a downstream direction. Sometimes larvae entered the arm containing control water. If one larva chose the arm which was not the source of the stimulus, following larvae also swam into the same arm. In this case they often stayed in the wrong arm for a considerable time. Then some of them pulled back to the point-of-choice and finally found the way to the release point of the stimulus.

Similar experiments were conducted with individual larvae at 18 d after hatching. In this case larvae also showed restlessness when stimulant water was introduced into the waiting chamber and then swam toward the arm of the source of stimulus. During the experiments, larvae sometimes moved into the control arm. Then the larvae usually pulled back to the point-of-choice and entered the arm containing stimulant water. But sometimes the larvae stayed in the wrong arm for long time.

In addition to the experiments with the Y maze, a small circular aquarium of 2 l was used to examine the reaction of larvae of *Tilapia* to *Tubifex* water in still water. Stimulant water from a small tank of *Tubifex* was introduced into the aquarium through a glass capillary. Stimulant water caused a positive response in 14-day-old larvae. At first, swimming speed increased and the larvae searched for food in the stimulant cloud for a while. Then the larvae reached the vicinity of the release point, and some of them bit at the glass capillary. As they were unable to see moving *Tubifex* at the release point, they gradually dispersed again in the aquarium.

The pelagic larvae of *Pagrus* begin to swim continuously by 4 d after hatching, and are randomly oriented in the surface layer of the aquarium. They still have a reduced yolk sac, but are able to feed on small organisms such as rotifers. They respond to moving particles in the water. These larvae, like many other teleost larvae, seem to react visually to food.

Similar preliminary observations were made with 8- and 16-day-old larvae of *Pagrus*. A small aquarium of 2-l capacity was used to examine their reaction to the squeezed juice of clam meat. Clam juice dissolved in sea water was released through a glass capillary at one side of the aquarium. Larvae 8 d old, in which the olfactory sensory epithelium was present but taste buds were lacking, did not show any remarkable reaction to the inflow of stimulant water. Sporadically some larvae were active and swam near the release point. The 16-day-old larvae, having both olfactory and gustatory receptors, became active when the clam juice was introduced into the aquarium. In this series of experiments, special searching movements of larvae were not observed, but some larvae sporadically gathered around the release point and stayed within the stimulant cloud.

There are comprehensive works confirming that adult fish use chemical senses in feeding. In catfish, gustation plays a primary role in the orientation and location of food (Bardach 1967; Bardach et al. 1967; Bardach and Todd 1970: Atema 1971; Bardach and Villars 1974). The catfish have many taste buds on the barbels and body surface as compared with the oro-pharyngeal cavity. They can search for the chemical stimulus release point by extended maxillary barbels near the water surface, even if the olfactory epithelium is cauterized. The marine goatfishes, *Upeneus bensasi* and *U. spilurus*, are able to sense and detect hidden food by taste buds on the chin barbels (Sato 1937, 1938). My observations indicate that in many teleost larvae, no taste buds are present on the outer sides of the body (Fig. 4A). Considering the distributional and developmental patterns of taste buds, searching for potential food by the gustatory sense is impossible for many larvae at the stage of initial feeding.

On the other hand, fish larvae probably rely on the olfactory sense in feeding. Kleerekoper (1969) reviewed a number of papers which indicate that olfaction is instrumental in the procurement of food, and that the scent of food acts as an arousal substance. Atema (1977) emphasized the olfactory function in the feeding behavior of highly visual fish such as yellowfin tuna. The scombrid fish *Euthynnus* respond to food flavor (Magnuson 1969). Hiyama et al. (1955) suggested that jack mackerel and mackerel can locate their foods with the olfactory sense. Bardach and Villars (1974) discussed the question of how fish detect absolute concentration differences in a stream of water by narrowly separated bilateral nares. Nevertheless, in nature salmonid fish discriminate between the chemical odors in water from different streams (Hasler 1966). They learn the home stream odors during the sensitive period at the smolt stage prior to the downstream migration. Juvenile coho salmon imprint to single artificial chemicals, morpholine or phenethyl alcohol, and utilize olfactory chemical cues for homing (Scholz et al. 1976). Thus, olfactory receptors of fish may be functional in rather early stages. As is seen in feeding behavior of *Tilapia*, olfaction in fish larvae appears to play a role in searching for prey.

Remarks

In Japan, mass production of fry for aquaculture has been successful with some fish. For instance, rearing experiments produce more than one million larvae of *Pagrus* annually at one hatchery. In these rearing experiments, a series of foods for growing larvae has

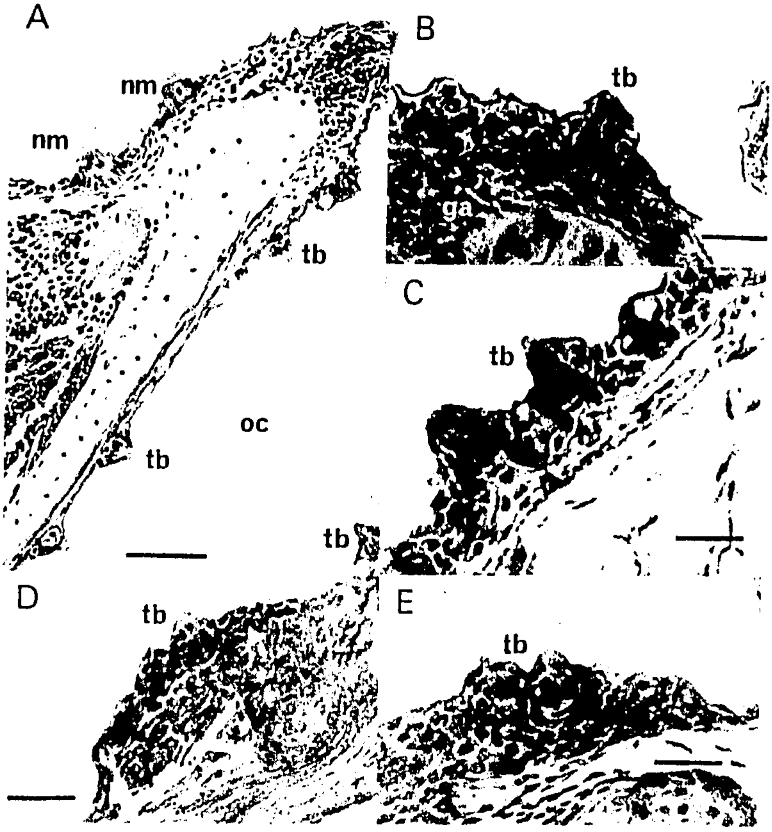

FIG. 4. Photomicrographs of oro-pharyngeal regions of teleost larvae, showing development of taste buds. A, longitudinal section of head of 6-day-old larva of *Carassius auratus*. Note the naked neuromasts (nm) lying in epidermal layer of outside of mouth. B, C, sections of pharyngeal region of 2-day-old larva (B) and 6-day-old larva (C) of *Tilapia mossambica*. D, E, sections of pharyngeal region of 16-day-old larva (D) and 25-day-old larva (E) of *Pagrus major*. ga, gill arch; nm, neuromast; oc, oral cavity; tb, taste bud. Calibration bars: 50 μm for A and 20 μm for B-E.

been established. During the period of about 25 days after hatching, cultured rotifers are first offered, and then copepods, *Artemia* nauplii, minced clam meat, and others, with periods of overlap from one food type to the next.

In the mass production of fry, the shortage of suitable food organisms is a constraint. May (1970) pointed out problems of food associated with large-scale fish culture, especially in relation to preparation of sufficiently large quantities of a suitable food. In this respect, manufactured diets will be of much value in culture of fry. Adron et al. (1974) were successful in rearing plaice larvae using an artificial diet, though survival rates were lower than in those fed with *Artemia*. Recently, research scientists in Hiroshima Prefectural Fisheries Experiment Station tried to use a dried manufactured diet made mainly of the northern fish meals, euphausid paste and cod-liver oil (T. Fushimi, Hiroshima Prefectural Fisheries Experiment Station, personal communication). Those larvae measuring 5 mm (11 d) and 8 mm (21 d) fed on the manufactured diet, but the survival rates and growth rates were not so good as compared with those fed with live organisms. It is of interest to note that these larvae certainly feed on the manufactured diet at younger stages before the formation of taste buds. Once food particles are engulfed by larvae, these are conveyed to the mid and posterior portions of the gut. In many teleost larvae, the mid portion of gut is involved in fat absorption and hind gut is involved in protein absorption (Iwai 1969). The hind gut is especially characterized by absorbing proteinaceous material by vigorous pinocytosis, though O'Connell (1976) obtained contrasting results with anchovy larvae. Therefore, it will be harmful if larvae ingest indigestible substances.

If a suitable food for larval fish is to be made it should provide sufficient nutrients for growth and contain effective chemical substances attractive to larvae. Basic studies on the manufactured diet for young yellowtail revealed that the amino acids, proline, alanine, and methionine, induce a remarkable feeding response, and combined use of these amino acids with inosine monophosphate is more stimulative than use of the jack mackerel chips alone (M. Takeda, Kochi University, personal communication). In adult fish, a mixture of compounds is more stimulative than any single compound at the same concentration (Hashimoto et al. 1968; Pawson 1977). Such active substances may be attractive to the chemical senses of fish larvae. That the taste buds are not developed in early larval stages suggests that one must determine what substances are more attractive to the olfactory sense than to the gustatory sense. The olfactory plasticity in searching for food was recognized experimentally in several fish (Atema 1977). These substances can then be used as attractants in the preparation of food for fish larvae.

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Discussions

BARDACH

Is it easier to feed artificial feed to fish larvae before their taste buds have begun to develop than after?

IWAI

According to the experimental data given by T. Fushimi, *Pagrus* larvae measuring about 5 mm in length will feed on artificial diets, especially early in the morning. *Pagrus* larvae at this stage apparently do not have taste buds.

BARDACH

You have told us of different types of development of sensory systems according to habits or characteristics of the larvae. Is it possible to make some kind of a scheme where one correlates relative degrees of development of vision, neuromasts, and the olfactory system with demersal, pelagic, and other characteristics of fish life history?

IWAI

It is very difficult to make an exact table indicating species differences in sensory equipment of newly hatched larvae, because of effects of environmental factors on organization in these larvae. It seems to me, however, that there are some differences of sensory equipment between larvae from demersal eggs and those from pelagic eggs. Similar differences may be seen between marine larvae and freshwater larvae. Generally speaking, in pelagic larvae, neuromasts precede the pigmented eyes and taste buds, and in demersal larvae, pigmented eyes appear earlier than neuromasts and taste buds. In most species, the olfactory organs appear in comparatively early stages.

BARDACH

How does the development of the olfactory organ compare with the development of both neuromasts and eyes? In particular, as the olfactory organ develops do some of the neuromasts disappear?

IWAI

I don't think they do. In larval stages, the number of neuromasts on the body surface increases as the larvae grow. But in juvenile stages these neuromasts gradually sink into the pits and canals. In many species eyes are well developed at the stage of onset of feeding and probably play the most important role in searching and catching food, as comprehensively explained by Dr. Blaxter (1975). The olfactory organs develop in early stages, too.

BARDACH

The neuromasts on the body may have a slightly different function than those on the head, and I would speculate that neuromasts on the head would be more geared to locating food than those on the body.

IWAI

I don't know exactly, but I can say that they are lying in a good position to perceive the direction of mechanical stimuli.

FISHELSON

If you compare bottom spawners and mouth breeders of *Tilapia*, there are beautiful differences in neuromast development. In a 5-day-old fry of the bottom spawning *Tilapia zilli*, all the system is developed, but in a 5-day-old fry of a mouth breeder, nothing is visible. During development in contact-making larvae of mouth-breeding *Tilapia*, there is a jungle of neuromasts on the head and these develop first, but not in the bottom spawners. Concerning feeding, the larvae of bottom spawners start to feed much earlier than mouth breeders, and for this not only do the taste buds appear at an earlier stage, but the diaphragm between the mouth cavity and esophagus opens earlier. Now I would like to ask Mr. Iwai about the retractor lentis, because as I know it's not enough to have a retina for vision. You must have accommodation. Now I know *Tilapia* start to feed as soon as the striation of the retractor lentis is visible. Have you seen this in marine fishes?

IWAI

In many species the development of the eye progresses very fast after the onset of feeding, but I have not examined the visual senses in detail. Accommodation may certainly be part of the visual system in some teleost larvae.

BLAXTER

But I think most teleost fish are myopic; in other words, they see things close to the eye and so it may not be too important to accommodate if they are feeding on organisms very close to the head. They need to accommodate only to see distant objects. But do we know any predatory fish larvae that can feed only using the neuromast organs?

FISHELSON

Anoptichthys jordani is a blind cave fish that I have grown for several years by feeding them nauplii of *Artemia*. Without eyes, they immediately react to nauplii passing by. I don't know with which system they react.

ATEMA

You need a quite complex retina to form an image, and if you are going to use an eye for feeding discrimination, you need a very sophisticated eye.

BLAXTER

In my experience the fish will much more readily take moving food which they can see. The eye can detect movement much more easily.

IWAI

Dr. Schwassmann (1965), working with sardine larvae, pointed out that retinal axons in the optic tectum for true shape perception and good visual acuity are not fully formed in larvae at the beginning of the feeding stage.

FISHELSON

What about Mauthner cells? I've got a feeling that the larvae start to feed with some coordination between detecting organs and the stroke of the caudal fin, and this goes together with the development of the Mauthner cells in the brain.

BLAXTER

Do we know when they occur in the larval stage?

IWAI

In some species, for example, zebrafish, bullhead, and *Salmo*, Mauthner cells are said to be functional at hatching (Eaton, R.C., and R.D. Farley. 1973. Development of the Mauthner neurons in embryos and larvae of the zebrafish, *Brachidanio rerio*. Copeia 1973: 673-682).

ATEMA

I'd like to ask another question about taste buds because on theoretical grounds it would seem unlikely that a larval fish would not have taste buds to discriminate the food that it puts in its mouth. Is that true? Does it feed before there are taste buds?

IWAI

Many marine pelagic larvae do not have taste buds at the stage of initial feeding. But *Tilapia* larvae are provided with taste buds when they begin to feed, and are presumably able to discriminate the food in the oral cavity.

ATEMA

What a risky existence. How do they do it then?

IWAI

Probably they detect the food by vision and gulp it. The material taken by jaws may pass through the oral cavity without gustatory discrimination.

HUNTER

You never see a very young larva rejecting a prey once it enters the mouth. Many larvae feed using a sinuous feeding posture—they rapidly strike and engulf the prey with an open mouth. There is no handling of prey.

ATEMA

There must be a great risk factor of getting something unpalatable.

IWAI

In many marine species, larvae are interested in moving particles. They can search for food by sight in early stages.

ATEMA

Yes, but how do they discriminate what's good and what's bad?

IWAI

It seems to me that it is impossible for them to select good material or harmful material at the first stage. But the period is of short duration. Taste buds develop within a few days after beginning of feeding even in such larvae.

MAY

Early larvae can accept only a very small range of sizes because of their small mouth opening and there's very little to choose from within that size range.

BLAXTER

I don't think there's any rejection of particles once they take them into their mouth.

MAY

But in any case there are very few naturally occurring particles of that size range which are not edible by them.

BARDACH

Assume that a foundation were to put up a large amount of money to help solve the question of larval nutrition. Would you perfect systems of live food or systems of artificial food? Or would you ply the trade on both sides of the street? Where do you think we have most to gain?

IWAI

I think at the present time, combined use of live food and artificial feed is effective for the successful rearing of fish larvae. But in mass-production of seedling fry, we are in need of sufficiently large quantities of a suitable food at hatching. Thus there will be increased demands for a manufactured larval diet.

BARDACH

Let me go one step further. If you can develop artificial diet particles that move because of the coating they have, would that be a strategy to take? It seems theoretically possible to manufacture artificial diets by pressure spray and coat them with something that would make the particles move once they get into the water. Would that be an interesting proposition?

IWAI

There are many problems in developing the manufactured diet as you mentioned. They have other difficulties such as decay of leftovers, and cost-effectiveness. Although an ideal diet is not available as yet, actually some manufactured diets, whose food particles measure 80-150 μm in diameter, have been used successfully in rearing not only freshwater fish larvae but also marine fish larvae. It goes without saying that such diets should provide a sufficient amount of nutrients and attractive substances, and we are preparing to collaborate with biochemists on this problem.

LILEY

What is the problem with the artificial diets? Is it a matter of palatability, or is it the lack of movement? What you're telling us seems to suggest that the fry will take the artificial diets until they can taste them. That suggests that palatability is the problem, in which case you might be able to coat the food particles with something that is palatable. This does raise the question, why is the food unpalatable? Is it because it is nutritionally inadequate? Work with birds and mammals suggests that some animals very quickly learn to avoid nutritionally inadequate foods. If the fish are able to learn that these particles of food are not adequate nutritionally, then whatever you do to the food without making it nutritionally adequate will not solve the problem.

BLAXTER

I think it's a mistake to look for anything too sophisticated in fish larvae. I think if you look at the stomach contents of fish larvae in the field they very often reflect the plankton; it is a question of the size of the particles that is vital. There's the question of microencapsulation of artificial food. This is being done now, isn't it?

HUNTER

The problem with microencapsulation is that as soon as you encapsulate a particle it becomes rather difficult to digest. Larval fishes vary in their ability to digest particles. In clupeoids and other larvae, gut clearance may be very rapid, and one needs a coating that will break down rapidly. Fouling of the water is another problem and requires rather elaborate plumbing to solve. Neutrally buoyant particles would be ideal but they are difficult to produce.

BARDACH

You assume the relative simplicity of a plankton diet, but take for granted a complete nutritional sufficiency which is one of the more difficult things to achieve in microencapsulation, that is, in very small particles.

BLAXTER

It's surprising how you can accustom fish to completely strange diets. For example our herring, once they metamorphose, are entirely fed on trout meal. If you put *Calanus* into the water, which is their normal diet, they're not happy about it.

FISHELSON

Why not try microhabitats with planktonic fish larvae in the natural environment, provided the net of this microhabitat would permit planktonic organisms to invade the habitat and serve as food?

MYRBERG

I would say if you can make a manufactured food as nutritious as live food, then why use live food? The only reason to use live food is if the sensory systems demand the characteristics of the food organism itself. When you say the survival on artificial food is not as good as the survival on live foods, was it because the larvae starved because they did not eat, or was it because they ate but still starved?

IWAI

In many cases, they feed on manufactured diets as well as live food such as rotifers, but sometimes they starve when diets sink to the bottom. Diets are taken by larvae when these are suspended as particles in the water column. Furthermore, even in larvae satiated with food, the growth rates are lower than those of larvae which are fed rotifers.

FISHELSON

Is there any evidence that fish larvae are able to feed from dissolved organic matter, let us say amino acids, in seawater like a lot of invertebrates are able to do?

BARDACH

At Michigan, we used marked amino acids and plugged guts, not with larvae but with juvenile goldfish of about 5 cm. There is no evidence that once the esophagus is plugged, there is absorption of amino acids, at least through any other epithelium.

HASLER

It depends on how much they drink, and even if they drink a lot, the percentage of their total energy budget that they get that way is miniscule. It's only 1% or something like that. The drinking species can take essential vitamins that way. Freshwater species don't drink much.

FISHELSON

But in larval stages, they don't need to drink because all they are is two plates of epithelium with something in the middle.

BARDACH

What about the concentration of amino acids in sea water?

JOHANNES

Very low. A few tens of micrograms per liter. Most of the published experiments that have purported to demonstrate that dissolved organic matter is an important energy source for marine animals do not in fact demonstrate anything of the kind (e.g., Johannes et al. 1968). In fact, a net *release* of dissolved organic matter has been demonstrated for numerous marine animals (e.g., Johannes and Webb 1970; see References after Atema's paper for complete citation).

BLAXTER

Very often they excluded the possibilities of ingesting bacteria. There have been very few good experiments. I think the hangup with artificial food is this movement question. I think most fish larvae will probably take moving food better.

MYRBERG

There have been some noteworthy studies on the importance of prey movement to predatory action with animals the size of fish larvae (e.g., Feigenbaum 1977; Horridge and Boulton 1967; both dealing with chaetognaths and copepods). Such work has demonstrated that the frequency of the vibratory movement of prey is clearly important to attack and capture by predators.

MAGNUSON

Dr. Harold Calbert of Wisconsin was able to stimulate feeding on artificial foods in walleye (*Stizostedion vitreum*), a crepuscular feeder, simply by reducing the light level in the aquarium. This suggests that one should examine how closely the captive environment mimics the natural habitat in which the animals are typically feeding, with regard to light intensity and perhaps other parameters.

HUNTER

A number of nonactive foods are frequently eaten by larvae. Copepod eggs are common and sometimes very abundant in the stomachs of larvae. We feed mackerel larvae anchovy eggs and they grow well on them. These foods certainly are not motile, but they probably provide olfactory stimuli.

BLAXTER

A colleague of mine has blinded herring and plaice larvae by removing the eyes. Normally in the early stage these are visual feeders. He finds that if he puts in a sufficient concentration of, say, *Balanus* nauplii, they will eat some. I think the larvae are swallowing water for osmoregulation and just take them in with the water. I think you're most likely to make progress with microencapsulation by getting a firm to do it—a big firm.

HUNTER

Some time ago, I heard that bacterial flocs were being tested as larval fish foods in Japan. Do you have any more information about this?

IWAI

Nutritional effects of bacterial flocs have been recognized in some marine zooplankton. Scientists of the Seto Inland Sea Fish Farming Association have been studying the effects of bacterial flocs on the rearing of fish larvae. In this case, they expect that bacterial flocs are not only useful as larval fish food but also effective in improving water quality, especially in relation to the prevention of *Vibrio* disease.

ATEMA

I still find it hard to believe that no chemoreception occurs. Why then do the taste buds develop later on? What changes in the animal's food habits, that at different stages for different animals taste buds do develop?

MAGNUSON

If you look at the food habits of fishes, I would think the fishes are perhaps most specialized when they are juveniles. When they get larger, the size range of food particles eaten tends to become broader, and this may give them a greater array of things that they need to choose from.

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Sensory Mediation of Social Recognition Processes in Fishes

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Myrberg, A.A., Jr. 1980. Sensory mediation of social recognition processes in fishes, p. 146-178. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

The experimental studies which have contributed to our knowledge of social recognition processes and the means whereby they are achieved in fishes are reviewed. Social recognition involves differing levels of organization: interspecies, species, sexual, and individual; and its mediation is served by one or more of the multitude of sensory modalities available to any given species. One might well expect, based on the great diversity of fishes and the widely differing habitats in which fishes are found, that recognition of conspecifics, mates, territorial neighbors, members of other species, etc., would be accomplished by a widely varying set of "tactics." Although that can be noted, it is also evident that there exists a rather remarkable consistency among diverse groups to use a similar "tactic" when dealing with a common recognition process. It is also apparent that intersensory integration is involved in many such processes; its importance has already been demonstrated in a few noteworthy cases. The complexity of cross-modality investigations, unfortunately, leaves them, to date, only as a tiny "glimmer" of important things still to come in the field of sensory biology.

Introduction

The fundamental goals of survival and reproduction require, throughout the life of any organism, countless decisions relative to given courses of action. These decisions depend, in turn, upon accurate and relevant information from that sensory world to which each organism is attuned. Where adaptive radiation has been extensive, such as that evidenced by fishes, it is reasonable to expect that different species will vary as to the degree that each relies on specific modalities to provide the information needed to answer given sets of problems. This is especially evident when one considers the staggering array of different habitats in which fishes are found.

Social recognition and the means whereby it is achieved in fishes are the subjects of this report. They constitute only one of many sets of problems faced by such animals, but the set is rather extensive. It includes recognition processes at the interspecies, species, sexual, and individual levels among a great diversity of fishes, each species possessing a variety of sensory channels (e.g., visual, olfactory, gustatory, auditory, near-field displacements, electrical, touch), any one of which is, at least, potentially available for use. This in itself creates a serious problem. It is often exceedingly difficult, and probably impossible in most cases, to establish that a given stimulus-quality is the sole arbitrator for a specific process. This is due not only to the difficulties concomitant with the requirement for appropriate controls within any experimental design, but also to our ever-increasing awareness that such processes may actually involve cross-modality compliance among different sensory data in the form of gestalt schema. Unfortunately, our ignorance is profound at this level of analysis. Because of this probable integration, any review of our knowledge must be cautious so as not to invite misunderstanding, and yet it must also be somewhat redundant based on the necessity to organize relevant findings and thoughts.

Some type of recognition process has been either found or suggested, wherever sought, throughout the gamut of the social activities recorded in fishes. These include feeding, schooling, migration, territoriality, social hierarchies, mate selection, pair bonding, spawning, and parental care. Certain activities will be treated lightly, e.g., feeding, schooling, and migration, since some of my colleagues will deal specifically with them during this conference. Also, an enormous literature exists on fishes relative to color and behavioral changes that herald the occurrence of still other acts or activities. Although such changes may well also provide "keys" to various recognition processes, their existence alone, in the absence of appropriate experiments, does not constitute direct evidence of discriminative processes. I shall, therefore, bypass the great majority of such studies, emphasizing instead those findings which have revealed relevant processes through controlled, experimental analysis.

The Sensory Mediators

VISION

Since man is a "visual animal," most of his attempts to analyze recognition processes in other animals have been concentrated on that modality. Despite this bias, there is little question that many fishes depend heavily upon vision to guide their countless daily activities. Present evidence suggests that this is the prime modality used in social recognition. Experimental analyses in fishes extend back to the initial studies by Lissman (1932) on the fighting fish, *Betta splendens*, and by ter Pelwijk and Tinbergen (1937) on the threespine stickleback, *Gasterosteus aculeatus*. These authors used appropriate models to elicit responses from their subjects and such a technique is still used in tests of social recognition based on active discrimination. These early results showed that only certain portions of the stimulus field contributed the highest measure of response (e.g., in the case of the stickleback, courtship in males was elicited only by a model possessing a silvery color, a swollen abdomen and no red color anywhere; shape and size meant little). Thus, the male had responded to the features characteristic of the reproductively active female.

Since these early studies, various projects have been undertaken to establish visual recognition processes at various levels of complexity.

Interspecies recognition

Until recently, interest at this level of interaction was centered primarily on the fascinating and highly complex cleaning symbioses that have been reported to involve numerous species from a variety of habitats (see Abel 1971; Darcy et al. 1974; Eibl-Eibesfeldt 1955; Feder 1966; Hobson 1969, 1971; Limbaugh 1961; Losey 1971, 1972; Okuno 1969a and b; Potts 1968, 1973a and b; Randall 1958). We now know in a number of these cases that the occurrence of "posing" by the given host is dependent upon the visual presence of the particular cleaner in question (Losey 1972; Potts 1968), and the particular course of "inspecting" the host by the cleaner is also species-specific (Potts 1973a). The host, at least, appears to achieve visual recognition of cleaners by learning through tactile reinforcement (Losey 1972). Another type of commensal relationship involves the goatfish, *Pseudopeneus macronemus* (= *P. forskali)*, and five different species of commensals that follow it and feed upon organisms in the sand cloud it stirs up while searching for food (Fricke 1975). A simple but elegant experiment using appropriate visual models showed that greatest response by the "followers" occurred when the model possessed the shape and color of the goatfish in the presence of the sand cloud.

Until recently, reports of interspecific interactions in other contexts were sparse (Gerking 1959). Although such interactions involving agonistic activities were initially noted in various freshwater habitats (e.g., Newman 1956; Stringer and Hoar 1955; Winn 1958), most recent reports concern fishes from coral reefs. These studies have shown that the phenomenon of interspecific territoriality is a stable system of sustained aggression maintained by a resident against members of numerous species (see Brockmann 1973; Colin 1971; Cummings 1968; Ebersole 1977; Low 1971; Moran and Sale 1977; Myrberg 1972a; Myrberg and Thresher 1974; Patterson 1975; Thresher 1976a). In the threespot damselfish, *Eupomacentrus planifrons*, for example, this system is expressed by a resident fish's defending a series of territorial perimeters, the arrangement of which is species-dependent (Myrberg and Thresher 1974; Thresher 1976a). The cues necessary for the recognition processes required of such a structural organization were investigated by Thresher (1976b). His field experiments showed that the shape or form of the intruder was critical, with movement being required for attack to be elicited. Color of the heterospecific was apparently not critical (we shall see later that the process of species recognition in this damselfish differs in that regard). The finding that shape was the important factor for this recognition process fitted well previous findings by Thresher that similar-sized defense perimeters were usually maintained for fishes having similar shape, but not necessarily similar colors.

Species recognition

The tremendous variety of colors and shapes found among fishes has led many observers to speculate on its probable meaning (e.g., Barlow 1974; Cott 1940; Hamilton and Peterman 1971; Longley 1917; Lorenz 1962; Myrberg 1972b; Potts 1973b; Wickler 1967). Most have concluded that such characters are used by conspecifics to recognize one another, as well as to provide information about the sex and physiological state of the individual concerned. It is noteworthy, however, that specific behavioral actions (i.e., movement) often accompany the above-mentioned features and some believe that such actions are more important in recognition processes than the species-typical color patterns so often mentioned (see Fryer 1977; Fryer and Iles 1972). Such an idea is especially pertinent to nocturnally active animals or those living under conditions of low light intensity.

In those instances where species recognition per se has been tested, results have been reasonably consistent. Fricke (1966) found that territorial individuals of two species of butterflyfishes (*Chaetodon fasciatus* and *Chelmon rostratus*) and one damselfish (*Amphiprion bicinctus*) showed heightened aggressive response to models displaying their species-characteristic shape and color pattern, compared to that of other models. Ono (in Zayan 1974) noted that body shape was important for species recognition in the rice fish *Oryzias latipes*, with speed of movement increasing the aggressive responses shown by territorial individuals. Thresher (1976b) likewise found that the territorial damselfish *Eupomacentrus planifrons* recognizes conspecifics by shape, but it also uses color pattern. Size and movement were apparently not critical. Potts (1974) also concluded that shape and color pattern were essential for species recognition in the wrasse *Crenilabrus melops*, as did Keenleyside (1971) for territorial male longear sunfish *Lepomis megalotis*. The latter author found that color was important specifically to certain body structures (the eye, the opercular patch, and the pelvic fins). Markl (1972) also found that shape was critical in the recognition of conspecifics by pirhanas, and similar to the previous case, he demonstrated that a dark eye and a protruding fin enhanced recognition. Body color was apparently not critical. Brockmann (1973), on the other hand, concluded that territorial beaugregories *Eupomacentrus leucostictus* did not use body shape in their discriminations; rather size and one particular color pattern of the species were the determinants for heightened aggression. Her findings and experimental design suggest that the level of recognition may well have differed from that examined in the previously mentioned studies. Testing an individual's ability to differentiate members of one's own species is somewhat different than testing discrimination between one's own species and others.

Species recognition based on visual cues has also been examined in a few species under nonaggressive conditions. Keenleyside (1955) noted in the characin, *Pristella riddlei*, that individuals chose as schoolmates only those conspecifics that possessed the dark, dorsal fin characteristic of the species. Timms (1975), also noting the prominent role that vision plays in species recognition by goldfish *Carassius auratus*, established that shape was indeed the most important discriminant but that size and some movement also played a role. Since the models in his case were simple geometric designs (ovals, squares, and rectangles) some might question whether approach responses to such objects of varying size can be considered equivalent to approach responses to conspecifics. In any case, his technique of monitoring and establishing levels of locomotory response appears useful for future studies of similar problems.

Problems of species recognition extend into other phases of social activities, including the period of parental care which characterizes a number of families of fishes. The members of one such family, the Cichlidae, show an extended period of parental care and consequently they face unique problems. The first is, can parents differentiate the eggs and minute young of their own species from similar eggs and young of other species? The second question is, can such tiny young recognize adults of their own species? An answer to the first question must be given in two parts. Parents of *Cichlasoma nigrofasciatum*, *C. octofasciatum*, and *Hemichromis bimaculatus* can apparently tell their own eggs apart from those of other species. Such discrimination is apparently based primarily on size differences, but shape and color may play a role. Heterospecific care will nevertheless be shown so long as the differences are not great (Collins 1965; Greenberg 1961; Myrberg 1964; Noble and Curtis

1939; Weber 1970). Parents of those species, as well as others (*C. bimaculatum, C. citrinellum, C. cutteri, H. fasciatus*), can also visually differentiate such tiny, free-swimming young under a variety of conditions (Greenberg 1963; Myrberg 1964, 1966, 1975; Noakes and Barlow 1973; Noble and Curtis 1939). This discrimination is apparently based, at least in certain species, on the association of parental care with certain visual cues of the young in the presence of specific chemical factor(s) of these same young (Myrberg 1966). This particular case clearly suggests the operation of intersensory correlates to environmental adjustment, a fact rarely appreciated or studied in fishes (Atema et al. 1969).

The second question, mentioned above, has also been studied in some detail. Tiny, free-swimming young of a number of species show a clear, initial preference to approach objects that possess only the breeding colors of their own species. For example, young of *H. bimaculatus* approached red (Baerends and Baerends-van Roon 1950; Kühme 1962; Noble and Curtis 1939), *Apistogramma reitzigi*—yellow (Kuenzer 1966), *A. borelli*—yellow and black (Kuenzer 1962); *C. octofasciatum*—black (Kühme 1962); and *Nannacara anomala*—dark color (Kuenzer 1966, 1968). The ease by which such preferences can be modified varies among species (Kühme 1964), as does the importance of still other species-typical features, e.g., shape (see Kuenzer 1968). Similar problems have been likewise clarified in the more specialized, mouth-brooding cichlids of the genera *Haplochromis* and *Tilapia* (e.g., Peters and Brestowsky 1961).

Finally, an interesting case of circumstantial evidence for visual mediation of species recognition has recently been described by Losey (1976): there exist two separate species-pairs within the blenniid genus *Hypsoblennius* in which the sympatric pair shows highly divergent systems of coloration, while those of the allopatric pair are highly similar.

Sexual recognition

Circumstantial evidence from many dimorphic species indicates that sexual recognition exists at, or near, maturity. These differences include color (males are usually the "showiest"), size, and shape. Color differences may exist more or less permanently or only during the breeding period, involving all or most of the entire body (e.g., many parrotfishes, wrasses, cyprinids, nandids) or restricted to limited regions (e.g., sunfishes, cichlids, sticklebacks, lanternfishes). If a size difference exists, it is often the male that is the largest, as is often noted in blennies, cichlids (clarified by Barlow 1968, 1974), damselfishes, gobies, and wrasses. There are, however, exceptions to this general rule, as witnessed by members of such diverse groups as parrotfishes, sea basses, ceratoid anglers, and sharks. Differences in shape are sometimes obvious, such as the trailing edges or other modifications of the fins (e.g., chaenopsids, many characins, many cichlids, emblemariids, poeciliids, and sharks), nuchal humps and horns (e.g., some cichlids and acanthurids), breeding tubercles (pearl organs) (e.g., catastomids, cyprinids, many percids), and the modification of jaws (e.g., many salmonids). Sometimes, the differences are not so obvious, such as the well-known "hooks" of many male characins, the glandular enlargements of the glandulocaudines and surfperches or even the teeth in certain sharks. Nevertheless, there remain numerous species which show no apparent sexual differences (noteworthy here are many pelagic species). This does not mean that such differences do not exist for the "eyes" of the fishes concerned. Also, cases are known where color polymorphism exists, but in only one sex (e.g., in a number of cichlids—Barlow 1973; Fryer 1977; Heiligenberg 1965—as well as in many wrasses and parrotfishes .

Where confusion exists for the scientist, a question often arises: do the fishes recognize sexual differences and, if so, how do they do it? Since the obvious answer to the first question seems to be yes, a not unreasonable answer to the second question is by differences in behavior. Perhaps this is why precious few studies have attempted answers to such questions experimentally. A major problem is to find a way to determine that members of one sex will, within reasonable limits, identify all members of the opposite sex. Unfortunately in many cases, one sex shows a preference for one segment or class of the other sex. Such results, therefore, amply demonstrate that a recognition process is operating but not necessarily one of sexual recognition. One example in point: Weber and Weber (1975) clearly showed that males of the cichlid, *C. nigrofasciatum,* prefer to spawn with dominant females, most of which are dark. Thus, a recognition process is involved and it appears to be operating at the level appropriate for mate selection. However, no conclusion can be made about sex recognition in this case. Noble and Curtis (1939) showed their understanding of this particular problem in one of the few studies that has considered both sexual and mate recognition processes. They concluded that sexual recognition was operating in the cichlid *Hemichromis bimaculatus*, and that slight differences of movement served as the necessary cues. Noble (1934) also stressed behavior as the discriminating factor in the pumpkinseed *Lepomis gibbosus* but concluded that color was definitely used in male-male interactions by the guppy *Poecilia reticulatus* (Noble 1938). Breder and Coates (1935) also argued that size and shape were used by males to recognize females of that same species. Ter Pelwijk and Tinbergen (1937) concluded from their experiments that the threespine stickleback *Gasterosteus aculeatus* used color as the major cue for sexual recognition—the red belly, in the case of the male, and the silvery body (and swollen belly) for the female.

However, males without red bellies did not elicit attack, and that again raises the question about recognition being afforded to only one class of a given sex.

Tavolga (1955, 1956) critically examined this problem in the frillfin goby *Bathygobius soporator*, finding no evidence that sexual recognition was based on morphological cues alone. He did mention, however, that the behavioral differences shown by conspecific intruders in the presence of territorial residents would eventually lead to mating. Reyer (1975), while studying the cichlid *Etroplus maculatus*, provided experimental evidence that sexual recognition was being mediated visually but he did not consider the relevant cues. Oehlert (1958), working also on cichlids, concluded that sexual recognition was occurring and the process involved behavioral differences. This was also the conclusion reached by Zayan (1974) for the poeciliid *Xiphophorus helleri*; and I'm reasonably sure that the six species of damselfishes of the genus *Eupomacentrus*, with which I'm reasonably experienced, are employing the same method. An important point to remember in this regard is that behavioral differences may be the direct effect of a relative size difference between males and females during interactions (Barlow 1968; Barlow and Green 1970; Miller 1964). Therefore, appropriate controls of this particular variable are required before definite conclusions are made.

Although strong evidence is lacking, it does appear that in most cases behavioral cues mediate sexual recognition. Interestingly, the most detailed study of the phenomenon that I've come across shows that in at least one case, behavioral differences were not critical. Robertson and Sale (1976) conducted their study of sexual discrimination on males of the fighting fish *Betta splendens*. After a complex series of model experiments, followed by appropriate analysis, sexual recognition by males was shown through their awareness of the size and shape of fins and the presence or absence of body-patterning. Although the authors mentioned that behavioral actions might augment discrimination, such was unnecessary for the recognition process.

Steele and Keenleyside (1971) showed that females of the centrarchids *Lepomis gibbosus* and *L. megalotis peltastes* can clearly discriminate between males of the two species by visual means. Although the experimental design tested species rather than sexual recognition, an interesting sidelight was that females of *L. gibbosus* preferred conspecific males even in the absence of visual cues. This suggests, at least, that sexual recognition might be occurring in certain centrarchid species through the mediation of another modality, such as a chemical sense. Interestingly, preferential discrimination of the females was not shown by males of either species. This contrasts with the results by Keenleyside (1967), but differences in response may have been due to differences in the stage of sexual maturity of the males.

Individual recognition

Although the problem of individual recognition by visual means has rarely been experimentally assessed in fishes, the few studies presently available have amply demonstrated the fact. Since dominance hierarchies are almost invariably based on a linear, size-dependent function in fishes, such an organization cannot, of itself, prove the existence of individual recognition. If, however, the size correlation is not maintained, evidence of the process can be obtained (e.g., as in the case of the bicolor damselfish *Eupomacentrus partitus*; Myrberg 1972a).

The first experimental evidence, based on appropriate controls, of individual (in this case, mate) recognition in fishes was obtained in the cichlid *Hemichromis bimaculatus* by Noble and Curtis (1939). They showed that males were recognized by their mates through some critical cue(s) located on the anterior third of the body (sans eye). Recognition was also accorded only when some movement (but not necessarily normal movement) was also present. Additional evidence of individual (mate) recognition has also been provided recently for another cichlid *Etroplus maculatus* by Reyer (1975).

An elegant series of field experiments, centering on mate recognition by the damselfish *Amphiprion bicinctus* was conducted by Fricke (1973, 1976). Not only was such recognition established and found to be visually mediated, it was also not based on behavioral differences. Rather the critical cue(s) was located on the head region (reminiscent of Noble and Curtis' study). Subsequently, Fricke found that the anteriormost color bar behind the eye in the test species was unique to an individual and changed with age in a consistent fashion. Finally, he demonstrated that such recognition was established by these fishes within 24 h and that it was not forgotten, even after 30 d's separation.

Thresher (in press) has also recently demonstrated individual recognition in the threespot damselfish *Eupomacentrus planifrons* in another context—territorial aggression. Again, working in the field, he clearly showed that residents were individually identifying their territorial neighbors by their specific color pattern and their location in space; size and behavior appeared not critical for recognition.

Finally, Zayan (1974) has also amply demonstrated such recognition among males of the poeciliid *Xiphophorus helleri* by critically analyzing dominance-subordinate relationships. Although he did not investigate the specific cues involved, Zayan believed that they were probably "...very small differences in morphology and/or in behavior."

Overview

Vision is commonly used to mediate social recognition processes in many fishes. It is also clear that different species can use different "tactics" to obtain the same result. Nevertheless, despite certain exceptions, an interesting trend is apparent and its consistency is rather remarkable, considering the different taxa involved.

Body shape seems to be the most important factor used in interspecies recognition, with color either not critical or of secondary importance. Movement appears necessary for a given response to be elicited, but recognition does not require it. Color pattern and shape are both apparently necessary in most cases of species recognition, but size cannot be discounted in some instances. Movement appears less critical at this level.

Behavior per se seems to be the overriding visual cue for sexual recognition in fishes. Although some early evidence exists that color and possibly even size and shape are all involved, much of that evidence must remain suspect because of the lack of appropriate controls.

Finally, individual recognition seems to be mediated by small differences in the chromatic pattern of the species concerned.

As already mentioned, there are exceptions to this general scheme and it may well break down when hard-won experimental data become available from major groups that are not as yet represented in the relatively small sample. These include, above all, most of the rapid moving and obviously highly visual pelagic fishes, such as the mackerels, tunas and their relatives, the salmon, and the herrings and their relatives, to mention only a few. Also conspicuous by their absence are the sharks, the eels, the flatfishes, and representatives from deeper waters.

MECHANORECEPTION

The density of water certainly provides the opportunity for fishes to use a wide variety of mechanical stimuli in their daily social activities. It is not unreasonable to suggest that fishes possess a three-dimensional "representation" of their surroundings, based on the reception of the incessant changes in near-field displacements about them (see Tavolga 1977).

For reasons of convenience, I shall henceforth equate mechanical and acoustical energy and refer to them simply as sound, regardless of the known differences between pressure and displacement functions.

The importance of the visual field to many social activities cannot be denied. Yet, such stimuli probably often act in concert with those affecting the acoustico-lateralis system to provide the most appropriate information to the fish about numerous activities, including schooling, feeding, agonism, and reproduction. A fine example of such intersensory mediation involving those two classes of stimuli has been supplied by Tavolga (1956). While working with the frillfin goby *Bathygobius soporator*, he found that simply the visual presence of another goby (in a stoppered flask) had no effect on the actions of gravid females. However, when the sounds of a courting male were added to the tank, such females not only became active but oriented their courtship activities toward the stimulus fish.

Acoustical stimuli are obviously involved with schooling, feeding, predation, and predator avoidance (e.g., Banner 1972; Chapman 1976; Hashimoto and Maniwa 1967; Moulton 1958, 1960; Myrberg et al. 1969, 1972, 1976; Nelson and Gruber 1963; Nelson and Johnson 1972; Protosov and Romanenko 1962; Richard 1968; Steinberg et al. 1965). Yet, in many cases, interpretations are difficult. For example, Banner (1972) found that young, free-ranging lemon sharks *Negaprion brevirostris* showed equal response to sounds of prey and nonprey alike. Although reasonable interpretations can be arrived at regarding these or other findings, it does indicate that the total adaptive response involves an integration of inputs from various modalities. To remain within my stipulated bounds, however—social recognition processes—means to relate to a region of relatively limited study. Few investigations have been undertaken in that direction.

Interspecies, sexual and individual recognition

Leaving aside predator-prey relationships, I'm unaware of any experimental study that relates to any mechanoreceptive mediation of interspecies recognition (tactile stimulation in cleaning symbiosis does not appear to involve recognition). The same holds true for individual recognition, but I am presently testing this particular point in one species of Caribbean damselfishes.

Since courtship sounds are often emitted only by the males in many species of fishes, it might be assumed that sexual recognition is afforded by such sounds. This need not be true. In the case of Tavolga's (1956) gobies, females showed increased activity and apparent courtship responses when the courtship sounds of males were presented, even in the absence of males. This is the only case where sexual recognition has been suggested, and it must remain so since other sounds were not presented to the females. Females of the bicolor damselfish *Eupomacentrus partitus* show no apparent response to the sounds of males when they are presented in the absence of males. Intersensory mediation is therefore suggested in the latter case.

Species recognition

Although intraspecific communication can certainly be suggested by the analysis of visual observations and passive monitoring of sound production, confounding variables almost invariably result in equivocal evidence.

Moulton (1956) was probably the first to use the sound playback technique in the field, thereby obtaining vocal responses of sea robins *Prionotus* spp. to sonic patterns having a temporal structure similar to their own sounds. Since then, various experimental studies dealing with a variety of fishes have considered intraspecific communication by sound (e.g., cichlids—Schwarz 1974a and b; cyprinids—Delco 1960; Stout 1963; damselfishes—Ha 1973; Myrberg 1972b; Myrberg and Spires 1972; Spanier 1970, 1975; gobies—Tavolga 1956, 1958; squirrelfishes—Horch and Salmon 1973; sunfishes—Gerald 1971; tigerfishes—Schneider 1964; toadfishes—Fish 1969, 1972; Winn 1964, 1967). Although many of these studies have demonstrated species recognition by sound, some must remain equivocal because of insufficient controls.

The specific, sonic properties (or cues) that provide the necessary discrimination, and thereby recognition, are known in only a few cases. When these are added to the few cases where circumstantial evidence is present, another trend is noted and it indicates an avenue for future research.

Sounds made by fishes are similar, with few exceptions. Their general structure consists of a series of brief pulses whose spectral content, though quite broad, has its greatest energy somewhere between 75 and 500 Hz (related species show similar energy peaks). Frequency modulation is weak, if present. Such acoustical signals lend themselves well to the coding of information through temporal patterning (Winn 1964, 1972), and not only is such an idea reasonable, it actually works.

Laboratory and field experiments (Ha 1973; Myrberg 1972b; Myrberg and Spires 1972; Spanier 1975) on five species of damselfishes in the genus *Eupomacentrus* have provided incontrovertible evidence that the members of each species recognize their own species' sounds ("chirps") by the unique temporal pattern of the brief pulses of each sound (pulse duration ~ 12 msec; "off-time" between pulses ~ 25 msec). The elements included within the brief sound (usually 3 to 5 pulses), e.g., the pulse interval and the pulse number, differ in importance in the communicative process. Species recognition is accomplished by the precise information obtained from the pulse interval and/or the "off-time;" the pulse number provides information about the major motivational state of the actor, while pulse duration per se and spectral content appear to play no critical role so long as they are held within reasonable limits (Myrberg et al. 1978). One of the most exciting findings of the entire investigation was that these little coral reef fishes can rapidly discriminate between sounds whose pulse intervals differ by only 9 to 10 msec (Spanier 1975). This strongly suggests that "time" is a most important factor in the lives of these little fishes.

Only one other major investigation has been conducted on a similar problem in fishes (Fish 1969, 1972; Winn 1967, 1972).

Although it did not deal specifically with species recognition, interest was directed at those temporal factors within the courtship sound of oyster toadfish (*Opsanus tau*) that caused them to respond sonically. Results showed that the communication system rested also upon a temporal organization, based on unit durations (= sound duration) and repetition rate (basically equivalent to pulse interval).

Of the remaining studies on fishes, only two others have speculated about the possible acoustical cues responsible for species recognition in their respective subjects. After analyzing the natural sounds of their subjects, Delco (1960—cyprinids) and Gerald (1971—sunfishes) both concluded that cues were of a temporal nature. Gerald went so far as to mention pulse rate, pulse number and pulse duration.

Overview

The temporal organization of a species' own sounds apparently provides the cue(s) for species recognition in at least a few species. I hope additional studies will soon be made to examine this function in other species. Finally, although the entire field constitutes a frontier, possible acoustical mediation of other social recognition systems must be examined, especially in regard to individual recognition. This appears to be an extremely fruitful area for future research.

CHEMORECEPTION

If one wished to illustrate the complexity, and perhaps even the individuality, of the sensory worlds of animals, no better example could be found than that comprising the chemical senses of fishes. Not only does convincing evidence exist that no less than five separate receptor systems operate in many species (i.e., olfaction, "vagal" taste, "facial" taste, "common" chemical sense, and the "cation" receptors of the lateral line), but certain of them overlap in capability and probably also in function (e.g., olfaction and taste—see Bardach and Villars 1974; Bardach et al. 1967). Such overlap appears redundant, suggesting that one or more biological functions is now, or was once, highly dependent on minimizing error. The diversity of the functions presently subserved by chemoreception in fishes include general arousal, avoidance of noxious agents, feeding, schooling, homing, migration, minimizing social disturbance, mating, parental care, and mediating most types of social recognition processes. This should not imply that such functions are mediated by chemoreception in most species, nor that each chemical sense is responsible for providing information about each of those functions. Such is clearly not the case. It does mean, however, that when so many functions involve similarly reacting sensory systems, the experimentalist is hard-put to unravel the "Gordian knot" of relationships in a way acceptable not only to his peers but to himself as well. Probably for that reason the more recent and accurate advances in our knowledge will force much (but certainly not all) of the early behavioral work on chemoreception to be reinterpreted or to be of historical interest only.

Those of us deeply interested in this field are extremely fortunate in having available a wealth of thorough reviews on all aspects of the subject in fishes (Atema 1971; Atema et al. 1969; Bardach and Atema 1971; Bardach and Todd 1970; Bardach and Villars 1974; *Experientia* 1976; Hara 1971; Kleerekoper 1969; and Scholz et al. 1973).

Therefore, rather than being presumptuous enough to "review the reviews," I shall provide here only a brief summary of our present information on the mediation and facilitation of social recognition processes by chemical means. I do this only to "round out" the present report.

Interspecies recognition

Hunter and Hasler (1965) have provided us with a fascinating instance of interspecies recognition in the redfin shiner *Notropis umbratilus*. Chemical recognition of the milt and ovarian fluid of the green sunfish *Lepomis cyanellus* apparently provides the means whereby these minnows find appropriate sunfish nests within which to spawn. Leaving aside the wealth of information dealing with the chemical facilitation of predator-prey relationships, the only other case that I'm aware of that has experimentally shown interspecific recognition in fishes is the early work of Göz (1941), who showed by an operant learning technique that the minnow *Phoxinus laevis* was capable of such recognition. Although mediation was demonstrated to be olfactory, the significance of such recognition in this particular species is still unclear.

Species recognition

Various experimental studies have shown this process being facilitated by chemical means. Probably the best known case in fishes is that accompanying the "Schreckstoff" reaction, as shown by cyprinids, silurids, and the majority of characins (von Frisch 1941; Gondolfi et al. 1968; Pfeiffer 1960, 1963; Schutz 1956). Based on their evidence, Tucker and Suzuki (1972) have suggested that such recognition involves the awareness by conspecifics of a species-specific ratio of certain substances contained in their skin, with the degree of subsequent reaction being dependent upon that known ratio. This explanation fits well the point that degree of relatedness affects the degree of reaction in such fishes. Although evidence is available that a few poeciliids also possess a similar reaction (Schutz 1956), other cases remain in question (e.g., certain atherinids—Rosenblatt and Losey 1967; Skinner et al. 1962; Steven 1959). In all fishes examined thus far, the "Schreckstoff' reaction has been found to be mediated strictly by olfaction.

Various behavioral actions associated with schooling and aggregating have also shown their dependence upon chemically mediated, species recognition processes. Experimental evidence for this includes work by Wrede (1932) and Keenleyside (1955) on cyprinids (*Phoxinus laevis* and *Scardinus erythropthalmus*, respectively) and by Kühme (1964) on one cichlid—the young of *Hemichromis bimaculatus*, and by Capron (1974) on another—the adults of *Haplochromis burtoni*. In those cases examined, olfaction seemed clearly the mediator.

Such recognition has also been demonstrated or strongly implicated in the migratory movements of eels (*Anguilla vulgaris*—Miles 1968) and salmon (the chinook—*Oncorhynchus tshawytscha*—Oshima et al. 1969; the coho—*O. kisutch*—Cooper et al. 1976; Dizon et al. 1973; Scholz et al. 1976). In the chinook, response was mediated by olfaction.

Finally, though pheromones were implicated in the parental recognition of young by a small brown bullhead (*Ictalurus nebulosus*—Breder 1935) and a blind goby (*Typhlogobius californiensis*—MacGinitie 1939), such recognition has been conclusively verified only in parental cichlids, e.g., *Nannacara anomala*—Kuenzer, Zoologisches Institut, D-3400 Göttingen, Berlinerstrasse 28, Federal Republic of Germany, pers. comm.; jewelfish *Hemichromis bimaculatus*—Kühme 1963; convict cichlid *Cichlasoma nigrofasciatum*—Myrberg 1966, 1975; and *C. citrinellum*—McKaye and Barlow 1976. The experimental designs used in many of the tests strongly suggested that olfaction was the mediating modality; however, gustation was strongly suggested in the first case mentioned, as well as elsewhere (Myrberg 1964). The intersensory interaction existing between the chemical and visual senses in this context has already been mentioned. Adding to the complexity, Kühme (1964) has additionally shown that tiny, free-swimming young of *H. bimaculatus* also demonstrate clear chemical discrimination between scents emanating from their own brood and broods of other species.

Sexual recognition

Although for many years, few examples of chemically mediated sex recognition existed in fishes (e.g., the blenny *Blennius pavo*—Eggert 1931; the lamprey *Petromyzon*—Roule 1931; the frillfin goby *Bathygobius soporator*—Tavolga 1956), recent interest in this relationship has expanded our knowledge considerably. We now have experimental evidence that chemical factors facilitate such recognition in other blennies (various species of the genus, *Hypsoblennius*—Losey 1969), catfishes (channel catfish, *Ictalurus punctatus*—Timms et al. 1972), cyprinids (goldfish, *Carassius auratus*—Partridge et al. 1976), characins (Mexican tetra, *Astayanax mexicanus*—Wilkens 1972), poeciliids (guppy, *Poecilia reticulata*—Amouriq 1964, 1965; Gondolfi 1969; *Mollienesia sphenops*—Parzefall 1970, 1973; Zeiske 1968), and anabantids (the gouramis—*Colisa lalia*—Mainardi and Rossi 1968; Rossi 1969; *Colisa labiosa*—Rossi 1968). In most cases where the specific mediator was considered, olfaction was either demonstrated or strongly suggested; *Mollenesia* was exceptional in that gustation appeared to be the modality involved. Also, in a number of cases involving widely divergent species (e.g., gobies, cyprinids, and poeciliids), females were recognized by their scent. Finally, and in the same "light," only sexually receptive fishes within any of the above species showed sexual discrimination. This should not infer, however, that others were incapable.

Individual recognition

Individual recognition by chemical means has been demonstrated by only a few species as yet. There are, nevertheless, some exciting implications.

Göz (1941) clearly demonstrated olfactory recognition in the cyprinid *Phoxinus laevis*; but the possible significance of such a process in fishes had to wait until Todd's (1968) study of the yellow bullhead *Ictalurus natalis*. Not only did his subjects demonstrate individual recognition by olfactory means, the process involved unmistakable correlates with the social order among individuals within a given community (e.g., dominance-subordinate relationships involving specific behavior *even* in the physical absence of an individual). Even overt aggression seemed to be controlled by the olfactory sense. The cues responsible for this incredibly complex, chemically controlled social order apparently exist within the mucus covering each fish (Bardach and Todd 1970; Todd 1971; Todd et al. 1967). Bardach and Villars (1974) have suggested, in line with Tucker and Suzuki's (1972) reasoning, that there may well be mixtures of compounds in the mucus, the concentration of which is specific to a given individual. The one point that seems still unclear, however, is whether a specific chemical signature is identifying a given individual or a given physiological state of an individual. From observations by Todd, the latter seems perhaps the more reasonable alternative.

It might be construed by some that such an intricate relationship could only be found in fishes such as the bullhead, whose "visual worlds" have been greatly reduced and/or are nocturnally active. Such may not be the case, however. By carefully manipulating individuals of two species of gouramis (*Colisa lalia* and *C. labiosa*), Rossi (1969) was able to show that the reproductive behavior of a given male (A) (normally initiated and maintained by the scent of females) would not occur if the scent of another male (B) accompanied that of a female. Such behavior would begin immediately, however, if male A could establish dominance over a third conspecific, male C, despite the ever present scent of male B. Although a few interesting tests should be considered in any future investigation of this particular story, present implications suggest than an intricate relationship exists between chemical information and social order.

Four other studies have each shown that members of a given species can chemically discriminate different groups of individuals within their own species. In each case, reasonable evidence was supplied that recognition was based on the olfactory sense. Miles (1968) found that elvers of *Anguilla vulgaris* were attracted to tidal waters holding adults, but withdrew from waters holding elvers. Kühme (1963) showed that parents of the cichlid, *Hemichromis bimaculatus*, readily differentiated different broods of their own species' young by chemical means alone, and in 1964, he also showed that tiny young of the same species can do the same thing. Finally, McKaye and Barlow (1976) have also shown discrimination of conspecific broods by parental midas cichlids, *C. citrinellum.* Although these studies did not demonstrate individual recognition, each clearly showed an operative process that was more precisely "tuned" than those dealing with species recognition.

Overview

Based on present knowledge, chemical agents mediate and facilitate all levels of social recognition in fishes. And although a few exceptions exist, such processes are usually mediated by the olfactory sense. It is also clear from specific cases that intersensory mediation of social processes may well involve chemoreception because of the tremendous specificity that it can display. In fact, the system would appear to fit well any process that depends on minimizing error.

ELECTRORECEPTION

A relatively small group of fishes possesses receptors that are specialized for the detection of electric fields: the gymnotids, mormyrids, the nile-perch (*Gymnarchus*), and some catfishes, as well as the sharks and their relatives (Bennett 1971). Certain of them possess what are called passive systems, in that they detect only signals of external origin; such animals lack electric organs, e.g., the catfishes and most elasmobranchs. Those fishes that do possess such organs (i.e., their own energy source) can control, to some extent, the electric field surrounding them; their systems are termed active. Of course, receptors of an active system can detect signals of external origin.

Since social recognition should require in most instances active systems, I shall limit my remarks to only those groups possessing such systems and for which we have some information available relative to such processes—the gymnotids and mormyrids.

As was the case in dealing with the other systems, this sensory system also possesses at least two groups of quite separate, functional receptors. One type is apparently insensitive to the high frequencies usually predominant in electric organ discharge (EOD) and operates only passively (detecting signals of external origin). The other group(s) operates actively by monitoring its owner's electric organ(s) (Bennett 1971; Bullock 1973). The neural projections are not quite so nicely delineated, however, as in other systems; all electroreceptors are innervated by the lateral line nerve.

It is also evident that we have still another "sensory world" with which to deal; but in this particular case, because we lack the necessary receptors (i.e., to sense voltages in the μ V range), we can't perceive its nature. One thing is certain, however; experiments have shown it to be a finely structured and a highly ordered "world."

Although the properties of the EOD and its receiving systems are highly amenable to mediating and facilitating all types of social recognition processes, we have precious little information about them. Therefore, I shall not subdivide this section.

Hopkins (1974a and b) found during the nonbreeding season that aggressive behavior in the gymnotid *Eigenmannia virescens* is elicited primarily by electrical stimuli within the characteristic frequency range of the species. When such signals, as well as those from other species, were played back to such fish, they showed their highest levels of aggression to the conspecific signals (instrumental signals mimicking signals from conspecifics were equally effective). During the breeding season, the same signals from conspecifics elicited courtship behavior. Sexual recognition was not apparent. However, another gymnotid *Sternopygus macurus* showed both species and sexual recognition. Adult males and females of the species have nonoverlapping ranges in their EODs, and when natural signals within the "female" range were played back to males in either the laboratory or field, courtship was seen immediately. If, however, EODs from the "male" range, from *E. virescens* and from *Apteronotus labifrons* were played back, courtship was not seen (Hopkins 1972, 1974a and b).

Black-Cleworth (1970) concluded that the unmodified discharge of *Gymnotus carapo* conveys information about its species, its size, and its location. Although evidence was not brought forth in support of species recognition, she did record the interesting fact that dominant individuals did not attack subordinates that interrupted their EODs in their presence. Also, thereafter, such subordinates enjoyed reduced attacks even when not interrupting their discharges. If this phenomenon happened not to possess a strictly linear relationship, it would certainly suggest individual recognition in the species.

Circumstantial evidence of individual recognition (and even species recognition—Bennett 1971) has also been suggested by the "jamming avoidance response," as noted in the gymnotids—*Eigenmannia virescens* and *Sternarchus albifrons,* the mormyrids—*Brienomyrus niger* and *Gnathonemus petersii* and the nile-perch *Gymnarchus niloticus* (Bullock 1970, 1973; Bullock et al. 1972; Heiligenberg 1976; Moller and Bauer 1973). Although experimental evidence is still lacking, the idea is reasonable.

Some behavioral evidence also exists among the mormyrids that suggests operative, recognition processes are being mediated by electrical means (even in schooling, Moller 1976). Malcolm (1972) working with *Gnathonemus petersii,* noted that one facet of the temporal structure of the EOD, monitored during the day, was individually distinct among his fishes. Additionally, Kramer and Bauer (1976) noted an interesting sexual difference apparently existing in the species-typical discharge rate during interspecific aggression by that same species. Yet, it is noteworthy that although communication processes are obviously affected by EODs in various species (e.g., *Gnathonemus petersii, Marcusenius brachyistius* and *Brienomyrus niger* (Kramer 1976; Kramer and Bauer 1976; Moller 1970a and b, 1976; Moller and Bauer 1973), results do indicate that response is dependent only on the presence of another EOD and its respective changes. So long as the frequency content of the discharge is reasonable, the species involved in the interaction seem not critical to the issue (Kramer 1976; Moller 1970a). This latter interpretation is strictly speculative, however, based not only on our limited knowledge, but also on the inefficiency that would "seem" to be present (but interspecific interactions certainly may not be inefficient—see the section on vision).

Overview

There can be no question that the electrosensory system is capable of mediating and facilitating a variety of social recognition processes. It only remains to be seen which processes they are. Answers to this problem involving various weakly electric fishes will no doubt soon be forthcoming since electroreception is one frontier of sensory science that promises fascinating research for many biologists for a long time to come.

Discussion

This rather hurried journey through the "sensory worlds" of fishes has revealed a wide array of receptor systems that mediate and facilitate the processes of social recognition. Apparently, in many cases more than a single system operates to provide necessary information. However, since sensory investigations demand adequate control of variables, a given study is often of necessity limited to but a single sensory modality; to handle the complexity required when two or more systems covary simultaneously could, and often does, invite an unmanageable situation. Also, as often as not, one finds that a single system alone can perform a task. However, such a result, though gratifying, should not be construed as demonstrating that only that particular system is actually used for such a task; the constraints of testing are not the same as those faced by animals in their natural environment. Synergistic processes may, for example, be imposed only on demand, such as in cases of "error-checking" (due to added costs because of redundancy or "noise") or they may be on-going, but an adequate "answer" to a given problem may require little or no intersensory integration.

I agree with Kleerekoper and his colleagues (e.g., Kleerekoper 1974, 1976a and b; Kleerekoper et al. 1973; Rand et al. 1975) that possible, even probable, synergistic interactions among sensory systems should not be neglected. But in many cases our knowledge at the behavioral level is still too fragmentary to attempt complex cross-modality manipulation. Yet, each worker has the responsibility, at least, to consider how the "knot" of the sensory gestalt might be effectively unraveled, even in part. We know that the phenomenon often exists (Tavolga 1976), and therefore scientists must find ways to describe it, to predict it, to understand it, and when necessary, to control it.

When dealing with man's effects on the animal kingdom or when attempting to control activities of selected species, such as directional movement, feeding, aggression, and reproduction, we tend to treat animals as if their "views" of the world were the same as ours. In the case of vertebrates, such an interpretation isn't unreasonable during a simple, first analysis; but such an interpretation is often not true, nor is it necessarily productive. Also, we invariably consider physical and chemical factors whenever survival and reproduction are in question. This is understandable in counteracting man's continuing efforts to debase the environment.

Even a cursory review of the massive literature on fishes shows the problems that beset the survival of stocks (e.g., de Sylva 1969; Doudoroff and Katz 1950, 1953; Fujiya 1965; Johnson 1968; Katz 1964; Sutterlin 1974). Effects have been shown on visceral organs, biochemical function, locomotion (i.e., approach-avoidance), and even learning (e.g., Warner et al. 1966). Complex social activities involving recognition processes are rarely if ever involved in such studies because of the confounding variables that must be considered. In aquaculture, where the level of production often reflects the level of control, social relationships and their concomitant recognition processes should be considered. If a corresponding modality facilitates a given process and that modality is inoperative or malfunctioning, one can predict that normal activity will not occur. A perfect example of that in fishes is the aggressive chaos seen in a community of yellow bullheads (*Ictalurus natalis*) following removal of their "olfactory world." Unfortunately, we know very little about such effects in fishes. In fact, aside from locomotion per se, behavioral effects of sensory malfunction are largely unknown, except at the gross level. Also, what little we do know is almost invariably about fishes that rarely can be considered food fishes. Information on social processes is unknown among most of the world's major fish stocks (e.g., anchovy, haddock, hake, herring, mackerel, menhaden, and tuna), with little information available on two others (cod and salmon). This unfortunate circumstance is understandable since studies of the social activities of such animals usually require not only expensive facilities but also extensive descriptive analyses prior to any experimentation. Such analyses have not been done. Whether or not these major obstacles to further knowledge will persist remains to be seen.

Social processes are better known for some species used in aquaculture, but again, we know surprisingly little about the effects of specific factors on particular sensory systems.

Timms (1976) has shown the subtle effects that various types of visual deprivation have on locomotion in the goldfish *Carassius auratus.* Hanyu and Ali (1963) and Pavlov et al. (1967) have clearly implicated changes in visual functions due to temperature alone. Weis and Weis (1976), following the leads of Smithberg (1962) and Stockard (1907, 1910), have shown that pesticides can bring about optical malformations in the Atlantic silverside *Menidia menidia.* Apparently antibiotics, even in low concentration, can do the same thing (the zebrafish *Brachydanio rerio*—Anderson and Battle 1967). Even high levels of certain dissolved gases, e.g., nitrogen, can damage the eye (e.g., Poston et al. 1973).

Bardach et al. (1965) and Haider (1975) have shown that taste buds in various catfishes of the genus *Ictalurus* can be damaged by extremely low levels of various caustic agents. Hara et al. (1976) have shown depressed neural response from the olfactory bulb in goldfish (*C. auratus*) following stimulation by very low concentrations of metallic salts. Hara (1967) and Oshima and Gorbman (1968, 1969) have investigated the effects of hormonal action on evoked responses from the olfactory bulb of the same species, while Godet and Dupe (1965) have investigated a similar relationship in the lungfish *Protopterus annectens.*

Ha (1968) and Popper and Clarke (1976) have shown that noisy conditions can result in temporary hearing loss in the lane snapper *Lutjanus synagris* and the goldfish *C. auratus*, respectively, while Banner and Hyatt (1973) have shown that such conditions can affect both survival and growth in young topminnows (*Cyprinodon variegatus* and *Fundulus similis*). Bahr (1973) has noted that very low levels of cyanide severely depress both the spontaneous and evoked activity of the lateral line nerve in rainbow trout, *Salmo gairdneri.*

At the level of practical fishing, strong implications have been raised between changes in vessel noise and differences in hauls of herring, capelin, mackerel and other commercially important fishes (Maniwa 1971; Olsen 1971).

Thus, what little knowledge we do possess on factors affecting sensory systems rests largely with species that are easily studied under controlled laboratory conditions, e.g., the goldfish. Although the information gained may as yet not be generalizable, it does provide, nevertheless, an important beginning and an awareness of problems that if solved, might well aid in revolutionizing aquaculture, ocean-ranching, and other management efforts throughout the world.

Acknowledgments

Preparation of this report was supported by the National Science Foundation through Grant BNS76-80168, Division of Psychobiology. The visual and bio-acoustical studies carried out by the author and his colleagues, Samuel Ha, Sue Patterson, Ehud Spanier, and Ronald Thresher, and which are summarized here, were conducted under Grants GB31000X and BNS74-200067, Division of Psychobiology, the National Science Foundation; the shark investigations of Arnold Banner and the author, also summarized here, were sponsored by the Oceanic Biology Program of the Office of Naval Research, Contracts N00014-67-A0201-0008 and N00014-76-C-0142. Appreciation is also directed to James Todd and James Tilmont for their interest and cooperation while many of our studies were being carried on within the Biscayne National Monument, National Park Service, U.S. Department of the Interior. I am also extremely grateful to Sue Myrberg and Juanita Spires for their aid in bibliographic research.

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Discussion

BLAXTER

What are the examples of real chemical individual recognition? Do fish, for example, come together individually year after year for spawning?

MYRBERG

There is no evidence of such long-term individual recognition by chemical means. One can conclude, based on some recent findings with salmon, that such might be occurring at the population level.

JOHANNES

What about *Amphiprion*?

MYRBERG

Individual recognition has been demonstrated by members of one species (*Amphiprion bicinctus*-Fricke, 1973, Naturwissenshaften 4: 204-205) and immediate recognition remained even after 30 d. However, the modality involved clearly appeared to be vision, not chemical in nature. By the way, the same species showed site recognition 6 mo after removal. Again, the recognition process seemed to be mediated by vision, not chemoreception. Definitive tests of the role of chemoreception in such activities have not been made.

HARDEN JONES

There are a number of examples known of fish being tagged and released together and subsequently being recaptured several years later in the same haul, or in the same set of lines or net, or on the same day and in the same place. This is recorded for Pacific halibut, spurdog, and cod. For spurdog this "evidence" suggests association for up to 7 yr, but the evidence should be interpreted with care.

BARDACH

When we found individual recognition in *Ictalurus*, it had been reported in one way or another before we did our work. It was clear that individual recognition had significance in this species. Might it occur in a wide range of species or is it a rare occurrence? Might there be some ecological or selective advantage to such recognition, even among schooling fishes?

MYRBERG

That is a difficult question to answer. Even in your studies, were the test subjects truly recognizing invariant individual signatures or were they responding to substances that accompanied specific physiological or behavioral states? An answer to such a question has not, as yet, been found and will demand, of course, a greatly expanded experimental design. In any case, there are numerous ways that individual recognition could aid social relationships among fishes; one that comes to mind immediately is reducing unnecessary expenditure of energy.

REINBOTH

Can you give any general definition of individual recognition? What justifies stating that individual recognition is involved in a particular type of social interaction? For a long time we have had difficulty making the evidence convincing.

MYRBERG

A general definition of individual recognition would be consistent behavioral reaction to a specific individual by another, regardless of spatial or temporal function. Also, it must be determined that the consistent reaction is not dependent on either the sex or the species of the individual being recognized. If one sees variation in the reaction or cannot exclude other recognition processes (e.g., sex, species), demonstration can be difficult indeed.

REINBOTH

In spite of what I have seen on the reef I still remain reluctant to speak of individual recognition. I cannot deny that there are other factors involved. I do not know what the fish are telling apart. All we see is a particular type of behavior towards a certain individual which may be characteristic. Is it then individual recognition?

MYRBERG

There have actually been only a few cases in which individual recognition has been show experimentally to occur in fishes. One might argue, at times, with the controls or just what was individually recognized, but reasonable evidence for the process is available.

HENDERSON

The sort of circumstance in which individual recognition is important is when there has been learning going on between two individuals which will be used at a later time.

FISHELSON

Individual recognition is important with regard to fisheries. Mouth breeding tilapias have no individual recognition. A male can be paired with any other female with no problems. Contrary to this, bottom spawners, especially *Tilapia zilli*, are strong monogamic fishes forming constant pairs for years, and if you were trying to culture *Tilapia zilli* in ponds you would lose your money. I will give you another example. We are working with 16 *Tilapia nilotica*, each of them individually marked. The experiments showed that there was among them a typical pyramidal hierarchy with a single alpha, two betas, and so on. In our experiments, we distributed them in aquaria and maintained each fish separately for 2 wk. When we put them together, after 2 d the same hierarchical pyramid was formed again.

MYRBERG

You should publish these results. It is the only case that I am personally aware of in fishes.

FISHELSON

We will publish this very soon. Now I will give you still another example. I have observed a pair of *Heniochus intermedius* living together for 7 yr in Elat. They must recognize one another.

Artificial Imprinting: A Procedure for Conserving Salmon Stocks

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HASLER, ARTHUR D., and ALLAN T. SCHOLZ. 1980. Artificial imprinting: A procedure for conserving salmon stocks, p. 179-199. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

The olfactory hypothesis for salmon homing states that juvenile salmon become imprinted to the unique chemical odor of their natal stream during the smolt stage and subsequently use this cue to locate their stream during the spawning migration. We tested this hypothesis by exposing (i.e., artificially imprinting) 18-month-old hatchery-raised coho salmon, rainbow trout, or brown trout smolts to a synthetic chemical (morpholine or phenethyl alcohol) in place of natural home-stream odors to determine if they would return to a stream scented with that chemical. After treatment the fish were stocked in Lake Michigan along with equal numbers of control fish. (Controls enabled us to determine if the experimental fish would return to the scented stream independently of the chemical cue). In six experiments with coho salmon, three with rainbow trout, and one with brown trout, higher numbers of experimental fish than controls (ratios of 8-17:1) returned to the stream scented with the imprinting chemical. Ultrasonic tracking experiments showed that morpholine-exposed fish could detect and discriminate morpholine while control fish did not react to the chemical. As these studies were conducted in the field, they provide direct evidence that salmon and trout use an olfactory imprinting mechanism to achieve successful homing. In addition these studies demonstrate that salmon and trout can be artificially imprinted with a synthetic chemical. Hence, our findings have direct practical applications for salvaging endangered stocks of salmon.

Introduction

Since 1966 salmonids native to the West Coast of North America and Europe have been stocked annually in Lake Michigan. Principal species are coho salmon *(Oncorhynchus kisutch)*, chinook salmon *(Oncorhynchus tschawytscha)*, rainbow trout (steelhead) *(Salmo gairdneri)*, and brown trout *(Salmo trutta)*.

These salmonids are a beneficial predator on overabundant forage fish and the basis of a welcome sport fishery. However, because Lake Michigan's tributary streams are not suitable for their natural spawning (Avery 1974), its salmonid populations, coho and chinook in particular, must be sustained by hatchery-released fish.

Typically, coho salmon hatch and grow in a hatchery for 1.5 yr before transfer to "smolting ponds" along the lake's tributary streams. There, in a 4-wk period from mid-April to mid-May, the young fish undergo smolt transformation—a series of characteristic changes of physiology and behavior which precede downstream migration. At the same time they become "imprinted" to the river system.

The fish are then allowed to migrate from the ponds downstream to Lake Michigan. After 18 mo in the lake, about 5% of the fish return to their respective stream system to spawn. Few stray into other streams, according to Wisconsin authorities.

Although homing salmon may employ different sensory cues in open water migrations (Hasler 1966; Harden Jones 1968), it has been theorized that they use olfaction to identify and relocate their home stream. The "olfactory hypothesis" (Hasler and Wisby 1951) postulates that each stream has a unique odor or bouquet arising from the characteristic mix of vegetation and soil types in the stream's drainage basin, to which young salmon become "imprinted" during the smolt stage. Indeed, awareness of the home stream appears to be acquired and not inherited, insofar as young salmon transferred to a second stream *prior* to smolting will return to that second stream where smolting actually took place (Donaldson and Allen 1957; Carlin 1968; Jensen and Duncan 1971; Vreeland et al. 1975).

In 1951, A.D. Hasler and W.J. Wisby of the University of Wisconsin-Madison proposed to imprint smolting salmon artificially with synthetic chemicals and later to use the scent to lure the salmon during spawning migrations to new locations.

Here we summarize the results of our experiments on the artificial imprinting of Lake Michigan salmonids, primarily coho salmon, from 1971-1974. In this research we used two separate methods to determine whether salmon could be imprinted to a synthetic chemical odor: field census investigations and ultrasonic tracking experiments.

Imprinting Experiments

Our basic approach was to imprint coho salmon smolts by exposing them to a synthetic chemical, morpholine, while leaving an equal number unexposed as controls. The two groups of fish—imprinted and controls—were marked with different fin clips and stocked directly into Lake Michigan.

During the spawning migration 18 mo later, we introduced morpholine into a river near the stocking location and determine the number of morpholine-exposed as well as control fish returning to this simulated home stream. We hypothesized that if the salmon were using odor cues to relocate their home stream, then only the fish exposed to morpholine would interpret the river as their home stream and return there to spawn. The control fish would indicate the level of random straying into the stream that might be expected.

METHODS

Coho salmon, hatched and raised for 1.5 yr at a Wisconsin fish hatchery, were divided into two equal sized groups marked with different fin clips and held in separate raceways.

Odor Environment. We relied on a single source of artesian spring water to supply both raceways. This water was considered "neutral" because it was not connected with any river draining into Lake Michigan and, therefore, could not provide the homing adult fish with any information about the location of a lake Michigan tributary.

Imprinting Chemicals. We metered a synthetic organic chemical, morpholine (C_4H_9NO—a heterocyclic amine) into one of the raceways to imprint the salmon. Unexposed or control fish were held in an adjacent raceway. Morpholine was selected as the imprinting chemical because (1) it is not known to occur in natural waters; (2) it is highly soluble in water; (3) it is relatively stable in the natural environment; and (4) our earlier work (Wisby 1952) indicated coho salmon could detect this compound at low concentrations)about 1 x 10^{-6} mg/L). Therefore, we maintained a steady state concentration of 5 x 10^{-5} mg/L for our experiment so that waterflow could fluctuate to some degree without concentrations dropping below a level detectable by the fish. A second chemical, phenethyl alcohol ($C_6H_5CH_2OH$), was also used as an imprinting odor for some experiments.

Imprinting Period. We exposed the fish to morpholine for approximately 5 wk (mid-April to mid-May) during their presmolt and smolt stages. We chose this development phase in the life cycle of coho salmon because earlier studies demonstrated that fingerling coho salmon taken from their natal tributary or hatchery before undergoing smolt transformation and transplanted to a different stream would subsequently return to the river of release. After smolt transformation we trucked them to Lake Michigan and released them.

Stocking Procedures. Although stocking locations depended on the experiment being conducted, in most cases we stocked the fish within 12 km of the mouth of the test stream—that is, the stream to be scented later during the spawning migration. By stocking the fish directly into the lake, we eliminated their downstream migration and thereby reduced the possibility of the fish's gaining any information about the test stream which could have served to identify it independently of the imprinting chemical. On the other hand, we felt it necessary to have the stocking site near the test stream because it is not known how the fish return to the general area of the home river. Our testing procedures assumed that other sensory systems guide the fish from distant points of the lake to shore areas near the home stream, a region to which the fish presumably became familiar at the time they were stocked.

Monitoring the Return. For most experiments the test stream was Oak Creek in South Milwaukee, Wisconsin (Fig. 1). During the spawning migration 18 mo after the fish were released, we metered morpholine into the stream at the same approximate concentration to which the fish had been initially exposed, although this concentration may have varied to some extent with changes in rainfall or other impacts on stream flow.

Adult salmon were collected in Oak Creek by electrofishing, gillnetting, and creel census survey (angler catch). Each day we conducted creel surveys in Oak Creek starting at sunrise and continuing every 2 h until dark. Electrofishing trips were conducted once or twice a week.

Because fish were unable to move past a dam 1.5 km from the mouth of Oak Creek, only a small portion of the stream had to be monitored. This made census surveys relatively easy. In fact, we believe these surveys, which continued until no salmon were left in the river, captured a high proportion of the salmon returning to Oak Creek.

CONTROLLING FOR ERROR

In planning our experiments, we took into consideration several situations which could have biased the results by causing differences in the return of imprinted and control groups independent of chemical odor. These situations included:

- differences in genetic background and early life history between imprinted and control groups. In our experiments, both groups of fish had similar genetic backgrounds, being eggs from fish taken at one location of Lake Michigan and raised under uniform conditions until separated.
- careless or incorrect marking of young fish. We assumed that any errors in fin clipping were equivalent for each group.

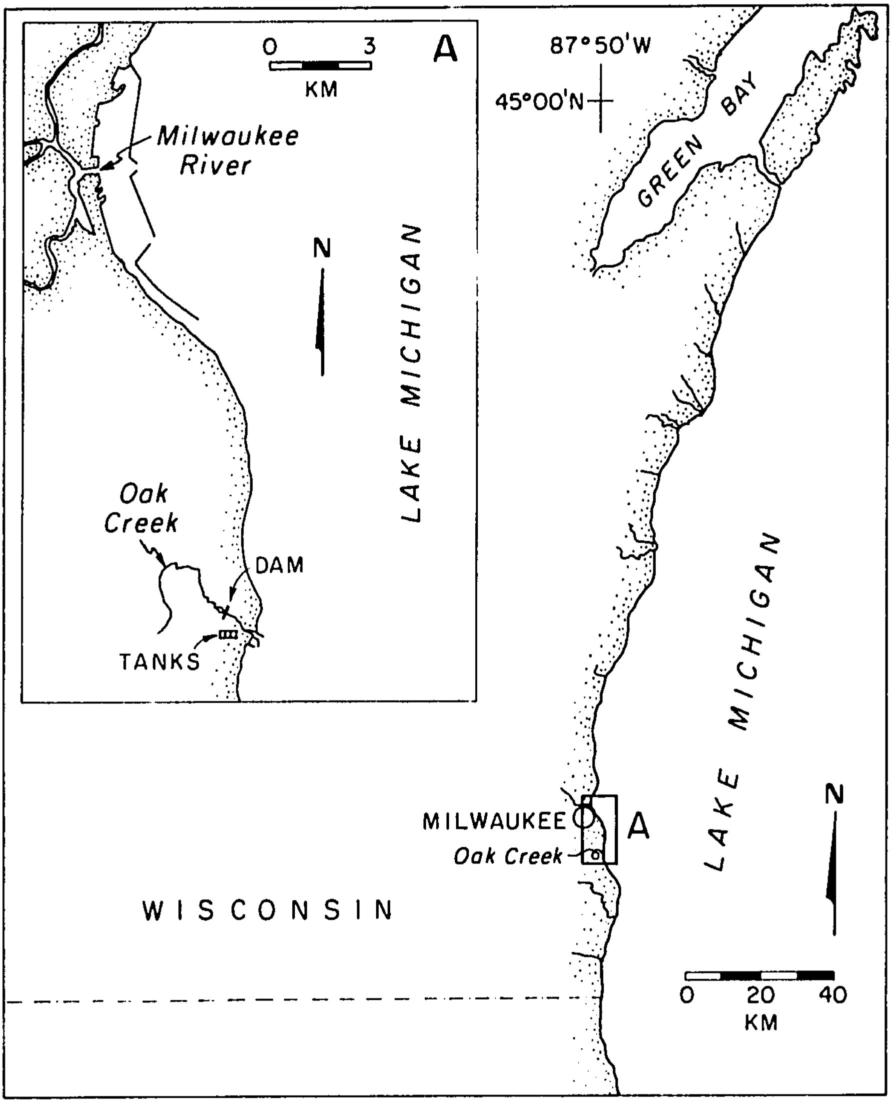


FIG. 1. Oak Creek research site, South Milwaukee, Wisconsin (44°30′ N, 87°30′ W). Morpholine was metered into Oak Creek near the water filtration plant (tanks in inset). The hatchery where the fish were reared was located 215 km NW of Oak Creek.

- differential mortality because of different fin clips. To control for this possibility, paired groups usually received symmetrical clips. Because the Great Lakes Fishery Commission in Ann Arbor, Michigan assigns fin clips in Lake Michigan to avoid duplication of clips, we could not always use symmetrical clips for imprinted and control groups. However, the incidence of mortality, which usually occurred immediately after fin clipping, was low and similar for all groups. Therefore, we assumed that differential mortality did not bias the results. The possible mortal effects of fin clipping or other factors after the fish were released into the lake are not known.
- problems with identification because of regeneration of clipped fins. Rich and Holmes (1929) and Stuart (1958) reported that double fin clips can reduce difficulties of identification. Therefore, we used double fin clips in most experiments, further assuming that regeneration would be similar for each group.

OAK CREEK EXPERIMENTS

In April of 1971 we transported 8,000 morpholine-exposed and 8,000 control coho salmon smolts from a fish hatchery to South Milwaukee and released them 1 km south of the mouth of Oak Creek (Fig. 1). During the spawning migration of the fall of 1972, we added morpholine to Oak Creek and monitored the stream for returning fish. As a result, we captured 216 morpholine-exposed fish in Oak Creek (2.68% of the 8,000 imprinted fish originally stocked) compared to only 28 control fish (Table 1), a ratio of 7.7:1 (Scholz et al. 1973, 1975; Cooper et al. 1976). A ratio of 1:1 would be expected if morpholine had no effect on the experimental group.

We repeated this experiment in 1972 in order to replicate the 1971 study (Scholz 1975; Cooper et al. 1976). An imprinted and a control group, each comprising 5,000 marked fish, were released at Oak Creek in the spring of 1972. In the fall of 1973, we recovered 437 imprinted fish (8.7% of those stocked) and 49 control fish. This recovery ratio of 8.7:1 confirmed the results of the previous experiment (Table 1). Furthermore, the recapture of imprinted fish (2.7 and 8.7% of those originally stocked) compares favorably with the 5% return of smolting pond fish usually experienced.

Concurrently with this second experiment, we administered morpholine to another group of 8,200 fish. Instead of being stocked at Oak Creek, however, they along with 10,000 control fish were released at an alternate stocking location 13 km north of Oak Creek (Fig. 1). Even at this distance, 647 imprinted and 65 control fish returned and were captured at Oak Creek (Table 1). This 10:1 ratio indicates that salmon can search an area within a radius of at least 13 km to locate a simulated home stream.

In 1973 we conducted a control experiment to determine what

TABLE 1. Results of experiments conducted at Oak Creek. Morpholine was present in Oak Creek in 1972 and 1973 (Expt. 1-3) but not in 1974 (Expt. 4).

Experiment number	Experimental group	Fin clip	Number released	Location	Date	Number recovered	Date	Percent of fish stocked
1	Exposed	Dor A+RP	8,000	Oak Creek	May 71	216	fall 72	2.68
	Controls	LV+RV	8,000	Oak Creek	May 71	28	fall 72	0.35
2	Exposed	RM	5,000	Oak Creek	May 72	437	fall 73	8.74
	Controls	LM	5,000	Oak Creek	May 72	49	fall 73	0.95
3	Exposed	D+LV	8,200	Milwaukee Harbor	May 72	647	fall 73	7.89
	Controls	D+RV	10,000	Milwaukee Harbor	May 72	65	fall 73	0.65
4	Exposed	A+RP	5,000	Oak Creek	May 73	51	fall 74	1.00
	Controls	A+LP	5,000	Oak Creek	May 73	55	fall 74	1.10

would happen if morpholine were not added to Oak Creek at the time of spawning (Cooper et al. 1976). Five thousand morpholine-exposed and an equal number of control coho smolts were again released near the mouth of Oak Creek. But this time we did not add morpholine to Oak Creek during the fall 1974 spawning season. The result was that 51 exposed and 55 unexposed salmon were captured at Oak Creek, a ratio of about 1:1, with both imprinted and control fish returning in about the same numbers as controls in previous experiments (Table 1). These results demonstrated unequivocally that morpholine was the operative factor in attracting fish to Oak Creek.

MANITOWOC AND TWO RIVERS

We modified the methods used at Oak Creek and conducted additional experiments at Manitowoc and Two Rivers, streams about 125 km up the lake Michigan coastline (Scholz et al. 1976) Here we used three groups of smolts—one group exposed to morpholine; a second group to a different chemical, phenthyl alcohol (PEA), at a concentration of 1 x 10^{-3} mg/L; and the third group left unexposed as a control.

The 5,000 fish in each group were stocked in Lake Michigan halfway between the Little Manitowoc River and Two Rivers (Fig. 2). We selected this location instead of Oak Creek for stocking the fish because the two nearby streams provided individual targets for our two chemically imprinted groups of fish, each being about 4.8 km from the original stocking point.

During the spawning migration in the fall of 1974, morpholine was metered into the Little Manitowoc River and PEA at the Two Rivers breakwater and we monitored both streams for returning fish. Additionally, we surveyed 17 other streams to evaluate the degree of straying by imprinted fish (Fig. 2). The results (Table 2) supported our expectations:

- Of the 218 morpholine-imprinted fish recovered, 207 were captured in the Little Manitowoc River. This represented 4.1% of the morpholine-imprinted fish originally stocked and 95% of their total number *recovered.* (Eleven morpholine-imprinted fish were recovered at other locations.)
- Of the 146 PEA-imprinted fish recovered, 133 were captured at Two Rivers, the PEA-scented stream. This represented 2.7% of this group originally stocked and 91% of their total number recovered. (Thirteen PEA-imprinted fish were captured at other locations.) As an indication that imprinted fish can be attracted to a very specific area, we captured 118 of the 132 PEA-imprinted fish at the breakwater area at Two Rivers where PEA was being metered into the water (Table 2). Only 15 fish were captured upstream despite considerable effort in sampling.
- Of the control fish, 24 were taken from Little Manitowoc River, 22 from Two Rivers and 79 at other locations, demonstrat-

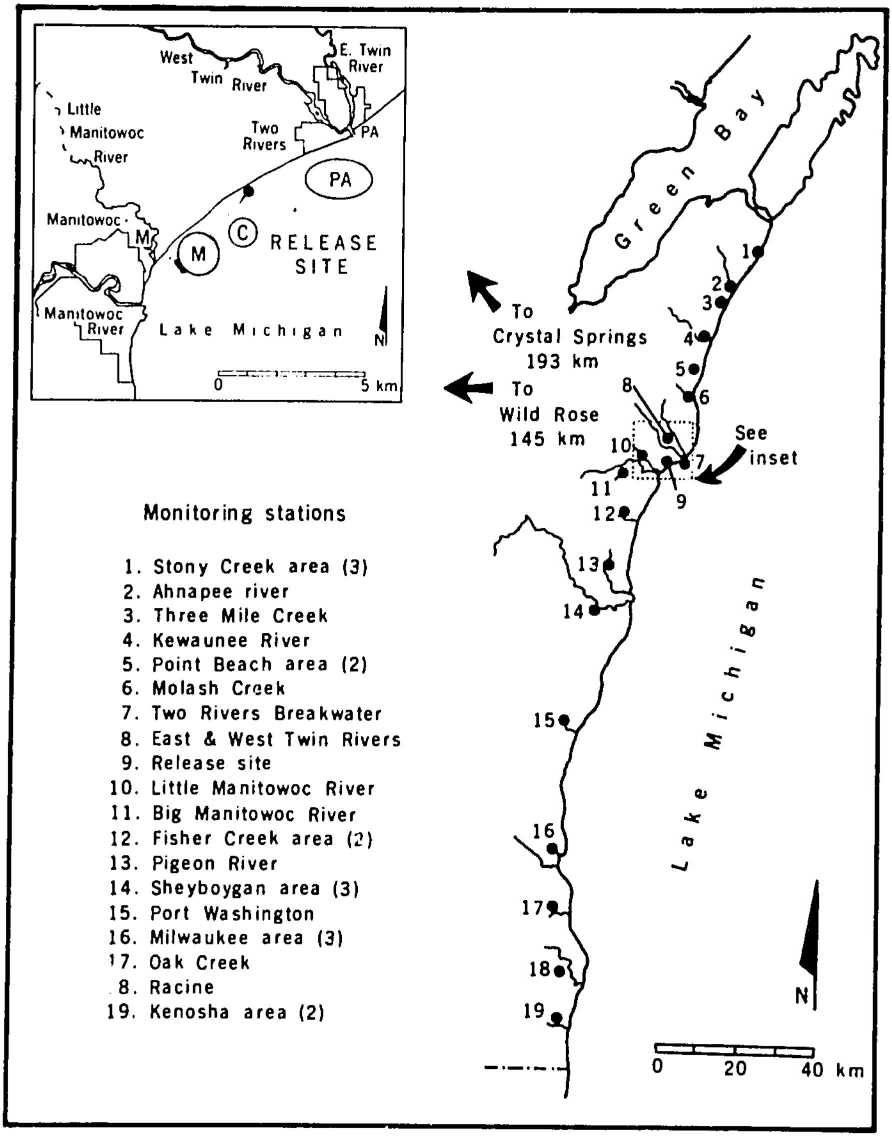


FIG. 2. Research area, Wisconsin shore, Lake Michigan. Numbers in parentheses behind monitoring stations represent the number of streams surveyed in that general area. Inset shows detail of stocking site, morpholine-scented Little Manitowoc River, and PEA-scented breakwater area at Two Rivers.

TABLE 2. Total number of morpholine-exposed (M), phenethyl alcohol-exposed (PEA) and control (C) salmon captures at individual locations. Boldface type represents the stream scented with morpholine (Little Manitowoc River) and italics represent the area scented with PEA (Two Rivers). Fishing effort is summarized by type and number of collecting trips at each location. Five thousand fish per group were released in 1973 and 10,000 per group in 1974. Numbers in parentheses represent the number of streams surveyed in that general area.

Location	1974						1975					
	Effort—no. trips			No. recovered			Effort—no. trips			No. recovered		
	Creel census	Gill net	Electro-fishing	M	PEA	C	Creel census	Gill net	Electro-fishing	M	PEA	C
1 Stony Creek (3)	90	13	13	1		4	40					12
2 Annapee River	138	3	5		2	7	224	4	14	6	1	37
3 Three Mile Creek	27	5	5	2	1	1	26					2
4 Kewaunee River	71		5				9					
5 Nuclear Power Plants (2)	123			1		4	3					2
6 Molash Creek	8					2	1					
7 *Two Rivers Breakwater*	*184*	*3*	*1*	*3*	*118*	*15*	*126*	*14*	*1*	*3*	*192*	*12*
8 *East & West Twin Rivers*	*123*		*9*		*15*	*7*	*17*		*14*	*3*	*8*	*21*
9 Stocking Site	90	1		1		7	30					1
10 Little Manitowoc River	**189**		**8**	**207**	**6**	**24**	**135**			**452**	**14**	**52**
11 Big Manitowoc River	44		5	2	3	31	7				1	26
12 Fisher Creek (2)	44					3	2					1
13 Pigeon River	23											
14 Sheboygan River (3)	75		1	1		3	1					3
15 Port Washington												
16 Milwaukee area (3)	65											
17 Oak Creek	306		5		1	7						
18 Racine	11					1						
19 Kenosha (2)	14											
Totals recovered				218	146							

ing considerable straying.

Clearly, morpholine and PEA-imprinted fish utilize chemical cues for homing and are attracted to streams or to specific areas scented with the appropriate odor.

The experiment was repeated in 1974-1975 using 10,000 fish per group, with similar results: 452 morpholine-imprinted fish were recovered in the morpholine-scented Little Manitowoc River compared to 12 captured elsewhere; 200 PEA-imprinted fish were taken at Two Rivers and 16 elsewhere; and of the controls, 52 were captured in the Little Manitowoc, 33 at Two Rivers and 84 at other locations.

ULTRASONIC TRACKING EXPERIMENTS

In 1971-1973, we conducted a different type of behavioral experiment at Oak Creek to test the imprinting hypothesis (Scholz et al. 1975). Essentially this involved releasing imprinted fish along the Lake Michigan shoreline and tracking them into an area scented with morpholine. As a control, we tracked imprinted fish through the same area when morpholine was not present or when a different chemical was present, as well as controls with morpholine present.

Adult salmon, captured in Oak Creek as part of the census experiments previously described at that site, were transferred by boat to a point 3.2 km north of Oak Creek. There, before releasing them, we inserted an ultrasonic transmitter through the esophagus into their stomach. A directional hydrophone, connected to receiving equipment on a tracking boat, enabled us to follow signals from the tagged fish.

We selected the release site assuming that fish released near the shore would follow the shoreline to Oak Creek, and intercept an intervening site where a small stream flowed into the lake (Fig. 3). Acting on this assumption, we dripped morpholine into the lake in a line extending from the mouth of the stream to about 100 m offshore, creating an odor plume through which the fish had to swim. To determine how long the chemical remained in the scented area, we measured water currents with drogues.

We tracked 56 fish through the test area. Most of them remained near the release point for about 1 h before moving. Thereafter they travelled usually at a constant speed and without changing direction. This migratory route usually paralleled the shore, typically within 50 m. In all cases (20 tracks), when morpholine was present in the test area, the imprinted fish stopped their migration and remained in the scented area from 1 to 4 h (Fig. 3a). Their stay roughly correlated with the time it took for currents to dissipate the chemical. When no odor was present (Fig. 3b), imprinted fish moved through the same area without stopping (13 tracks).

These results demonstrate that morpholine invariably arrested the

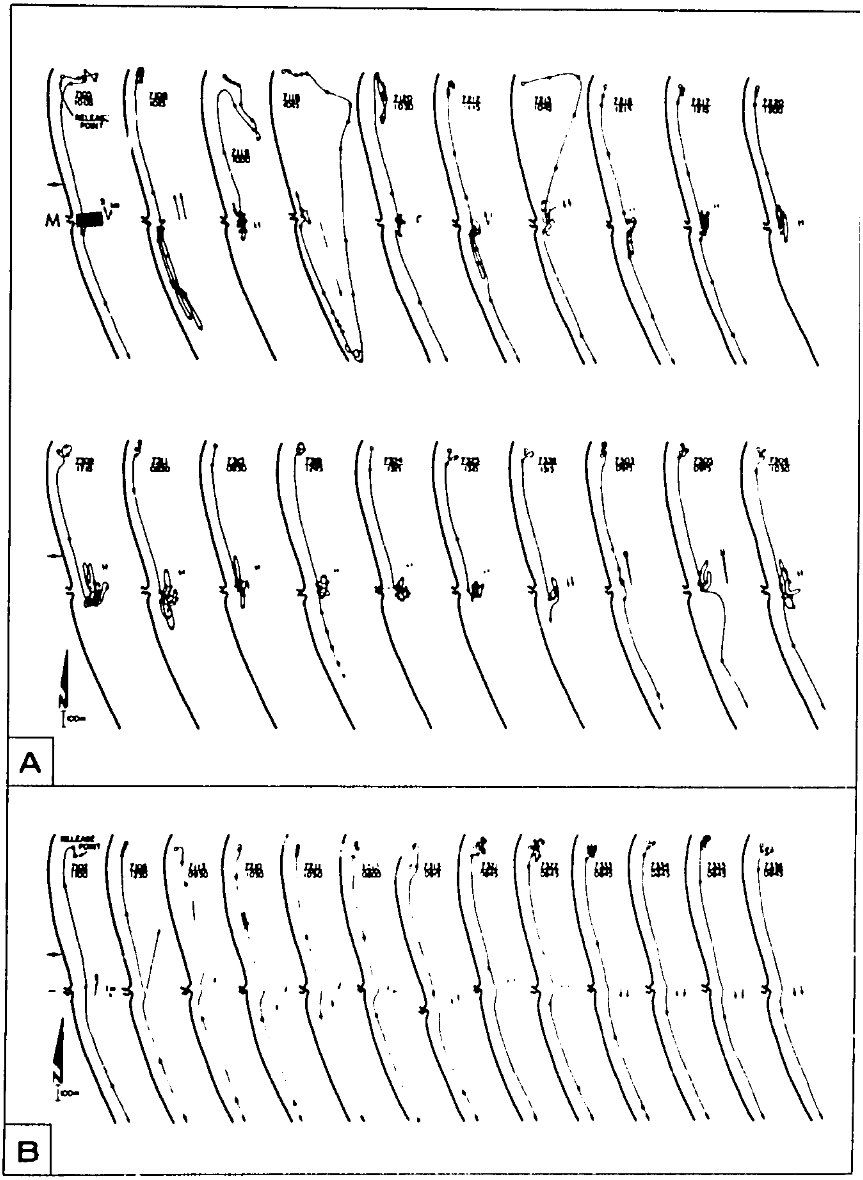


Fig. 3. Ultrasonic track plots of (A) imprinted salmon with morpholine present, (B) absent or (D) with a different chemical present, and (C) control salmon with morpholine present in the test area. The first two digits of each track number identify the year in which the track was recorded. Time when the track was started is recorded immediately below the track numbers; dots along the track path present 15-min intervals. Arrows beside the test area represent 1-h current vectors.

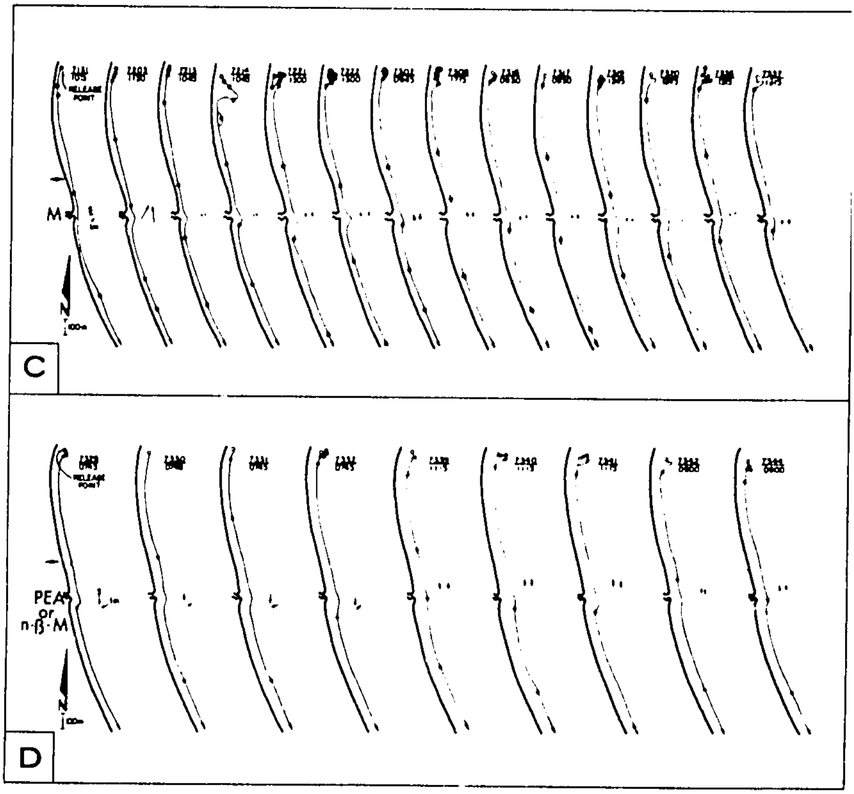
progress of the imprinted fish. However, it was also possible that th fish reacted to morpholine simply because it was not the same a Lake Michigan water. If so, their behavior was not necessarily associated with a long-term memory of morpholine.

To test this possibility, we tracked nonimprinted fish through th area when morpholine was present (Fig. 3c). All 14 fish moved through the morpholine-scented area without stopping. In addition morpholine-imprinted fish were tracked through the area when it was scented with a different chemical; none of these fish stopped their migration (Fig. 3d). In these tests the chemicals were N-β hydroxyethyl-morpholine (7 tracks) and PEA (2 tracks).

Thus, it appears that imprinted fish were not reacting to morpholine as a unique shoreline odor. Rather, their reaction to morpholine in the water seems to be associated with olfactory imprinting and long-term memory responses.

COROLLARY EXPERIMENTS

We conducted several corollary experiments at the same time as the work so far described. In a preliminary experiment (Cooper et al. 1976), coho salmon exposed to morpholine for 2 days at the onset of



smolting returned to a simulated home stream in about equal numbers as fish exposed for 30 days. Thus, very short periods of morpholine exposure seem sufficient to imprint fish successfully.

Additional field census and ultrasonic tracking experiments (Scholz et al. 1975) were aimed at determining just how close salmon had to be stocked to the simulated home stream in order to be attracted to it during spawning migration. Again, these studies utilized basic imprinting methods, the fish being imprinted to morpholine at a fish hatchery. The difference lay in increasing the distance between the stocking site and the test stream. We found that salmon stocked within 40 km of the stream homed to it, but salmon stocked 64 km away did not. Apparently salmon as a first stage must return to a generalized region near the location where they were stocked. Only then do they home to a stream scented with the imprinting chemical. This accords with the hypothesis that fish use other sensory systems to return from distant places in the lake to shore areas near the home stream.

We have also conducted three experiments with rainbow trout (Cooper and Scholz 1976; Scholz et al. 1975, 1978b) and one with migratory brown trout (Scholz et al. 1978a). In all cases, significantly higher numbers of morpholine-exposed, as opposed to unexposed trout, returned to a stream scented with morpholine.

Imprinting Methods and Equipment

Although we selected morpholine and phenethyl alcohol, it is theoretically possible to utilize other synthetic chemicals for imprinting, provided the odor can be detected by the fish. The concentration level at which a fish can detect a chemical is usually determined by behavioral conditioning techniques or by observing the reactions of fish when a chemical is added to their tank. Ideally each chemical should be tested with respect to the target species because each species of fish may detect that chemical at a different concentration level.

Our experiments used morpholine because Wisby (1952) had previously determined that it could be detected by untrained coho salmon at low concentration (1×10^{-6} mg/L) and PEA was chosen because Teichmann (1962) reported that rainbow trout could be trained to respond to phenethyl alcohol at a concentration of 3.6×10^{-4}mg/L.

Through experience and considerable experimentation, we have gradually refined our procedures and equipment for delivering these chemicals. This delivery system uses glass containers and peristaltic or, alternately, piston pumps to meter the chemicals into the raceway or test stream. We also had to develop heating and insulating systems to prevent freezing of the chemicals as well as select appropriately "neutral" water for the imprinting phase of our work. Detailed discussion of our procedures and equipment appears in our imprinting manual (Scholz et al. 1975).

Probably the most critical factor and worth discussing briefly here is the determination of the sensitive period during which salmon can be successfully exposed to an imprinting chemical.

In our experiments we exposed salmon to an imprinting chemical before and during smolting, which occurred usually in late April or early May. This meant we began imprinting operations in early April and continued for about 5 or 6 wk until 1 or 2 wk after the first signs of smolt transformation. In Lake Michigan's coho salmon, smolting characterized by loss of parr marks and changes in body coloration from dark green or black to silvery. In addition, the smolts form tight schools at the downstream end of ponds or raceways whereas presmolts were scattered throughout the raceways. The total length of the fish at the time of smolt transformation is approximately 100 mm.

Smolting behavior is complex. During this period of transformation, the actual imprinting process is probably rapid and may be stimulated by the increased endocrine activity that initiates smolting (Hoar 1976). Endocrine development usually coincides with growth because Atlantic and sockeye salmon will remain in the stream another year before smolting if they do not reach a certain minimum size. The standard size at smolting for coho and sockeye salmon and rainbow trout is reported in several papers to be about 100 mm. This is more variable in chinook or Atlantic salmon. At the same time, size does not appear to be the only factor which controls smolting insofar as some fish reach smolt size 6 mo before smolting occurs. Because smolting occurs about the same time every year, it is possible that photoperiod (day length) and temperature might be more basic influences in smolt transformation. In order to control salmon migrations effectively, especially with regard to chemical imprinting, smolt behavior needs to be researched more fully for each species.

Management Applications

Results from our experiments imply that the olfactory identification of the home stream by salmon is rapidly learned and retained until adulthood. Moreover, artificial scents can be used for imprinting in place of natural odors. It is evident, therefore, that the final stages in the migration of some species of salmonids can be manipulated by artificially imprinting smolts to a synthetic chemical.

With respect to Lake Michigan's salmonids these findings suggest several applications:

- Artificial imprinting at Wisconsin hatcheries reduces the need for smolting ponds, an advantage both in operating cost and survival of young fish; e.g., water quality and temperatures can be carefully controlled in a hatchery.
- Artificial imprinting permits manipulation of salmon and trout runs by selecting specific locations for harvest, whereas fish stocked in smolting ponds return only to the river of release. In addition, fish can be stocked at sites within a metropolitan area which does not have adequate facilities for smolting ponds, and thereby insure a lively fishery 18 mo later for metropolitan residents. By careful planning, such programs can spread out or concentrate sports fishing pressures as may be desirable.
- Artificial imprinting can improve the returns and harvest of steelhead trout and other species which normally must be stocked directly in the lake because of unsuitable stream temperatures at time of stocking. Unless they are imprinted artificially, such fish exhibit a poor return to the stocking site and a high degree of straying since they are not exposed to a unique odor during the imprinting period.

Our findings may also be valuable with respect to conservation of Atlantic or Pacific Ocean salmon stocks, where fishery biologists could use artificial imprinting for attracting adult salmon to suitable areas for spawning or commercial harvest, or diverting them from power dams, warmwater discharges, or other potential hazards. For example, in the Pacific Northwest's Columbia River, artificial imprinting could be used to identify artificial spawning channels or to re-establish spawning streams where dams or pollution have eliminated ancestral stocks. Once spawning salmon are lured to these streams, perhaps too remote for direct stocking, the offspring would be naturally imprinted to their home stream system. In addition, fish may be attracted to specific sites along the coast for harvest before they enter the river, hence utilizing them in prime condition at their best commercial value.

Indeed, much of this promise is being realized. The widespread adaptation of our imprinting techniques in fish management programs—from Scotland to New Zealand—has been a rewarding outgrowth of basic research on anadromous fish migration.

Acknowledgments

We thank Warren Downs, University of Wisconsin Sea Grant Editor, for collaboration in preparing this digest of our original article, Wisconsin Sea Grant Advisory Report No. 414.

Our research is supported by the University of Wisconsin Sea Grant College Program, U.S. Department of Commerce—National Oceanic and Atmospheric Administration, the National Science Foundation, and the Wisconsin Department of Natural Resources.

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Discussion

BARDACH

Do you think your method of artificially imprinting salmon can usefully be applied in other parts of the world?

HASLER

In the Baltic, especially where there are many streams inaccessible to salmon, our method should bring them to the mouth of the stream for harvesting; hence I think that we ought to try it there, also probably in Nova Scotia and Great Britain. Our studies should be repeated for Atlantic salmon to determine if the runs could be increased by a factor of 10. It promises to be very profitable. I think it could be done in Japan and New Zealand. There are sites where rivers are either choked by dams, spoiled by pollution, or too turbid.

HENDERSON

Do you have any evidence that the increased return in your Lake Michigan experiments was primarily because of lack of straying, or is there a real difference in mortality as well?

HASLER

I don't know. We haven't had enough returns of marked fish caught on the high sea to evaluate them.

HENDERSON

Someone has suggested that there is a lot of straying and that that is the reason they're not caught.

HASLER

Our most recent study shows only 1% straying to 26 streams. If I were 40 yr younger, I would work on the "cussedness" of fish, i.e., the fish that go astray. Certainly the Pacific salmon would have become extinct long ago because of volcanic eruptions if a straying component were not inherited.

MURPHY

Did you try imprinting by releasing fish in, for example, Oak Creek? I think the experience on the Pacific Coast in releasing trout and salmon would suggest that you can imprint by releasing your animals in the stream you want them to come back to.

HASLER

Of course. We have transplanted smolts from a hatchery into a tributary of Lake Michigan and found that they returned to that tributary to spawn. I think probably the most beautiful examples of that are those of Carlin on the Atlantic salmon in Sweden. His records indicate that about a week residence in the adopted stream is adequate for homing, but he died before working up those data. In fact I'm asking for a grant from NSF to go to Sweden next year to work over Carlin's data. Carlin has hundreds of thousands of records on returning fish that were marked with metal tags, transplanted from their home tributary or hatchery to a second steam, and subsequently recaptured. These data should yield information about the critical period for imprinting.

HARDEN JONES

I think it's time you called this the home steam odor theory and not hypothesis. I think it's a proven fact and I don't think anyone would dispute that anymore. But artificial imprinting will only guide, or decoy, those salmon which return to coastal waters; and the gain cannot exceed the loss that is attributable to straying. No one disputes that stray rates are low (that's what the home-stream theory is all about), so the gain by artificial imprinting is going to be low, say no more than 5%. There cannot be a 10-fold gain unless there is an increase in the proportion of fish that return from the high seas to coastal waters.

BARDACH

Is there any point in imprinting with an artificial chemical if the fish can be imprinted to a natural stream?

HASLER

Probably not, but there may be situations where it is not possible to imprint fish to a natural stream. For example, many stocks of salmon in streams of the Rocky Mountains in Idaho which feed into the Columbia River became depleted after the building of hydroelectric dams. Now fish ladders have been built to allow passage upstream, but before salmon populations can become reestablished, young salmon must be stocked in the rivers. Now many of these rivers are inaccessible to hatchery trucks and therefore cannot be restocked by normal methods. However, it would be possible to imprint young fish in a hatchery and then decoy them into one of these rivers simply by setting up a drip station on that river. Someone walking in with a backpack could set it up. The beauty of it is that this procedure needs to be done only once because subsequent generations of fish will be able to become imprinted to natural river waters.

BLAXTER

I think I can see one problem, for example in Scotland. You could use morpholine or some other substance or substances to imprint salmon specifically or to reinforce the natural odor in a particular stream. Different people would use different substances to imprint their own salmon populations. I think in Scotland, where we have a lot of rivers in private ownership, there would be a great problem with "specialized" poaching. Poachers would release these substances for their own illegal purposes.

HASLER

I know what you're talking about and I haven't any answer to it. Four states border Lake Michigan, all of which want to use morpholine to imprint salmon. Regulations governing the use of the chemical will need to be set up. This will require the cooperation of all participating agencies.

FISHELSON

This is a general question and may be more for the future. Atlantic shallow waters are more and more polluted by various strong chemical substances, and I don't see any hope that in the near future it will become better; maybe it will become worse. So how do you think this will affect imprinting and the chemical situation along the shoreline where a fish returns from the ocean?

HASLER

There may be little possibility of masking the odor of one nontoxic chemical by another. Just recall your own experience of being in a locker room with all kinds of people and with the odor of their sweat permeating the whole room: if a woman wearing perfume walks through you are alerted instantly. Our attempts to mask odor of one aquatic plant with another species failed. Another thing I've often thought about is what if the chemical has some caustic action on the olfactory system?

BARDACH

We have some indication that chemical confusion does not make much difference. Take salmon near Seattle; the fish have to go up a river that goes right through the Boeing plant with high levels of chemical pollution, and yet the salmon go through it and come to the decision point Art was talking about. So it appears that the specific chemicals or mixtures of chemicals on which the animals have been imprinted override confusing stimuli.

ATEMA

It appears that either one chemical or a mixture of chemicals facilitates neural networks and sets the motor pattern working. This can be in the case of salmon imprinted and locked up in the brain at a certain time. It's opened up again later on and is very selective. This is a hypothesis, but I think there is indeed, as Dr. Bardach said, evidence that there would be pollution interference only if there were chemicals that were very similar to those involved in the original imprinting, especially if the latter were not a complex mixture but only one compound so that the chances of confusion would be theoretically great.

MAGNUSON

Another problem could be avoidance responses to particular compounds, for example copper ions, far below toxic levels. At such levels the animals respond to copper and avoid it. There could be competition between avoidance of certain compounds and following the home stream odor.

KEMMERER

Are the fish responding to a single odor, a combination of odors, or a specific sequence of odors? In spawning and nursery areas, fish are exposed to one odor. When they swim downstream they are exposed to combinations and sequences of odors. Does the imprinting mechanism take these changes into account such that when fish return from the ocean they first look for one odor and then others to guide them back up the rivers?

BARDACH

It looks as if the fish are looking for a single odor. It looks as if once the imprinting has been done, other odors are disregarded.

MYRBERG

How do you think salmon make upstream progress using odor as a guiding mechanism? Do they respond to the active substance by gradient searching, or are they responding rheotactically?

HASLER

The odor may act as a releaser for rheotaxis. If you observe the confluence of a stream and introduce a dye upstream of the confluence, it hangs on for miles downstream, staying on the margin. I visualize a salmon's behaving like a zigzagging hunting dog to avoid becoming fatigued (accommodated) to the odor. I have a student working this fall on what salmon do when they reach a place in the river where they have to make a decision, such as at the first fork. We should have some data on that point forthcoming.

MYRBERG

Do salmon fall back?

HASLER

Yes, there are several examples in the literature of fish bypassing their home stream or ascending the wrong stream but later turning around and returning to the home stream.

BLAXTER

The Norwegians have shown by the EEG technique that *Coregonus* respond preferentially to their own population, so it might be that salmonids are particularly sensitive to pheromones or substances produced from their own population. If you wanted something to which they are very, very sensitive, it might be worth screening that sort of substance rather than something like morpholine.

HASLER

Your colleague Solomon has published a review in *Nature* on the possible role of conspecific pheromones in salmon migration. It's an old hypothesis, going back to Huntsman and even before.

MAGNUSON

I think that a substance from the fish themselves would be a poor odor to use, because fish would tend to follow the odor of the fish ahead of them. In most situations it would be unlikely that other fish of the same species were upstream. The key would be the first fish to make the choice.

HASLER

It would probably also not work for juvenile fish in the river to give off the cue because they would be genetically unrelated to the adults coming back. I can't visualize then how they could provide a unique conspecific cue. Remember the cue has to be unique, not just species specific, or the fish would turn up the first tributary they came to that had salmon in it instead of returning to their home tributary.

ATEMA

One thing that puzzles me is that when the fish were imprinted in a hatchery situation with morpholine there were other odors present as well. The whole complex is an odor bouquet. If they are put from the hatchery into the field, they have to disregard all the other odors and yet remember morpholine. How is it possible that they recognize the morpholine, and it's not necessary to have the whole hatchery chemical surroundings?

HASLER

I don't have a good answer for the question. Maybe the morpholine is different enough that it overrides the bouquet effect. Also the background water that the fish were being held in was spring water which might not have a lot of organic material in it. We know that the active component which the fish detects is contained in the organic fraction.

HENDERSON

One of the nice things about this Michigan experiment is that the fish were raised in water from a different watershed.

HASLER

Yes. The reason we did this was so that we would not run into the bouquet problem. It may be that the natural odor of a watershed might be dominant over morpholine and the fish would return there if it were available. By imprinting the fish in a different watershed we reduced this problem.

Training of Fishes Applied to Ranching of Red Sea Bream in Japan

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FUJIYA, M., S. SAKAGUCHI, and O. FUKUHARA. 1980. Training of fishes applied to ranching of red sea bream in Japan, p. 200-209. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Experiments were conducted to determine if a red sea bream, *Pagrus major,* could be trained to respond to underwater sound pulses for possible application to fish farming.

Sound pulses of 200 Hz generated by a frequency oscillator were recorded on tape and emitted by an underwater speaker in an experimental tank. Red sea bream about 2 cm total length were kept in the tank and fed four times a day. Thirty sec before food was given, sound pulses were started, continued for 2-5 min while fish were feeding and then stopped 10 sec after feeding ended. At the first feeding on the second day of the experiment, several fish appeared to gather around the underwater speaker before the food was given. Almost all sea bream in the tank were trained to respond to the sounds after 2 wk. Individuals as small as 20 mm long could be trained, and conditioning lasted at least 2 mo. Shock from handling did not usually reduce the effect of conditioning, but sudden temperature changes sometimes affected the sea bream's response.

Sea bream have comparatively high powers of discrimination of sound frequency and respond best to 200-700 Hz.

Introduction

Aquaculture production of the world was over 6 million metric tons in 1975 (FAO 1976) of which 66% was freshwater and marine fishes, 16% molluscs, 18% algae, and 0.3% crustaceans. Production is still increasing in many regions and improvement of methods is a significant responsibility of fisheries scientists. Many governments are interested in improving and developing aquaculture to provide protein and aid in economic development. It is believed that fish ranching should be the focus of future aquaculture development.

Fish ranching requires the application of many fields of science. This paper describes the application of conditioned reflex training to marine ranching of red sea bream *(Pagrus major)* in which the animals are reared in their natural environment to avoid the costs of feeds and facilities. However, some degree of control of the fish is still required in nature, especially at harvest time. Training the fish to aggregate at a place of capture might reduce the vulnerability of the young stages to the commercial fleet and thus increase the efficiency of sea ranching.

The red sea bream *Pagrus major* is traditionally considered as an especially highly valued food fish in Japan. Thus, it is not surprising that research on farming red sea bream has been conducted since 1887. Artificial propagation procedures were studied as early as 1902, but little success was achieved and the work waned. In 1958 fundamental research on propagation began again with more modern techniques and facilities, and success came on an experimental scale in 1962. Since then, farming of red sea bream has advanced rapidly and is becoming a valuable program in the development of coastal aquaculture. A flow chart for the procedure appears in Fig. 1. At present, farming techniques, especially seed production, are most advanced for red sea bream in comparison to those for other species.

Egg and Fry Production

Fertilized eggs are obtained by stripping wild fish or from natural spawning of captive animals. Stripping of wild stock is most common and is conducted at sea immediately after the mature fish are caught. Males and females are easy to identify. To obtain natural spawning in captivity, equal numbers of male and female breeders are held in a tank through the spawning season. Water temperature should be 15-21°C and the specific gravity less than 1.02 g/cc. Oxygen must also be sufficient. Fecundity of age-4 (1 kg) fish is 300,000 eggs. Spawning continues for several days at dusk.

The mature egg is about 1.2 mm in diameter. The specific gravity of seawater is about 1.024 g/cc at 15°C and eggs should float. The egg surface is covered by sticky material that is removed by soaking

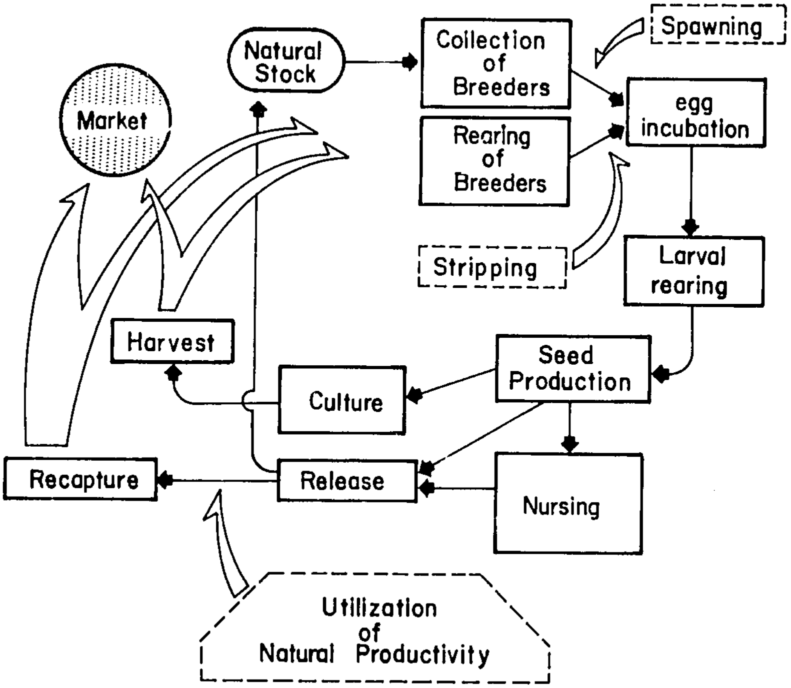

FIG. 1. Flow chart of steps in farming red sea bream in Japan.

the egg in seawater. The fertilized egg or zygote is pelagic, colorless, and transparent, has a diameter of 0.97-1.1 mm, and contains an oil globule about 0.25 mm in diameter.

Zygotes are sensitive to bright light, physical shock, and fluctuations in temperature. Black pigments on the oil globule change with light intensity and may control light penetration. Light intensities allowed into the egg by the pigment range from 100-3,000 lux. Thus, hatching tanks should be illuminated with a maximum of 3,000 lux at the water surface. Physical shock produces abnormal development, and consequently care in transportation is required. Hatching occurs in 60 h at 15°C and 40 h at 18°C. Below 10°C development ceases. Zygotes sink to the bottom if the water has a specific gravity less than 1.023 g/cc. Eggs that lie on the bottom have a poor percent hatch.

Recently hatched fry are inactive for 1 d, after which they are transferred to a rearing tank of "green seawater" which supplies their first foods, phytoplankton and small zooplankton. To prepare "green seawater" an outdoor tank with a capacity of 1,000 l is filled with new, clean seawater; 500 g of fertilizer and an innoculant of phytoplankton are added. Within 10 d the green seawater is ready and 40,000 fry can be added.

After a few days the green water should gradually be replaced with new seawater. From this stage on the fry must be fed. Initially the swimming stage of oyster larvae and zooplankton such as rotifers are suitable. About 10 d after hatching, the fry become more active, and nauplii of brine shrimp and copepods should be provided. When the body length exceeds 20 mm, minced shrimp and fish meat can be fed and the fry are ready for transfer to growing facilities in the sea.

During the rearing of fry, water quality control, light intensity, and dissolved oxygen are important. Dead eggs, fish, and food organisms must be removed from tanks as often as possible. Light requirements differ between individual fish and growth stages. Consequently, rearing tanks should have a range of light intensities available from 0 to 2,000 lux so that larvae can choose the best conditions for themselves.

Growing to Marketable Size

In cage culture the red sea bream are held in a floating cage about the same size as the yellowtail cages. The cage is made from a wood or steel pipe frame and a synthetic fiber net. In August, 6-8 kg of fry per cubic meter of water are placed in the cages. They are fed thawed fishes such as anchovy and sand eel. Artificial diets are becoming more popular with the growers, but are more expensive than thawed, low-value fishes. Marketable sizes are reached in 12 to 18 mo.

In more extensive ranching, fry are held in floating cages until they reach 5 to 7 cm in total length, but are then released into the natural environment. Oceanographic and ecological studies are used to assess the suitability of the release area beforehand.

Although these released fishes should contribute to recruitment of natural stocks and become the object of traditional fisheries, it is feared that too many may be captured before they attain a commercial size. For example, in the Seto Inland Sea, about one-half of the natural stock of red sea bream are caught within the first year by small trawlers. An intensive fish stocking program is in practice there, but if the red sea bream are caught within a year they contribute nothing to the fish ranching program. Thus, there is logic in keeping the released fish away from the trawling areas. An attempt to do this is described below through use of an audio signal to train the fish. The project has been applied at the demonstration level.

Training Procedure—Preliminary Experiments

Experiments were conducted to test whether or not the young red sea bream could be conditioned to aggregate around an underwater sound source, whether they retained the response without reinforcement for several months, and whether handling of the fish or other stresses destroyed the response.

A small floating cage (2 x 2 x 1 m) in an outside aquarium (4 x 4 x 2 m) served as a test facility. Fish 20 mm total length and about 1 mo old were put in the cage. An underwater speaker (pioneer UL-3S) and tape recorder (Sony TC-860) transmitted 200 Hz at an intensity of 20-30 dB. Conditioning was conducted four times per day, twice in the morning and twice in the afternoon. Sound emission began 30 sec before and continued through each of the four 2 to 5-min feeding periods.

Some fish were conditioned within 2 d, and within 2 wk almost all gathered around the speaker immediately after sound emission. The response persisted at other frequencies without retraining but was not as strong. The response to 200 Hz was retained for 2 mo without further reinforcement to sound. Various manipulations of the fish such as dipnetting, anesthetizing, or treatment to prevent disease, did not change the response. Responses were altered by changes in water temperature, salinity, rain, and storms, but were not seriously lessened. The largest change in response to sound occurred when water temperature was lowered below 10°C. From these results we concluded that it should be possible to usefully train the fish to aggregate near a sound source in the natural environment.

After the fish had been trained with 200 Hz sound, their response to other frequencies ranging from 20 to 1,000 Hz was observed. Response was strongest to 200 Hz and diminished as frequencies increased. A range of 200 to 700 Hz was found to be suitable.

Field Training and Demonstration

Field trials were conducted in a small bay near a fishermen's village at southern Shikoku Island. A floating cage (10 x 10 x 5 m) was placed in the bay supported on a steel pipe framework and styrofoam floats. An automatic food-pellet dispenser was installed at the center of the cage 1 m above the water. The underwater speaker, immediately below the feeder, was 1 m below the water surface. Feeding and sound emission were remotely controlled from a small shoreside house.

The chronology of the 1971 experiments was:

Sept. 10 —	10,000 juveniles from the hatchery released into the floating cage; began feeding with pellets.
Sept. 28 —	stopped practice feeding.
Oct. 23 —	began conditioning fish to sound.
Oct. 29 —	about one-third of fish respond to sound.
Nov. 10 —	almost all fish respond.
Nov. 16 —	100% of fish respond to sound.

Jan. 29 — fish released from cage.
May 3 — a few fish can be attracted to the sound source.
May 7 — 100 fish attracted to speaker.
May 15 — several hundred fish attracted.
June 15 — 3,500 to 4,000 fish observed by diver.
June 28 — fish attracted and recaptured by seining; 1,494 released fish caught, 285 wild fish also caught.

Loss of about one-half of the fish at recapture time might have been prevented if we had more experience with the seining method in this particular situation. Regardless, significant numbers of released fish remained in the area over the winter.

Based on these results, we conducted a demonstration-level experiment in the Seto Inland Sea. Similar methods were used but fish were released after 2 mo of conditioning. Initially, released fishes ate mostly pellets; later, they began eating natural foods as well, such as crustacea, polychaetes, and larval molluscs. Conditioned fish usually remained within 1 km of the release site but occasionally wandered as far as 5 km. Wild sea bream migrate over much longer distances. Some of the conditioned fish were caught by commercial boats, mostly by angling or gillnetting. Only a few were caught by longliners or trawlers. Apparently training with the conditioned reflex technique was quite effective in protecting the released fishes from ordinary fishing enterprises.

Future improvements could include providing less food in winter since the fish are so inactive then; reducing the intervals between training sessions; and conducting the projects near seaweed culture plantations. The first two possibilities would reduce the cost of the project; the third would provide shelter as well as natural food for the fish. Some success has been achieved in the latter approach.

Recommendations and Conclusions

A number of recommendations can be made for application of conditioning to actual commercial fish ranching. A protected site in an inner bay undisturbed by currents, heavy seas, or high noise level should be chosen, with oceanographic conditions suitable for fish life. Water should be less than 10 m deep for ease in construction and servicing the cages. A floating cage with synthetic fiber netting is ideal. Red sea bream juveniles 20 mm long are large enough for conditioning with sound. Frequencies of 200 to 700 Hz can be used and intensities of 20-30 dB are sufficiently loud. Fish can be trained in 2 wk in shoreside tanks or about 2 mo in the field. Fish should be allowed to swim over the top of the cage after training is complete by pulling a side of the net beneath the surface to minimize stress on the fish. After the fish are released, the same conditioning procedures should be used but the amount of food should be reduced to encourage the use of natural foods. Capture methods must be refined for the recapture of the fish at the time of harvest. Recapture in winter works poorly in Japan. The recapture operation should be repeated several times but at intervals to be effective.

While the procedures tested here were specifically for ranching of red sea bream, we believe the methods can be applied to other species and aquacultural operations, because some wild fish responded to the field training along with the sea bream. An ability to maintain fishes on a commercial scale in nature without having to build large facilities has economic appeal. Our findings might also be especially applicable to maintenance of fishes in marine parks. The method when applied to larval fishes may help in initiating feeding of tank-raised fishes.

We hope that the data and information obtained in these experiments will be applied to the future development of commercial fisheries.

Acknowledgments

We thank the scientists of the Nansei Regional Fisheries Research Laboratory and Hiroshima Prefectural Fisheries Experimental Station with whom these studies were conducted.

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Discussion

BARDACH

How far did you track the fish?

FUJIYA

The trained fish stayed in the 1-km area but the untrained fish sometimes went 10 or 20 km away.

BARDACH

If you saturate that 1-km field with released fish you may work against yourself because you may have to feed too much.

FUJIYA

Well, in this case, we don't have any such plans because we don't like to feed fish food for this purpose; we just give a small amount as reinforcement.

ATEMA

Do you have an estimate of the percentage of natural food they eat vs. what you gave?

FUJIYA

Well, sometimes 50%, sometimes 100% natural food because I think the natural food is much more tasty than pellets, even for farmed fish. They prefer the natural food.

ATEMA

Do you have any idea of what these fish are displacing in that habitat? They are grazing the environment in enormous numbers, so what are they displacing that is naturally there?

FUJIYA

Usually, we use as ranching fields certain areas where there was much natural stock in the past, or else new, artificially produced fields. For all these, we calculate roughly what the carrying capacities are and then we release certain numbers of fish on this basis.

ATEMA

Do you know what fish were there before?

FUJIYA

Yes. Also, in some fields where sometimes several fish occupy a habitat, the first comers usually get the better positions. In Japan we are now thinking about how to get the seed much earlier than the natural spawning time of the fish.

KEMMERER

How many times did you try to recapture the fish? Just once?

FUJIYA

We tried twice: the first time we got about 2,000, and the next time only 500 because we made the first collection in the morning and the second in the afternoon. But this was too close an interval. So, we'd like to suggest that recapture trials must be done once a day and continued for several days.

HENDERSON

I'm not sure how your reinforcement procedure works after the fish has been released. If the fish is at a great distance from the feeder when it hears the sound, again it's not going to have a chance to see whether there's any food there or not.

FUJIYA

That's true, but for instance within 1 or 2 d in situations like this some fish go out 1 km away and some days they come back to the original point. That's already checked by the migration investigations.

BARDACH

Did you reinforce at random or did you reinforce every day at the same time?

FUJIYA

Every day, same time.

BARDACH

In that case, the fish learned the time of feeding and came then.

HENDERSON

They do this in China in moderate-sized lakes when they are feeding fish with supplementary food. Part of the reason for this feeding is to concentrate the fish for capture. They feed in a fixed place at a regular time.

FISHELSON

If this place is so shallow and great in length, why can't you cut it out off from the sea by net? Then you will not lose fishes. Also, is it possible to transport the fish in the sea by sound and bring them into enclosures for capture?

FUJIYA

Yes.

MYRBERG

Your findings clearly show how underwater sound might well be applied to a fishery problem. I'm pleased that you have applied such a technique, especially since the basic facts pointing to such applications have been around for more than 10 yr with little interest being shown in such possibilities—at least in the United States. A major problem confronting such applications has been, however, the development of an inexpensive, underwater speaker that is durable, portable, and capable of transmitting appropriate low frequency sounds (e.g., bands between 100 and 600 Hz) with reasonable power. Such is needed for any expanded fishery application. Another point regarding your interesting talk. . . why are you training the very small fishes? If you collected somewhat larger individuals and trained them, you'd save on food costs and the time of harvest would be relatively shorter.

FUJIYA

We did some experiments with larger fish.

BLAXTER

It seems to me that there are two problems in the long term. One is that you will gradually collect unwanted species. You did in fact show that you had 30% or so "contamination" by unwanted fish. And I think the other thing is that you will get a gradual dispersal as they range farther and farther from the loudspeakers. If they find that the natural food is more tasty, they won't come back to the loudspeakers, so that when you want to harvest them, they are lost.

FUJIYA

For this kind of purpose, we should select some very suitable site for release. The site is extremely important. If there are lots of natural fish, that's not a good site.

BLAXTER

We are doing this type of recall feeding, too. One of our ideas is to put rainbow trout into an oligotrophic lake where there are no indigenous fish. In other words, we are using the lake as a big aquarium. We are feeding the fish on artificial food, but we do not have the problem of diluting the stock with indigenous fish.

BARDACH

Ten years ago you did an experiment with rainbow trout in the sea which also fed, in part, on natural food. Are you still doing this anywhere with trout?

FUJIYA

No. This training method is very applicable to the trout also, but in the summertime in Japan the water temperature goes up and that makes it very complicated.

BARDACH

Are you doing it with any other fish than the sea bream?

FUJIYA

Some prefectural stations tried the yellowtail, but that doesn't work. Also, in Kyushu they are trying this method in a marine park with many different species, so I think it is quite possible.

BARDACH

The experiments you showed were done in 1972. Since then, have you improved, perfected, or carried on some new experiments?

FUJIYA

No. We worked on the special research plan from the federal government at the time, and that project continued until 1975. Since then the federal budget for this work has been cut, but the method is now used by local governments.

BARDACH

Have others, commercial fishermen or fishing companies, begun to use it?

FUJIYA

No.

MYRBERG

I believe that a Japanese squid-fishery is presently using underwater sound as an attractant with excellent results (Maniwa *In* A. Schuijf and A.D. Hawkins (eds.) Sound reception in fish, 1976, Elsevier, 271-282; Y. Maniwa and Y. Hatakeyama, 1975, Technical report of fishing boat 28 (Serial No. 64), Fishery Agency, Chuo-ku, Tokyo, 22 p.).

FUJIYA

But that is not training.

MYRBERG

No, it is not training but it uses sound as an apparent attractant.

BARDACH

What kind of sound is played to the squid?

MYRBERG

They tested broad bands such as propeller noise as well as pure tones (150, 200, 300, 600, and 1,000 Hz). The 600 Hz pure tone increased catches by 56 to 108% (different trials involved) and was considered the best "attractant."

Patterns of Hormonal Control in the Reproductive Behavior of Fish, and Their Relevance to Fish Management and Culture Programs

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LILEY, N.R. 1980. Patterns of hormonal control in the reproductive behavior of fish, and their relevance to fish management and culture programs, p. 210-246. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Gonadal hormones have been implicated in the regulation of secondary sexual characteristics and reproductive behavior of male and female teleosts. There is some evidence that pituitary hormones may also be directly involved in the control of some components of spawning and postspawning behavior, and nonreproductive aggressive behavior.

The endocrine system is in turn responsive to environmental and behavioral stimuli. In this review emphasis is placed upon the distinction between two stages in the gonadal events preceding breeding. Annual changes in photoperiod and (or) temperature appear to be the major environmental factors responsible for entraining the growth phase of the gonadal cycle which brings fish into a condition of prebreeding readiness. The onset of reproductive behavior and spawning depends upon the occurrence of ovulation and spermiation. A variety of physical and biotic factors, ranging from 'floodwater' to pheromones, may serve as triggers releasing this second phase.

Stress, crowding, and pollutants have all been shown to affect the endocrine system. The behavioral effects of these endocrine changes have only rarely been considered.

Attempts to control teleost reproduction for aquaculture and management purposes include manipulation of environmental conditions to control gonadal development, induction of ovulation and spermiation in fish which become gravid but fail to spawn in captivity, and treatment with steroids to induce sex-reversal or enhance growth. The behavioral consequences of these procedures have been largely ignored. It is suggested that if aquaculturists are to obtain maximum benefits from their attempts to control breeding, it is essential that more attention be directed to understanding the behavioral component in the endocrine-behavior axis.

Introduction

Most recent work on the endocrine control of reproduction has been concerned with the regulation of gonadal growth and maturation, with very little attention to behavior. Furthermore most attempts to apply endocrine techniques to fish culture are aimed specifically at circumventing "behavioral problems," such as the fact that many species of fish fail to spawn in captivity. Nevertheless, there seem to be many points in the relationship between endocrine system and behavior which might be exploited for the benefit of fish management programs.

The basic hormonal repertoire of teleost fish is essentially similar to that of other vertebrate groups (Hoar 1969; Donaldson 1973; Fontaine 1976; Idler 1973; Reinboth 1972). There are, of course, differences in the pituitary and gonadal hormones, and certain gonadal steroids are evidently peculiar to teleosts (Donaldson 1973; Idler 1973).

Baggerman (1968), Liley (1969) and Fiedler (1974) have reviewed the literature concerned with the hormonal control of behavior in fish. In addition to a role in the regulation of behavior, the endocrine system governs the development of secondary sexual characteristics which in turn are intimately involved in behavioral interactions. The following account summarizes the principal findings in the earlier reviews and introduces more recent studies.

Role of Hormones in Control of Behavior

DEVELOPMENT OF SECONDARY SEXUAL CHARACTERISTICS

Males

Experiments involving hormone therapy with or without gonadectomy have established clearly that gonadal steroids play an important role in the development of secondary sexual characteristics. These include breeding coloration which may function in attracting a mate, inter-male competition, and perhaps in maintaining reproductive isolation. Structural features include pearl organs, breeding tubercles (Wiley and Collette 1970) and fin modifications ranging from simple elongation as in the case of the gourami (Johns and Liley 1970; Kramer 1972) to more elaborate structures such as the gonopodia of poeciliid fish (Turner 1960). Smith (1974) found that treatment with methyltestosterone will induce the formation of breeding tubercles and the mucus-secreting dorsal pad in fathead minnows *Pimephales promelas.* The appearance of this pad normally coincides with the onset of breeding behavior during which the male rubs the dorsal surface against a rock surface which eventually serves as a spawning site. It is suggested that the mucus coating may serve to lubricate the site and prevent damage and (or) perhaps assist in attachment of the eggs. Smith (1976a) suggests that a similar but more widespread epidermal thickening in several cyprinid species may provide protection during their "abrasive" spawning behavior. The thickening of the skin and increased mucus production in spawning salmonids may serve a similar function. These changes can be induced in nonspawning fish by androgen treatment (Yamazaki 1972).

Males of several cyprinid species lose their alarm substance cells during breeding, presumably an adaptation to prevent misfiring of the fright reaction during "abrasive" spawning (Smith 1976a). The loss of alarm substance cells appears to be under androgen control (Smith 1973). Interestingly, in the case of the fathead minnow the male retained the fright response to alarm substances (Smith 1976b).

In addition to their role as alarm substances it is becoming increasingly clear that chemical signals (pheromones) also provide an important means of sex recognition, attraction and excitation in fish (Bardach and Todd 1970; Pfeiffer 1974). Male pheromones which attract and excite both males and females have been described in rainbow trout *Salmo gairdneri* (Newcombe and Hartman 1973) and Pacific herring *Clupea harengus pallasi* (Stacey and Hourston MS). In *Blennius pavo* (Laumen et al. 1974) and three species of *Hypsoblennius* (Losey 1969) the male pheromones appear to attract and excite only other males, and in two species of *Colisa* (Rossi 1969) and *Betta splendens* (Ingersoll et al. 1976) there appears to be a chemical released which inhibits reproductive or aggressive behavior.

Only in one study has there been an attempt to identify both the source and possible endocrine control of male pheromone production. Laumen et al. (1974) demonstrated that a male pheromone is secreted by appendices of the anal fin spines of mature males of *Blennius pavo*. As a result of experiments in which immature males were injected with mammalian LH and methyltestosterone, these authors concluded that the development and function of the glands is under the direct influence of hypophysial gonadotropin. In *Hypsoblennius* there are anal secretory pads which may be the source of pheromone. But it was also noted in these species that ejaculation occurred at the same stage of courtship that the pheromone first appeared (Losey 1969), and Stacey and Hourston (MS) note that in Pacific herring spawning can be triggered by the presence of herring milt. These observations suggest that the pheromone may be produced in the genital system and perhaps released with the milt.

Females

In most teleosts hormone-dependent secondary sex characters are 'male-positive' (Yamamoto 1969). There are a few unequivocal examples of gonadal hormones' governing the development of female characteristics, although it is clear that treatment with estrogen is effective in inducing sex reversal in genetic males of many species tested (Schreck 1974). One group of sexual characteristics which may prove to be under hormonal control is the sexual pheromones. Pheromones which attract and stimulate conspecific males have been demonstrated in the frillfin goby *Bathygobius soporator* (Tavolga 1956), channel catfish *Ictalurus punctatus* (Timms and Kleerekoper 1972), several anabantids (Mainardi and Rossi 1968; Rossi 1969), several species of poeciliids (Amouriq 1964; Liley 1966; Zeiske 1968; Gandolfi 1969; Parzefall 1970, 1973; Crow and Liley 1979), rainbow trout (Newcombe and Hartman 1973), *Astyanax* (Wilkens 1972), and goldfish *Carassius auratus* (Partridge et al. 1976). Several of these studies suggest that the pheromone is produced in, or under the control of, the ovary at about the time of ovulation and is released shortly before or during spawning (see in particular Tavolga 1956; Amouriq 1965; Partridge et al. 1976). In the case of the guppy *Poecilia reticulata,* Crow and Liley (1979) found that the release of the pheromone is restricted to the short period of receptivity following parturition.

REPRODUCTIVE BEHAVIOR

Teleosts display a bewildering variety of patterns of reproductive behavior. At one extreme species such as the Pacific bonito *Sarda chiliensis* form temporary pairs within a school and release gametes freely into the water (Magnuson and Prescott 1966). Other species prepare a nest site, defend a territory, and go through elaborate pair formation and mating ceremonies. These activities are often followed by extended care of the eggs and young involving one or both sexes (Baerends 1971). Not surprisingly the various components and phases of the breeding cycle may be governed by different causal factors and, in considering the role of endocrine agents, it is convenient to distinguish three major phases in the breeding cycle: prespawning, spawning, and postspawning care of eggs and young.

Prespawning behavior: males

Included here are nestbuilding, territorial defense, and courtship, activities which normally precede the actual release of gametes (spawning) by hours or days. These activities appear to be androgen-dependent in most species examined. In a few studies there are suggestions that some or all of these behaviors persist after castration. For example, Aronson (1959) reported that in *Aequidens latifrons* all elements in the mating pattern were still present up to 6 wk after castration. The most striking change was a decline in nest-digging. Other examples are reviewed by Liley (1969) and Fiedler (1974).

Fiedler (1974) concludes that in fishes, in contrast to mammals, gonadotropins have a direct effect upon sexual behavior. However, I believe that for a number of reasons this conclusion is premature. Firstly, experiments involving castration rarely include adequate checks on the completeness of castration. Aronson (1959) stressed the danger that even very small fragments of gonadal tissue may regenerate and provide sufficient hormone to induce reproductive behavior. This is believed to be the explanation of the persistence of breeding behavior in 5 of 13 castrated male gouramis *Trichogaster trichopterus* in a study by Johns and Liley (1970).

Secondly, there is a danger of erroneously classifying as reproductive those behavior patterns which function in a nonreproductive context. Agonistic behavior occurs in a variety of behavioral situations: defense of a territory or nest site, and as a component in courtship, but it is also involved in a variety of nonreproductive roles, including intraspecific competition for food and nonbreeding space, and the maintenance of individual distance and dominance status. Behavior patterns involved in these different agonistic contexts may be quite similar in form, but it should not be surprising if causal mechanisms prove to be different. Thus, in contrast to the variable effects of castration on sexual behavior, all castrated male gouramis in Johns and Liley's (1970) study were as aggressive as controls. However, the agonistic behavior observed was not directed to the defense of a territory or nest-site, but simply resulted in the establishment of dominance relationships. In other words, the agonistic behavior has a nonreproductive function. This interpretation may be applied to other studies, particularly those with sticklebacks by Hoar (1962), Baggerman (1966), and Wootton (1970), which reveal a persistence of agonistic behavior after castration, in immature animals, or in the nonbreeding season (Liley 1969).

Thirdly, Fiedler's (1974) conclusion is based in part upon the results of the application of hormones and inhibitory agents (antiandrogens and antigonadotropins) to intact animals. Interpretation of the results of such studies relies heavily upon conjecture as to the effectiveness of the stimulatory, inhibitory, and negative feedback effects of such treatments.

In conclusion, the available evidence suggests that the occurrence of prespawning behavior in male fish is governed by gonadal hormones. Although there does not appear to have been any attempt to identify precisely when in relation to gonadal and endocrine events prespawning behavior commences (as has been possible with some female teleosts, see next section), it seems likely that the onset of male prespawning activity coincides closely with the occurrence of spermiation (release of spermatozoa into the sperm duct by thinning of the semen). Some experimental studies suggest that spermiation is a direct effect of pituitary gonadotropin; other observations indicate that spermiation is mediated by gonadal androgens secreted in response to gonadotropin (see de Vlaming 1974). The fact that treatment with androgens alone is sufficient to restore sexual behavior of castrated males in several species studied (e.g., Johns and Liley 1970) indicates that stimuli from the gonads or ducts are not essential to the onset of reproductive behavior in spermiated males.

There is little unequivocal evidence that pituitary hormones are involved in regulating prespawning behavior other than through a tropic control of androgen secretion. However, pituitary hormones do appear to play a direct role in spawning and postspawning behavior, and in the control of agonistic behavior not directly involved in reproduction. In the latter case, experiments involving treatment with gonadotropins (mammalian) suggest that gonadotropin may be the factor responsible (Hoar 1962). On the other hand Smith (1969, 1970) found aggressive behavior in *Lepomis* was not affected by treatment with androgen or Human.Chorionic Gonadotropin, whereas both hormones increased nest digging behavior.

Just how androgens exert their effect on prespawning behavior has hardly been considered. Studies with *Bathygobius* (Tavolga 1955) and the goldfish (Partridge et al. 1976) indicate that responsiveness to sexual pheromones produced by the female is governed by the male's endocrine state. Partridge et al. (1976) found that unspermiated male goldfish failed to respond to the pheromone, whereas spermiated males did react. However, they also noted that spermiated males exhibited an increased sensitivity to food odor, suggesting that perhaps the increased response to a pheromone reflects a general increase in olfactory responsiveness induced by physiological changes associated with spermiation. Work by Goff (1979) provides some support for this suggestion. Recording from the olfactory bulb he found a nonspecific increase in responsiveness to odors in spermiated male goldfish. Earlier investigations by Oshima and Gorbman (1968, 1969) and Hara (1976) established that administration of sex steroids to goldfish augmented the response of the olfactory epithelium to chemical stimulation. The effects induced by sex hormones involved changes in amplitude and patterns of response rather than a change in threshold.

Numerous studies (references in Schwagmeyer et al. 1977) have demonstrated that ablation of the telencephalon of fish results in severe impairment of reproductive behavior. Experiments involving electrical stimulation of the brain in *Lepomis* (Demski and Knigge 1971; Demski et al. 1975) implicate the preoptic area of the brain in nest-building, courtship, spawning and sperm release. Macey et al. (1974) and Peter (1977) also indicate that the preoptic region is involved in the control of the spawning reflex in *Fundulus*. Recently Demski (1978) using autoradiographic techniques has demonstrated that the parvocellular region of the preoptic area of *Lepomis* contains testosterone-concentrating neurons. On the basis of these findings, Demski (1978) suggests that higher forebrain influences on reproduction may be mediated by activation of small neurons in the preoptic area of the brain, an area known to receive afferent inputs from the olfactory bulbs, optic, trigeminal and vagus nerves, and the telencephalon and spinal cord (Peter 1977). Thus, these studies, although limited to a small number of species, strongly suggest that in fish as in mammals (Davidson 1972) and birds (Hutchison 1976) the preoptic area is involved in the integration of hormonal, olfactory, and behavioral inputs, and plays a key role in the organization and control of reproductive behavior.

Prespawning behavior: females

As in most vertebrate species female fish assume a less distinctive breeding coloration and play a more passive role in the mating process. Perhaps because of this, hormonal regulation of female behavior has received far less attention than that of the male. Nevertheless, the female does contribute actively in the breeding interaction and, as in the case of the male, it is useful to distinguish between prespawning and spawning phases in the breeding process.

Apart from an obvious correlation between ovarian maturation and spawning readiness (e.g., Lambert and van Oordt 1974; Polder 1971; Schreck and Hopwood 1974; Yaron et al. 1977), there is still relatively little direct evidence of a role of gonadal hormones in the control of female sexual behavior. Ovariectomy results in a loss of sexual responsiveness in the small number of species investigated (Liley 1969). But, apart from causing an increase in locomotory activity in goldfish and guppies (Liley 1969) only in two species has it proved possible to demonstrate a direct effect of estrogen treatment on behavior. Nevertheless, the results of both of these studies appear to have important general implications.

One of these studies concerns the viviparous guppy *Poecilia reticulata*. Liley (1966) demonstrated that the female undergoes regular cycles in sexual receptivity and displays maximum responsiveness to male courtship in the few days following parturition. The female also produces a pheromone which attracts and excites males (Amouriq 1964; Gandolfi 1969; Crow and Liley 1978). Release of this pheromone appears to be restricted to the period of receptivity following parturition (Crow and Liley 1978).

The period of receptivity and pheromone production coincides with vitellogenesis in the ovary and, according to histochemical studies (Lambert and van Oordt 1974), with maximum steroidogenesis. Ovariectomy causes a decline in sexual responsiveness and pheromone production. The behavioral response is restored by treatment with estrogens (Liley 1972). (The effect of estrogens on pheromone production has not been examined.) Hypophysectomy results in a loss of the sexual response which is restored by estrogen treatment alone, an indication that the pituitary is not directly involved in controlling sexual behavior.

Some long-term ovariectomized females (Liley 1968), and most virgin females ovariectomized 1 to 3 wk earlier, respond sexually to male courtship (Liley and Wishlow 1974). This response disappears after a few days. Thus, although experiments involving hormone administration establish clearly that sexual responsiveness is affected by estrogens, the occurrence of sexual behavior in ovariectomized fish leads to the conclusion that sexual responsiveness is not completely dependent on gonadal hormones. Liley and Wishlow (1974) suggest that sexual responsiveness in the female guppy is the outcome of an interaction between the effects of ovarian hormone and the influence of nongonadal factor(s). The nongonadal factor is sensitive to 'experience' and serves to adjust the female's response to the social environment.

The second study concerns the oviparous goldfish *Carassius auratus.* Injection of estrogen into intact females does not by itself induce increased sexual behavior. However, Stacey and Liley (1974) established that a key factor in the onset of spawning readiness is the stimulus provided by a mass of freshly ovulated eggs in the lumen of the ovary or in the oviduct. The clearest demonstration of the role of eggs is provided by experiments in which eggs were taken from an ovulated female and injected through the ovipore into the ovarian lumen of another female. Provided the ovaries of the recipient were in a vitellogenic stage (but without ovulated eggs) the recipient female performed normal spawning behavior when paired with a sexually active male. Females with regressed ovaries failed to respond to egg injection; however, treatment of regressed fish with a variety of gonadal steroids, both estrogens and androgens, restored the spawning response to egg injection. Evidently the gonadal steroid governs the responsiveness of the female to the stimulus provided by the mass of eggs. This effect may be mediated at the level of sensory receptors in the oviduct or abdominal cavity and (or) by areas of the hypothalamus implicated, in studies cited earlier, in the regulation of sexual behavior.

Hypophysectomy eliminates the response of goldfish to the injection of ovulated eggs. This response is not restored by steroid treatments alone, but can be induced by a combination of gonadotropin preparation and steroid hormones (Stacey 1977).

Correlated with the increase in sexual responsiveness of female goldfish at ovulation is an increase in attractiveness to the male. This attractiveness appears to depend largely upon the release of a pheromone produced in the ovary around the time of ovulation (Partridge et al. 1976).

It is of interest to compare the cause of sexual behavior in the guppy and goldfish. In the former the increase in sexual responsiveness is specific to estrogens, is not affected by hypophysectomy (as long as estrogens are present), and evidently does not depend upon stimuli from the ovary and oviduct. Androgens as well as estrogens will induce responsiveness in the female goldfish, but this also requires the stimulus provided by a mass of eggs and a pituitary contribution. Perhaps these differences in causal mechanisms reflect differences between the oviparous, presumably primitive, teleost condition and the specialized ovoviviparous mode exemplified by the guppy. Thus, it appears that the female goldfish remains in an endocrine state appropriate for breeding for several weeks, but spawning is normally synchronized with ovulation by the stimulus of a large intra-ovarian mass of ovulated eggs which acts as a fine control in the timing of sexual responsiveness. In the guppy, perhaps because mating does not have to be so closely synchronized with ovarian events—mature eggs remain viable and may be fertilized over a period of several days—the gonadal steroids have become more directly involved in the control of sexual response, resulting in the situation analagous to that in female mammals.

Preliminary studies with the flagfish *Jordanella floridae* (Crawford 1975), rainbow trout *Salmo gairdneri* (Liley, unpublished), and Pacific herring *Clupea harengus pallasi* (Stacey and Hourston MS) confirm the importance of ovulation and presence of eggs in the onset of prespawning and spawning behavior, but whereas prespawning and spawning behavior follow within hours of ovulation and may be complete within 2-4 h (goldfish) or 4-5 days (trout), in the Pacific herring it appears that ovulated and spermiated individuals can retain their gametes in viable condition for long periods (N.E. Stacey, Dept. of Zoology, Univ. of Alberta, Edmonton, Alberta, pers. comm.). In the lab ovulated and spermiated fish could be held for at least 2 mo and still exhibit apparently normal spawning behavior, although it is likely that in the sea fish would spawn within 1-2 wk of ovulation or spermiation.

Spawning in the herring is actually triggered by the presence of herring milt; addition of a small amount of suspension of milt induces extension of the genital papilla, and in the presence of appropriate substrate, the onset of spawning by both males and females within as little as 2-3 min (addition of ovulated eggs has no effect on spawning). These observations suggest that the milt contains a pheromone which stimulates spawning within a school. The mass spawning which results is sufficient to cause a conspicuous milky discoloration of the water over the spawning grounds (Hourston and Rosenthal 1976).

Although the consequences of ovulation are less immediate, the limited evidence suggests that as in the other oviparous species studied it is the presence of the ovulated eggs and the associated endocrine conditions which determine the response of the female herring to the pheromone and spawning substrates: nonovulated females do not show the increased swimming activity, or the extension of the genital papilla in response to herring milt, typical of ovulated females.

In conclusion, although there is ample evidence of the occurrence of estrogens (and in some cases androgens, Reinboth 1972; Katz and Eckstein 1974) in teleost ovaries there is still a remarkable paucity of information regarding the function of these steroids in morphological development, metabolism and behavior. Work with the guppy and goldfish provides a clear demonstration of the influence of estrogens on behavior, but, in the case of the goldfish, provides a warning that in an oviparous fish it may not be sufficient to inject a hormone and look for behavioral effects. Unless appropriate stimuli from genital tracts are present, such treatments are almost certain to yield negative results.

Corticosteroids have been implicated in the control of ovulation and spawning. Sundararaj and Goswami (1966) treated sexually mature but unovulated female catfish *Heteropneustes fossilis* with several steroids; only the corticosteroids induced ovulation, and in some cases oviposition, in the absence of males. Since then, other workers have shown that corticosteroids may induce ovulation (Jalabert 1976). However, there is no evidence that corticosteroids exert a direct influence on reproductive behavior. Corticosteroids were without effect when administered to ovariectomized female guppies (Liley 1972) and ineffective in priming regressed female goldfish prior to the injection of ovulated eggs from a donor female (Stacey 1977). Jalabert (1976) reviews the evidence in favor of a 'direct gonadotropic route' triggering oocyte maturation. The effect of the ovulatory surge of gonadotropin is believed to be mediated by 17α-hydroxy-20β dihydroprogesterone produced by follicular envelopes in response to gonadotropin action. Jalabert (1976) suggest that in *H. fossilis*, and perhaps other species, there is an alternate 'indirect corticotropic route' involving corticosteroids which in turn mediate oocyte maturation, perhaps by increasing follicle sensitivity to 17α-20β Pg. Thus any effect of corticosteroids on spawning behavior is indirect: the female (presumably with high levels of endogenous estrogen) responds to the stimulus provided by the mass of eggs ovulated under the influence of corticosteroids.

Spawning behavior: males and females

Involvement of neurohypophysial hormone in spawning behavior of the killifish *Fundulus heteroclitus* was proposed by Wilhelmi et al. (1955) when it was discovered that intraperitoneal injections of large doses of mammalian neurohypophysial hormone preparations induced a "spawning reflex response." This response occurs in gonadectomized, hypophysectomized fish and is not preceded by pair formation or any distinct prespawning behavior (a prominent feature of "normal" spawning). Comparable results have been obtained with females of *Oryzias* (Egami 1959) and *Rhodeus* (Egami and Ishii 1962) and male and female *Jordanella floridae* (Crawford 1975). The same treatments appear to be without effect in several species tested: *Carassius* (Pickford in Macey et al. 1974; Stacey 1977); *Misgurnus fossilis* and *Salmo* (Egami and Ishii 1962); *Gasterosteus aculeatus* (Lam, Nagahama, and Chan, pers. comm.); *Heteropneustes fossilis* (Sundararaj and Goswami 1966).

Treatment of *Fundulus* with teleost neurohypophysial hormones arginine vasotocin and isotocin confirmed the earlier results obtained with mammalian preparations (Macey et al. 1974) and revealed that arginine vasotocin was the more potent of the two prinicipal components (Pickford and Strecker 1977).

Macey et al. (1974) found that destruction of the preoptic nucleus reduced or eliminated the reflex response to exogenous neurohypophysial hormone preparations. They suggested that the preoptic nucleus is involved in the spawning behavior of the killifish and that neurohypophysial hormones exert their effect by their action on the preoptic nucleus.

However, a more recent study casts doubt on that interpretation: Peter (1977) reports that arginine vasopressin injected directly into the third ventricle of the brain was no more effective in eliciting the reflex response than intraperitoneal injections, suggesting that the hormone exerts its effect through a peripheral action. Peter (1977) concludes that in view of the large doses normally required to elicit a spawning reflex response, the activation of a peripheral receptor by neurohypophysial hormones is probably not part of the normal mechanism for triggering spawning behavior in teleosts, although the possibility remains that neurohypophysial hormones may be involved via their ability to stimulate oviduct and ovarian smooth muscles in teleosts (Heller 1972). In this regard it is perhaps significant that the three species in which neurohypophysial hormones have the most striking effect, *Fundulus, Oryzias* and *Jordanella,* are all killifishes of the family Cyprinodontidae. A characteristic of this group is that during a breeding season they may spawn daily for several days or even weeks, the female depositing relatively few eggs at a time. In *Jordanella,* in which the female 'places' the eggs individually or in small groups, this type of oviposition appears to be associated with the presence of a large muscular oviduct (Crawford 1975). In view of the ability of neurohypophysial hormones to stimulate oviduct and ovarian smooth muscle in teleosts, it seems likely that these hormones induce spawning-like responses through their effects on oviduct and ovarian smooth muscle, and perhaps comparable muscular tissue in the male.

Whereas oxytocin has no effect on spawning in either male or female goldfish, intraperitoneal injections of prostaglandins, particularly PG $F_{2\alpha}$, induced spawning responses (without release of eggs) in females with vitellogenic ovaries but without ovulated eggs (Stacey 1976). Spawning activity developed within 1/2 hour, but unlike the induced spawning reflex of *Fundulus,* occurred only when females were paired with sexually active males. This same i.p. treatment was without effect when applied to male goldfish, but Stacey (pers. comm.) reports that intramuscular injections of PG $F_{2\alpha}$ induced female spawning movements in male fish!

A number of recent studies suggest that prostaglandins may be of general importance in the spawning of oviparous fish. Crawford (1975) observed spawning responses in unpaired male and female *Jordanella* after administering prostaglandin, PG $F_{2\alpha}$. Indomethacin, a prostaglandin synthesis inhibitor, blocks digging and spawning behavior in female rainbow trout (Liley, unpublished) and inhibited spawning in response to milt in ovulated Pacific herring (Stacey, pers. comm.). Prostaglandin treatments induced sexual responses in female sticklebacks (Lam and Nagahama, pers. comm.). In contrast, neither prostaglandins nor indomethacin had any effect upon the viviparous guppy (Liley, unpublished).

What is the role of prostaglandin in the control of spawning? Prostaglandins are known to stimulate contraction of smooth muscles and have been implicated in parturition and oviposition in mammals and birds (Labhsetwar 1974) and in ovulation in goldfish (Stacey and Pandey 1975). In addition it has been shown that stretching of uterine muscle stimulates prostaglandin release (Poyser et al. 1971). Against this background Stacey (1976) hypothesized that distension of the oviduct following ovulation (or injection of ovulated eggs) results in the release of prostaglandin (most likely PG $F_{2\alpha}$) which then acts directly or indirectly to induce spawning behavior.

The source of endogenous prostaglandin is not known. Prostaglandin may be released from the oviduct following physical stimulation or it may be released centrally in response to afferent signals generated in the oviduct. Equally little is known as to the mode of action of prostaglandin in inducing behavior. Perhaps the prostaglandin acts directly on central nervous system mechanisms, or it may act less directly, perhaps by causing the release of the teleost equivalent of mammalian LH RH (Ojeda et al. 1975) which has been shown to induce or increase lordosis behavior in hypophysectomized, estrogen-treated female rats (Pfaff 1973).

It is clear that much further work is required before concluding that prostaglandins play a physiological role in causing spawning in teleosts. In addition there remains the question as to how the link provided by neurohypophysial hormones in killifish fits into what may prove to be a more widespread causal mechanism in teleost reproduction.

Postspawning behavior

In the great majority of teleost species spawning is followed by a break-up of the temporary pair, and neither partner pays any further attention to the eggs. However, in other species spawning is followed by a period in which one or both sexes guard the eggs and young. Several studies have implicated a prolactin-like hormone in the regulation of this parental behavior (reviewed by Liley 1969; Fiedler 1974; Blum 1974). These studies show that in a variety of species of cichlids, and in the wrasse *Crenilabrus ocellatus,* in which one or both parents fan the eggs, this fanning behavior can be induced by injection of mammalian prolactin. Prolactin also stimulates an increase in mucus secretion, which in *Symphosodon* serves as a nutrient for the young. Blum (1974) has confirmed that these same behavior patterns and mucus-stimulating effects can be induced by paralactin prepared from the fish hypophysial material.

Smith and Hoar (1967) injected male threespine sticklebacks *Gasterosteus aculeatus* with prolactin and found no evidence that the pituitary is directly involved in the regulation of parental behavior. Their finding that castration early in the parental phase resulted in a decline in fanning led them to conclude that parental fanning is regulated by a testis hormone. However, in a study by Molenda and Fiedler (1971) it was found that low doses of prolactin increased fanning in male sticklebacks, whereas high doses similar to those applied by Smith and Hoar inhibited fanning in males with nests.

A number of studies implicate gonadal hormones in the control of parental behavior. Machemer and Fiedler (1965) concluded that in the paradise fish *Macropodus opercularis* full nestbuilding activity depends upon two hormones. Androgen increases building activity, but this effect is expressed fully only in the presence of a prolactin induced increase in mucus production. Kramer (1972) confirmed the effects of androgen on nestbuilding of another anabantid, *Trichogaster trichopterus.* He found also that female gouramis, which do not normally perform nestbuilding or parental care, would build nests and could be induced to retrieve eggs to the nest after treatment with androgen. A synergism between prolactin and estrogen is believed to be involved in the control of mouthbrooding behavior of females of *Tilapia mossambica* (Fiedler 1974).

HORMONES AND MIGRATION

Woodhead (1975) has provided a thorough review of the extensive literature on the endocrine physiology of migration. Although there is little reason to doubt that the endocrine system plays an essential role in mediating the osmoregulatory and metabolic responses necessitated by migration, there is still no clear evidence that hormones play a causal role in the onset and maintenance of migratory behavior.

Environmental and Behavioral Influences on the Endocrine System

It is well established that the endocrine system regulates many aspects of behavior, but it is equally clear that the endocrine system is itself responsive to behavioral and environmental stimuli. The interaction between environment, endocrine system, and behavior ensures breeding at an appropriate time and place and maintains a smooth progression through the different phases of the breeding cycle.

A majority of teleost species, even in tropical regions, are seasonal breeders. This is an evolutionary response to the fact that certain periods of the year may be more favorable to survival of eggs and young, and may involve not only suitability of the physical environment and food supply, but biotic factors such as predation, inter- and intraspecific competition, and a species' social system (Kramer 1978). These are the "ultimate" factors to which breeding seasons are adapted. The actual timing of breeding is determined by the "proximate" environmental factors which "predict" the favorable season in advance (for full discussion of the relationship between ultimate and proximate factors, see Immelmann 1971). Considerable evidence suggests that the influence of proximate external factors is mediated by neuroendocrine mechanisms which govern the pituitary-gonad axis (Donaldson 1973; de Vlaming 1974).

In considering the role of these exogenous factors, it is important to recognize that gonadal development is usually a lengthy process, taking place over weeks or months before the breeding season. Only at the end of the growth phase do ovulation and spermiation occur and prespawning and spawning behaviors more or less suddenly appear. This suggests that it is important to distinguish two developmental phases, each governed by the endocrine system, and each with its own set of causal factors. These phases will be referred to as (a) gametogenesis and gonadal growth, and (b) final maturation of the gametes, and ovulation and spermiation. Sexual behavior appears to be mainly associated with the second phase, whereas behavior in preparation for breeding such as migration towards the breeding grounds must be initiated in the first phase of gonad development.

FACTORS GOVERNING GAMETOGENESIS AND GONADAL GROWTH

Photoperiod and temperature have been implicated in the timing of gonadal cycles and sexual maturation of many species of fish (reviews by Schwassmann 1971; de Vlaming 1972, 1974). De Vlaming (1972), critical of many of these investigations, points out that although photoperiod has frequently been credited as the dominant environmental regulatory factor, photoperiodic responses seem to be temperature-sensitive in most species studied. Furthermore, the short-term nature of many investigations may result in misleading conclusions, especially as the effect of photoperiod and temperature may vary with season and phase of reproductive development.

With the above reservations, de Vlaming (1972) tentatively suggests that in salmonids photoperiod may exercise a dominant role in regulating reproductive cycles, whereas in cyprinodontiform fishes temperature may play a more critical role. Changes in photoperiod appear to play some role in the gasterosteids. Both photoperiod and temperature may be significant regulatory factors in the reproductive cycles of cyprinid and perciform fishes.

It is apparent that even among the relatively small number of species studied there is considerable diversity in reproductive timing mechanisms. No doubt this is in part a reflection of the diversity in phylogeny, geographic distribution, and ecological adaptations of the species concerned.

De Vlaming (1972) stresses the fact that the effect of photoperiod and temperature vary with the season. The mechanism underlying such changes in sensitivity may lie in the existence of an endogenous circannual rhythm. Bullough (1940) concluded that in the European minnow *Phoxinus laevis* there is an internal reproductive rhythm which under normal circumstances is reinforced and brought into phase by seasonal variations in the environment. Ahsan (1966) argues that in the lake chub *Couesius plumbeus*, the fact that the final stage of testicular maturation could be induced only by experimental photoperiods and temperatures as the normal time of spawning approached, suggests that there is an endogenous rhythm of reproduction which is timed by temperature and photoperiod but not completely governed by them. Baggerman (1972) noted seasonal changes in response to photoperiod manipulations in the stickleback. The most direct evidence for the existence of an endogenous rhythm comes from the work of Sehgal and Sundararaj (1970) and Sundararaj and Sehgal (1970). In experiments in which female catfish *Heteropneustes fossilis* were held in total darkness at constant temperature, ovarian recrudescence followed by regression occurred. The ovarian cycle became out of phase with the "natural" cycle by as much as 2 months in animals kept in total darkness for 536 days.

Experiments involving manipulation of both temperature and photoperiod indicate that although gonadal development may be accelerated or delayed, in some species there are definite limits to the extent to which breeding can be rephased, suggesting that limits may be imposed by an endogenous rhythm. For example, Sundararaj and Vasal (1976) found that although they could accelerate the ovarian cycle so that *Heteropneustes fossilis* spawned

5 mo early, they could not postpone postspawning regression by more than 2 mo. In contrast, Lasker (1974) reports that with a fixed photoperiod of 4 h light per day and a temperature of 15°C it is possible to maintain laboratory populations of the northern anchovy *Engraulis mordax* in which some fish are sexually mature and spawning every day of the year. However, it is perhaps significant that under natural conditions this species has a prolonged breeding season, and although there is a marked peak in spawning early in the year, some eggs may be found in any month.

It seems likely that the relative importance of the endogenous rhythm and exogenous factors in controlling the breeding activity will vary considerably, depending upon the ecology and geographical distribution of the species concerned. In environments with profound, reliable, seasonal changes in temperature and photoperiod these external factors are likely to play a dominant role in phasing the breeding cycle, with the endogenous rhythm playing a permissive role. In locations where seasonal changes in photoperiod and climate are less marked and reliable, the endogenous rhythm may be paramount. Thus Schwassmann (1971) suggests that perhaps in tropical species a long-term, externally-timed phasing is absent and that an internal physiological rhythm proceeds on its own and maintains a "mature" condition for some time, with the actual onset of breeding being released by a particular stimulus such as rainfall.

In addition to annual rhythms, it is well known that most fish species display a circadian rhythm in many aspects of their behavioral activities. Circadian rhythms in spawning activity have been noted in the medaka (Egami and Nambu 1961) and in several species of anabantid fish (Hall 1966; Johns and Liley 1970). The physiological basis of these spawning rhythms is unknown.

A number of investigators have demonstrated the existence of circadian rhythms in response to light and hormones, and in the release of hormones. Baggerman (1972), Chan (1976), and Sundararaj and Vasal (1976), by introducing light pulses into the night phase of an experimental photoperiod, have demonstrated in threespine stinklebacks, medaka, and *Heteropneustes fossilis*, respectively, that a circadian rhythm in sensitivity to light may provide the basis for the gonadal response to photoperiod. Investigations involving goldfish (Breton et al. 1972), cutthroat and rainbow trout (O'Connor 1972), and the golden shiner *Notemigonus crysoleucas* (de Vlaming and Vodicnik 1977a) have resulted in data which suggest that release of gonadotropin from the pituitary is related to the daily light cycle. De Vlaming and Vodicnik (1977a) noted that the rhythm was evident in fish held at long photoperiod (15.5 h L) but not under short days (9 h L). De Vlaming and Vodicnik (1977b) found that the daily rhythm in pituitary gonadotropin was altered by pinealectomy, and postulate on the basis of this and other effects of the operation that the pineal is involved in mediating the response to photoperiod.

Endogenous rhythms may also influence responsiveness to circulating hormones. De Vlaming and Vodicnik (1977a) found that salmon gonadotropin was more effective in stimulating gonadal development in the golden shiner when administered early in the light phase; the same dose given late in the day was ineffective. In the medaka gonadotropin proved to be more effective in stimulating ovulation late in the light phase than at other times of the day (Hirose and Donaldson 1972).

De Vlaming and Vodicnik (1977a) also found daily rhythms in response to ovine prolactin. At 24°C and long photoperiod prolactin retarded gonadal development in golden shiners independent of injection time, whereas at 15°C injections of prolactin given early but not late had an antigonadal effect.

Although fragmentary at present these studies of circadian and circannual phenomena serve as a reminder that temporal aspects of hormone production and responsiveness to hormones must be examined further. The work of Meier (1972, 1975) indicates that an understanding of the timing of long-term rhythms of reproduction and migration may depend upon an appreciation of the interaction and synergism of endocrine rhythms having a circadian periodicity.

FACTORS REGULATING FINAL MATURATION OF GAMETES, OVULATION, AND SPERMIATION

Jalabert (1976) has shown that in at least some female teleosts, oocyte maturation (resumption of meiosis) and ovulation (expulsion of the matured oocyte from the follicular envelope) can be experimentally dissociated and shown to depend on different endocrine processes. However, as both processes depend upon pituitary gonadotropin, for present purposes it is convenient to consider the two components as part of a single event referred to here as ovulation.

The more or less sudden onset of prespawning and spawning behavior appears to be correlated with spermiation and ovulation. It is possible that these gonadal events occur as the final stage of a continuous process of gonadal growth, and are under the control of the same causal factors as the earlier stages. However, there are reasons to believe that in most species spermiation and ovulation are regulated by biotic and/or physical factors distinct from those responsible for gametogenesis and gonadal growth. This is most apparent in the control of ovulation; the situation is less clear with respect to spermiation.

Spermiation and ovulation are both induced by pituitary gonadotropins. Ovulation has been associated with a surge in plasma gonadotropin (Breton et al. 1972). This poses the question: What are the exogenous factors which act through the brain-pituitary mechanism to time the occurrence [illegible] and spermiation?

This question is of particular importance [illegible] fish culture programs. For example, many of the widely cultivated species of Indian and Chinese carps do not breed in captivity (Chaudhuri 1968). In most cases fish mature and remain in a state of preovulatory and prespermiation readiness but fail to spawn, presumably because of the lack of the factor which normally induces ovulation and spermiation and the "release" of spawning. Treatment with pituitary gonadotropin preparations (hypophysation) is usually sufficient to induce ovulation and spermiation. The treated fish are then stripped or allowed to spawn.

Investigations involving many species indicate that both physical and biotic factors may be involved in the "release" of breeding. One of the best studied species is the goldfish. Yamamoto et al. (1966) found that goldfish held under long photoperiod (16 h light/day) and at 14°C or less develop to a prespawning stage but neither ovulate nor spermiate. Raising the temperature to 20°C results in most fishes' spermiating or ovulating. Spawning commences within a few hours. Ovulation may occur with or without males present, but the presence of males and green plants are necessary for spawning and oviposition (Yamazaki 1965).

Thus we see that in the goldfish a rise in temperature appears to be the factor which stimulates ovulation and spermiation; thereafter the fish become responsive to a variety of stimuli from the partner and the environment. A sudden rise in temperature appears to be a key factor in the induction of spawning in captive *Bairdiella icistia* already brought into a prespawning condition by photoperiod and temperature manipulations (Lasker 1974). Dodson and Young (1977) report their own investigations with the common shiner *Notropis cornutus*, and the work of others with the common shiner, redside shiner *Richardsonius balteatus*, and the brook stickleback *Culaea inconstans*, which indicate that upstream spawning migrations of these species occur in response to increasing water temperatures. In none of these studies reported by Dodson and Young (1977) is there information on the gonadal condition of fish initiating the spawning migration.

Numerous tropical and subtropical species of freshwater teleosts are known to breed soon after the onset of heavy rainfall at the start of a wet season. Frequently spawning coincides with the occurrence of flooding (Chaudhuri 1968; Sinha et al. 1974; Schwassmann 1971; Lake 1967; van der Waal 1974). Should the floods fail, the fish may not spawn that year as happened in Lake Malawi (Lowe-McConnell 1975) and as Khanna (in Sinha et al. 1974) reported for cyprinids in India.

Attempts to correlate the onset of spawning of Indian carps with the physical and chemical changes which accompany heavy rain and flooding (changes in depth, current, temperature, turbidity, dissolved oxygen, etc.) do not reveal any consistent pattern (Chaudhuri 1968; Sinha et al. 1974). However, a number of reports note that spawning in several species of carp occurs shortly after mature but unovulated carp are released into shallow earth-lined ponds (bundhs) recently filled by floodwaters. Dubey (1969, in Sinha et al. 1974) found that carp would often commence breeding within hours of introduction into bundh water whether the weather was cool after rains or warm without rains.

These observations on Indian cyprinids parallel those of investigators in Australia and Africa. Lake (1967) studied the spawning of five species representing four families present in the Murray-Darling drainage system in Australia. Lake stresses the fact that there are enormous fluctuations in water levels and other factors in that river system. Experiments indicate that specific water temperatures and floods act as triggering mechanisms for spawning. For example, *Plectroplites ambiguus* would spawn in ponds only if water temperatures remained above 23.6°C, but spawning did not occur at that temperature (or above) unless the pond had been recently filled. Interestingly, Lake (1967) postulates that the native species of fish are stimulated to spawn by a factor resulting from the inundation of dry ground. He hypothesizes that this factor may be petrichor, an oil which has been isolated from silicate minerals and rocks by Bear and Thomas (1964). Petrichor is believed to be responsible for the characteristic odor associated with rain falling on dry soil.

Van der Waal (1974) reports his own and other observations which indicate that spawning of African catfish (*Clarias* spp.) is triggered by factors associated with flooding of previously dried out shallow ponds.

Thus there are firm indications that some factor associated with floodwater, perhaps washed out of dry soil, may be the effective stimulus inducing spawning in many species of tropical and subtropical fish. However, it is equally clear that this explanation cannot apply in all cases. Of six species of characids inhabiting a tropical forest stream in Panama, Kramer (1978) found that two species, *Bryconamericus emperador* and *Piabucina panamensis,* spawned in temporary tributaries with the first floods of the rainy season. *Brycon petrosus* and *Hyphessobrycon panamensis* spawned in the dry season. The majority of adult *Gephyrocharax atricaudata* were mature in most months, but fry appeared in several peaks scattered through both dry and rainy seasons. *Roeboides guatemalensis* seemed to breed throughout the year but with a dry season peak.

In spite of the large number of studies on environmental control of breeding in coldwater teleosts such as salmonids and gasterosteids, nothing is known regarding the factor(s) releasing spermiation and ovulation in those species, if indeed such a specific factor exists. Peterson (1972) attempted to relate the time of entry of rainbow trout into a spawning trap to a range of environmental variables. On the basis of a 3-yr study, Peterson concluded that there was no evidence that water temperature is the controlling factor it was once thought to be. He did find evidence that spawning activity coincided with an increase or decrease in barometric pressure (but not with high or low pressure as such). Unfortunately, there is no information as to the gonadal condition of the fish moving into the trap.

Factors associated with the lunar and tidal cycles may serve to time breeding in some marine species (reviewed by Schwassmann 1971). The best studied example is the California grunion *Leuresthes tenuis* which undergoes successive semilunar spawning runs onto the beaches of Southern California from March to September. The external factor responsible for the precise timing of the run are not known. May et al. (1979) reported a lunar periodicity in spawning of threadfin *Polydactylus sexfilis* held in net enclosures.

Most of the species considered so far fall into Lowe-McConnell's (1975) "total spawner" category which includes fish which spawn all their eggs of one season in a single batch. However, many teleost species are "partial" or "small-brood spawners" which spawn several batches of eggs during a more or less extended breeding season. A characteristic of many of these species, especially those in the latter category, is the possession of an elaborate repertoire of pre- and postspawning behavior. This may include territorial defense, preparation of a nest-site, and prolonged pair formation. Spawning may be followed by care of eggs and young. Correlated with the more elaborate behavioral interaction characteristic of these species is the fact that behavioral stimuli provided by conspecifics may influence endocrine activity and perhaps trigger ovulation and spermiation, and thereby time breeding episodes.

The role of behavior in stimulating endocrine and hence gonadal activity has been demonstrated in a number of laboratory studies. Aronson (1951), Polder (1971) and Chien (1973) have shown that in three species of cichlids, visual stimulation provided by the sight of a mate or mirror image accelerated the ovarian cycle and deposition of unfertilized eggs. A chemical stimulus from the males was also effective in stimulating ovarian cycles in *Pterophyllum scalare* (Chien 1973). Lambert and van Oordt (1974) indicate that the presence of the male is necessary to maintain the 5-day ovarian cycle of *Brachydanio rerio*. They noted that activity of the pituitary gonadotrophs may be related to the presence or absence of males. Johns and Liley (1970) found that 2 or 3 days exposure to a nest-building male was necessary before a female gourami *Trichogaster trichopterus* would spawn. The relatively dramatic change in the female's response—a switch from hiding from the male to approaching and butting him—appeared to coincide with the occurrence of ovulation.

Social stimulation is probably responsible for the synchronization in spawning cycles in natural populations of green sunfish *Lepomis cyanellus* and threespine stickleback described by Hunter (1963) and van Mullem (1967), respectively. Van den Assem (1967) found that male sticklebacks in winter condition came into breeding more readily if paired with one on each side of a glass partition than did solitary males. The presence of vegetation also had a stimulatory effect upon nest-building. Reisman (1968) also noted that social conditions had a marked effect upon the secondary sexual characteristics of the male threespine stickleback.

In the case of the Pacific herring it appears that the female may remain in an ovulated condition for some time (Stacey and Hourston MS). Spawning and oviposition occur in response to a pheromone in milt and perhaps to visual and tactile stimuli from suitable spawning substrates. It is not known if there are special environmental factors responsible for induction of ovulation. Aronson (1965) refers to other work involving salmon, herring, whitefish, and minnows which suggests that social facilitation may occur in the synchronization of breeding.

Conclusion:

In this section emphasis has been placed upon the distinction between two stages in the gonadal events preceding breeding. The two phases appear to be governed by different causal factors.

Annual changes in photoperiod or temperature, or both, appear to be the major environmental factors responsible for entraining the growth phase of the gonadal cycle. The relative importance of the external entraining agents and endogenous rhythms in maintaining the seasonality of reproduction varies considerably and may be assumed to reflect species differences in ecology and geographic distribution.

The growth phase of gonadal development brings fish into a condition of prespawning readiness, but the onset of reproductive behavior appears to be determined by the final maturation of the gametes and the occurrence of ovulation and spermiation. The list of physical and biotic factors already implicated in triggering this second phase suggests that only broad generalizations can be made about the nature of the cues triggering breeding. Presumably each species responds to an ecologically appropriate combination of stimuli which act through a common neuroendocrine mechanism responsible for inducing ovulation and spermiation.

Other Endocrine Changes Induced by Environmental Stimuli

There is considerable evidence that stress, such as that caused by handling, has a marked effect upon endocrine activity (Mazeaud et al. 1977; Simpson 1976). All kinds of stress result in an increase in circulating catecholamines, mainly adrenalin. In mature male coho salmon, struggling and hypoxia resulted in an increase in plasma corticosteroids (Mazeaud et al. 1977). Interrenal activity may also be affected by behavioral interactions. Noakes and Leatherland (1977) reported that isolated rainbow trout showed evidence of lower levels of interrenal activity than did crowded fish. Furthermore interrenal activity was inversely correlated with rank in a stable dominance hierarchy, except in the case of the dominant.

There are no reports of behavioral effects of these changes in corticosteroid hormone level in fish. However, the fact that administration of ACTH is known to facilitate passive avoidance learning in rats (De Wied and Weijen 1970) suggests that it may be of interest to examine the behavioral effects of stress on fish, particularly as it affects conditioning to factors associated with stress.

A small number of investigations have shown that crowding of fish may reduce fecundity or inhibit spawning (reviewed by Solomon 1977). These effects appear to be mediated by unidentified chemical factors. Although not investigated, these chemicals probably exert their effects by influencing the activity of the brain-pituitary-gonad axis.

Donaldson (1976) reviews investigations into the influence of sublethal levels of environmental pollutants upon reproductive processes. Many contaminants including heavy metals, pesticides and radiation have been shown to affect hormone synthesis and metabolism, though virtually nothing is known of any behavioral consequences of these effects. Chan (1977) presents evidence that sublethal doses of methyl mercury inhibit spawning in *Oryzias latipes* by blocking release of gonadotropin from the pituitary.

Hormones and Behavior in Fish: Relevance to Management and Culture Programs

Considerable effort has been devoted to the application of endocrine manipulation, either to induce breeding in species which are difficult to breed in captivity, or to control breeding and behavior in fish which are too prolific. For obvious technical and environmental reasons these procedures have been applied mainly to captive or semi-captive fish.

There has been almost no consideration given to any behavioral problems or implications presented by the use of endocrine manipulations. The following summarizes some of the principal approaches in attempts to regulate reproduction in teleosts. In each case some of the possible behavioral implications are considered.

MANIPULATION OF ENVIRONMENTAL CONDITIONS TO CONTROL GONADAL DEVELOPMENT

"Controlled" environmental conditions may be used to "reschedule" breeding or to induce breeding in species which fail to develop and mature in captivity and (or) in a non-native location.

Early attempts to accelerate or deccelerate reproductive development were applied mainly to salmonids (Donaldson 1976). By compressing the photoperiod cycle it has proved possible to advance breeding of brook trout by 3 mo (Hazard and Eddy 1951). Similar photoperiod manipulations are being applied to pink and coho salmon to extend the spawning season and allow production of salmon eggs and milt at 3- or 4-mo intervals throughout the year (Donaldson et al. 1977). Sundararaj and Vasal (1976) were able to extend the spawning season of catfish *Heteropneustes fossilis* and obtain 2.6 times more eggs than are usually available from each female during the spawning season.

The chief problem with these approaches is to determine *for each species* the important conditions of photoperiod and temperature or other unknown factors responsible for phasing the gonadal cycle. Nevertheless, the success achieved so far, e.g., Donaldson (1976) Sundararaj and Vasal (1976), Kuo and Nash (1975) and Lasker (1974), suggests that the control of breeding through manipulation of environmental conditions will prove increasingly important to fish culture programs. However, they do raise one interesting and possibly serious problem, that is: to what extent are the fish, produced out of phase with the natural cycle, maladapted to the natural environment into which they may be released? Do brook trout hatched in September instead of December (Hazard and Eddy 1951) and planted 19 mo later have any detrimental effect upon the natural populations into which they are introduced?

INDUCTION OF OVULATION AND SPERMIATION

Injections of pituitary preparations (hypophysation) have been used successfully on a routine basis for many years to induce final maturation, ovulation, and spermiation in fish which have completed gonadal growth (Chaudhuri 1968; Donaldson 1976). Other chemical agents may prove suitable and perhaps preferable to pituitary materials. Clomiphene citrate (Pandey and Hoar 1972), prostaglandin (Stacey and Pandey 1975), corticosteroids (Sundararaj and Goswami 1966) metapirone (Pandey et al. 1977) and a combination of steroid hormone and pituitary extract (Jalabert et al. 1977) have all been shown to induce ovulation.

Hypophysation is usually necessary in situations in which the exogenous factor which normally triggers spermiation or ovulation is missing or ineffective. In such cases as the riverine breeding of Indian major carps, it may be possible to induce spawning by releasing breeders (gonad growth complete) into recently flooded bundhs (Chaudhuri 1968). However, it is not always possible to provide suitable conditions on the necessary scale, and hypophysation may be the only alternative. Moreover, hypophysation allows a control over breeding which facilitates selection of breeding stock and hybridization.

Hypophysation is often followed by stripping and artificial fertilization, and thus behavior associated with breeding is bypassed. In other cases treated fish are released to spawn naturally in enclosed areas or in large containers. Apart from the observation that the sex play of such fish is less vigorous (Chaudhuri 1968) there seem to be no other observations which suggest that spawning behavior of treated fish differs from that of natural spawners. Thus, "in actual practice the main bottleneck in freshwater fish seed production and collection has been overcome" (Sinha et al. 1974). Nevertheless Sinha et al. (1974) comment that a knowledge of spawning requirements of these carps is essential, not only for scientific exploitation of natural seed resources but also for ensuring a dependable source of seed supply. Therefore, in spite of the obvious success of hypophysation techniques, it is desirable to know more about the environmental cues—physical, chemical or biological—which normally trigger spermiation and ovulation. Knowledge of these factors may allow more widespread breeding of desirable species and reduce the need for access to the relatively sophisticated facilities required by hypophysation procedures.

APPLICATION OF STEROID HORMONES OR THEIR ANTAGONISTS

Induction of sex reversal

There are a number of situations in which it may be advantageous to obtain unisexual or asexual populations of fish (reviewed by Schreck 1974). For example, the prolific *Tilapia,* when raised as pondfish, are considered a nuisance because many of the fish produced are unacceptably small. Guerrero (1975, 1976) demonstrated that it is technically and economically feasible to use androgens to obtain all-male cultures of Tilapia. Treatment resulted in higher standing crops and larger individual weights compared with untreated controls (Guerrero 1976).

Administration of heterologous sex steroids to induce sex reversal has been applied successfully to a wide range of teleosts (Schreck 1974) including several species of salmonids (Yamazaki 1976; Simpson 1976).

Sex steroids as growth promoters

In addition to their effects upon sexual differentiation, some steroids, particularly androgens, have marked anabolic effects when administered to salmonid fry under hatchery conditions (McBride and Fagerlund 1976; Fagerlund and McBride 1977; Simpson 1976; Yamazaki 1976). The dose and timing of treatments in these investigations were such that in most cases androgenic effects were kept to a minimum.

The behavioral effects of treatments with gonadal steroids appear to have been largely ignored, perhaps because it is assumed that changes in behavior parallel the "reversal" in gonads and morphological features. But while it is clear that sex-reversed fish do frequently display behavior typical of their assumed sex, there are reasons to suspect that there may also be important quantitative and qualitative differences which could have important implications for fish management practices.

Treatment of intact juvenile or gonadectomized adult male and female threespine sticklebacks with methyltestosterone induced male coloration and kidney tubule development (Wai and Hoar 1963). None of the treated juveniles and only 6% of the masculinized adult females began nest-building. Masculinized females never displayed sexual responses towards introduced females. Clemens et al. (1966) treated guppies with testosterone from birth to 60 days and obtained sex reversal in a considerable proportion of the females. But only 14% of males (both genetic males and females) sired young even though they showed full coloration and yielded viable sperm on stripping.

These two examples emphasize the need for careful examination of behavior before concluding that the behavior of sex-reversed fish is the same as that normally shown by untreated individuals displaying the same genetically determined sex as the reversed individuals. Almost certainly the extent of development of heterologous behavior will depend upon the time and duration of hormone treatment. Yamamoto (1969), Hackman and Reinboth (1974) and Yamazaki (1976) demonstrated the importance of the timing of steroid treatment: to be fully effective steroid treatment must be administered before sexual differentiation of the gonads commences. This also raises the question: Is there a process in early development of teleosts comparable to the hormone-dependent differentiation of sexual behavior in mammals (Davidson 1972)?

It is well established for a number of mammals that perinatal androgen suppresses the potential for the development of female behavior patterns in genetic males and exerts some degree of early organization on male behavior (Davidson 1972). At present it is not clear whether these findings with mammals have any direct relevance to fish. Lindsay (1974) in a preliminary study obtained some evidence that treatment of guppies with androgen in the first week after birth, although it did not masculinize the females, resulted in a slight increase in responsiveness to the masculinizing effects on behavior of androgen administered to the females after they had matured.

If there are common mechanisms in the development and differentiation of sexual behavior and gonadal function in teleosts and mammals, then there are important implications regarding the administration of sex steroids (and anti-steroids) to young fish. For example, it is possible that treatment with steroids at a critical stage in development may influence the form and intensity of adult sexual, aggressive, and territorial behavior, even though there are no obvious morphological signs of sex reversal. Indeed, if fish can be induced to react less aggressively or show reduced sexual behavior, energy devoted to the maintenance of these activities may be diverted into enhanced growth (or do such fish become stunted because of a failure to compete for food or space?).

Finally, it would be of interest to determine whether stress-induced changes in corticosteroids (and any other steroids?) at an early stage of development affect subsequent development and differentiation of behavior.

In addition to the specific effects referred to above, a number of investigators have noted an increase in "general" activity following treatment with gonadal steroids (Liley 1969; Donaldson, Pacific Environmental Institute, Dept. of Fisheries and Oceans, West Vancouver, B.C., pers. comm.). These activity responses have not been studied carefully, but it appears possible that they may have important consequences in hatchery and pond environments.

Pheromones

Pheromones have been implicated in social, sexual and individual recognition, as sex stimulants and attractants, and as alarm substances. In spite of their obvious importance in so many facets of behavior, remarkably little is known of the control and site of production, and the chemical nature of any pheromones except alarm substances (reviewed by Pfeiffer 1974). Investigation of these problems may eventually make it possible to utilize pheromones, natural or synthetic, as tools in the control of fish behavior. For example, Stacey and Hourston (MS) suggest that it may be practicable to add herring milt to spawning ponds or in the sea to induce spawning in Pacific herring at a time and place convenient to the fishery managers.

Conclusion

In spite of the fact that hormone treatments and hypophysation and photoperiod manipulation procedures have been "available" and in limited use since the 1930's (Pickford and Atz 1957), only recently has there been a dramatic and widespread increase in interest in applying these procedures to improve upon what are, in many cases, long established fish culture practices. The results obtained so far promise the following benefits:

(1) less reliance by aquaculturists on natural fry ("seed") production for stocking fish ponds.

(2) production of large numbers of fry from a relatively small stock of selected breeding fish.

(3) year-round production of fry for pond rearing.

(4) culture of desirable species which at present are difficult to rear and breed in captivity.

(5) enhanced productivity by stimulation of growth and/or by suppression of breeding.

Although most techniques for controlling reproduction are still at an experimental stage, the last 10 years have seen a dramatic increase in our knowledge of the endocrine mechanisms which govern the gonadal cycle. Unfortunately, this appreciation of endocrine mechanisms has not been accompanied by a comparable interest in the behavioral link between the organism and its environment. This is surprising in view of the fact that it is generally recognized that not only does the endocrine system regulate behavior, but that behavioral and other environmental stimuli also affect the endocrine state. At present the behavioral components in this link are largely ignored, perhaps because in many laboratory investigations "behavioral problems" may be readily by-passed. For example, the induction of ovulation and spermiation by hypophysation is usually followed by stripping and artificial fertilization. However, the apparent success of this technique should not be allowed to discourage attempts to determine the natural factors which regulate the gonadal cycle and trigger spawning behavior. A better understanding of these factors may make it possible to reduce the dependence upon hypophysation procedures and access to the relatively sophisticated facilities which they require.

Where steroid hormones are administered to induce sex-reversal or promote growth it is essential to know more of the behavioral effects of these treatments. These hormones are likely to influence the behavioral interactions and activity of fish being raised in ponds and hatcheries. Appropriate management procedures may be necessary to take into account any potentially beneficial or adverse effects of these changes in behavior. In the case of fish intended for release, it is particularly important to determine the effects of hormone treatments upon survival and reproduction, and perhaps the impact of treated fish upon the native untreated population.

It follows from the above that if aquaculturists are to obtain full benefit from their attempts to control breeding in teleosts, it is essential that more attention be directed to understanding the endocrine-behavior axis in reproduction, i.e., both the endocrine regulation of behavior, and the behavioral and environmental regulation of the endocrine system. In addition it is important to

investigate the possibility that a particular endocrine treatment may have an impact on behavior not directly related to reproduction, but which may nevertheless affect the efficiency of pond or hatchery operations.

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Discussion

FUJIYA

I would like to make a comment regarding the possible role of pheromones in molluscs. We have an extensive program in which artificially produced scallop and abalone "seed" is placed into the sea. If we put 10,000 scallops into an area, the following year we may find three to five times as many scallops there. The same applies to abalone. Evidently, natural seed settles in the vicinity of the established scallops and abalone. We believe that there may be pheromones produced which attract the larvae, and that if we could just put pheromones into the sea it might be possible to establish new stock without establishing artificially produced seed. From your experience do you think that this is really a pheromone or not?

LILEY

It seems as though there is definitely some form of signal, probably chemical, which attracts larvae to the area where scallops and abalone are already established. If there is such a chemical attractant, I would be satisfied to call it a pheromone, though it doesn't seem to me very important whether such an attractant falls within a narrow definition of pheromone or not.

BLAXTER

But we need to know what these substances are so we can use them, especially in aquaculture.

LILEY

I agree. We definitely need to identify the effective components and determine the specificity of such chemical signals. In the case of our goldfish study, we used thin layer chromatography to follow up a suggestion that the pheromone produced by an ovulated female may be a steroid metabolite. We were not able to come to any conclusion on the basis of that approach.

BARDACH

In the case of induced breeding by photoperiod manipulation with salmon and perhaps mullet, you are obviously into a fairly advanced technology. Can these procedures be applied relatively easily? Is a rough control of photoperiods sufficient?

LILEY

I believe it may be possible in some cases. Let me give an example reported to me by Dr. E.M. Donaldson of the Pacific Environmental Institute in West Vancouver. He visited Malacca in Malaysia where they have been attempting to breed Chinese carp. It was pointed out that carp which are native to a region with marked photoperiod and temperature cycles were being held under tropical conditions with minimal changes in light and temperature. Interestingly, a few carp were coming into reproductive condition throughout the year. Dr. Donaldson suggested that they put lights over the holding tanks and give the fish an extended photoperiod for part of the year. It will be interesting to see if these relatively rough procedures are sufficient to induce breeding. If they are not successful then it may mean that it is necessary to turn to more complex manipulations involving both photoperiod and temperature.

ATEMA

Do you think it is worthwhile pursuing injecting individual fish as a tool?

LILEY

As these hypophysation techniques require relatively sophisticated facilities and expertise, I believe that it is desirable to find an alternative to a reliance on hypophysation. For a farmer in India who might be 100 km from the nearest hatchery, it would be better to provide tools or know-how which he can apply for himself. In particular, I think that we should be finding out more about the natural spawning triggers. For example, it would be interesting to pursue Lake's (1967) work on flood spawners. If there really is something leached from dried-out soils, it should be possible to find out more about these factors and perhaps make use of that knowledge.

HENDERSON

I would like to make two comments. Once these techniques for a particular species are well in hand, they are not really too complicated for farmers to carry out. You see this in China: wherever they are producing Chinese carp, they are also producing fry locally. Problems arise in developing the methods for new species or in applying them to a different region. And this brings me to the second point, and that is whether or not we are at a stage now in our understanding of the induced maturation and spawning where it is possible to lay down some quite general guidelines to people who are trying to apply these techniques to different populations or different species. We at FAO have been thinking that it is about time to prepare a manual to assist such people. Do you think we are at the appropriate stage to do so?

LILEY

The range and diversity of ecological adaptation in the control of breeding are too great for it ever to be possible to provide a set of specific instructions which if carried out could be used to induce gonadal growth in any species of fish of interest. However, I believe that it should be possible to provide general guidelines as to how to go about determining for each species the photoperiod and temperature manipulations which may prove effective in stimulating the growth phase of gonadal development. Once fish have become gravid, it may be necessary to take additional steps to induce ovulation and spermiation before spawning or artificial fertilization can occur. As I have suggested previously, a greater knowledge of the natural spawning triggers may suggest ways in which this may be achieved without resorting to hypophysation.

BARDACH

In a number of cultured fish, the problem is not how to get them to spawn, but how to prevent them from spawning. A second possibility is that if you can prevent gonadal growth by hormonal treatment you might obtain enhanced somatic growth. Are there promising possibilities in those two directions?

LILEY

Steroid hormones have been used in attempts to produce unisexual populations and (or) to stimulate growth. For example, the prolific breeding of *Tilapia*, when raised as pondfish, results in large numbers of undersized fish. It appears that it may be economically feasible to feed androgens to young *Tilapia* and obtain an all-male population in which fish grow rapidly to a usable size. Estrogens may be used in hatchery feed to obtain a greater proportion of the more economically desirable female salmon. Steroid hormones are also being tested for their anabolic effects. Now I see two problems with these procedures: What are the immediate and what are the subsequent effects of these treatments on behavior? In my paper, I have mentioned two studies which indicate that behavioral reversal may not be complete in spite of apparently complete morphological sex reversal.

BARDACH

There are probably other manipulations that are easier and more practical, for example, the production of all-male populations by hybridization in *Tilapia*. In certain cases, especially in stock enhancement and release, the situation may conceivably be different, and the feeding of steroid hormones may be in order.

LILEY

I would like to emphasize just how little attention is given to the possible behavioral effects of these hormone treatments. Yet it is clear that there are effects which might be important for the overall success of these procedures. For example, it seems to be common knowledge among people doing this type of work (Fagerlund and McBride, pers. comm.) that fish which are receiving methyltestosterone are more active and aggressive, at least in competition for food. They show an increase in appetite. There is also an increase in food conversion efficiency. Another unpublished observation by Fagerlund is relevant here. He fed methyltestosterone to chinook salmon fry and found that at low fish density the treatment resulted in enhanced growth as expected, but the fish held under high density conditions did not differ from controls. Dr. Fagerlund did not attempt to explain this, but it seems reasonable to suggest that if the hormone increases activity, and perhaps aggressive behavior, the resulting increase in metabolism of these fish, particularly under crowded conditions, may be sufficient to counteract the anabolic effects of the steroids. Perhaps it would be worthwhile to examine ways of reducing this increased activity to get the full growth effects of these steroid treatments. That is just a thought—I don't know how practical that would be considering the scale on which these fish are raised in hatchery operations.

Using Knowledge of the Reproductive Behavior of Reef and Lagoon Fishes to Improve Fishing Yields

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JOHANNES, R.E. 1980. Using knowledge of the reproductive behavior of reef and lagoon fishes to improve fishing yields. p. 247-270. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

During their spawning periods, otherwise fragmented populations of reef and lagoon food fishes gather in large, often docile aggregations at predictable times and locations. These aggregations not only provide exceptionally good and widely used opportunities for fishermen to make large catches, but also present unrealized opportunities for fisheries managers to study and manage the stocks they represent. Since many commercial species have spawning cycles that are similarly timed in terms of both season and lunar period, whole groups of species might be managed by simply closing the commercial fishery during some portion of their collective spawning periods. This approach could be pursued with a wide range of options depending upon the value of the fishery and the economic and technical resources available. At its simplest level, and where the bulk of the catch goes through central markets, enforcement could be carried out very inexpensively at the market. In underexploited fishing areas remote from fishing centers, exploitation could be encouraged through exploratory fishing programs designed to locate spawning aggregations in time and space.

Introduction

Coral reefs, seagrass beds, and mangrove swamps form a widespread, highly productive complex of shallow marine communities in the tropics. The total production of fish in these communities has never been calculated, but it is undoubtedly substantial. Coral reefs are thought to be the most extensive shallow marine community type on earth (Goreau 1961) and areal yields of reef fish compare favorably with yields in productive temperate waters (Stevenson and

Marshall 1974). Mangrove communities also support importan fisheries (e.g., Heald and Odum 1970). Often interposed betwee intertidal mangrove communities and offshore coral reefs are sea grass beds. No measurements of fish production are available for thi community, but it is known that primary production is exceptionall high (e.g., Odum et al. 1973; Zieman 1975).

Where these communities occur together, their fish faunas overla considerably (e.g., Olsen et al. 1973; Vivien 1973). Many specie which spend their adult lives in reef communities live as juveniles i adjacent mangrove swamps (e.g., Austin 1971) or seagrass bed (e.g., Munro 1974; Ogden and Zieman 1977). Various species whic spend the day in reef communities move into seagrass beds at nigh to feed (e.g., Randall 1965; Starck and Davis 1966). Many specie which occupy reef habitats during low tides move up onto seagras flats or into mangrove swamps to feed on high tides (pers. observ.). Because the greatest species diversity in reef-mangrove-seagras complexes is found in reef communities, and for the sake of brevity, I shall refer below to the fishes of these communities as reef, or ree and lagoon fishes.

Most countries bordered by these communities have neither enough money nor enough adequately trained people to mount sophisticated fisheries management programs. Under such conditions practical management schemes must be unusually simple and inexpensive. But reef and lagoon fisheries present management problems that appear to be anything but simple. Species diversity is much higher than in temperate waters and no one or few species generally dominate the catch. As Munro (1974) states, "The problems of assessing the potential harvest 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." Management programs tailored separately for each species would require far more knowledge concerning their biology than is presently available, and in any event would be prohibitively complex and expensive.

Treating groups of species as single management units has often been suggested as a possible solution under such conditions. Some progress has been made in the analysis of tropical trawl fisheries over soft-bottom communities by treating groups of jointly harvested species as single populations (e.g., Tiews et al. 1967). But this approach is not applicable in its original form to reef, mangrove, and tropical seagrass fisheries. Harvesting of these communities involves working over a wide variety of substrate and bottom contours. Thus, no single method generally accounts for the bulk of the harvest; the catch is shared by fishermen using traps, trolling lines, droplines, gill nets, seine nets, spear guns, and a variety of other devices. Size selection and species selection differ with each fishing method. Consequently, if a reef fisheries management program were patterned after that proposed for tropical trawl fisheries, a different set or regulations would be required for each method, creating a scheme of utterly impractical complexity.

In short, if reef and lagoon fisheries are ever to be exploited efficiently, then managing groups of species as single units seems unavoidable. Yet the wide variety of fishing methods employed precludes management based on existing models. So at present there are simply no generally accepted principles of reef and lagoon fisheries management.

Under such conditions it is inappropriate to think of management in terms of the refined goals characteristic of fisheries management theory. Achieving a maximum or optimum sustained yield in a multispecies reef and lagoon fishery borders on the impossible. A less precise goal, but one to which we can realistically aspire, is simply to achieve moderately stable increases in the yields of heavily overharvested fisheries.

To adjust catch levels effectively in reef fisheries which are only moderately overexploited would require a degree of knowledge and fineness of control over the fishery that we are not likely to possess in this century. Indeed at present it is very difficult even to identify moderate departures from optimum catch rates in such fisheries because of the problems of obtaining the necessary data. It is sometimes possible to do so for single species, but it is rarely if ever practical to do so for the bulk of the species that make up significant portions of the fishery.

But there comes a point in the deterioration of a fishery when it is no longer necessary to gather detailed catch and population statistics in order to know that the fishery is seriously depleted. In Western Samoa, for example, 8 man-hours of spearfishing yields an average of only 0.3 kg of reef fish (Lindsey 1972). Many other reef and lagoon fisheries are also grossly depleted (e.g., Clutter 1971; Lindsey 1972; Munro 1974). In such cases almost any regulations that bring about a general reduction in fishing pressure may be expected to improve future yields, and it is only to such areas that the following discussion is directed. (A later section of this paper deals with underharvested reef and lagoon fisheries).

It is possible that management of some of these fisheries would cost more than the results would be worth. But, for areas where some form of management seems desirable, I propose a relatively simple and inexpensive approach. It involves not only managing groups of species collectively, but also treating all fishing methods collectively as a single management unit. In its simplest version the scheme appears to be within reach of countries with only very limited management resources. It entails management, enforcement and research procedures based largely on certain collective features of the reproductive behavior of reef food fishes.

Reproductive Behavior

Reef fish populations are characteristically fragmented into numerous, small subpopulations. This suggests that it would be difficult to study or exert much control over their population dynamics. As Cushing (1968) has said, "the powerful theoretical weapons developed for analyzing the changes in fish populations are of little use if the populations cannot be delimited." During their reproductive period, however, the behavior of reef food fishes renders many of them more amenable to population analysis and also provides a practical means for controlling their exploitation. The following description of their reproductive behavior is condensed from Johannes (1978a).

The subpopulations of many larger species (25 cm total adult length) of reef fish migrate and converge to form large aggregations at spawning time. Among such species are albulids, chanids, mugilids, sphyraenids, serranids, carangids, lutjanids, lethrinids, gerreids, acanthurids and scombrids. The advantages of such aggregations for population studies are compounded by the behavior of the fish that form them.

First, these fish often gather year after year at the same locations to spawn. Favored locations are over the outer reef crest, over the outer reef slope, and in or near channels through the reef. Spawning at such locations facilitates the flushing of the eggs offshore and away from reef predators.

Second, spawning aggregations often occur at predictable times of the lunar month and of the year. Spawners typically aggregate on the spawning ground for 3 to 5 days around new and/or full moons and spawn on outgoing tides. In addition, peak spawning seasons for many species have been found to occur simultaneously and regularly in various parts of the world at times of the year when prevailing winds and/or currents are at their minimum velocities. In regions affected by monsoon or trade winds, peak spawning periods typically coincide with one or both of the twice-yearly wind shifts in spring and fall.

Finally, a number of these species are unusually approachable and unwary while in spawning aggregations. Some species with which a diver can normally establish only fleeting visual contact may actually be approached and touched while in spawning aggregations. This obliviousness to predators during the reproductive act is also found in certain other animals such as sea turtles and land crabs. Its function seems never to have been discussed. It may be a "flight override" mechanism which ensures that the reproductive act will not be aborted in response to threats from predators.

Because of their predictable concentrations in space and time, and in some species, their unusual docility, reef fishes are particularly vulnerable to fishermen during their spawning periods (e.g., Craig

1966; Razniewski 1970; Smith 1972; Johannes 1978a). They are therefore much more susceptible to overfishing than their typically diffuse interspawning distribution would suggest (cf. Murphy, this volume). But for the same reasons, their populations should also be easier to study and their exploitation easier to control than seems to have been recognized previously.

Management and Research

OVEREXPLOITED FISHERIES

Since peak catches of many species are made more or less concurrently while they are in their spawning aggregations, joint management of their stocks could be pursued by restricting fishing during some portion of their spawning period. [Closure of spawning grounds has been used as a single-species conservation measure for centuries in some traditional Pacific island reef fisheries (Johannes 1978b) and for many decades in the management of some continental freshwater and anadromous fishes.] The degree of control sought using this approach could vary with the needs and the technical and economic resources at hand.

Let us take a heavily depleted reef fishery and assume that, as is often the case, money and manpower available for management are extremely limited. Here management must take an especially simple form. In such countries fish must often be taken to the market within a short time of being caught because the fishermen lack refrigeration facilities or ice. Here enforcement of closure during spawning periods could take its simplest form, being restricted to the fish markets. It would thus require a minimum of personnel, and in many cases, no boat.

In areas where much of the catch does not go through a central market (e.g., areas dominated by subsistence fishing) or where the fish are preserved by salting, drying, or freezing, this method of catch limitation would be ineffective. Here enforcement could also be restricted spatially and temporally and costs thereby reduced substantially.

Since spawning aggregations occur at restricted times and locations, enforcement carried out only during spawning periods would cost substantially less than full-time enforcement. Management in this form would achieve only generalized control over the collective fishing stock. But, as discussed above, precise control of stocks seems beyond reach in reef fisheries.

A somewhat more rigorous management program could be undertaken in areas where more money and personnel are available. Year-to-year monitoring of fish on the spawning grounds would enable the fisheries manager to detect changes in population sizes of important species and vary the annual number or the length of closures. To a limited extent he might also manage certain species or groups of species independently. This is because, unlike trawl fishermen, reef and lagoon fishermen often focus on one species or small groups of species at a time, thereby giving the fisheries manager some ability to exert control over their separate catch levels. It would not be economically justifiable to single out more than a few particularly valuable species for separate management, however.

Where moderate amounts of money and trained personnel exist, the best management scheme would thus lie somewhere between managing all stocks collectively and managing each species separately. The point on this continuum at which the management of a particular fishery would fall would depend upon the size and value of the fishery and the economic and technical resources of the fisheries managers. In reef and lagoon fisheries it would always lie closer to the collective end of the spectrum.

It would not be appropriate here to recommend detailed specific management procedures within the general framework I am proposing. The number of potential variations on the basic scheme are very large owing to the large numbers of species involved and the wide range of geographical, cultural, economic, and technological differences to be found along tropical coastlines. However, it is appropriate to discuss some of the research that would aid the fisheries manager in formulating the proposed program.

The first step is to identify spawning times, and if enforcement is to be carried out on the fishing grounds, spawning locations. This latter information may be obtained from fishermen, although not always with ease. They may be secretive about spawning locations, being afraid of inviting additional competition. But only those aggregations known to fishermen will be heavily exploited and thus appropriate for management.

Palau, Western Caroline Islands is possibly the only place where biologists know enough about the timing and locations of spawning aggregations (e.g., Johannes 1978a) to initiate such a general management program before collecting much additional information. It is doubtful that Palauan waters are sufficiently overfished to benefit greatly at present from restrictions on fishing for most species on their spawning grounds, however. But the fishery for some species is clearly deteriorating in some areas. As a result fishing for several species of groupers on their spawning grounds has recently been banned. Some restrictions on harvesting of several other species while in their spawning aggregations would also be desirable (Johannes, in press).

Once spawning sites and timing are known, tagging of spawners, where affordable, could then be used to delimit the distributions of populations of important species during interspawning periods and provide information on growth rates, mortality rates, how often individuals spawned annually, and other information needed if management efforts are to be gradually refined.

Some species such as mullet migrate to the spawning grounds in large schools following predictable routes along which fishermen exploit them. Where enforcement on the fishing grounds is planned, migration routes of such species must also be determined.

Where resources permit it would also be desirable to monitor the effects of management. In doing so, it would be useful to differentiate between "growth overfishing" and "recruitment overfishing." When the mean size of a fish in a population decreases excessively in response to fishing pressure, growth overfishing has occurred — the fish are being caught before they have time to grow to optimum harvesting size (e.g., Cushing, 1972). Severe growth overfishing appears to be occurring around many reef and lagoon areas; the mean sizes of fishes harvested in heavily fished areas are often greatly reduced compared with those in other areas (pers. observ.). Since reef fish often spawn more than once and grow between spawnings, a reduction of the catch on the spawning grounds would obviously help reduce growth overfishing. The effect of this measure could be estimated by monitoring the mean size of important species caught before and after its implementation.

When the numbers of fish in a population decrease excessively in response to fishing pressure, recruitment overfishing has occurred; the fish are being caught before a sufficient number have time to spawn to replenish the population. A reduction of the catch on the spawning ground would obviously aid in reducing recruitment overfishing. Munro (1974) and Munro and Thompson (1973) provided evidence that high rates of exploitation with small-meshed traps depresses recruitment around Jamaica. But it is not generally clear to what extent this type of overfishing is a general problem in reef fisheries. One reason for this is that the larvae of most reef fishes are pelagic and dispersed over ill-defined areas in coastal and nearshore oceanic waters. After a variable period of pelagic existence (see below) the young settle and colonize reef, mangrove, or seagrass habitats. Recruitment is a function, in part, of the numbers of pelagic larvae that manage to reach suitable habitats in which to settle. Wide year-to-year variations in the numbers of young that settle are known to occur in reef and lagoon communities (e.g., Blanco and Villadolid 1939; Gosline and Brock 1960; Kuronuma and Yamashita 1962; Rao 1972; Popper and Gundermann 1975; Powles 1975; Kami and Ikehara 1976; Luckhurst and Luckhurst 1977; Russell et al. 1977) and may be related at least in part to year-to-year fluctuations in factors (see below) other than the number of eggs spawned. Such variations are liable to obscure the relations between stock and recruitment.

It would be desirable nonetheless to develop some ability to forecast future stocks, provided it could be done inexpensively. This might be accomplished in some cases by estimating the numbers of young settling inshore from year to year. Although very little research has been done on the inshore migration and settling of these fishes, a number of species are known to appear at specific nearshore locations during certain predictable seasons, tides, and lunar periods [see Johannes (1978a) for references; additional references are Blanco and Villadolid 1939; Kuronuma and Yamashita 1962; Rao 1972]. Among these are important food fishes — milkfish, acanthurids, gerreids, and siganids. As more observations are made, more species may be found to settle in shallow water at predictable times and places, providing an opportunity to estimate recruitment (e.g., Rao 1970). In some cases the relation between settling and recruitment may not prove to be simple, however. For example, in years of heavy settlement of juvenile rabbitfish *Siganus spinus* in Guam, they exhaust their inshore food supply and mass mortalities ensue (Tsuda and Bryan 1973). Knowing the timing and location of these movements would also enable biologists to estimate the number of juveniles available in a given area for aquaculture stocking purposes (e.g., Sivalingham 1975).

An even simpler method of making rough forecasts of recruitment is conceivable. Year-to-year variations in prevailing winds and currents are probably at least in part responsible for the observed year-to-year variations in numbers of settling reef fish larvae. Almost no research has been done on this relationship in the tropics, but observations on the relation between offshore winds and numbers of milkfish larvae moving inshore support the concept (Kumagai et al. 1976). A comparison of wind and current conditions with recruitment over a series of years would reveal if the relationship holds for other species. If it does, then wind and current measurement might provide a simple, inexpensive predictor of recruitment. [Saville (1965) reviews this approach as applied to temperate fisheries.] The relation between wind and current conditions and recruitment may be clearest around isolated oceanic islands where nearshore hydrography is relatively simple.

To study the effects of prevailing winds and currents on recruitment of reef fish larvae, it is necessary to know not only when they spawn, but also the length of their pelagic larval periods. This latter information is available for only a few species, whose pelagic stages last from 10 to 90 days (Table 1). It is clear that the pelagic period is flexible in at least some species; metamorphosis to the inshore juvenile stage can be delayed in some species until a suitable substrate is encountered (e.g., Breder 1949; Caldwell 1962; Burgess 1965). Other species have pelagic postlarval stages which spend a variable time in the open sea, often associated with drifting logs or other floating objects, until they encounter shallow water and take up residence there. As mentioned above, however, the pelagic larvae

TABLE 1. Pelagic larval periods of reef and lagoon fishes.

Species	Larval period[a]	Reference
Chanos chanos	about 10 days	Schuster 1960
Mugil cephalus	42 days	Kuo, et al. 1973
Mugil curema	12-16 days	Houde et al. 1976
Kuhlia sandvicensis	probably about 2 mo	Tester and Takata 1953
Caranx mate	48-52 days	Watarai 1973
Chaetodon miliaris	about 2 mo	Ralston 1975
Chromis dispilus	about 1 mo	Russell 1971
Abudefduf abdominalis	20-30 days	May 1967
Dascyllus spp.	"a few weeks"	Allen 1975
Acanthurus triostegus	about 2 1/2 mo	Randall 1961
Siganus canaliculatus	23-30 days	May et al. 1974
Siganus vermiculatus	22 days	Popper et al. 1976
Siganus lineatus	29-35 days	Bryan and Madraisau 1977

[a] The pelagic larval periods of these species were determined using various methods and under a variety of conditions. The limits of the duration of these larval periods may well exceed those listed here because (1) the time to metamorphosis into the inshore juvenile form can be delayed in some species until a suitable habitat is reached (references in text), and (2) development rates may vary with temperature and food (e.g., May 1967). Some species of reef fishes also have pelagic postlarval stages.

of some species regularly arrive inshore en masse during specific lunar periods. Such fishes are obviously not entirely at the mercy of offshore currents. How do they detect and move toward shallow water and how do they time their arrival there? Research on the behavior and general biology of reef fish larvae has been very limited and much useful information awaits discovery.

There is some evidence that despite their initial dispersion into offshore waters, the larvae of many of these fishes may settle largely in the general coastal areas from which they originated as spawn (Johannes 1978a), and that there may be a significant degree of genetic isolation between adjacent populations (e.g., Smith 1969). Work is currently underway in several laboratories on the genetic relations of tropical coastal fishes from different locations. Research into genetic relations of different spawning aggregations could provide valuable clues to the degree of their reproductive isolation.

Intensive fishing directed at spawning aggregations creates a new selection pressure which tends to favor the survival and reproduction of individuals which do not spawn at times and places typical for the species. Modern fishing gear and the increased demand for fish by expanding populations intensifies this pressure. It would be instructive to measure its impact on the spawning habits of exploited species.

UNDEREXPLOITED FISHERIES

Reef and lagoon areas exist around the globe that are far from fishermen's bases and go unharvested or underharvested as a result. Among such areas are offshore banks near Jamaica (Munro 1974), most of Australia's Great Barrier Reef and the leeward Hawaiian Islands. These areas are liable to grow functionally more remote as fuel costs continue to climb. New incentives are required to encourage their exploitation.

One such incentive might be provided by means of exploratory fishing projects designed specifically to locate spawning grounds. Being able to exploit large numbers of fish predictably concentrated in time and space would help offset the travel costs involved in reaching them. [For example, the fishermen in Belize (British Honduras) are familiar with the location and seasonal and lunar timing of a large spawning aggregation of Nassau grouper. Once a year several hundred boats converge from all along the coast of Belize and the fishermen establish a temporary fishing camp to exploit the aggregation (Craig 1966).] In such a research program the time element would obviously be of greater importance than has been the case with most conventional exploratory fisheries programs. In many instances diving surveys in suspected spawning areas would probably yield information on spawning aggregations faster than would fishing trials. Probable times and places at which to locate spawning aggregations have been described above.

In cases where profitable fisheries might be developed if spawning ground were located, and where sufficient funds and expertise are available, the use of biotelemetry (e.g., Stasko and Pincock 1977) to track fish to their spawning grounds might be worth trying. Attempts are currently being made in Hawaii to find the spawning grounds of milkfish using this method.

GEOGRAPHIC LIMITS OF APPLICATION

Reproductive behavior and timing are generally quite different in temperate marine fishes than in typical tropical species. The latitude, temperature, or intermediate habitat where the tropical reproductive pattern described here gives way to typical temperate patterns is not known, nor whether the transition is gradual or abrupt. Therefore, it is not possible at present to put geographic limits on the areas where the approach to management proposed here might reasonably be attempted.

Hawaii, a relatively well studied subtropical marine area with a depauperate Indo-Pacific fish fauna and moderately developed coral reefs, would seem like a likely spot in which to obtain some clues to this problem. Spawning of Hawaii reef fishes seems to follow seasonal patterns similar to those found at lower latitudes (e.g., Watson and Leis 1974; Johannes 1978a). But only one large food fish, *Polydactylus sexfilis*, is known for certain to have a predictable lunar spawning rhythm (Santerre and May 1977). If other Hawaiian food fishes exhibit lunar spawning rhythms as some of the same species do in lower latitudes, this fact is unknown to local fisheries biologists. This could be because lunar aggregations do not commonly occur in Hawaii, or it may be because fishing pressure and competition among fishermen has been so intense for so many years that the spawning aggregations are either too small, or their locations too well guarded by fishermen, to be generally known. Fish market surveys in which investigators looked for lunar periodicity in catches and in gonad development would help to clarify this problem.

COMPLICATING FACTORS

Management of fisheries according to the present scheme will depend upon being able to predict accurately the occurrence of spawning aggregations. There are several possible complicating factors.

1. The day of the lunar month on which spawning commences and the duration of spawning activity may vary by several days from month to month and year to year (e.g., May et al. 1979; Hasse et al. 1977).
2. Peak spawning seasons differ in different localities within certain tropical areas such as Jamaica (J. Monroe, P.O. Box 4820, University P.O., Papua New Guinea, pers. comm.), Cuba (Roig and de la Maza 1952) and southeast India (Bapat 1955).
3. Occasionally spawning aggregations do not occur in the anticipated month. Off Belize (British Honduras) there is some evidence suggesting that unusually bad weather may interfere with the seasonal timing of spawning of two species of reef food fish. In the last 50 yr the predictable spawning aggregations of the silk snapper *Lutjanus vivanus* have twice failed to materialize according to fishermen. Both failures followed severe hurricanes. In 1974 the well-known spawning aggregations of the Nassau grouper, *Epinephelus striatus*, formed 2 mo later than is customary. Two major hurricanes occurred in the area a few months earlier (I.J.B. Robertson, UNDP/FAO Fishery Development Project, P.O. Box 24, Mogadiscio, Somali Democratic Republic, pers. comm.).

At present, too little is known about the timing of spawning of most species in most localities to enable us to say how great the difficulties posed by such complicating factors may be.

An additional complication pertains to all species which exhibit both seasonal and lunar reproductive rhythms. Such species must insert an extra month into their "physiological calendars" on the average of approximately once every 3 yr to keep their reproductive rhythms in phase with the seasons. (The problem is identical to that of human cultures with lunar calendars; the intercalation of a 13th month roughly every 3 yr has been standard practice). Consequently a spawning season that usually starts around (for example) the new moon in March, will be found to start around the new moon in April in roughly one year out of three. This factor renders the prediction of the first month of the spawning season uncertain but does not affect the accuracy of prediction of the timing of subsequent spawnings. This phenomenon is discussed in more detail in Johannes (in press).

UNTAPPED SOURCES OF INFORMATION

Almost ignored as a source of information on the biology of reef fishes is the tropical fish market. Large and valuable amounts of information on reproductive timing could be gained inexpensively within a year by monitoring the state of maturity of the fish brought to market, provided of course that they arrive ungutted.

A second, sometimes encyclopedic source of this and other information of value to fisheries managers is fishermen, and it is a great pity that their knowledge has not been more actively sought and recorded in the tropics. Some possess much more practical knowledge about the species they catch than do biologists (e.g., Johannes 1978a). An hour's discussion can sometimes elicit more information of practical value about a species than a year's expensive conventional research.

In areas where native cultures are still more or less viable, talking with fishermen may also reveal whether traditional marine conservation measures exist or existed. Patterning modern conservation measures after indigenous ones, if they appear to have merit, deserves consideration. Such regulations are more liable to gain local support than regulations unfamiliar to local fishermen, who will sometimes even enforce them themselves, taking some of the burden off government enforcement personnel. In various parts of Oceania closure of fishing during spawning periods has been used for centuries as a conservation measure (Johannes 1978b). Fishermen of Palau, Micronesia have recently and on their own initiative pushed through legislation prohibiting fishing for groupers on one of their spawning grounds.

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Discussion

ATEMA

If chiefs of the local areas regulate their own fisheries, why are we here at Bellagio?

JOHANNES

The answer is complicated. I'll give you part of it briefly. We Westerners brought about the destruction of these management methods. Pacific Islanders invented limited entry, for example, many centuries ago, and then we came and told them, "This is primitive. This is not the way we do things in the civilized world. The sea should be open to all." We also introduced the profit motive and export markets into their self-contained, communal subsistence economies. A conservation ethic can no longer thrive under such conditions, so government regulation of fisheries becomes necessary.

HENDERSON

Local limited entry management has also been characteristic of African inland fisheries. Every bit of water belonged to somebody and only certain people could fish this water. These rights were very cleverly controlled. This system has also been destroyed by "modern" approaches.

BLAXTER

May I ask also a rather destructive question? Is it realistic to make spawning surveys by SCUBA diving?

JOHANNES

You don't need SCUBA. Mask and snorkel will do it.

BLAXTER

How do you do it—just count the fish?

JOHANNES

Yes. It's a well-established technique among reef biologists. Reef waters are typically very clear. The method was pioneered by Brock (1954) and Bardach (1959) and has been most recently discussed by Thompson and Schmidt (1977).

BLAXTER

I don't think you could count the fish in a tight clump.

JOHANNES

Certainly you could make useful relative estimates. Tagging with highly visible tags on the spawning grounds might enable one to make pretty good absolute estimates too.

BLAXTER

I have trouble even trying to estimate the number of fish swimming in a tank.

MAGNUSON

Significant papers are being published based on visual observation, or comparing visual observations in streams and lakes with catch per unit of effort by conventional trap and gill nets. The visual observations are giving a much wider species array and are providing a better estimate of community structure than fishing gear. I think it's becoming not only a popular but also a verified method.

JOHANNES

We must also keep in mind that the degree of accuracy sought when gathering fisheries statistics in the temperate zone is just plain out of the question in most tropical fisheries.

HARDEN JONES

In the North Sea the sand eel occupies the niche of a reef fish; it is nonmigratory and the annual value of the catch is about 18% of the North Sea landings. My colleague Mr. Tim Wyatt believes that sand eels spawn with a lunar periodicity and he suspects that this may prove to be the case for plaice and other commercial species in temperate latitudes. I think that you have rightly drawn our attention to the large body of information which must be known to and held by fishermen. I believe that the science would go forward if they could be persuaded to share this knowledge with us. But in practice this is a difficult problem and has bedeviled us all, whatever latitude we live in.

JOHANNES

In my experience it is much easier to obtain this information from fishermen in areas where the profit motive has not taken over completely, where competition is therefore not so intense and the fishermen are still willing and often proud to volunteer their knowledge. I've given up in Hawaii because the fishermen there, in an intensely competitive fishery, won't give you the time of day.

In response to your statement that lunar periodicity is not limited to the tropics, I have found references to only six species of temperate zone fishes that exhibit lunar spawning periodicity, in contrast to more than 50 species in the tropics. Considering that orders of magnitude more research has been done in the temperate zone, one would expect to find reference to more fishes that spawn in lunar cycles there if it were as important a phenomenon there as it is in the tropics.

HARDEN JONES

I think in the North Sea there are probably not more than eight species that are of sufficient commercial importance to be studied intensively.

JOHANNES

That's fair enough. Diversity is much lower in the temperate zone. But of course I am talking about the entire temperate zone, not just the North Sea.

HASLER

You made mention of predation by sharks several times and I was startled by it because I thought there was quite an active and intensive fishery for sharks.

JOHANNES

In some limited areas.

HASLER

Would this be some way of improving survival, by getting at the main predator?

JOHANNES

That's a cultural problem. In some areas sharks are considered a prime fish but in many others people won't eat them and so the sharks there are just as abundant as they ever were.

HASLER

There's an awful lot of protein in the shark. You'd think they would have used it.

JOHANNES

There is another problem too. Many shallow water sharks have rather limited home ranges and most have extremely low fecundities. For both these reasons one can deplete a shark fishery in very short order. Furthermore it is often difficult to convince fishermen to fish for species for which there has not been a traditional fishery. By and large sharks don't keep very well and don't fetch high enough market prices to justify exporting them from areas in which they are not appreciated locally. Dried shark fins sent to Chinese markets are an exception.

REINBOTH

You suggest that apparently most of the species that are aggregating towards the reef edge towards the open sea have limited spawning periods. But is it really true? I remember having long discussions with Dr. Erdman from Puerto Rico. According to what I heard from him, there is a tremendous variety: some species spawn all the year round; others do it for a very limited time only. As far as I could gather from him, there is no clearcut correlation in this with particular families or particular species, and I am wondering whether it is true that most of the species you are dealing with have a very limited annual spawning period.

JOHANNES

I did not intend to suggest reef fish have very seasonally limited spawning periods. But there are certain seasons when particularly large numbers of species—and large numbers of individuals within species—spawn. And if you look at Erdman's (1956) data you will find that they support what I am saying. At other times of the year, some of the same species spawn, but smaller numbers of species, and individuals within species, are involved.

HENDERSON

Do you have any evidence on the degree of localization in island areas of the stocks of larger reef fishes? To what degree are the offspring that are produced from a particular island returning to the same island to spawn? Your remark about fishermen protecting stocks of grouper suggests there may be this localization. It is a critical factor in management.

JOHANNES

That's a very important question. Smith (1969) presented evidence that genetically distinct populations of *Decapterus bipinnulatus* exist around different Hawaiian islands. Genetic studies of populations of other species from different localities in the tropics are currently underway in a number of laboratories and I expect we'll know a lot more about this within the next 5 yr. There is another interesting series of observations which I touched on in my paper. Several weeks after a major spawning occurs the larvae of some species will migrate inshore in the same general area where the adults spawned. This occurs in Palau, for example, an area to which these larvae could not have travelled or been carried in their brief lifetime from neighboring islands; the nearest islands are too far away. These larvae almost certainly originate locally and somehow manage to find their way back to the area from which they originated as eggs, after having been transported many miles out to sea.

BARDACH

Isn't it most clearly correlated with length of pelagic larval period? The longer the pelagic larval period, the more unlikely that a very strong tendency would be noticed to return to the spawning site.

JOHANNES

One might certainly think so. But one of the fish whose postlarvae migrate inshore like clockwork at predictable times of day and of the lunar period is the surgeonfish, *Acanthurus triostegus* (Randall 1961). And it has a 2 1/2-mo oceanic larval period, which is rather long for a reef fish. So although what you surmise seems reasonable, it may not always be the case.

BARDACH

What if the larvae are not as pelagic as one thinks?

JOHANNES

While it is true that not much is known about the behavior of these larvae, enough is known about their distribution to say that the larvae of many species of reef fishes are found a long way from shore. Off Hawaii, for example, larvae of reef fishes such as labrids or synodontids, which tend to be absent from nearshore plankton tows, begin to show up in tows once you move several kilometers offshore (Leis and Miller 1973). If you look at the literature on tuna stomach analysis you find that more often than not, reef fish larvae and juveniles constitute an important fraction of their food.

One interesting observation relating to the ability of these fish to find their way back to shallow water concerns fishermen from Tobi, a tiny island in the southwest corner of Micronesia, who frequently fish for tuna and other fish aggregating around logs that float past their island. These men are real students of the behavior of the fish found around these logs. And reef fish larvae and juveniles are typically found in abundance clustering under them. These fishermen volunteered that the young reef fish leave the logs and swim toward the island many hundreds of yards prior to establishing visual contact with it or with the bottom. Presumably there is some chemical cue that enables them to detect an island or shallow water at a distance.

HUNTER

When you say larvae are migrating in to shore, are you really talking about larvae? Many tropical larval fishes have rather short larval periods, and you may be considering juvenile fishes or prejuveniles to some extent.

JOHANNES

I'm talking about larvae, postlarvae, juveniles—what have you—as long as the fish are still in the young pre-demersal stage. The terminology used to distinguish different stages of young fish is very useful in some circumstances but terribly awkward in others. There seems to be no general term. The term "juvenile" has grown to mean something much more specific among ichthyologists than one might guess from consulting a dictionary.

MYRBERG

When one is talking about closed seasons and open seasons in tropical subsistence fisheries, how does this relate to our experience in the temperate zone?

JOHANNES

In the tropics one deals with fisheries running the gamut from primitive-subsistence to industrialized-commercial, with the two types intermingling or overlapping in many areas. This makes it hard to generalize. Enforcing fishing regulations is generally more difficult in subsistence fisheries because of the large number of small boats involved, the lack of a central market where one can keep tabs on the catch, and lack of money.

MYRBERG

Are you saying that fisheries managers should impose closed seasons on these island fisheries?

JOHANNES

"Seasons" is not quite the right word here. Call it "periods." One would not need to close the fishery for a group of species for a whole season, but simply for the few days of the lunar period during which they spawn. And keep in mind that during these periods the fishery would remain open for other species which did not exhibit the same lunar and seasonal spawning rhythm or which for other reasons were not judged to require management. In some areas this approach might even stimulate the utilization of previously underutilized species while the fishery was closed for other species. The great multiplicity of species in tropical fisheries offers a lot of flexibility here.

MURPHY

It's easy to find evidence of populations of these coral reef communities decreasing in the face of pressure, but the evidence that they're being overfished in the sense that they're yielding less protein than they might if they were fished less intensively just isn't there.

In the case of Palau I understand that while it was being administered by the Japanese they actually caught a lot more fish in the area around the archipelago supplying a very much larger population than at present with all their fish needs.

JOHANNES

According to the old fishermen in Palau, during the Japanese period, the reef fish population went down drastically. It was several years after the war that they began to experience a repopulation.

MURPHY

Yes, but we still don't know about the total harvest from the reefs. The standing stock, of course, was small during the Japanese regime.

JOHANNES

One recent study demonstrated that in a very heavily exploited shallow reef fishery in American Samoa the catch per unit area was still remarkably high, but the fish were so tiny that the catch per unit effort was simultaneously extremely low (Hill 1977). Such a fishery has little commercial potential despite the high areal yield. And although efficiency is often not as important in artisanal fisheries as it is in highly mechanized fisheries, there comes a stage when the amount of effort involved in harvesting is simply too wasteful of manpower. In the Samoan fishery studied by Hill the yield to line fishermen, for example, was only about 0.5 kg/h. Such unrewarding fishing is pursued only in the vicinity of villages. No one would bother travelling more than a few hundred meters to exploit such a resource even though the yield-per-unit area was still high.

LILEY

From your introduction I rather expected you to be telling us that what you can pin down precisely is not the time of spawning but the places of spawning and that you can pick out zones off the reef edge where most of the spawning is occurring. If that is the case, why can't those areas be closed to fishing at certain times of the year?

BARDACH

Implementation of such measures is a problem. If you have to police on such occasions you will have difficulty.

JOHANNES

This is why I would restrict the surveillance to the times when the fish are particularly vulnerable in those areas, because there is so little money and so few personnel available to enforce the laws in tropical areas.

MURPHY

I think another important aspect of these fisheries in Hawaii, and almost everywhere in the Pacific, is that there are refugia which are difficult to get at, and these refugia, even with intense fishing elsewhere, could easily supply enough larvae to maintain the productivity of the heavily fished reefs. Lobsters are a good example of that. There are big stretches of uninhabited coastline in Palau or stretches that are difficult to fish because of the configuration of the beach. Those are natural refugia.

JOHANNES

Refugia can reduce the problems of recruitment overfishing. But in reef areas, where many species tend to have comparatively limited home ranges, refugia won't do much to reduce the problems of growth overfishing. In other words, whereas pelagic larvae may move from refugia to fishing grounds, the more reef-bound adults are much less likely to do so.

BLAXTER

What's known about the fecundity of these fishes, particularly ones that you say are spawning inshore, clupeoids?

JOHANNES

Nobody really knows because many species are multiple spawners. Reef species typically spawn several times a year. But nobody knows just how many times per year the individual fish spawn. To measure fecundity one needs to know not only how many eggs are carried but how many batches are produced annually.

KEMMERER

The implication of a closure form of management is that it promotes inefficiency. Fisherman should be allowed to fish when fish are aggregated to reduce operating costs.

JOHANNES

Increasing the cost of capture today may decrease it tomorrow. Any conservation scheme, if applied after the resource has begun to dwindle, requires short-term sacrifices for the sake of long-term gains.

ATEMA

Also, what are you going to do with the surplus of people? Let's say that the ultimate inefficiency is that you could go out one day a year and catch a certain amount of the stock and that's it. That means one boat, one captain and and a small crew, absolute efficiency in harvesting that stock. But what are the other people going to do that are not fishing?

KEMMERER

That is a valid point. It is for that reason the term "optimum yield" was coined. Every fishery cannot be managed for maximum yield. A subsistence fishery probably should be managed to maximize social as well as economic benefits. The point I want to make relates to a principle, which is that it is basically wrong to promote inefficiency unless there is a reason for inefficiency.

HENDERSON

I think one must examine the economic and social questions of whether you need employment or efficiency. In some cases you may need one and in some you may need the other.

REINBOTH

I wonder how reliable the data are when we assume a lunar control in the onset of spawning activities. From the literature which I know I get the impression that the observations are more or less casual, but when we observe in a given species a very extended spawning period and when you claim that outside this period there remains a smaller percentage of fish that are spawning, then I am wondering how we can talk about lunar control of spawning activity.

JOHANNES

The majority of species with which I am familiar spawn largely within a 2- to 5-day period around a given phase of the moon. Small and usually insignificant portions of the stock of some species may spawn at other times.

MAY

There are cases where spawning is tightly packed around certain phases of the moon with absolutely no spawning taking place in between. This is definitely true in polynemids and siganids.

REINBOTH

But when we have these gradations and when we remember the examples among invertebrates in which the whole story started, it seems to me that we must be very careful and introduce perhaps a better definition of the term lunar control of reproduction. There are great differences between various species. I don't consider it to be sufficient when we simply uncover some relationship to the lunar cycle.

BLAXTER

Is it likely that some fish in fact spawn every new moon or every full moon?

JOHANNES

In most cases we don't know. Individuals of two species of rabbitfishes held in captivity in Palau spawned on three successive months.

ATEMA

To what extent can this argument be applied to high seas fisheries? Is it possible that we will terminate a high seas fishery too by tremendous efficiency?

KEMMERER

Overfishing is due to efficiency and effort, not just efficiency. Efficiency in itself is not bad. Effort can and should be managed.

JOHANNES

Introducing "efficiency" into tropical artisanal fisheries has been the downfall of many of them. You bring in nylon nets, outboard motors, and various other gear to enable the fishermen to fish more efficiently, and you end up with overfishing and overcapitalization time and time again. This kind of narrowly conceived "efficiency" proves often to be a bane rather than a boon.

MAGNUSON

Efficiency must be somewhat important or they wouldn't have concentrated their fisheries on spawners.

BARDACH

Some increased efficiency is necessary; otherwise you will not be able to supply the increasing urban concentrations with the fish they need. If you had these fisheries only supply the local villages, what you say is correct.

JOHANNES

Certainly modern equipment has given artisanal fishermen in some areas access to previously underexploited resources and markets. But introducing modern boats and gear into tropical artisanal fisheries that cannot tolerate much expansion has proven many times to be socially, economically and/or biologically disastrous. The phenomenon has been dealt with in a paper entitled, not facetiously, "Do fisheries experts aid in fisheries development?" (Alexander 1975; see also, for example, Cole 1973; Nietshmann 1973; Cordell 1974; Hadikoesworo 1977).

BARDACH

I think we have to be very careful to make prescriptions for subsistence fisheries in light of the fact that there are social tendencies in those subsistence fisheries to make them more efficient. The tendency exists because the world is one. Of importance here are tradeoffs in the goals of management.

MURPHY

I think you're right. I think that the islanders might have a very sophisticated goal even though they don't realize they have it. They may actually, when left alone, be adjusting the level of fishing effort to maximize the economic yield. By that, in the context of an islander, I mean holding fishing down to a level so that somebody going out fishing for a day comes back with a worthwhile catch. Now that level of fishing is almost certainly much less than that which would yield the maximum pounds of fish from the reef, and so when they talk about overfishing they may be talking about it in that sense. That is now becoming the management goal in all types of fisheries, not just island fisheries.

ATEMA

I think there is one more principal point. Do we really believe we can manage fish stocks by knowing everything? Will we know everything, or should we have preserves of stocks that are not touched just in case something goes wrong?

FISHELSON

I think by knowing more about the biology of single species, we will be able to make predictions, providing the environment that we are predicting remains stable. By putting together information about the important fishes—all the biological information, physiological, and so on—you can begin to make some predictions.

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Acknowledgments

I am grateful to John Gulland for reading and criticizing the manuscript. This research was supported by grants from the John Simon Guggenheim Memorial Foundation and the National Science Foundation. Hawaii Institute of Marine Biology Publication No. 568.

Behavioral Aspects of Sex Inversion in Certain Fishes

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REINBOTH, R. 1980. Behavioral aspects of sex inversion in certain fishes, p. 271-286. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Sex inversion is unique to teleost fishes; certain species initially reach maturity as males and later turn into females (protandry) while others are first females and become males thereafter (protogyny). A unique teleost species fertilizes itself. The phenomenon is more prevalent in the subtropics and tropics than in the temperate zone, and far more marine than freshwater species are reported to show sex inversion. Certain families, especially the wrasses *(Labridae)* and the parrotfishes (Scaridae), are sexually dichromatic as well as sex-inverting. Their color phases and their spawning behavior, that is, group and/or pair spawning, are functionally related to genetic constitution and endocrine states of individuals. Sex-inverting species in the other families *(Serranidae, Centropomidae)* exhibit prominent spawning migrations and aggregations which provide opportunity for commercial fisheries. Such fisheries may require special attention to gear selectivity so as to conserve a sufficient number of individuals of both sexes for reproduction of the species. Sex inversion also underscores the fact that sex is labile in fishes and that it can be manipulated by hormone treatments. Such treatments are important in aquaculture for the production of unisexual populations. These manipulations in aquatic animal husbandry are discussed as they relate to sex-inverting and other species of cultured fishes.

Introduction

It is the purpose of this paper to discuss the behavior of fish species in which individuals change from males to females or from females to males in their life cycles (Reinboth 1970). Some species are first males and then females and certain others turn from females to males in the course of their life histories. The phenomenon is called sex inversion but simultaneous hermaphroditism, that is, the occurrence of ripe male and female gonads in the same individual, has also been reported from several orders. My present treatment will stress spawning behavior, certain aspects of migration, and endocrine control of sex in ambisexual fishes, and relate these components of the biology and life histories of selected ambisexual species to fisheries management in capture and culture fisheries.

It ought to be noted at the outset that teleost fishes are the only group among vertebrates in which simultaneous hermaphroditism and spontaneous sex inversion occur (Reinboth 1970). This deviation from the usual reproductive pattern in vertebrates poses problems broadly related to genetics, developmental physiology, comparative ethology, and evolution; these, however, are beyond the scope of the following paper.

There are three main types of ambisexual organization among teleosts: (1) simultaneous hermaphroditism in which an animal may change its functional sex (release of sperm or ova) within minutes; in one species only, the killifish *Rivulus marmoratus*, self-fertilization appears to be the rule (Harrington 1975); (2) protogyny in which fish of a species first show ripe ovaries and later in life develop functional testes; and (3) protandry in which fish first develop functional testes and later functional ovaries. Such species occur mostly in the marine environment with an overwhelming preponderance of them in tropical and subtropical waters. No hypothesis has been advanced to explain why the number of ambisexual species in fresh water is low (less than 10 reported to date).

Although ambisexual species occur in various orders of fishes (Smith 1975), the Perciformes are the only group in which all three types of ambisexuality exist in a large number of species. The list of ambisexual teleosts increases steadily; the latest additions come from the pomacentrids reported by Fricke and Holzberg (1974), Fricke and Fricke (1977), and Fricke and Reinboth (unpublished) and the pomacanthids (Shen and Liu 1976).

The gonads of ambisexual fishes vary greatly from species to species. Their histology demonstrates a bewildering variety grading from spatial separation of ovarian and testicular tissues in the same gonads, albeit in different proportions, to germinal tissues with the characteristics of a typical gonochoristic (sexually separate) reproductive organ in which the elements of one sex appear first, mature, and then change over into the gonads of other sex after the first period of reproductive activity or later. Protogynous ambisexuality (females turning into males) seems to be more frequent than the other two main types. Both types of changeover have been called sex inversion. As one sex succeeds the other in any one individual, this term, rather than sex reversal, is correct.

Physiological mechanisms of sex inversion are unknown even though speculations have been made about the evolutionary significance of this remarkable phenomenon (Smith 1967, 1975; Barlow 1975b; Heath 1977). Environmental factors can hardly be envisaged to trigger change of sex. This is especially true for species of tropical coral reefs where the animals spawn throughout the year and individuals undergoing sexual transformation can be found at any time.

Except for the unique self-fertilizing hermaphrodite *Rivulus marmoratus* (Harrington 1975), no ambisexual species has been reared under laboratory conditions. Thus, considerations of the genetics of sex determination in ambisexual teleosts are speculative. A cytogenetic approach by Mehl and Reinboth (1975) implicates a possible polyploid sex chromosome; further studies are badly needed.

Certain ambisexual species are also markedly sexually dichromatic. Intraspecific differences in coloration of males and females, especially among certain species of parrotfishes and wrasses (Scaridae, Labridae), are so great that the color variants have been described as different species (Winn and Bardach 1957, 1960). Barlow (1975a) corrects such a taxonomic confusion also in serranids, deleting *Hypoplectrus nigricans* as a valid species after observing it to spawn with *H. chlorurus* in the open sea. To complicate matters, wrasses and parrotfishes also have males of two types (diandry) (Reinboth 1973). One is a primary, i.e., genetically "pure" male which first resembles the female in color and later with age assumes the male color phase. The other is a secondary male, that is, a male which was first a female and upon gonad transformation assumed the usually more resplendent male color phase. Even more confusion is thrown into the matter by the observations of Randall and Randall (1963) who noted that two types of spawning behavior exist in some species of parrotfishes, namely group and pair spawning, respectively, which will be discussed in more detail later.

Patterns of Reproductive Behavior in Ambisexual Fishes

Parrotfishes and wrasses are unique among ambisexual fishes in that they have two distinct patterns of spawning. In fact, group and pair spawning may even occur in the same species. Only a few details have emerged about the relation of spawning behavior to sexual dichromatism, diandry, and sex inversion, even though many observations have been made attempting to elucidate the relationship between ambisexual patterns and behavioral traits among these prominent families of coral reef fishes (Reinboth 1957, 1962, 1967, 1975b; Choat and Robertson 1975; Robertson 1972; Robertson and

Choat 1974; Robertson and Warner 1978; Warner 1975; Warner and Robertson 1978). The protogynous wrasses of the Caribbean and the Atlantic have provided some of these details.

The original goal of our study of *Thalassoma bifasciatum,* the most common such wrasse in the Caribbean (Reinboth 1967, 1973, 1975b, 1977), was to determine whether behavior of primary and secondary males in their terminal color phase differed. Prolonged observations of individually tagged specimens and later histological examination of their gonads clearly revealed that neither male type can be distinguished as being either the group or pair spawning partner exclusively. On the basis of this study and others on the reef (Reinboth 1973, 1977), we concluded that the dualistic mode of reproduction was not related to diandry as such but to male dichromatism. Corresponding results obtained by Kuhn (1976) on *Thalassoma pavo* from the Western Mediterranean and the comparative survey by Warner and Robertson (1978) confirms our findings. Two Caribbean wrasses, *Halichoeres bivittatus* and *Halichoeres maculipinna,* in which group spawning was observed by Warner and Robertson, are clearly dichromatic and diandric. Yet it may well be inferred from Warner's and Robertson's (1978) data that monandry (one type of male only) excludes group spawning behavior regardless of whether a given species is dichromatic (e.g., *Clepticus parrae)* or not (e.g., *Bodianus rufus).* But observations are still insufficient to ascertain whether simultaneous occurrence of dichromatism and diandry necessarily means that pair and group spawning occur in the same species.

Another behavioral feature prevalent among the parrotfishes and some wrasses is the formation of a "harem" (Robertson 1972). He observed that males of *Labroides dimidiatus* were territorial during the spawning season only, a condition reminiscent of the "lek," a temporary male territory described by Lack (1940) for certain birds. He then advanced the idea that sex inversion is socially controlled. Barlow (1975b) favors a similar interpretation, and Warner et al. (1975), Warner and Robertson (1978) and Robertson and Warner (1978) also believe that social factors play a major part in the timing of sex inversion in other species. My sporadic observations on *Thalassoma bifasciatum* do not contradict this suggestion (Reinboth 1973). The first report on social control of sex inversion has been made by Fishelson (1970, 1975) in the serranid *Anthias squamipinnis* which first matures as a female. These results have recently been confirmed by Shapiro (1977b). Fricke and Holzberg (1974) suggest similar events occur in the sex inversion of the pomacentrid *Dascyllus aruanus.*

Social interactions may be of temporary or of long duration, including pair bonding. None of these seem to be peculiar or exclusive to ambisexual species but they bear some relation to the mode of egg dispersal or protection, regardless of sex inversion.

A frequent pattern of spawning behavior among teleosts is the annual aggregation of males and females, often in distinct places and involving migrations to special locations where spawning itself occurs. Such spawning in large or very large groups also occurs among the ambisexual species of commercial importance, namely the groupers and the threadfins, as well as *Lates calcarifer*, the catadromous giant perch for which sex inversion was noted in Papua New Guinea by Moore and McFarlane (1976). These species have shorter or longer seasonal spawning aggregations as described by Smith (1972) for the Nassau grouper in Bahamian waters. The excerpt from the description of annual spawning migrations of *Epinephelus striatus* along the coast of British Honduras by I.J.B. Robertson (Project Manager, UNDP/FAO Fisheries Development Project, Mogadiscio, Somali Democratic Republic, personal communication) further highlights how masses of these fishes gather for spawning.

> "As far as the spawning concentrations in the waters of Belize are concerned. . .there are some five areas where this takes place, all of which are very restricted in size and very specific in location and timing. Normally the fish concentrate and are caught by the fishermen commencing at the first period of the full moon in December of any year and the season lasts through to March. They only appear to take baited hooks for two or three days either side of the full moon and to a lesser degree two or three days before and after the period of a new moon during this period. Efforts to catch the fish at any other time are unsuccessful although it has been tried time after time. The fish concentrate in the fore reef area in depths around 30 meters ± 5 m, sometimes rarely coming into waters of 20 m. The reef formation in the areas is of the spur and groove formation and the fish tend to concentrate in only two or three of the channels at any one time although they may move along the reef to nearby channels from time to time. The concentration areas are characterized by often strong eddy zones and are all located where the bottom and general reef topography favours either an upwelling condition or a zone close to two or more surface or subsurface current lines. Needless to say, the conditions are not very favorable for comfortable fishing and present a real danger to the small boats which are the only sort capable of approaching the reef at those points where the fish are concentrated."

This species, like most marine fishes, has pelagic eggs and larvae. There has been shown, as yet only among certain of them, a connection of the spawning site with the hydrography (as above) and the exact time of spawning in relation to the moon and therefore the tide (Johannes 1978 and this volume). This relation of spawning location and time, apparently to assist in the dispersal of pelagic larvae, is also well described by May et al. (1979) for the threadfin

(*Polydactylus sexfilis*).

As parrotfish and wrasses occur in shallow, well-lit, transparent waters facilitating numerous observations of their spawning habits, we may once more turn to them for evidence of exact timing of the spawning act even though they are of lesser commercial importance. The peak of spawning activity during the day in these groups appears to be correlated with tidal conditions favorable to transport of eggs away from the spawning site. For instance at Aldabra in the Indian Ocean I observed that *Thalassoma hebraicum* spawned exclusively on the outgoing tide. Aside from the relation of spawning time with optimal opportunity for egg dispersal by current, the spawning act itself contributes to having the eggs reach the surface where the current is strongest. Randall and Randall (1963) were the first to describe the upward gyrations of spawning pairs of *Sparisoma*, later to be confirmed by several others for other parrotfishes and also for wrasses.

Even though ambisexuality including diandry has no proven cause-and-effect relation to the mode of egg development and larval life of a species, I would draw attention in this regard to some observations of certain species with demersal or protected eggs. Genera like *Labrus*, *Thalassoma*, *Halichoeres*, *Coris* and *Novaculichthys* share the peculiarity of spontaneous sex inversion from female to male, whereas representatives of *Symphodus* and *Labrus* but no other genera mentioned above produce demersal eggs, and both genera display parental care. Does a similar pattern apply to sparids also? There is no answer to that question at this moment but it may be noted again that the only sparid for which protogyny has been established unequivocally is the black sea bream *Spondyliosoma (Cantharus) cantharus* (Reinboth 1962). In contrast to other porgies (either protandric or gonochoristic) this species shows parental care (Wilson 1958) and has demersal eggs. Demersal eggs are typical for the protogynous emmelychthiids (=centracanthids) (Reinboth 1962).

Observations so far suggest that diandry does not occur in species with demersal and/or protected eggs and also that protogyny might be somehow related to this same mode of egg development. But there are the many protogynous groupers with their long juvenile pelagic lives and also the protandric *Lates* with pelagic eggs which spawns in places that permit the young to seek shelter in the mangroves at an early age (Moore and MacFarlane 1976 and R. Moore, Department of Primary Industry, Fisheries Research, Box 5, Daru, Papua New Guinea, personal communication). Thus, there seems to be less of a pattern here than appeared at first glance and explanations cannot yet be made that tie causally one or another kind of ambisexuality to distinctly corresponding patterns of life histories. These explanations, and with them interpretations of the evolutionary significance of sex inversion, will have to await far greater insight into the phenomenon that we now possess.

The Ambisexuality of Fishes and Problems of Fishery Management

The difference in the sizes of the sexes in ambisexual species is the main aspect of their biology which relates to fishery management in capture fisheries. The main groups involved here are the groupers and the porgies as well as the threadfins and *Lates*. When gillnets are used as is the case with the giant perch (*Lates*) in some locations, the drastic difference in size between sexes could eliminate or seriously reduce one sex within a population or spawning aggregation. Although fishermen teach professional biologists a lot about the biology of fishes (Johannes 1978), and have taught me facts as well, I have been surprised that the normal occurrence of sex inversion among certain commercially important species is largely unknown to fishermen. It is also surprising that no scientific paper exists about reproductive features among Western Atlantic porgies, even though representatives of this family (e.g., *Archosargus, Stenotomus*) are abundant near active North American research stations. Fortunately, an interesting study (Malo-Michéle 1977) of the protandric porgy (*Boops salpa*) for which a fishery exists in Frànce sheds some light on relations of way of capture and regional variations to the sexual organization and to some extent to the population dynamics of a common ambisexual species.

Fishing may have a selective effect on the size of fishes remaining in a population after heavy fishing pressure; the mean size of *Tilapia (= Sarotherodon) nilotica* in Lake George in the landed catch decreased from 900 to 400 g, while the length range at maturity decreased from 20 cm to 18 cm (Gwahaba 1973). Silliman (1975) showed comparable results with *S. mossambica,* where fishing pressure operated towards the survival of smaller and slower growing individuals. These observations were not made on ambisexual species but they underscore the fact that heavy, even partially selective, fishing on species that show sex inversion with smaller and larger individuals of different sexes could lead to highly skewed sex ratios, even to endanger the survival of certain populations. There emerges a clear need for greater attention to the phenomenon of ambisexuality in fisheries investigations than it has received so far.

If one tries to relate research on teleost ambisexuality to the basic and applied sides of fisheries biology and management, it soon becomes obvious that the questions which remain to be answered frequently relate to broad problems faced by all marine ichthyologists. Detailed knowledge of larval ontogeny (development) of many species is one of them, strongly tied to the difficulty of rearing marine fish artificially. These information gaps are further caused by ignorance of the entire reproductive cycle of a given species. It is more often the rule rather than the exception that we are either informed incompletely or not at all about the biology of juvenile stages. Often we do not find small fish below a certain size because we do not know their habitat. In other cases we cannot reconstruct the full reproductive cycle(s) because the animals are located by fishermen at limited periods of the year only. In my own area of research the exact type of sexual organization in certain ambisexual species remains obscure due to such problems. The influence of exogenous and endogenous (hormonal) factors on gonad maturation and spawning is another point which awaits further clarification. Investigators in Israel pay much attention to the gonochoristic euryhaline *Mugil* (Blanc-Livni and Abraham 1969). When those fish are kept in fresh water, gonadal development is arrested and the fish do not reproduce when they are prevented from seaward migration. The protandric sea bream *Sparus auratus* from the Mediterranean also migrates between waters of different salinity, but little is known in this case about a relationship of this behavior and reproductive phenomena. Rearing experiments with the same species are in progress in the Red Sea at Eilat. Preliminary data suggest that the experimental set-up may even influence the process of sex inversion (Zohar and Gordin, Israel Oceanographic and Limnological Research Ltd., Mariculture Laboratory, P.O. Box 212, Eilat, Israel, pers. comm.) The results obtained by the Israeli workers differ partly from earlier data that have been collected from animals living under natural conditions (D'Ancona 1940/41, 1949).

A correlation between environmental conditions (salinity being but one example) and the functioning of the endocrine system have been intimated (see also Liley this volume). But how these factors are integrated is poorly understood.

Heiligenberg (1965) remarked on a profound influence of acidity of the water on the sex ratio in the African cichlid *Pelmatochromis;* to my knowledge this observation has not been followed up by other workers, but it clearly demonstrates how a peculiar variable that could be inherent to particular techniques of fish culture may bear upon its outcome.

The use of hormones for the induction of certain reproductive phenomena has been treated in this book by Liley. The case of ambisexual species draws our attention to the application of sex steroids as potential tools to manipulate sex. Protogynous teleosts are the only vertebrates among which functional sex inversion can be brought about by administration of testosterone to adult females (Reinboth 1962). We know this fact but do not yet understand the underlying mechanism. Its eventual elucidation might give us a clue to determine the direction of sex differentiation in a planned way even in gonochoristic species instead of relying on trial and error as one has up to now. The experiments by Yamamoto (1965) on *Oryzias* *latipes* have proved that fertile YY males can be produced experimentally and this is a crucial step when it should appear desirable to obtain a purely male offspring from matings with normal females. Similar experiments with other species have not been equally successful but finding out the correct time and effective dosage for hormonal interventions may enable comparable manipulations with them (Hackmann and Reinboth 1974; Nakamura 1975). In species for which social control of sex inversion is assumed, investigations about the quality of sensory inputs and their transduction into morphogenetic events on the level of the gonad are badly needed. But once such a relationship can be established in a sufficiently precise way, the hope is justified that new ideas will emerge for controlling sexual development for practical purposes and thus give new scope to aquaculture practices.

Sex inversion also has profound bearings on certain manipulations that are already practiced in aquaculture: the relatively greater anatomic and histologic attention which the gonads of sex-inverting fishes have received are likely to be of service in the general quest of eliciting sex changes and/or the development in controlled rearing of only one sex, usually the male. Sex changes or unisexual development of gonochoristic mixed populations have been reported especially in *Sarotherodon (Tilapia)* where early maturity and efficient parental care easily lead to crowding in ponds. Tayamen and Shelton (1978) offer a summary of earlier such experiments and add some critical ones of their own involving *Sarotherodon niloticus.*

The existence of sex inversion allows, however, successful manipulation of sex in adult animals, a condition unique among vertebrates (Reinboth 1970). Chen et al. (1977) have brought about early sex inversion in a commercially important, sex-inverting, caged-reared grouper (*Epinephelus tauvina*). They stress that they have opened a new field in endocrinological research on various forms of fish hermaphroditism. Although this can be disputed, the authors may contribute in their experiments to answering another question, namely whether there are differences in the growth rate depending on the sex phase of the fish.

The isolation in time and sometimes in space of males from females among ambisexual species facilitates certain manipulations in culture, such as the rearing of one sex only, and also permits easier application of certain hormonal techniques which would channel food into body instead of gonadal growth by blocking gonadal maturation. For various physiological reasons and following common experience, males are reported to grow faster than females. Even when commercially farmed fish in coastal waters are harvested before they are sexually mature (as is the case in *E. tauvina)*, eventual positive results of hormonal treatment of ambisexual fishes may become applicable to other species. Parallel systematic investigations on sex-specific growth rates among gonochoristic species could, in turn, encourage new efforts to elicit sex inversion by appropriate application of sex steroids to undifferentiated ambisexual fish. Thus, research into the endocrine mechanisms that determine sex inversion among ambisexual species may assume further importance especially when cryogenic storage of sex products of fishes becomes perfected. Then the bringing about of a sex change in any one individual will facilitate the establishment of inbred lines and thus broaden both scope and method of fish breeding.

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Discussion

MAGNUSON

More and more studies seem to be finding that what were once considered two closely related species are really sex-inverting forms of the same species.

REINBOTH

We have examples of this. When I studied the gonadal organization of *Coris julis* from the Mediterranean the discovery of protogynous sex inversion in that species solved an old taxonomic problem. From two species one could be deleted. The same might happen with others, too.

JOHANNES

The few ambisexual species in the temperate zone tend to belong to typically tropical families like the ones you mentioned, serranids for example.

REINBOTH

I am not sure that one can say this. For example, sparids and wrasses are fairly common in temperate waters. On the other hand it is true that there are only four serranid species in the Mediterranean. Beyond any doubt, the number and diversity of ambisexual forms is much larger in the tropics.

BARDACH

It is interesting to note that two closely related families, the Serranidae and Centropomidae, show different forms of ambisexuality. Serranids are protogynous, while at least one centropomid, *Lates calcarifer*, is protandric.

REINBOTH

Lates calcarifer, I learned from you and Dr. Murphy, is supposed to be protandric. But I have not seen any publication concerning this. Up to now simultaneous hermaphroditism or protogyny are the only ambisexual deviations from gonochorism among serranids. Let's take the porgies as another example. The species from the Mediterranean are either gonochoristic or protandric. As I mentioned before, *Spondyliosoma cantharus* is the only species for which protogyny has been established with certainty. As far as we know, it is the only porgy with demersal eggs and it shares this peculiarity with the protogynous emmelichthyids.

MURPHY

I'd like to comment on the giant perch *Lates*, which starts out as a male. You alluded to the possibility of management problems associated with this. There is concern with respect to this animal because females are the large members of the population and commercial fisheries are notoriously biased towards larger members of a population. This same species is artificially propagated in Thailand, so that it would be possible to examine the genetic control.

FISHELSON

I think Dr. Reinboth should not apologize for not contributing information of use in commercial fisheries. Today we know that spearfishing on the large serranid fishes in the Red Sea creates a problem of management for the natural populations. There is a growing number of spearfishermen and all of them are shooting the larger fishes and so eliminate the males. This is now a matter of concern in Israel.

REINBOTH

In this context some statistical data by Thompson and Munro (Part Vb, The biology, ecology and bionomics of Caribbean reef fishes: Serranidae (hinds and groupers), Res. Rep. Zool. Dep., Univ. West Indies No. 3, 1974) may be interesting. The authors compared the male/female ratio in the protogynous *Epinephelus striatus* and *Mycteroperca venenosa* taken from relatively unexploited oceanic banks with catches of *E. guttatus* and *Petrometopon cruentatum* from heavily exploited reefs at Port Royal (Jamaica). In the area with high fishing intensity the share of females became more than seven times larger. If there were a social control of sex inversion like in *Anthias*, an earlier transformation should be expected. But no indications for this have been found. Whether or not the hypothesis is correct that high fishing pressure decreases the inversion rate and thus increases the number of females remains to be investigated. In my opinion it is an important question which merits great attention from the practical point of view also.

BARDACH

Would you care to give us some speculations as to what the evolutionary advantages of either one or the other mode of inversion might be, in connection with certain ecological conditions?

REINBOTH

No, I can't. And in spite of the invitation which you made at the beginning of the session to speculate freely, I even refuse. Once again I refer to the porgies. If you take the protandric *Pagellus acarne* and the protogynous *Spondyliosoma*, both are coastal species, and at the Marine Biological Laboratory at Banyuls-sur-Mer (France) both species can be found frequently in the same haul of the trawl net. We don't know details about the life habits of those fish, but there are also no indications for conspicuous differences that could be taken as environmental clues. Both *Pagellus* and *Spondyliosoma* appear to be quite successful in their biotope. It seems that it is equally advantageous being either protandric or protogynous. How this is brought about, nothing is known.

BARDACH

Well then one should not be surprised that there isn't very much information on it, because apparently from a management point of view, with some exceptions such as the largest groupers and, potentially, *Lates*, it isn't very important.

REINBOTH

No, here I wouldn't go along with you. We simply don't have sufficient information for a statement on this matter. How about hormonal manipulations in order to produce unisexual populations when sizeable commercial advantages might be related to one specific sex?

HARDEN JONES

Knowing nothing about this subject I can step in where those who know something needn't say anything. I would have thought it possible to say what the biological significance is, because making all your female fish larger increases their fecundity.

FISHELSON

Except that the smaller fishes are much more preyed upon. Our studies in the Red Sea show a great loss in fish population during the juvenile stages, and waiting several years until one female can spawn will cause a great loss. The predator pressure in tropical waters is one of the main factors in population regulation, and in many species, increasing reproduction in small size groups seems to be an answer to this.

MURPHY

The other aspect with almost the same explanation is the one that is used to explain grilsing in salmon. In addition to increasing absolute fecundity, having more males than females assures that a female will always be attended. But the embarrassing thing is that the opposite case (protogyny) is also viable in nature.

FISHELSON

Roberson described *Labroides dimidiatus* as harem-living and sex-reversing, with the largest fish being male. And the same species in the Red Sea lives in pairs, being a permanent monogamist.

MURPHY

I think that in order to explain the opposite case you really have to look at the behavior patterns of the animals. In herding vertebrates there is usually a large herd of females and only one extra large male.

MAGNUSON

If mortality were high and only a few got big enough to be males, that would be fine because the numbers of smaller females breeding would be large. Arguments can be developed for either life history strategy—protogyny or protandry.

REINBOTH

For making reasonable speculations about the eventual advantage of one particular direction of sex change you really have to know more physiological and ecological parameters of the fish you are dealing with.

BLAXTER

Does one know anything about the spawning behavior? Does one male fertilize many females?

REINBOTH

I can answer the question at least partly for the protogynous wrasse *Thalassoma bifasciatum*. It has two types of males with regard to gonadal ontogeny: primary males (born as males) and secondary males which develop from females by sex inversion. But with regard to the behavior, only a second form of male dichotomy seems to be important: male dichromatism. The smaller males cannot be distinguished from females, whereas the larger ones turn into terminal males with a conspicuous poster coloration. Those terminal males don't really court the females. They give optical signals by which they invite the females to come to the place where the male has established its territory. If there are many females ready to spawn, the male spawns with these females 30 times, 50 times, it doesn't matter. But the same species indulges in group spawning, provided that some minimal population density is assured. Group spawning takes place only between animals with the same color pattern. But neither from catching eggs released after group or pair spawning nor from the analysis of slow motion movie pictures could we find any basic differences related to pair or group spawning. Group spawning also can be performed many times within short intervals. But we do not know whether the same male (or males?) participates in successive spawning rushes.

HASLER

In the southern part of the United States there is a great deal of fish culture of bluegills (*Lepomis macrochirus*) which have about a 4-wk spawning period. Frequently they'll continue to spawn throughout that period, so that if you don't have a predator to thin them out you'll have stunting of the fish. Would it be possible to change these fish to a single sex after 1 or 2 wk so that the density of fry in the pond is at an optimum, avoiding crowding and thus increasing yield?

REINBOTH

I am not sure whether I can answer your question in a satisfactory way. In the case of the bluegills I don't see any chance of manipulating the sex of the fish after they have passed some critical stage during their juvenile period. Bluegills are normally gonochoristic and there is not a single example known in which gonochoristic fish can be induced to change sex after gonadal sex determination. (The stage of definite sex determination may well be reached before the appearance of histologically discernible features in the gonad.) But if you are interested in the production of unisexual offspring, this probably can be done by appropriate treatment of undifferentiated fish with sex steroids. After having succeeded in obtaining fish in which the phenotypical sex differs from its genetic constitution, the appropriate choice of certain individuals as mating partners would guarantee offspring consisting of one sex only. And it is finally another question whether you think of modifying the sex of juvenile fish in large ponds by adding sex steroids (or other drugs) to the food. Such a procedure is likely to end up by producing many pathological individuals.

MAGNUSON

Is it safe then to say at the present time that we don't know the endocrine mechanism of sex reversal?

REINBOTH

That's unfortunately entirely correct.

HASLER

But I asked if it's possible to stop wild spawning as an aid to fish culture. Why not feed pellets containing testosterone? Has this been done?

MAY

Yes, this has been done with *Tilapia*. Dr. Liley referred to this earlier. Feeding testosterone will produce all male broods.

HASLER

How do you do that?

LILEY

Well you just add the hormone to the feed. The point in their life at which you feed them with hormone is very critical. To obtain complete sex-reversal it is necessary to start the treatment before the gonad differentiates, and this seems to be a rather short period early on.

REINBOTH

Experiments designed to find out more about this have been done in my laboratory. In *Hemihaplochromis (Pseudocrenilabrus) multicolor* the critical period didn't last longer than 48 h, maybe even shorter.

LILEY

But I think you're unable to get any effect from estrogen.

REINBOTH

On the contrary, with estrogen it's relatively easy to obtain effects, but estrogens are extremely toxic. If you treat the animals with them they may grow normally but don't reproduce successfully.

MYRBERG

How strong is the correlation between demersal eggs and protogyny which you mentioned?

REINBOTH

I don't dare to describe it as a firm correlation. But it seems interesting to me that among the wrasses you find demersal eggs in the protogynous genus *Labrus*. Other representatives of the family (e.g., *Symphodus*) also produce demersal eggs but they don't change sex, unfortunately. In the genus *Labrus* the production of demersal eggs is closely related to parental care. In *Spondyliosoma cantharus* there is also parental care which is known, unfortunately, from occasional observations only by Dr. Wilson in the Plymouth Laboratory. I don't know of any report about parental care in this species in the open sea but when I remember the short comments of Zei on the emmelichthyids—they have demersal eggs, too—nothing is known about parental care among them.

MYRBERG

I mention the point only to suggest that species with demersal eggs may also have a strong tendency toward territoriality. This in turn may be one reason for the large males. It's an interesting point.

The Feeding Behavior and Ecology of Marine Fish Larvae

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HUNTER, JOHN R. 1980. The feeding behavior and ecology of marine fish larvae, p. 287-330. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

The behavioral-ecological traits of pelagic marine fish larvae diagnostic of specific ecological roles are discussed. Topics considered include: parental effects (egg size, yolk quantity, spawn distribution); swimming behavior; feeding and searching behavior; prey size relationships; and abundance and distribution of prey. Pertinent literature is reviewed and unpublished data on the larvae of northern anchovy, *Engraulis mordax,* and Pacific mackerel, *Scomber japonicus,* are presented. These two species are used as examples of two distinctly different ecological roles exhibited by marine fish larvae.

Introduction

Natural fluctuations in the size of fish populations are caused primarily by annual variability in the strength of incoming year classes. These may vary from about 0.3 to 2.0 orders of magnitude and this variability often has no obvious relation to size of parent stock (Cushing 1977).

Lack of understanding of the relation between stock and recruitment has hindered effective management of marine fish stocks. The loss in production from collapse of fisheries over the years has been huge. Murphy (1977) estimated a loss in production of clupeoid fishes of 600 million tons not including recent declines in Peruvian anchovy production. Many of these declines in production may be attributable in part to overfishing due to the failure of existing models to provide adequate management guidance owing to lack of understanding of recruitment. Many experts believe that studies of mortality in early life history stages, particularly that of eggs and larvae, hold the key to understanding the stock and recruitment relation (Hunter 1976a). Principal sources of larval mortality are generally believed to be starvation and predation. Thus, studies of behavior and ecology of larval stages in relation to these sources of mortality and stock size may provide much of the needed information. Aquaculture of marine fishes also depends upon adequate knowledge of the behavior of early life stages, for it is these stages that produce greatest technical difficulty in culture and highest labor costs. The objective of my report is to discuss behavioral-ecological traits of pelagic marine fish larvae that are diagnostic of specific ecological roles, and to consider such roles in relation to causes of mortality.

Parental Effects

EGG SIZE-YOLK QUANTITY-STARVATION

The size of a larva at the time of first feeding and the amount of time available to find food before onset of irreversible starvation are largely determined by the maternal influence of egg size and by water temperature. Shirota (1970) found that the length in mm of 40 species of marine and freshwater larvae at onset of feeding was related to egg diameter in mm by the simple relationship L=4D. Large size at onset of feeding is an advantage because larger larvae are able to swim faster and search a greater volume of water for food.

Larvae from large eggs generally have more time to find food before the onset of irreversible starvation because yolk persists for a longer period after feeding begins and/or the larvae have greater reserves in their body which can be used in metabolism (Blaxter and Hempel 1963). Larvae from small pelagic eggs are capable of existing for about 1-2 days after yolk absorption before onset of irreversible starvation, whereas larvae from large eggs such as herring and plaice are able to exist for 6 days and in grunion larvae starvation is reversible after 16 days (May 1971; Table 1). The ability to withstand starvation increases steadily from this point. At the beginning of metamorphosis, herring can withstand 15 days, plaice 23 days (Blaxter and Ehrlich 1974), anchovy 14 days, and Pacific mackerel larvae 5 days (Hunter 1976b and Hunter and Kimbrell MS). These differences reflect in part differences in activity; plaice are less active than herring at this time (Blaxter and Ehrlich 1974), and anchovy less than mackerel. Differences between older fishes reared in the laboratory must be considered only in a relative sense because of the striking differences in condition between reared and wild animals (Blaxter 1975).

TABLE 1. Vulnerability to starvation of eight marine fish larvae at the time of first feeding.

Species	Temp °C	Size at hatch		yolk absorption	Days to point of no return[a] relative to:			Authors
		Length mm	Dry weight mg	Period (days)	Hatch	Yolk absorption	Onset of feeding	
Grunion *Leuresthes tenuis*	20	9.0	362	4	12+[b]	8+[b]	12+[b]	May (1971)
Clyde herring *Clupea harengus*	7-8	8.2	189	8	25	6	22	Blaxter and Hempel (1963); Blaxter and Ehrlich (1974)
Haddock *Melanogrammus aeglefinus*	7	3.5	—	6-7	6	0-1	—	Laurence (1974); Laurence and Rogers (1976)
Pacific mackerel *Scomber japonicus*	19	3.1	40	3	4.0	1.0	1.6	Hunter and Kimbrell (MS)
Northern anchovy *Engraulis mordax*	16.5	2.9	21	4	7.7	1.5	2.5	Lasker et al. (1970); Hunter (unpubl. data)
Bay anchovy *Anchoa mitchilli*	24	2.5	18	1.7	3.1	1.4	1.7	Houde (1974)
Sea bream *Archosargus rhomboidalis*	22	2.3	28	2.2	3.4	1.2	1.7	
Lined sole *Archirus lineatus*	24	1.9	22	3.3	3.8	0.5	1.3	

[a] Time of irreversible starvation (Blaxter and Hempel 1963).

[b] 50% mortality from starvation, not a point of no return, because all survivors able to survive if fed.

The duration of egg incubation, although strongly affected by temperature, is also influenced by egg size. Ware (1975) found the relationship between the incubation time *(I)* at the water temperature for peak spawning, and egg diameter *(D)* for 14 species of Northwest Atlantic fishes was $D = 0.101 I + 0.67$. Similarly, the duration of the yolk sac stage is also affected by egg size (Blaxter and Hempel 1963). Thus, larger eggs improve the survival capabilities of a larva at the onset of feeding, but at the cost of decreasing fecundity and increasing the duration of stages most vulnerable to predation.

The optimum egg size must strike a balance between numbers and the risks of starvation and predation. At lower temperatures where incubation periods are longer, the advantage generally falls to larger eggs, whereas the reverse appears to be true at higher temperatures (Ware 1975). Fine adjustments in these tactics appear to exist within a species to meet seasonal and regional differences in environment. Egg size varies significantly among spawning groups of herring (Blaxter and Hempel 1963) and is known to vary seasonally in many species, with the largest eggs produced in the spring at the coolest temperatures and egg size declining as the season progresses (Bagenal 1971; Ware 1975).

The estimation of the days to irreversible starvation has generally been made from the time of complete yolk absorption but the time from onset of feeding provides more insight to survival strategy, as most larvae begin to feed before the yolk is completely exhausted. Herring larvae have a prolonged period in which they are capable of feeding but still have yolk (Table 1). Thermal optima in efficiency of yolk utilization is another way larvae may adapt to specific environmental conditions. Sea bream larvae retain more yolk at the onset of feeding at 26°C than at other temperatures and thus have more yolk to sustain them if food is not present (Houde 1974). Plaice larvae have a sharply defined thermal optimum in yolk utilization efficiency between 6.5-8°C, which could produce 10% larger larvae at the time of first feeding (Ryland and Nichols 1967).

SPAWNING TACTICS

Eggs of pelagic spawners are often distributed in extremely patchy patterns; 37% of Pacific sardine eggs taken in the years 1951-1959 occurred in only 0.6% of the samples (Smith 1973). Helfrich and Allen (1975) found the density of mullet eggs *Crenimugil crenilabis* to be 17/L at the surface after about 1-2 sec of intensive spawning. A high density of northern anchovy eggs taken in a neuston net was 31/L, corresponding to a density of 46,000 eggs/10 m^2 of sea surface, which is in the upper 5% of all samples of anchovy eggs collected with nylon nets (unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). Other high egg densities include 31,000 eggs/10 m^2 for Pacific sardine (Smith 1973) and 9,000 eggs/10 m^2 for Atlantic mackerel (Sette 1943). The eggs in such patches gradually disperse; dispersion is more rapid at the perimeter of the patch resulting in a denser centrum surrounded by a less concentrated corona. The horizontal mean distance between neighboring eggs increases in a patch from 1-2 cm at spawning to 15-20 cm in most several-day-old sardine eggs (Smith 1973). In the northern anchovy, dispersion of larvae as measured by the negative binomial *K* (Lloyd 1967) continues from hatching until the larvae reach about 10 mm, at which time they reach their most dispersed state and contagion increases thereafter (J. Zweifel, unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). This change from decreasing to increasing contagion coincides with the time anchovies begin nightly migrations to the sea surface to fill their swim bladders (Hunter and Sanchez 1976) and is close to the onset of schooling which begins at about 12 mm by concentrating larvae near the surface at night and thus increasing the frequency of social contacts.

Dispersion of larvae could progress to the point where it might influence onset of schooling or delay formation of schools of viable size. *Menidia* larvae reared in isolation took more time to form a school when brought together than socially reared larvae and the length of the delay was proportional to the period of isolation (Shaw 1961). Breder and Halpern (1946) showed that *Brachydanio rerio* larvae reared from the egg in isolation had considerable hesitancy to join a school. Thus, onset of schooling could be retarded if larvae are dispersed to the point where social contacts are infrequent.

Intraspecific competition and cannibalism also may be affected by initial spawn density and dispersion rates. Houde (1975) found that growth and survival of sea bream larvae decreased rapidly when stocking density exceeded 8 eggs/L at food levels of 1500-3000 microcopepods per liter. Food concentrations of 100/L did not sustain sea bream larvae except at 2 eggs/L stock densities. Bay anchovy larvae (*Anchoa mitchilli*) seem to be much less affected by stock density (Houde 1975, 1977). Sibling cannibalism is common in rearing larvae of large piscivorous fishes such as the scombroids (Mayo 1973) but is unreported and presumably rare in clupeoid fishes. Thus, larger and more active larvae seem to be more prone to cannibalism and competition for food and possibly better able to find schooling companions because of faster swimming speeds. Formation of dense patches of eggs and slow dispersion rates may favor clupeoid larvae, but lower egg densities may be more favorable to the more active larvae.

Swimming Behavior

The cruising speed of larvae is of major importance in their feedin ecology because it affects the frequency that larvae encounter prey and also accounts for the greatest metabolic expenditure. Swimmin of larvae may differ somewhat from adults due, in part, to the lack c mechanical support of the caudal fin. Tail beat amplitude and ta beat frequency are continuously modulated in northern anchov larvae (Hunter 1972) and Pacific mackerel larvae (Hunter an Kimbrell, MS), whereas in adult fishes amplitude is modulated les frequently, except during accelerations (Hunter and Zweifel 1971) Tail beat frequency is inversely proportional to length in fishe (Bainbridge 1958; Hunter and Zweifel 1971), and consequently, th frequency in early larval stages can be quite high, reaching 5 beats/sec in 4- to 5-mm anchovy and Pacific mackerel larvae. A their cruising speed, anchovy larvae use a beat and glide mode o swimming similar to that of adults. This mode of swimming is slow and thereby reduces the volume of water that can be searched, but it has a high metabolic efficiency (25% in a 15-mm larva; Vlymen 1974).

Temperature can have a major effect on activity or cruising speed. Two effects of temperature on activity are illustrated for the northern anchovy reared to age 12 days at various temperatures on a diet of *Gymnodinium splendens* (Fig. 1). Temperature affected the timing of the transition from the inactive yolk-sac stage to the active feeding stage as well as having a direct effect on activity of older larvae. At age 4 days, negligible feeding activity occurred in larvae at 15°C or lower and the speed-temperature relation was a function of developmental rate. At ages 8-12 days, all larvae were past this transition and a direct effect of temperature on activity is evident in the figure.

Cruising speeds increase markedly over larval life more or less in proportion to length. Blaxter and Staines (1971) observed that the cruising speed of herring larvae increased from 20 cm/min at the end of yolk-sac stage to 80 cm/min 8 wk later; in pilchard *(Sardina pilchardus)* speed increased from 10 to 30 cm/min in 3 wk; in plaice from 10 to 60 cm/min over 7 wk; and in sole *(Solea solea)*, from 5 to 40 cm/min over 7 wk. They also noted that cruising speeds of flatfish, sole and plaice dropped by 90% at metamorphosis. Similarly, oxygen consumption of winter flounder *Pseudopleuronectes americanus* was shown by Laurence (1975) to decline sharply at metamorphosis.

Specific comparisons in activity or swimming speed from the literature are difficult to make because of differences in temperature, methodology, and lack of data on larval size. Data collected in my laboratory on anchovy and mackerel show that anchovy larvae swim more slowly than mackerel larvae at all stages of development (Fig.

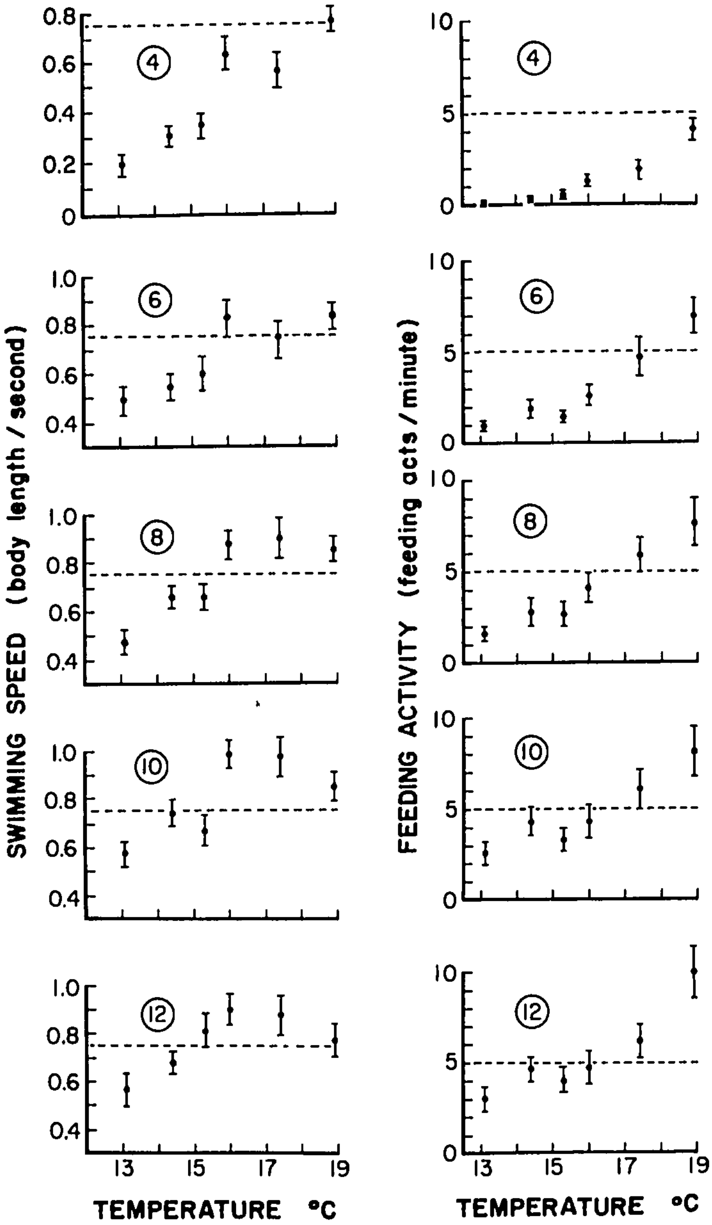

Fig. 1: Effect of temperature on swimming speed and feeding rate of northern anchovy fed *Gymnodinium splendens* (mean density 400 cells mL). Points are means, bars are 2x standard error of mean, panel numbers are larval age in days, and dashed line is a visual reference. Data based on direct visual observation of larvae for 5-mm intervals. Each point is average value for 15 fish in two or more rearing groups.

2). Such a striking specific difference in cruising speed is diagnostic of major differences in life history tactics because it implies marked differences in searching abilities and metabolic requirements. For example, at 18°C, anchovy larvae consume 4.5 μL 0_2. mg dry wt^{-1} h^{-1}whereas mackerel consume 6.1 μL 0_2 . mg dry wt^{-1} h^{-1} (Hunter 1972 and Hunter and Kimbrell MS). The actual difference in metabolic rate between these species is probably greater because the larvae were confined in small Warburg flasks which probably reduced the activity.

Blaxter (1969) concluded from his review that cruising speeds of larval fishes are on the order of 2-3 body lengths/sec and burst speeds, speeds that can be maintained for a few seconds, are on the order of 10 body lengths/sec. The cruising speed of the anchovy is close to 1 body length/sec and in mackerel it increases from 2 to 3 during the larval stage. Thus, these two speeds approach the upper and lower limits of the general range of cruising speeds.

Feeding Behavior

PREY PERCEPTION AND RECOGNITION

Marine fish larvae are visual feeders. All those studied so far, plaice, herring and anchovy, lack rods and retinomotor pigment migration during the first weeks or months of life (Blaxter 1968a, 1968b; C.O'Connell, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA). That feeding is confined to daylight hours is also indicated by stomach content analysis in other species (Arthur 1976).

To be perceived, a prey must be relatively near; first-feeding herring larvae react to prey at 0.7-1.0 body length (L) (Rosenthal and Hempel 1970) or 0.4L (Blaxter and Staines 1971); plaice at 0.5L and pilchard at 0.2L (Blaxter and Staines 1971). Ninety-five percent of the prey reacted to by northern anchovy were within 0.4L of the axis of progression (Hunter 1972).

It would be unreasonable to attach much importance to differences among these values between species. The factors controlling perceptive ranges in larval fishes have not been studied and size of prey was not isolated as a variable. In adult planktivorous fishes, perceptive distances appear to be a linear function of prey size (Confer and Blades 1975). If perceptive distances increase with prey size in larvae, this would certainly increase the effective searching volume of larvae specializing in such prey. In all these studies, the authors point out that perceptive ranges increase as larvae grow. Rosenthal and Hempel (1970) concluded that perceptive ranges in herring larvae also change with activity level, being greater during slow meandering swimming and shorter during faster swimming.

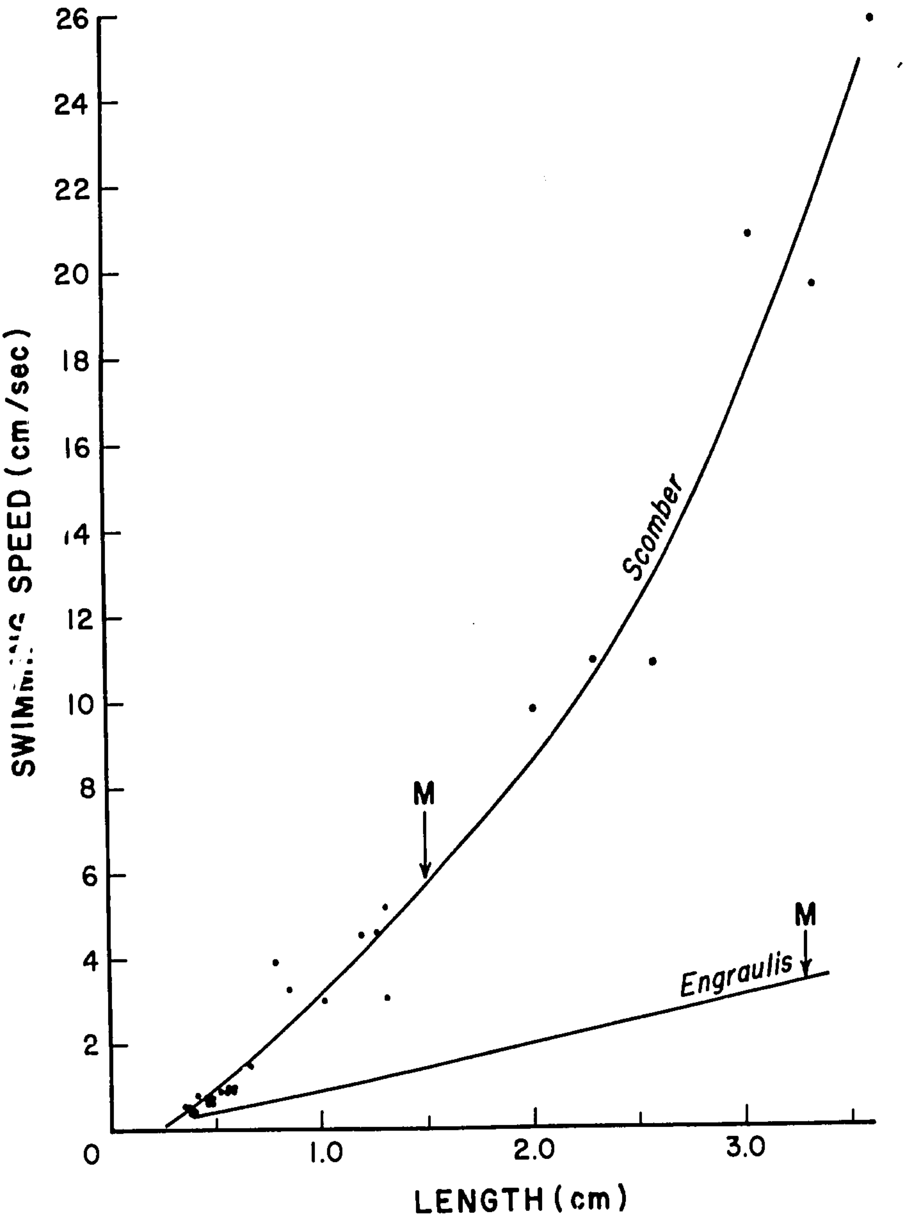

FIG. 2. Swimming speed of Pacific mackerel, *Scomber japonicus*, larvae and juveniles at 19°C; points are means for five or more observations; curve fit by eye; and swimming speed of northern anchovy larvae, *Engraulis mordax*, at 17-18°C from Hunter (1972). Speeds are total distance covered, including time spent in rest and feeding, and M indicates fish length at metamorphosis.

They also state that herring larvae do not perceive prey which are beneath the plane of the horizontal axis of the body, but this does not appear to be the case for northern anchovy larvae (Hunter 1972).

The stimuli eliciting prey capture have not been studied in larval fishes, but in adult fishes prey size is usually the strongest factor with movement seeming to direct attention of the fish toward the prey (Kislalioglu and Gibson 1976a). Almost all predators which are believed to depend upon prey movement are able to detect prey even when they are motionless (Curio 1976). The frequent occurrence of copepod eggs and other nonmotile foods in the stomachs of field-caught larvae and *Artemia* eggs and other nonmotile foods in laboratory-reared larvae (May 1970) clearly shows that movement is not essential in many species. Prey size selection so dominates selection patterns in larval fish that it is difficult to evaluate the role of other prey characteristics such as spines and other protective structures, color, or avoidance behavior. Bowers and Williamson (1951) concluded that some copepods with spiny appendages such as *Acartia* occurred in the stomachs of herring larvae less frequently than would be expected from their abundance in the plankton, and Arthur (1976) suggested that jack mackerel may select the more brightly colored copepods such as *Microsetella* which occur in their stomachs in greater abundance than in the plankton. It would be of considerable interest to study such characteristics under controlled laboratory conditions, both from the standpoint of larval feeding ecology and copepod evolution.

MOTOR PATTERNS

Upon sighting a prey clupeoid larvae assume a sinuous posture and advance toward the prey by sculling the pectoral fins and undulating the finfold while maintaining the body in the S-posture. When the prey is a short distance from the snout, the larva opens its mouth, straightens its body causing the body to drive forward, and the prey is engulfed (Breder and Krumholz 1943; Rosenthal and Hempel 1970; Hunter 1972). Larvae of plaice *Pleuronectes platessa* (Riley 1966) and northern sennet *Sphyraena borealis* (Houde 1972) and other fishes are also reported to assume a sinuous feeding posture but the behavior has been studied in detail only for clupeoids and for freshwater coregonid larvae *Coregonus wartmanni* (Braum 1964), and quite possibly differences exist among species.

Pacific mackerel larvae *Scomber japonicus* feed in a manner more typical of the biting attack of many adult fishes. Upon sighting a prey, mackerel larvae advance toward the prey, stop, draw back the tail, and hold it in a slightly recurved, high amplitude position. The rest of the body is straight; feeding is accomplished by opening the mouth and driving the tail posteriorly. Presumably many other larvae of similar robust body form feed in this way.

Anchovy larvae often assume and reassume the S-posture while maintaining their orientation to a moving prey; but my observations indicate that once the strike is made, larvae rarely strike again at the same prey. Mackerel larvae, on the other hand, frequently strike two or more times at the same prey if the previous strike was unsuccessful. Mackerel larvae often reposition for the second strike by moving backward; anchovies and other clupeoid fishes do not appear to have this maneuverability (Blaxter and Staines 1971). Large prey are more difficult to capture and are less abundant in the sea; consequently, persistence in a feeding attack as exhibited by mackerel may be an essential characteristic of a species whose strategy depends on larger prey.

The time spent poised in a striking posture is much longer at the time of first feeding than in later larval life, and gradually the strike becomes integrated with swimming movements. In the anchovy, duration of complete feeding acts declined from 1.5-2.0 sec to about 0.6 sec when larvae reached 17 mm and relative speed of the strike also declined (Hunter 1972). A poised striking posture seems to be a common tendency in young larvae and declines as the larva grows and could be an adaptation to low feeding success, and perhaps to a necessity to feed by engulfing prey that are relatively large for their mouth.

Handling times are negligible when copepods and other small zooplankton are prey because the prey are engulfed by the mouth instantaneously. Piscivorous fish larvae manipulate their prey and consequently handling times increase with prey size as is the case for adult fishes (Kislalioglu and Gibson 1976b). The appearance of piscivorous habits requires development of a new set of motor patterns associated with grasping prey and presence of sufficient numbers of teeth to accomplish this end. Larvae of the northern sennet *Sphyraena borealis* usually seize other larvae crosswise and, by a successive series of head shakes, move the grasp to either the head or tail. Then without losing grip, the prey is swallowed head or tail first (Houde 1972). Houde observed that newly hatched fish larvae were eaten by sennets at age 10 days and were the preferred food of sennets 9 mm and longer. I observed the same behavior in the Pacific barracuda *Sphyraena argentea* feeding on siblings in a rearing tank. In this case, piscivorous feeding began at age 5 days when larvae were only 4.4 mm. Pacific mackerel larvae become piscivorous when they reach 10 mm. They also seize other larvae from the side, carry them crosswise in the mouth, periodically release the prey, and grasp it again until it dies; then they release it and ingest it, usually head first.

FEEDING SUCCESS

Feeding success of fish larvae is often low at the onset of feeding. Estimates for herring are 6% (Rosenthal and Hempel 1970) and 2-6% (Blaxter and Staines 1971), for coregonid larvae 3-5% (Braum

1964), and 10% for northern anchovy (Hunter 1972). Feeding success gradually increases, reaching 90% in about 3 wk in the anchovy (Hunter 1972), and in about 7 wk in herring (Blaxter and Staines 1971). In contrast to these species, plaice larvae capture 32-62% of prey attacked at the onset of feeding (Blaxter and Staines 1971) and the relatively large larvae of *Belone belone* (12 mm) capture 60-100%, depending on prey type (Rosenthal and Fonds 1973).

Blaxter and Staines (1971) suggest that the initially high success of plaice larvae may be due to increased maneuverability of plaice relative to herring and to their ability to swim backwards. Feeding success of anchovy larvae dropped from 80% to 40% at age 17 days when the prey was changed from *Brachionus* to *Artemia* nauplii, but in 2 days their success increased to the former level (Hunter 1972). Changes in mouth size or other developmental changes could not occur so rapidly; thus, the difference appears to be attributable to experience.

SEARCHING BEHAVIOR

Food density requirements have been estimated from behavioral search models of the basic form outlined by Ivlev (1960). These models in their simplest form require an estimate of ration, swimming speed, perceptive field, and feeding success with many other parameters added as complexity increases. These models range in complexity from the simple models of Rosenthal and Hempel (1970), Blaxter and Staines (1971) and Hunter (1972) where only basic parameters are considered, to the increasingly complex models of Jones and Hall (1974) and the most complex to date, Vlymen (1977). Vlymen's model is the only one that does not assume a random search pattern and that addresses the problem of a contagious food distribution. In his model the larvae have no effect on food density and the model does not use a prey size dependent modulation of perceptive field and feeding success. All such models are extremely sensitive to assumptions regarding the perceptive field and swimming speed and to the accuracy of these measurements. For example, Blaxter and Staines (1971) estimated that the searching abilities of herring larvae increased from 0.1 to 2.4 L/h over 8 wk, whereas Rosenthal and Hempel (1970) estimated they increased from 1.5 L to about 10 L/h in 10 wk. The major difference in these results is in the differences in perceptive distances and rates of swimming (Blaxter and Staines 1971). It would seem to be of value to use such models to set up hypotheses that could be tested in the laboratory or at sea.

Owing to these problems and to effects of temperature, specific comparisons are difficult but these estimates do suggest that the volume searched by young larvae is often quite small: pilchard (5-7 mm) search 0.1-0.2 L/h, plaice (6-10 mm) search 0.1-1.8 L/h

(Blaxter and Staines 1971) and anchovy (6-10 mm) search 0.1-1.0 L/h (Hunter 1972). All studies show that searching abilities increase markedly with growth, since speed, capture success rates, and perceptive distances are functions of length or age.

In the two cases studied, search patterns in larval fishes were nonrandom. Larval anchovies decrease their speed and change their turning probabilities when they enter a dense patch of food. The probability of making a complete reversal in direction increased from 0.04-0.05 at low food densities to 0.23 in dense patches of *Gymnodinium* and to 0.07 in patches of *Brachionus* (Hunter and Thomas 1974). Wyatt (1972) showed that the time plaice spent swimming increased with a decrease in food density. Similar nonrandom search patterns have been described for adult fishes (Kleerekoper et al. 1970; Beukema 1968).

Prey Types

Naupliar through adult stages of copepods are the typical food of most marine fish larvae studied to date. Some notable exceptions to this rule exist: in the North Sea in normal years, the food of plaice larvae consists mostly of the appendicularian *Oikopleura dioica* (Shelbourne 1962) and larval fishes may be a common item in the diet of the more piscivorous larvae. Larvae are commonly eaten by larval Pacific barracuda (A. Ahlstrom, pers. comm., National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) and blue marlin *Makaira nigricans* (Gorbunova and Lipskaya 1975), and judging by high incidences of cannibalism under rearing conditions, they may be frequently eaten by many scombroid larvae (Mayo 1973). Blue marlin larvae begin feeding on fish larvae at 6 mm and they become the principal food by 12 mm (Gorbunova and Lipskaya 1975); under rearing conditions, the scombroid fishes, *Euthynnus alletteratus*, *Scomberomorus cavalla*, *Scomberomorus regalis* and *Auxis* became cannibalistic at about 5 mm (Mayo 1973), *Scomber japonicus* at 10 mm, and *Sphyraena argentea* at 4.4 mm (Hunter, unpublished data). Under aquarium conditions, sibling cannibalism appears to end as scombroid fishes become juveniles and begin schooling (Mayo 1973; Clemens 1956; Hunter and Kimbrell MS).

Larvae tend to be more euryphagous during the earliest stages and organisms such as tintinnids, phytoplankton, mollusk larvae and ciliates are often eaten as well as copepods (Arthur 1976; Bowers and Williamson 1951; Lebour 1921; R. de Mendiola 1974). Phytoplankton, often identified as green remains, is relatively common in the stomachs of clupeoid larvae at about the time of first feeding, but is uncommon soon after. In general, the use of phytoplankton in laboratory rearing studies as a sole source of food for first-feeding larvae has been unsuccessful (May 1970). Northern anchovies, on the other hand, are able to subsist on a diet of the dinoflagellate *Gymnodinium splendens* for up to 20 days, but at a greatly depressed growth rate (Lasker et al. 1970; Theilacker and McMaster 1971). Anchovies will feed on a variety of dinoflagellates, *Gymnodinium, Gonyaulax, Prorocentrum* and *Peridinium,* but not small flagellates, *Chlamydomonas, Dunaliella,* nor on diatoms, *Ditylum, Chaetoceros, Thalassiosira* and *Leptocylindrus* (Scura and Jerde 1977). That larvae fed *Gonyaulax* (40 μm diameter) did not survive, whereas those fed *Gymnodinium* (50 μm diameter) did, led Scura and Jerde to conclude that it was the small size of *Gonyaulax* which made it an inadequate food. Using the same line of reasoning, it seems doubtful that any of the other dinoflagellates they studied would support growth because they are even smaller in diameter.

The tendency for larvae to feed upon a greater variety of organisms in early larval life and subsequent specialization in stages of copepods may simply be due to the existence of a greater variety of small organisms of the proper size in the sea. The ability to subsist on the relatively small organisms such as dinoflagellates may be restricted to larvae of relatively modest energy demand, such as the northern anchovy, i.e., a larva of relatively low initial weight, low activity, existing in cool water.

Prey Size Relations

SPECIFIC DIFFERENCES

Size dominates prey selection patterns of larval fishes and is one of the best diagnostic characteristics for evaluating specific ecological roles. The critical dimension for ingestion of copepods and other oblong prey is the maximum width including appendages (Blaxter 1965; Arthur 1976). Evidence for this is based on the fact that copepods are frequently found in the stomachs of larval fishes which were too large to be ingested in any other way (Blaxter 1965; Hunter 1977). Copepods are usually found in the stomachs of clupeoid larvae with antennae folded back along the body (Blaxter 1965). Blaxter goes on to say that copepods with antennae folded in such a way are probably the only ones that are captured successfully. Inclusion of the appendages increases the maximum width of adult and copepodite stages by about 49% in *Pareuchaeta,* 25% in *Calanus, Pseudocalanus, Acartia, Microcalanus,* and *Metridia,* but has a negligible effect in *Temora, Oithona, Oncaea,* and *Microsetella* (Wiborg 1948a).

The increase in size of prey selected by marine fish larvae as they grow is well documented in the literature and occurs in every species studied. Often, prey length or life stage was used as a measure of size rather than the more informative measurement of maximum prey width. A striking feature of these data is the consistency of trends among related species and groups (Fig. 3). The small clupeoid larvae, *Sardinops*, *Engraulis*, and *Harengula*, consistently feed on small prey of the order of 50-200 μm width; both species of *Trachurus* show a tendency for a marked increase in the range of food sizes eaten with length; and *Scomber* shows a somewhat similar trend. In the three engraulid species, there appears to be a consistent tendency for a marked increase in the range of prey eaten between 8 and 12 mm. Hake larvae begin feeding on much larger foods than the rest with only a slow increase in average prey size. De Ciemchomski and Weiss (1974) point out that hake begin feeding on advanced copepodite and adult stages of copepods.

The consistency of these trends from different localities and species strongly suggests that these patterns are the result of positive size selection inherent to species or specific ecological groups of larvae. Stepien (1976) demonstrated that sea bream larvae select foods by size, with a slight positive electivity for prey of 100-200 μm width in larvae 4-5 mm and a stronger positive electivity for prey 200-300 μm in larvae 7-9 mm. The difference between sea bream and the two clupeoid larvae in the figure may be more marked under natural conditions because the food size preference of sea bream increased faster than the increase in size of the food in the rearing tanks.

Except for hake, specific differences are less marked at the onset of feeding with all larvae feeding on prey of 50-100 μm width although jack mackerel take much larger foods as well. Houde (1973) remarks that organisms 50-100 μm are eaten by a great variety of larvae at this time, including those with relatively large mouths such as the tunas and flatfishes. Arthur (1977) estimated the naupliar biomass in the California Current system and expressed it in terms of naupliar width. The naupliar biomass was at a maximum between 50-80 μm of naupliar width and declined sharply on either side even though there were many more nauplii of smaller sizes. He points out that the food size range of first-feeding Pacific sardines, northern anchovies and jack mackerel all overlap the naupliar biomass maximum and it appears that the feeding range of many other larvae do so as well.

Larvae in the above comparisons are relatively the same size at onset of feeding and hatch from relatively small eggs. Larvae from large eggs, for example, exocetid larvae and saury *Cololabis saira* are 6-7 mm at first feeding and feed on a range of prey equivalent to that of older jack mackerel or *Scomber* of about the same size (Yokota et al. 1961). None of the species in Fig. 3, other than hake, could eat newly hatched *Artemia* nauplii at the onset of feeding, but rearing studies reviewed by May (1970) indicate that plaice larvae, two species of *Fundulus*, a species of *Sebastes*, two cottid species, four species of atherinids, *Aulorhynchus flavidus*, and *Fugu pardalis*

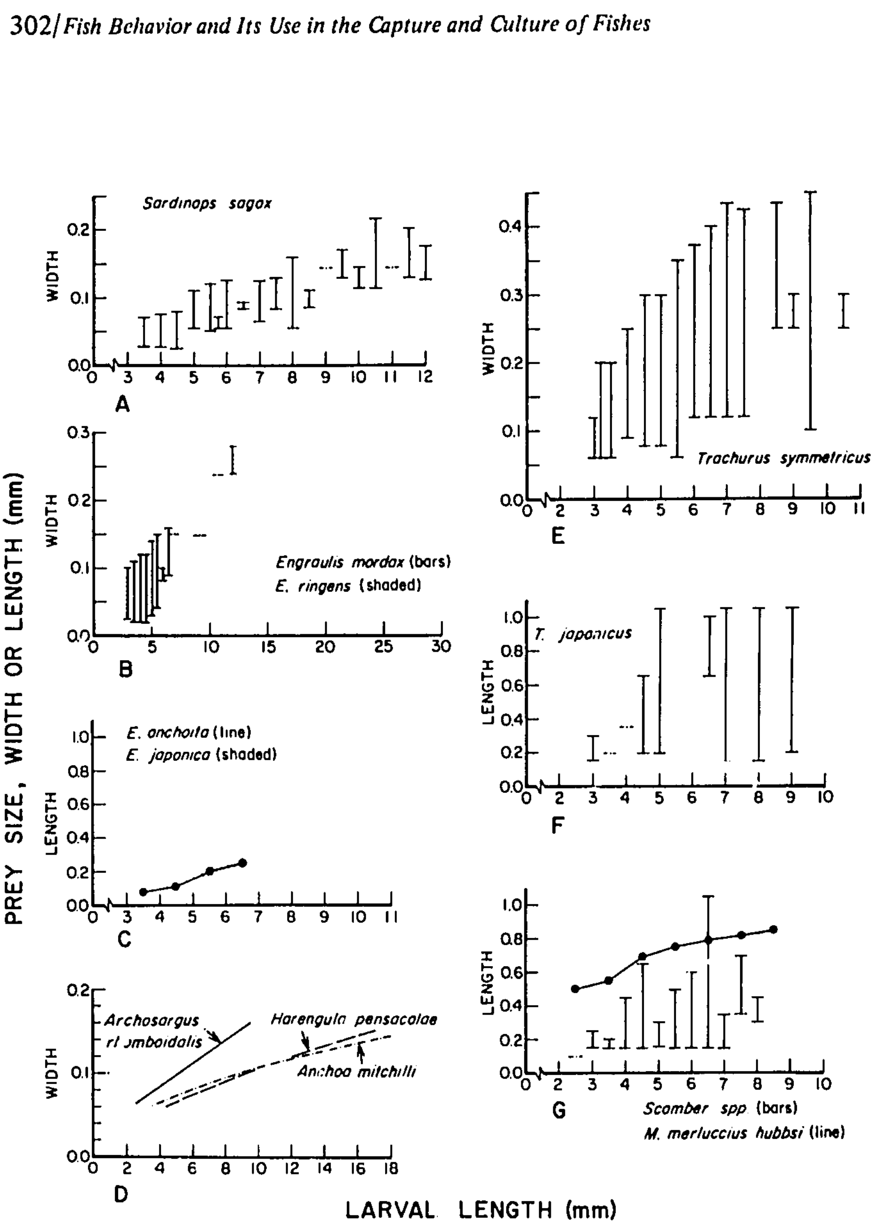

FIG. 3: Relation between prey size and larval length for 12 species of marine fishes; label on ordinate indicates if prey width or prey length were measured; vertical bars and shaded areas represent range of prey sizes; and straight lines connecting dots indicate average prey sizes. Plots were redrawn from Arthur (1976) for *Sardinops sagax, Engraulis mordax* and *Trachurus symmetricus;* from R. de Mendiola (1974) for *Engraulis ringens;* from Detwyler and Houde (1970) for *Harengula pensacolae* and *Anchoa mitchilli*; from Stepien (1976) for *Archosargus rhomboidalis*; from Cieschomski and Weiss (1974) fro *Engraulis anchoita* and *Merluccius merluccius;* and from Yokota et al. (1961) for *Engraulis japonica, Trachurus japonicus* and *Scomber* spp. Data are for sea-caught larvae, except panel D which were laboratory reared.

feed successfully on *Artemia* nauplii at the onset of feeding. Many of these species have large eggs, again emphasizing the importance of the maternal contribution in the feeding tactics of some larvae.

An additional feature of importance in these records is the slow increase in the minimum size of prey eaten in all species. The effect of this is to greatly expand the prey range in larvae that select larger prey. In summary, marine larvae select foods of increasingly larger size as they grow, but the average and range of sizes selected differ greatly among species and may be diagnostic of specific ecological roles.

EFFECT OF MOUTH SIZE

The size of the mouth and the rate it changes with length must be partially responsible for specific differences in food size selection. Shirota (1970) measured the gape of the mouth of 33 species of marine and freshwater larval fishes, correlated them with the size of natural foods and growth rates, and concluded that larvae with smaller mouths grew more slowly than those with larger ones. Blaxter (1965) showed that differences in gape of the mouth existed between different races of herring, and concluded that these differences could be of great significance in early survival.

Mouth size would be expected to set the upper size limit for prey. To define this relationship, Hunter (1977) and Hunter and Kimbrell (MS) determined for anchovy and Pacific mackerel the mouth size threshold for various prey. In these experiments, larvae were exposed to high densities of a single prey, *Brachionus, Artemia* nauplii, or anchovy eggs, for 2-4 h and the proportion of larvae that captured one or more prey was tabulated by mouth size classes. None of the larvae tested had any previous experience with the particular prey. The width of the mouth was closely correlated with the ability to capture these prey (Fig. 4). The first incidence of feeding occurred when the ratio of prey width to mouth width was close to unity, when *Artemia* or anchovy eggs were the prey. In the case of *Brachionus*, it was lower (0.63) which may have been caused by the fact that first-feeding anchovy larvae were used in this experiment to avoid the effect of rapid improvement of success that occurs over the first few days.

These experiments indicated that on the average, 50% of larval anchovy or mackerel were capable of feeding on these prey when the prey width to mouth width ratio was 0.76. The width of the mouth provided a good indication of the size of prey a larva was capable of ingesting. Mouth gape was also measured but width was preferred because it could be measured with greater accuracy. A different relation could be expected for piscivorous feeding or when ingestion involved manipulation of the prey because larvae are capable of greatly expanding their mouths under these circumstances. The

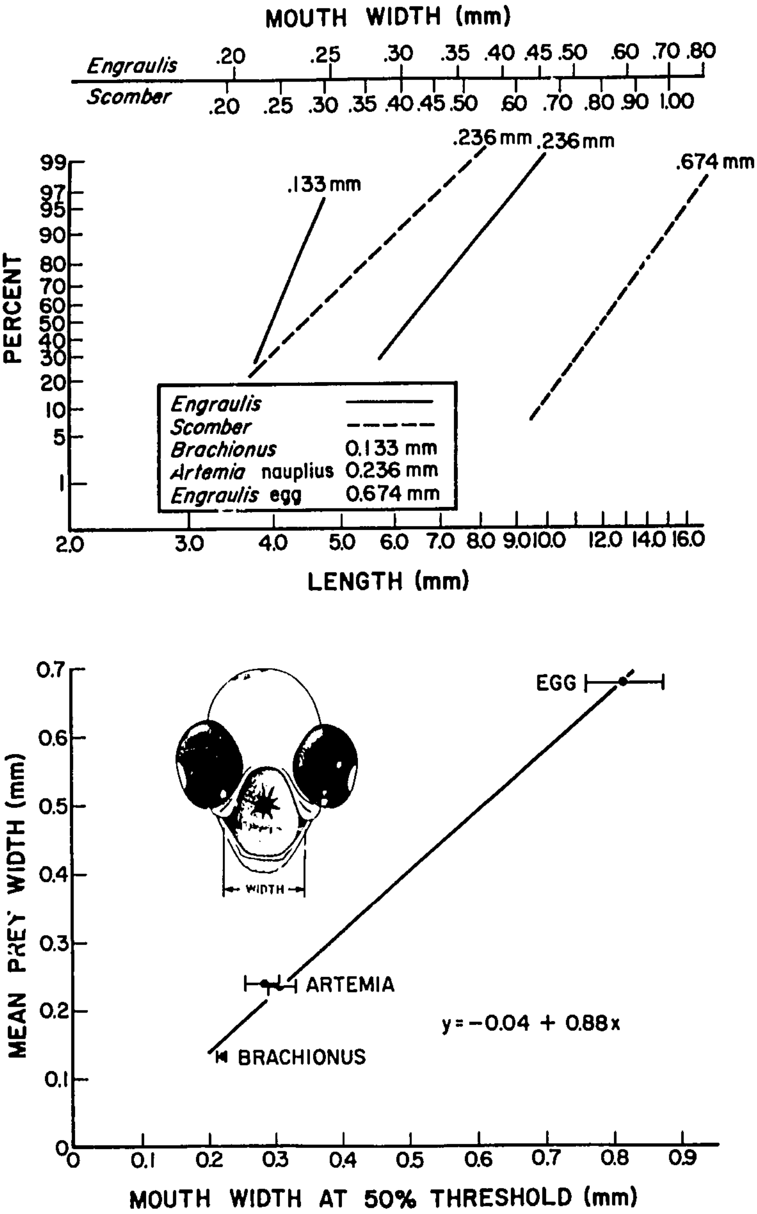

FIG. 4. Relation between width of mouth and ability of *Scomber japonicus* and *Engraulis mordax* to capture prey of various widths. Upper panel, percent of larvae that captured one or more prey shown as a function of mouth width (upper scales) and larval strength (lower scale); lines are for the regression of probit on log larval length. Lower panel, average width of prey shown as a function of the mouth width at which 50% of the larvae ingested one or more prey; estimates taken from probit lines given in upper panel; and bars are the 95% confidence intervals for the estimate. Density of prey in the experiments were: *Brachionus* 9/mL; *Artemia* 10/mL; and *Engraulis* eggs 10/L.

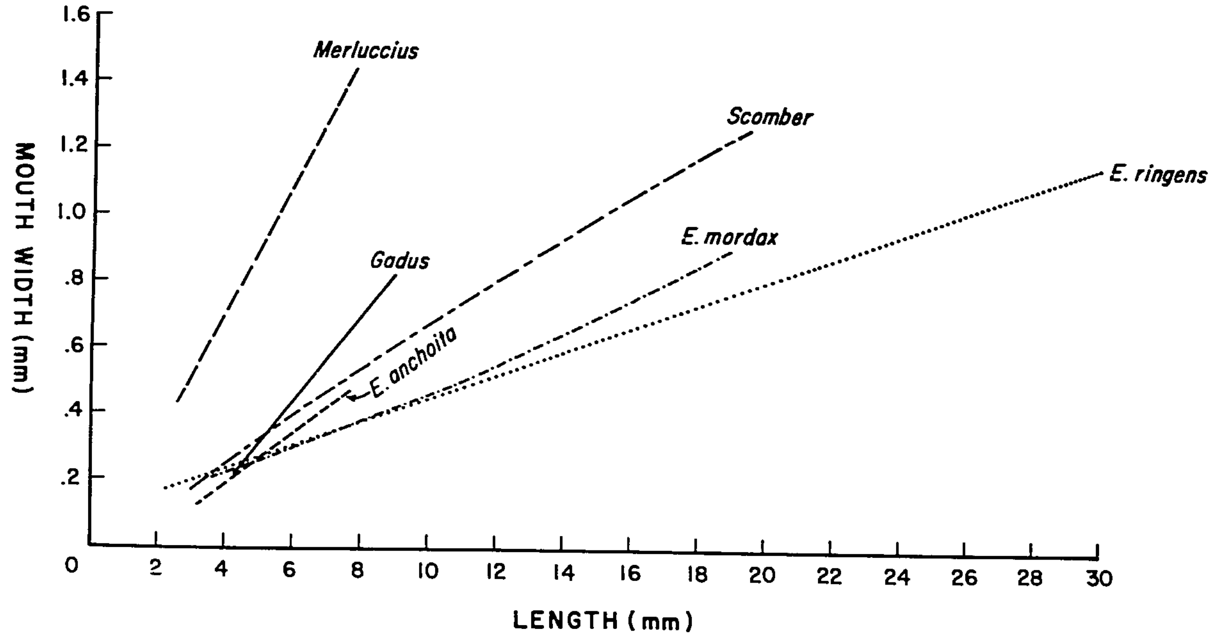

Fig. 5. The relation between mouth width and larval length of hake, *Merluccius merluccius* from de Ciechomski and Weiss (1974); cod, *Gadus morhua* from Wiborg (1948b); Pacific mackerel *(Scomber japonicus)* from Hunter and Kimbrell (MS); and three species of anchovy, *Engraulis anchoita* from de Ciechomski and Weiss (1974). *Engraulis mordax* from Hunter (1977) and *Engraulis ringens* from R. de Mendiola (1974).

gape of the mouth would be expected to be related to handling time in this case (Kislalioglu and Gibson 1976b).

These thresholds are also of interest because they indicate how feeding success is affected by prey size. They also show that prey are eaten "end first" because at the lowest success levels, the prey could be ingested in no other way. Many of the trends in size selection of prey discussed in the previous section are also suggested by the relationship between mouth width and length. The mouth sizes of the three engraulid species are similar to each other and differ markedly from those of the other species (Fig. 5). The mouth width of all species but hake are somewhat similar in the beginning but differences increase greatly with growth. Hake stand out as being distinctly different from the rest from the onset of feeding.

The sharp increase in food size that occurs in the engraulids between 8-12 mm occurs at a time anchovies become highly proficient in capturing *Artemia* nauplii and the increase in prey size is to one of that diameter. No evidence exists from mouth size information to explain the leveling of food size that occurs thereafter, despite the fact that the mouth continues to grow. It seems reasonable to assume larger prey would be eaten if the opportunity existed. Thus, other limits must be imposed; one such limit may be the slow swimming speed of engraulid larvae.

NUTRITIVE VALUE OF PREY OF DIFFERENT SIZES

The nutritive value of larger prey can be illustrated by considering the relation between width of copepods and their weight. Gruzov and Alekseyeva (1970) give a wet weight to length conversion for a group of copepods including species in Calanidae, Paracalanidae, Pseudocalanidae, and other families having a cephalothorax length to width ratio of 2.0-2.8. I transformed their data to show dry weight as a function of cephalothorax width by using the midpoint of their width ratio (2.4) and assuming a water content of 87% (Lovegrove 1966).

This calculation indicated that an increase of 2.5 in width produces an order of magnitude increase in dry weight. Thus, a larva feeding on copepodites 200 μm wide would have to capture 10 times the number of prey to obtain the same ration as one feeding on copepods 500 μm wide (Fig. 6). The effect of a slight increase in width of prey eaten is more marked if the change from feeding on nauplii to copepodites is considered. The change in body width of *Calanus* from nauplius VI to copepodite I is slight even when appendages are included in the measurement (Wiborg 1948a), but the dry weight about doubles. In *Calanus helgolandicus,* the dry weight of nauplius VI is 2.0 μg and that of copepodite I is 4.3 μg (Paffenhöfer 1971). The well-known seasonal and regional variation in copepod weight (Marshall and Orr 1955; Gruzov and Alekseyeva 1970) should be

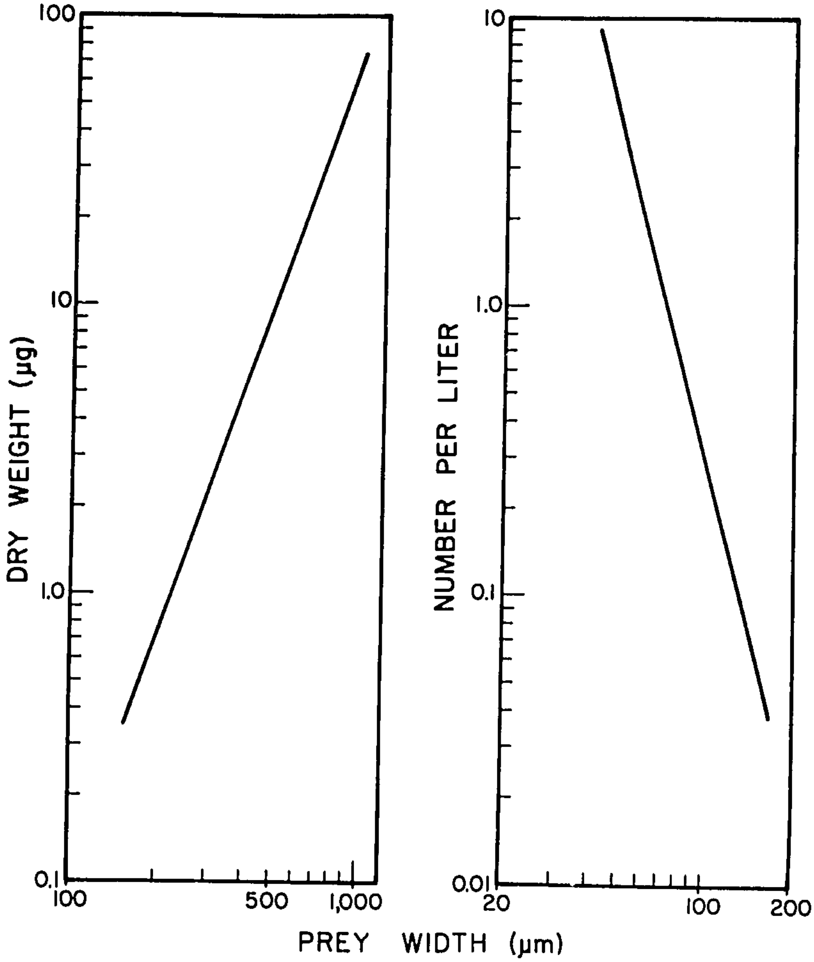

FIG. 6. Left panel, relation between copepod width and dry eight (excluding naupliar stages) calculated from data given by Gruzov and Alekseyeva (1970). Right panel, relation between number of prey per L in the sea and prey width, recalculated from Vlymen (1977).

considered in any study of food size relations in larval fishes.

The necessity for increasing prey size with growth is illustrated by comparing growth rates of larval anchovies (Hunter 1977) and Pacific mackerel (Hunter and Kimbrell, MS) fed different foods (Fig. 7). When anchovies are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm whereas when *Gymnodinium* and the rotifer *Brachionus plicatilis* are used, growth becomes asymptotic at about 20 mm and few larvae survive (survival drops from 46% at age 26 days to 6% at age 42 days). Similarly, Pacific mackerel growth slows on a diet of only *Brachionus* and few survive beyond 8 mm at age 15 days. Howell (1973) was able to grow plaice larvae through metamorphosis on *Brachionus* alone, but at a much slower growth rate than when *Artemia* was used, indicating that some species are able to grow through metamorphosis on rather small prey but at a depressed growth rate.

Vlymen (unpublished data, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA) estimated for larval anchovy the minimum caloric value of prey required to meet energetic needs for parameters in his 1977 paper. The model uses a 12-h feeding day, a temperature of 17°C, and the maximum feeding rate observed in the laboratory (about 10 attacks/min). Gut capacity was not included and consequently the limit was set by the maximum feeding rate. To calculate the minimum caloric value of prey necessary to meet energy needs, Vlymen used the model $E_1 + E_2 + E_3 + E_4 = 0.48\,R$ where:

E_1 = $(5.10 \times 10^{-2})\,L^{3.3237}$ (the basal metabolic rate in calories, where L = length (cm));
E_2 = $0.19\,L^{4.48}$ (the total energy cost of swimming);
E_3 = $0.05\,L^{4.48}$ (the total energy cost of feeding attacks at maximum rate during a 12-h day);
E_4 = $0.29R$ (the energy cost of mechanically processing food, intestinal propulsion, etc).;
$0.48\,R$ (the proportion of the ration (R) available for energetic needs).

The ration at the maximum attack rate was $R = (7.12 \times 10^3)\,C \times S$ where 7.12×10^3 is the total number of attacks at the maximum rate in a day of feeding; C = calories per prey; and S = the success of capture. By substitution he obtained $(3.78 \times 10^{-5})\,L^{3.3237} + (1.77 \times 10^{-4})\,L^{4.48} = C \times S$. The success of capture (S) is a function of age, not length, and is described by the function $S = 93.2\,\mathrm{Log}_{10}\,T - 33.3$ where T is larval age in days. To obtain the minimum caloric value of prey for larvae of various lengths, ages at specific lengths were obtained from laboratory growth rates (Hunter 1976). The origin of the data and the derivation of the parameters used in this model are described by Vlymen (1977).

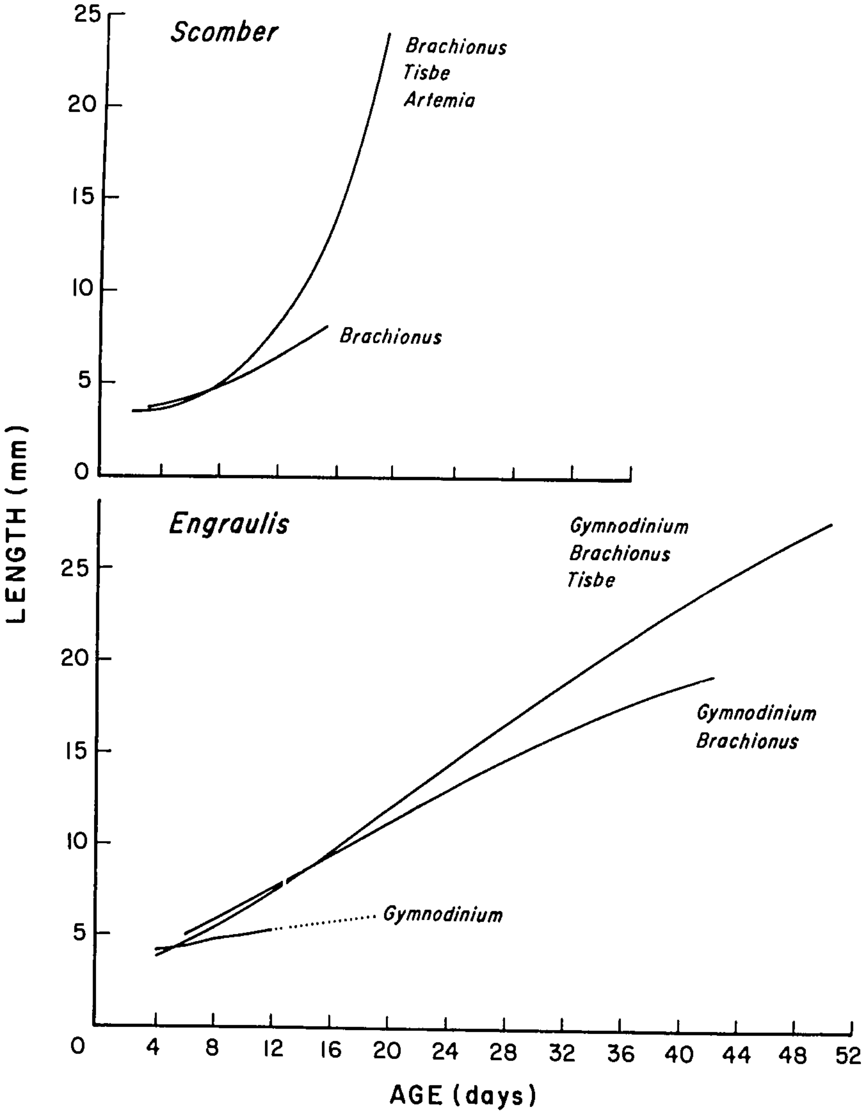

FIG. 7. Laboratory growth rates of *Scomber japonicus* at 22°C fed various foods, from Hunter and Kimbrell (MS), and of *Engraulis mordax* at 16°C, from Hunter (1977). Calorie values of prey were: *Gymnodinium* 0.00005 cal; *Branchionus* 0.0008 cal; and *Artemia* 0.0096 cal (Hunter 1977).

His results are reasonably close to those described above from rearing work. The model predicts no growth beyond a length of 6 mm on prey having a caloric value of *Gymnodinium* and none beyond 14 mm for *Brachionus* (Fig. 8).

Thus, the lower size limit of prey, at least over the first few weeks of feeding, appears to be set by metabolic relations, whereas the upper limit is controlled by mouth size.

Abundance of Food and Food Density Requirements

The density of particles in the sea declines rapidly with increasing size or diameter of the particle (Sheldon, Prakash and Sutcliffe 1972; Sheldon and Parsons 1967). Such a relationship was presented by Vlymen (1977) for particle size distribution from Niskin casts measured with a Coulter Counter by Richard Eppley (Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA) (Fig. 6). Sheldon et al. (1972) pointed out that roughly similar amounts of organic material exist in logarithmically equal size intervals in any water mass; hence, in any sample, many more small particles exist than larger ones. This implies that to feed on larger prey, a larva must search a much greater volume of water and it also may explain why the minimum prey size changes so slowly in larvae that select larger prey.

The density of particles in the size range relevant to larval marine fishes has been studied by a number of workers and their results have been reviewed by Blaxter (1965), May (1974), and Arthur (1977) and are presented here in tabular form (Table 2). These studies indicate that average density in the open sea ranges between 13-40 nauplii per liter and typically between 1-7 copepodites per liter. On the other hand, in enclosed areas such as lagoons, bays, and estuaries, much higher densities are found. Average densities in these areas of naupliar and post-naupliar stages combined can exceed 200 per liter.

Larval fishes have been maintained in the laboratory at various food densities to determine the density of prey required for survival. Some of these density experiments are summarized in Table 3. Most indicate a prey density of 1000-4000 microcopepods/L are required for high survival rates in the laboratory. These results agree in general with what has become standard rearing practice in recent years; in such techniques, the highest densities are used initially and are subsequently reduced to about 1000/L (Houde 1973). Much higher densities are required for very small prey such as phytoplankton. Lasker (1975) found that anchovy larvae required 5000-20,000 *Gymnodinium splendens* cells per liter at 19°C and 20,000 or more at 14°C for significant feeding to occur. Standard rearing

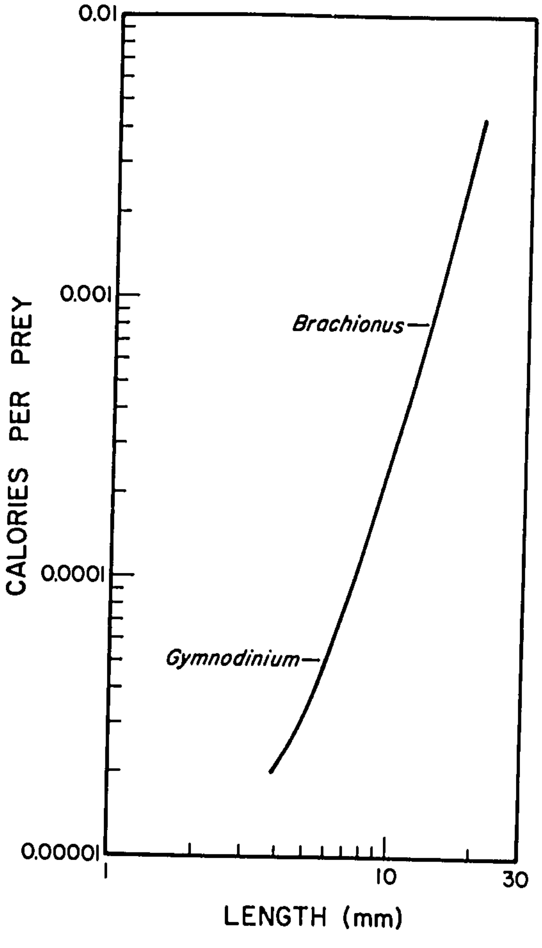

Fig. 8. Relation between minimum caloric value of prey required to meet energy needs of larval northern anchovy at 17°C and larval length. From model developed by Vlymen (1977) and Vlymen (unpublished), see text for explanation. The caloric value of *Gymnodinium* and *Brachionus* is indicated.

Table 2. Average[a] densities of microcopepods in the sea.

	Average density of microcopepods (number per liter)				
	Nauplii	Copepod-ites	Total	Location	Author
Open sea	13	2	15	Southeast Coast of Kyushu	Yokota et al. (1961)
	22	36	58[b]	California Current	Beers and Stewart (1967)
	40	5	45[b]	Southern California near shore	Beers and Stewart (1970)
	27	7	34[c]	Eastern Tropical Pacific	Beers and Stewart (1971)
	36	1	37	California Current	Arthur (1977)
Partly enclosed	76	19	95	Azov Sea	Duka (1969)
	—	—	223[d]	Gulf of Taganrog	Mikhman (1969)

[a] Mean for all stations, and years given in publication listed in table.

[b] Includes all copepods passing 202 μm mesh net.

[c] Includes all copepods passing 202 μm mesh net and caught on 35 μm mesh.

[d] Defined as food of *Clupeonella delicatula;* microcopepods account for over 90% of items eaten (Mikhman 1969).

TABLE 3. Food density thresholds for six species of marine fish larvae.

Species and common name	Container volume (liters)	Duration (days)	Food type	Stock density No./L	Survival at various food densities		Author
					Density No./L	Percent survival	
Plaice *Pleuronectes platessa*	5	14	*Artemia* nauplii	50 (larvae)	1,000	72^{a}	Wyatt (1972)
					500	72	
					200	54	
					100	32	
Northern anchovy *Engraulis mordax*	10.8	12	Wild zooplankton (nauplii)	10 (eggs)	4,000	51	O'Connell and Raymond (1970)
					900	12	
					90	0.5	
					9	0	
Bay anchovy *Anchoa mitchilli*	76	16	Wild zooplankton (nauplii-copepodites)^{c}	0.5-2 (eggs)	1,751^{b}	50	Houde (1977 and in press)
					75	10	
					17	1	
Sea bream *Archosargus rhomboidalis*	76			0.5-2 (eggs)	199^{b}	50	Houde (1975 and in press)
					28	10	
					11	1	
Lined sole *Archirus lineatus*	38			0.5-2 (eggs)	854^{b}	50	Houde (1977 and in press)
					115	10	
					44	1	
Haddock *Melanogrammus aeglefinus*	37.8	42	Wild zooplankton (nauplii)	9^{d} (larvae)	3,000	39	Laurence (1974)
					1,000	22	
					500	3	
					100	0	
					10	0	

[a] Survival was 100% at 50/L for first 7 days without a decrement in length; see also Riley (1966).
[b] Estimated food density for indicated survival levels.
[c] Plankton blooms of *Chlorella* sp. and *Anacystis* sp. maintained in rearing tanks.
[d] Estimated by adjusting for hatching success.

practice for northern anchovy requires 100,000 or more *Gymnodinium* cells per liter (Hunter 1976b), whereas 1,000 microcopepods per liter appear to be adequate (O'Connell and Raymond 1970).

Density thresholds determined by Houde (1975; 1977; in press) are markedly lower than those of the others listed in the table and are substantially below those used for routine rearing of larval fishes. He attributes his lower thresholds to use of lower stocking densities, general improvement in culture techniques, and frequent daily monitoring and adjustment of food density. He also maintains a dense phytoplankton bloom in his containers which may also contribute in some way to higher survival. Of particular interest is the very low threshold determined for sea bream, emphasizing the importance of specific feeding tactics. This species selects larger prey (Stepien 1976) than the other species studied by Houde, and judging by the density threshold, is much more efficient in finding and catching prey.

In general, the density thresholds determined for larvae in the laboratory are much higher than average microcopepod densities in the open sea, described in the previous section. On the other hand, the high microcopepod densities in enclosed areas are within the range that Houde (1975, 1977) found to support survival and growth. Thus, food may not be as critical for species, such as those he studied, which exist in such areas. Many problems exist in interpreting such laboratory findings and extending them to field conditions. The interactions of stock density, food density, and mortality are problems which may be overcome to some extent by use of low stocking densities and frequent monitoring of food density. Changes in ration with development and prey size distributions in the tank are also critical. The few larvae that survive at very low prey densities may be those that captured, either by good fortune or because of a larger mouth, the few larger prey in the container. Selection of the appropriate criteria also poses problems. Growth as well as survival declines with food availability; this is evident in all the food density studies cited but perhaps best illustrated by Riley (1966), Wyatt (1972) and Houde (1975, 1977). Reduction of growth may be nearly as lethal as starvation because of the increased exposure to predation.

The disparity between most estimates of food densities required by larvae and average densities in the open sea have led to the hypothesis that larvae may be dependent on small-scale patchiness of food. In the sea, large-scale sampling will always tend toward the mean concentration between such patches. Data collected by Yokota et al. (1961) on naupliar abundance provides one of the better examples of patchiness of larval forage because the samples were taken on a scale relevant to larval searching behavior. They counted all the nauplii occurring in 1-liter samples taken at the surface from an area off the southeast coast of Kyushu over 2 yr. The average naupliar density for their 4,730 samples was 13/L. The greatest number in a single sample was 524 and only 2% of the samples accounted for over 20% of the nauplii.

Laboratory experiments on searching behavior discussed previously indicate that larvae have the ability of remaining in patches of food if they find them. The search model of Vlymen (1977) indicated that the average anchovy larva could not exist in the sea if food were distributed randomly. He concluded that first feeding anchovy larvae require a food contagion of $K = 0.17$, where K is the negative binomial, just to meet minimum energy requirements. Thus, to meet minimum requirements, prey would have to be 1.3 times as "crowded" as they would be on the average, if the population had a random distribution (Lloyd 1967).

Lasker (1975) tested the patchiness hypothesis by exposing anchovy larvae to samples of water taken from the surface and from the chlorophyll maximum layers usually 15-30 m below the surface. Feeding by larvae was minimal in samples taken from the surface but extensive feeding occurred in water from the chlorophyll maximum layer when these samples contained prey of about 40 μm at densities of 20,000 to 400,000 prey/L. The prey were primarily the phytoplankter *Gymnodinium splendens;* microcopepods were never at high enough densities to be eaten by the larvae. Houde and Schekter (in press) exposed sea bream to simulated patch conditions in the laboratory by increasing the concentration of microcopepods to 500/L for periods of 2-13 h per day from a background density of 25-50/L. They found that survival at 10 days after hatching of larvae exposed to only 3 h of food at 500/L was similar to that of larvae fed at a constant 500/L. Thus, even very short-term patchiness could enhance survival in this species. Lasker (1975) has considered a much broader time scale; the bloom of *Gymnodinium* had persisted for at least 18 days until a storm obliterated the chlorophyll maximum layer. His measurements after the storm indicated that the density of food was insufficient for feeding.

Ecological Roles

In this section, I define two ecological roles based on the traits discussed in the preceeding sections. These roles, Engrauliform and Scombriform (Table 4), were selected because of their contrasting traits, by firsthand knowledge of the behavior of *Engraulis mordax* and *Scomber japonicus*, and because in the beginning they are of similar size and have similar yolk reserves. To fill in gaps of knowledge, I have used results for other species which I believe fall within these two ecological categories.

Table 4. Two contrasting ecological roles for marine fish larvae based on behavioral and physiological traits.

	Relative differences	
Trait	Engrauliform	Scombriform
Spawn		
Contagion of spawn	High	Lower (?)
Food		
Mouth size	Small	Large
Range of food size	Small	Large
Abundance of foods eaten	Higher	Lower
Calories obtained per attack	Lower Higher	Higher
Feeding behavior		
Feeding posture	Sinuous	Rigid
Persistence of attack	Infrequent	Frequent
Feeding capacity	Low	High
Ability to exploit short-term food patch	Low	High
Maneuverability	Low	High
Locomotion and metabolism		
Cruising speed	Slow	Fast
Metabolic rate	Lower	Higher
Social interactions (laboratory)		
Effect of larval density on growth	Low	High
Sibling cannibalism	Rate	Frequent
Time on onset of schooling	Late	Early
Growth	Slow	Fast
Instantaneous mortality	Lower	Higher

Food size preferences may be one of the best diagnostic traits for identifying ecological roles. To feed on large prey requires a large mouth and a greater and more efficient searching effort because of the exponential decline in density with prey size. Greater searching effort may require a faster swimming speed and this in turn implies a higher metabolic rate and energy requirements. Large prey are more efficient in satisfying energy requirements and promote faster growth (Kerr 1971a and 1971b). Faster growth reduces the duration of the larval stage and the time to the onset of schooling. A larva that is more dependent on large prey can ill afford to pass up prey if the first attack fails. Thus, persistence in attack and maneuverability would appear to be essential, and the sinuous mode of feeding seems to lack these characteristics.

The sparid *Archosargus rhomboidalis*, which seems to fit in many respects the scombriform role, is affected much more by laboratory stocking density and is better able to take advantage of short-term patchiness of food than is the engraulid fish *Anchoa mitchilli* (Houde and Schekter 1978). These tendencies are in keeping with the differences in searching power and efficiency of feeding implicit in these roles. Feeding rates and ration also could be expected to vary between these roles but few accurate measurements exist. Owing to the strong effect of food density, larval weight and temperature (Stepien 1976), specific comparisons are not possible. At least in younger larvae satiation mechanisms appear to be lacking. Death from overfeeding in the laboratory has been reported for grunion (May 1971) and the siganid, *Siganus canaliculatus* (May et al. 1974), and I have observed it in larval Pacific mackerel. Northern anchovy maintained at the same food density as mackerel did not die from overfeeding, suggesting a higher feeding capacity in the more active mackerel.

Although the evidence is weak for differences in spawn density that I have associated with these roles, it does make some evolutionary sense. At high spawn densities, suppression of intraspecific effects on growth would be adaptive as well as suppression of sibling cannibalism. Species of slow swimming abilities such as anchovy might require higher initial larval densities to assure the socialization necessary for the onset of schooling, or to form schools of viable size. Finally, Ware (1975) suggests that instantaneous mortality is proportional to growth rate. If Ware's argument is correct, then the slow growth of anchovies relative to mackerel (Fig. 9) is indicative of a lower mortality.

In these comparisons, many assumptions and simplifications were made and the very significant role of temperature was not considered. In a strict sense, such roles should only be defined within specific temperature ranges. Many other possible strategies exist. Those species that hatch from large eggs in a relatively large and mature state, such as flying fish, herring larvae, saury, and many others, do not fit into these categories. The flatfishes show major deviations from either pattern because of the striking changes at metamorphosis resulting in declines in activity and metabolic rate (Blaxter and Staines 1971; Laurence 1975). Another possible role is that of a larva dependent on large prey, but using a relatively passive hunting strategy at reduced metabolic cost and experiencing a slow growth rate. This contrasts with the fast growth, high metabolism, and active hunting of scombroid larvae. This more passive large prey strategy could be relatively common in cold water where metabolic costs are less.

My emphasis has been on specific differences in feeding ecology of larvae because I feel this approach is essential for understanding the cause and effect relationships underlying mortality. The apparent similarities in feeding habits among pelagic larval fishes are striking nonetheless. The characteristics emphasized here, such as preferences for size ranges of copepods, minor differences in larval

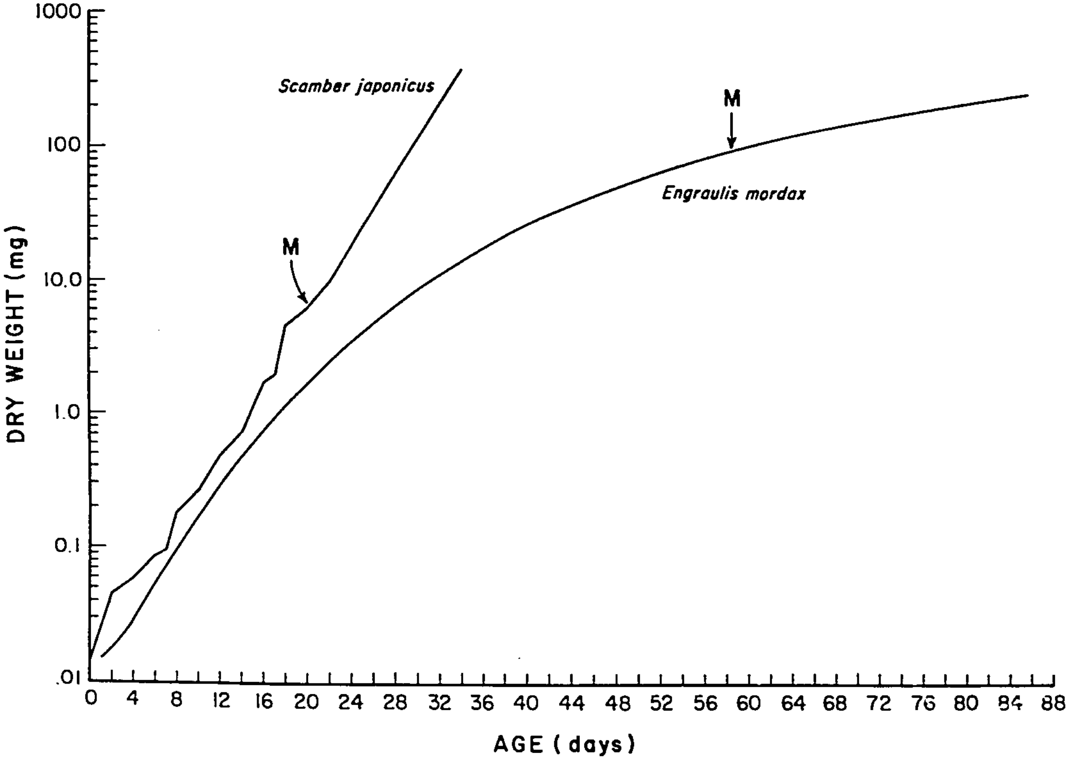

Fig. 9. Growth of larval *Scomber japonicus* and *Engraulis mordax* in the laboratory at 19°C. Data on *Scomber* is a line formed from connecting average length for three experiments and converted to weight by length-weight conversion (Hunter and Kimbrell, MS); data on *Engraulis* is a Laird-Gompertz fit (Hunter 1975) to unpublished rearing data at 19°C; and M indicates age at metamorphosis.

size and yolk reserves, and differences in swimming speed, seem subtle relative to the major differences that exist in feeding ecology of the parents. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods despite the fact that the feeding habits of the parents include benthic and epipelagic piscivores, filter-feeding and particulate-feeding planktivores, and many other specializations. The feeding habits of larvae, of course, are most similar at first feeding when larvae are least specialized, and distinctions become more obvious as development proceeds and fish approach metamorphosis.

Given proper phase relationships, many species could be dependent on the same food resource. Competition between species is regulated to some extent by the timing of spawning and its relation to the production cycle. In the California Current, peak spawning by the northern anchovy occurs in early spring, whereas peak spawning by the large-mouthed larvae, jack mackerel and Pacific mackerel, occurs later, although spawning of all three species broadly overlaps (Kramer and Smith 1970a, 1971). Vertical partitioning of the water column has not been discussed but is a tactic of major importance. *Scomber* larvae seem to be more closely associated with the upper surface layers than clupeoid larvae, whereas hake are located at greater depths (Ahlstrom 1959; Nellen and Hempel 1970). It is possible that the rapid metabolism, fast growth, large prey tactics of scombroids may be designed for near-surface existence and possibly the slow growth, large prey tactics of hake are limited to cooler or deeper waters. Clearly, vertical distributions of larvae and their foods need detailed attention.

Sources of Mortality, Approaches

A critical period for survival occurring around the time of first feeding has long been hypothesized as a possible determinant of year class strength (Hjort 1914; May 1974; Vladimirov 1975). Hjort's critical period concept, as restated by May (1974), is that the strength of year classes in marine fishes is determined by availability of planktonic foods shortly after the yolk supply has been exhausted. Low feeding success, low resistance to starvation, small size, and immaturity of larvae at this time suggest that they would be more vulnerable to starvation death than at any other time, but the evidence from estimates of natural mortality is inconclusive (May 1974). Although physiological and behavioral criteria indicate the highest vulnerability at yolk absorption, it is also the time when larvae feed upon the smallest and therefore most abundant food supply. Events in later life such as the necessity to feed on larger but less abundant prey, disruption of food patches by storms, and failure to form viable schools could also be sources of mortality. In the anchovy, a major risk may be involved in the shift from very small prey such as nauplii and phytoplankton to larger copepodites. This risk would be faced by larger-mouthed larvae at a much earlier age. This risk can be hedged to some extent if larvae continue to feed on smaller prey and take larger copepods when available, which seems to be a basic strategy as evidenced by the slow increase in minimum prey size in all species. Sooner or later, these large prey must be eaten or growth will be slowed, as laboratory work has demonstrated, and retarded growth leads to greater exposure to predation (Murphy 1961).

To isolate causes of natural mortality of larval fishes, estimates must be made of incidence of starvation and predation over the spawning range and these losses compared to estimated rates of mortality. Such models must account for egg mortalities of up to 29% per day and larval mortality rates of 2-10% per day (Jones and Hall 1974). Predation is probably the most common cause of mortality during the egg and yolk-sac stage, although other causes have been suggested (Vladimirov 1975). Predation by fishes on eggs is detectable by stomach examination because the chorion is relatively resistant to digestion but may be difficult with larvae such as small 3- to 5-mm anchovy where digestion is so rapid that larvae are unidentifiable in less than 2 h (Hunter, unpublished data). The study of predation by arthropods and other predators that injure or grind prey will also be difficult. Owing to the diversity of potential invertebrate predators, bioassays of samples from predator communities might be a productive approach, perhaps using large plastic enclosures containing fish larvae. It seems unlikely much progress could ever be made using a species-by-species analysis.

Studies of starvation in the sea seem to offer a better opportunity for isolating a cause of mortality than those of predation because of the difficulty of direct observation and detection of predation. Laboratory work indicates that incidence of starvation can be identified by chemical, morphological and histological criteria (Balbontin, de Silva and Ehrlich 1973; Ehrlich 1974; O'Connell 1976; Ehrlich, Blaxter, and Pemberton 1976). If absolute criteria are to be used, histological techniques may be preferable because deterioration of cell and tissue structure appears to be less affected by laboratory rearing and is independent of size (O'Connell 1976).

Morphometric techniques are desirable because they can be applied routinely over the spawning range of a species and can be easily incorporated into standard ichthyoplankton analysis. They have been used by Shelbourne (1957) and Blaxter (1971) to assess condition of sea-caught larvae, but Blaxter's work indicates that their application should be confined to a relative assessment. He found in herring that body depth and condition factor changed with starvation in the laboratory, but larvae captured in the sea had a lower condition factor than those dying of starvation in the laboratory. I obtained nearly identical results with northern anchovies using body depth (Hunter, unpublished data). Thus, the most practical approach for assessment of starvation on a population basis may be morphometric analysis calibrated in terms of starvation using histological analysis of sea-caught specimens. Finally, intensive studies in the laboratory and at sea are essential for defining ecological roles and causes of mortality, but in the long term these studies must lead to identification of parameters that can be measured routinely over the spawning range of the species.

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Discussion

FISHELSON

What do you think science may contribute after 5 yr or more to stock maintenance from the point of view of larvae?

HUNTER

I think we'll know the probable effect of the environment on year-class strength or at least know whether or not it is even practical to approach the problem from the standpoint of larval mortality. We have many field studies going on. We'll be able to assess the proportion of starving larvae in the sea in the next few years and perhaps separate starvation from predation as a cause of mortality.

BARDACH

When you talk about recruitment, do you talk about recruitment to the fishery?

HUNTER

Yes.

BARDACH

When is the onset of fishing?

HUNTER

When the fish are about 1 yr old and about 10 cm in length.

MURPHY

I don't think they're fully recruited until they're 2 yr old.

BARDACH

How does this compare with the Peruvian stocks?

MURPHY

Full recruitment occurs at 1 yr, but heavy fishing mortality starts at about 6 mo.

FUJIYA

You said something about cannibalism. Is that real cannibalism or just biting?

HUNTER

It's real cannibalism. Mackerel larvae eat fish about half their size.

BLAXTER

There must be a size hierarchy before that occurs.

HUNTER

It depends on the species: barracuda, for example, become cannibalistic at about 4 mm long when the larvae are all nearly the same size, and they prefer fish by the time they're 10 mm.

MURPHY

What is the thinking now with respect to the size of the larvae when the relative survival for a year-class is more or less stabilized? From what you told me, it's not just when they're starting to feed.

HUNTER

Correct. Paul Smith of our laboratory has preliminary estimates of mortality now of fish up to 20 mm for 25 yr. You can see a higher mortality at the onset of feeding and a great deal of differential mortality in different years, but the year-class strength is not established even at 20 mm.

MURPHY

You're talking about numbers of fish, and those have a tremendous variance. The estimate for a given year is pretty wide.

BLAXTER

How does growth in your tanks compare with that in the sea?

HUNTER

We're beginning to get data on growth of anchovies in the sea by counting daily rings on the otoliths. Differences between laboratory and sea growth can be as great as the difference caused by a 2-3°C difference in rearing temperatures. In general, larvae in the sea grow slower than larvae reared in the laboratory at the same temperature, but occasionally we find some samples in which sea-caught larvae appeared to be growing faster than laboratory-reared larvae.

BLAXTER

You might think there'd be stronger selection for size in the sea than in a tank where there are no predators.

HUNTER

Yes. Growth may appear to be faster in the sea because of predation.

LILEY

When you do have more information about the larval ecology and feeding behavior, how do you see its being applied? Are you not looking at the possibility of culturing these pelagic fish?

HUNTER

No.

LILEY

What do you think could be the long-term application of this? This helps you to make predictions, but I'm wondering if there are things that you can go into and do.

HUNTER

Our objectives are to learn what is causing the large fluctuations in the annual number of recruits in fish populations. We feel that if we had a better idea of the mechanisms, we could better manage fish stocks. Nobody as far as I know has yet been able to solve these problems.

HASLER

Is the Peruvian anchovy coming back?

MURPHY

They started to recover and then apparently faltered and are falling off. The data from Peru aren't as available as they used to be, but I understand they closed anchovy fishing and turned everybody on to sardines and mackerel.

HASLER

That fishery makes such a huge contribution to the world's protein supplies that it would seem important to focus on that.

HUNTER

Yes. The world's largest fisheries are based on these clupeoids, which is why we're working on them.

MYRBERG

How does your knowledge of these species provide information relative to those species that are cultured? Can we learn something from this that can be applied to those species that are well known in culture?

HUNTER

Many of us have reared fish larvae for a number of years, and I think collectively the techniqes from our own and others' research are beginning to follow certain patterns. A reservoir of information exists, and many of the techniques that are almost intuitive now were developed by hard work in many laboratories over the last 10 yr. For example, the rule of one nauplius per mL didn't always exist.

MAY

It seems to me that fish species that are now commercially cultured are primarily the species that are easy to rear through the larval stages. The kinds of fishes that John is talking about are not commercially cultured anywhere, but I think the information he and other people are gathering will provide the basic knowledge which will enable these species to be cultured in the future. I don't know if it will ever happen on a commercial scale, but it may, and if it does, it will depend fairly heavily on the kind of basic knowledge that's being accumulated now.

HUNTER

There are many incidental findings that may be useful for rearing other species. For example, we found the best way to reduce cannibalism was to rear mackerel at the highest temperature possible. Cannibalism stops at metamorphosis when they start schooling, and you can double the survival by reducing the time to metamorphosis.

FISHELSON

Is it possible then that we can use heated waters of reactors and power plants to farm in the sea, using large ponds in which we can grow the small larvae till they pass the cannibalistic stage and then let them out?

HUNTER

People working on tropical fishes have greater problems with water chemistry than those working on temperate, coldwater species. When I speak of warm water I mear about 22-23°C, which is warm for Pacific mackerel but is not warm by tropica standards.

BLAXTER

Surely cannibalism is partly an artifact of the crowding in the tank, isn't it?

HUNTER

Yes, although cannibalism is common even in adult scombroids. I don't think there's much doubt that if a scombroid encounters another it would eat it if it were the correct size. But I think spawn is much less dense than that of clupeoids and encounters may be infrequent.

MAGNUSON

I think that about 10% of the stomach contents of adult skipjack captured on the high seas consist of their own juveniles. You gave two strategies for pelagic larvae. Are these essentially the only two strategies? Or is there some continuum?

HUNTER

I think many larvae may fall into these classes, but hake would be a good example of one that does not, and there are many others. A continuum may exist, but other variables, especially temperature, would have to be considered before all differences could be accounted for in a continuous pattern. Some larvae that feed on large prey grow slowly and may have a more passive feeding strategy than scombroids, but these seem to be adapted to cooler temperatures. A continuum seems likely because the range of feeding strategies is more limited in larvae than adults. Nearly all larvae are diurnal, particulate planktivores specializing in the young stages of copepods.

BLAXTER

In the past the work on rearing larvae, at least Shelbourne's work, has led to a technology for rearing flatfish for farming; turbot are now at the point of being farmed commercially. The technology all comes from the general work that was done in the sixties, and so there's been a fairly rapid practical spinoff from that work. Of course it's for valuable fish; it's a luxury market.

MURPHY

If we succeed in artificially spawning milkfish, there's some guidance about how to go about rearing the larvae.

BLAXTER

I think with *Brachionus* as a food almost any species could be reared.

HUNTER

I think the critical element is a 240-μm-diameter particle. In other words, a food is needed as a substitute for *Artemia* nauplii, because many larvae do not grow well when fed *Artemia* nauplii, although plaice and others do. I think many major improvements can be made in the *Brachionus* system, and I think it's a waste of time to worry about artificial foods of the size of *Brachionus*.

ATEMA

I recall the famous story on the East Coast where they used to raise lobsters in hatcheries up to the fourth stage and then release them. Nobody has ever shown that the operation was successful. I suspect they released them in the wrong place, but another possibility is that if they raised them to the sixth stage, would they have been successful? I wonder about that in your fish stituation. How large is the dangerous window?

BLAXTER

All the early work on releasing plaice and cod never improved the fishery. In fact the only case where there apparently was some improvement was when Dannevig released cod into the Skagarak.

Behavioral Adjustment of Fishes to Release into a New Habitat

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HENDERSON, H. FRANCIS. 1980. Behavioral adjustment of fishes to release into a new habitat, p. 331-344. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

More attention should be given to the behavioral problems associated with the transplantation of fish. From perhaps an hour to several days may be needed for fish to adjust to new conditions. This period may be conveniently divided according to behavioral criteria into (1) a relatively stereotyped "fright response," (2) a period of tentative exploration, and (3) a period of learning about the new habitat. In my opinion further study of the behavior of fish under stress could contribute much to our knowledge of the evaluation of behavior patterns of fishes. Even more significantly, such studies should provide help to fishery managers by suggesting methods of handling which would lead to improved survival and growth of transplanted fish.

Introduction

The high costs of raising fish for use in restocking have been an important factor in limiting the effectiveness of stocking as a means of maintaining or rehabilitating fish stocks in the face of heavy exploitation. An important factor in this cost is the high mortality which occurs once the fish are transferred to the new habitat and before they reach harvestable size. Much work has been done on reducing the effects of physiological stresses on this transfer, e.g., temperature change, low oxygen, or a change in salinity. As a result, considerable care is usually taken to reduce such stresses in transfer operations. On the other hand, little is known about the time it takes for a fish to adjust its behavior to new surroundings so as to be able to cope with threats of predators while locating new food supplies. Consequently, little attention is given to assisting the fish in this adjustment.

It seems likely that more attention to the behaviors of fish under stress and of their adaptive significance could lead to a variety of techniques through which fish could be assisted in their adjustment to new conditions, thus improving their prospects of survival in transfer. The purpose of this discussion is to call attention to this thesis through reviewing the limited literature available, and to propose a classification of the recovery or adaptive responses of fish under stress which may be helpful in organizing further studies.

Background

The behavior of a fish under stress is different from that of a normal fish. A yellow perch when transferred to aquaria will dive to the bottom and press its nose into a corner (Nursall 1973). Presumably this is a behavior which, when it occurs in the wild, keeps the animal hidden. Bluegills behave similarly when frightened or sick. School formation may be altered by stress as well as color patterns, both of which have significance in relation to defense (Radekov 1973; Breder 1949). Feeding is commonly inhibited. Such reactions are particularly evident in aquaria and are well known to aquarists and laboratory workers. They are much more difficult to observe under practical field conditions.

When a fish is released into a new natural environment, attack by a predator would seem to be the most immediate threat to its survival. The first stocking of silver carp fry into Lake Kinneret, Israel, failed as the fry were quickly consumed by *Tilapia zillii*. The problem was solved by holding the fry behind a protective net for an hour or so until the fry formed into schools (M. Bar-Elan, Director, Department of Fisheries of Israel, 23 Amiel St., P.O. Box 21170, Tel Aviv, Israel, pers. comm.). Once schools had formed, predation was much reduced.

Predatory losses of newly introduced fish are a less important problem in intensive fish-culture operations, but even short periods of poor growth can seriously affect profit. Studies of acclimation to a new habitat are thus also apt to be of considerable value to culturists. A particularly crucial period of handling and transfer stress in fish culture is associated with artificial spawning. Spawners are especially valuable and warrant special attention to ensure survival and optimal reproductive performance. The Chinese, for example, concentrate spawners with a seine net into one corner of their pond and then release them in order to "train" them for subsequent removal to holding ponds preparatory to hormone treatment.

Food is clearly a secondary factor in ensuring survival after transplantation, as most juvenile and adult fish can withstand considerable periods of starvation. Fry, however, are not so well adapted to periods of starvation. They not only lack food reserves but quickly succumb to predation if poorly fed (Cuff 1977).

Several steps can be recognized in the establishment of normal feeding of a transplanted fish. First, there is a period of recovery of normal movement, secondly a period of familiarization with the new habitat, and finally a period of adjustment of feeding habit if the available foods are different from those to which the fish has been accustomed. While the second and third periods may run concurrently, it seems likely that free or normal feeding behavior would not be fully established until the fish has become fully acquainted with its new habitat. Pelagic fish might thus be expected to regain normal feeding rather more rapidly than inshore fishes that depend on cover for protection.

Other kinds of behavioral adjustments may also be significant. For species that establish home ranges or feeding territories, normal active behavior may not occur until these are established. A new spatial "map" may be required. Introduced fish will normally be disadvantaged in hierarchical relations, such as those associated with feeding at artificial feeding stations in fish ponds. It thus seems worthwhile to look more carefully at the adjustment period.

Protective Behaviors Immediately Following Transfer

There are a number of potentially useful strategies which a fish might adopt to gain protection against predators during the period of adjustment. These include freezing, hiding, seeking the company of other fish, and counterattack. The latter is uncommon (Breder 1949), but Fernet and Smith (1976) report that introduced goldeye assumed dominance over "residents" in experimental troughs. In this instance, however, no real residence was established (10 h) and the fish were not fed after capture. The other responses are much more typical.

Hiding is not only a typical response of inshore fishes but appears to be quite stereotyped. Yellow perch, as already mentioned, dive to the bottom but will remain motionless at the bottom corners of a pail (Nursall 1973), hardly a satisfactory hiding place. Bluegills, in my experience, do not even seek the bottom but will stay in a corner with contact on each side of the head. Holt et al. (1977) report that radio-tagged walleye released in deep water would sound for about 5 min, then return to the surface before moving off. Released in shallow water, the fish usually remained motionless on the bottom for up to 45 min before moving slowly to deeper water.

A number of fish such as the flounders are able to bury themselves very quickly in sand. The spiny eel *(Mastecembelus)* and the Japanese weatherfish *(Misgurnus)* show such behavior in aquaria (Adler 1975). While such behaviors are frequently described, there is less information on the length of time required for a released and frightened fish to begin to explore his new environment, leaving a secure refuge, or what sort of hiding places would be most attractive and or most easily found.

Pelagic fish have no hiding places but often descend to deeper strata when frightened (Radakov 1973). A related maneuver in some species is an alteration in color. In many cichlids, frightened fish develop vertical banding, perhaps to blend with vertical submerged vegetation (Baerends and Baerends-Van Roon 1950). The same authors note that *Cichlasoma meeki* darkens when ill or when chased over and over. I have noted that *Sarotherodon niloticus,* a cichlid of pelagic habit, tends to become lighter and more silvery when disturbed in aquaria. The flatfishes are particularly good at blending with the substrate whether frightened or not. Many of the "protective" color changes, such as lightening or darkening to match the general tone of the environment, are relatively fast in fishes but may vary from a few seconds in some species to many days in others (Breder 1949; Odiorne 1957).

Freezing also seems to be a common response of frightened fish, which, as remarked by Breder (1949), may give way to flight if a predator approaches too closely. In laboratory test apparatus, resumption of swimming activity is often taken by investigators as an indication that an experimental fish has resumed "normal" behavior after being moved.

Fish are thought to be safer in groups than as isolated individuals. While there has been considerable discussion over the nature of the protection afforded by a school to its members (Radakov 1973), there seems little doubt but that some protection is afforded. Hobson, quoted by Radakov (1973), observed a sardine school which was attacked by grouper in places within the school where confusion had resulted from a pelican attack. Once calm returned, the groupers abandoned their attack.

In addition to the tactical protection which the school seems to provide, the presence of other members of the species (or even surrogates) seems to confer a measure of calm and confidence in the behavior of fish. Werner and Hall (1974), in studying foraging behavior in the bluegill, found that if only one or a few fish were present in the plastic wading pools used as experimental tanks, the feeding procedure frightened the fish and produced erratic feeding. However, reproducible results and normal feeding behavior resulted when 10 fish were used together in the same tank. Olla and Samet (1974) found that mullet began feeding more quickly when they could see a group already feeding. Beyer (1976) found that *Scardinius* *erythropthalmus,* a schooling fish, learned color discrimination faster in groups than singly.

If, however, the shoal is ill-assorted, as in the experiments of Muzinic (1977), "social interference" (Miyadi 1960) may occur. In Muzinic's experimental tanks small and large sardines not only did not school together, but the small fish did not feed well in the presence of the larger ones. The length of time needed for normalization of behavior may vary considerably. Reynolds and Casterlin (1976) observed that the activity of largemouth and smallmouth bass in an experimental tank stabilized within 48 h after introduction. These fish had been captured by electrofishing. Fava and Tsai (1976) note that wild dace, acclimated to the laboratory for 1 wk, needed 30 min to 1 h to adjust to a transfer to a test chamber. Hartt (1966) noted apparent delays in movement of tagged salmon from the release site, concluding that a delay of 1 day was typical. He also cites evidence from direct observation of fish after tagging: ". . . tagged fish may often be seen collecting in loose schools a short distance from the trap or vessel from which they have been released. Such schools may remain almost stationary or mill slowly for a considerable length of time." Much worthwhile work could be done by studying the factors determining the duration of the initial fright response in species in which it is sufficiently stereotyped to provide a good measure.

The Onset of Feeding Behavior

Provided that the fish introduced into a new environment are able to avoid being eaten, the search for a reliable source of food is perhaps their next priority. General exploration of the habitat and familiarization with it may be especially necessary to inshore species. Most descriptions of behavior of fish after transfer to aquaria or test apparatus do not describe exploratory behavior as a usual component of acclimation. However, such apparatus is often featureless, perhaps calling for little exploration. In the wild, however, satisfactory feeding may require, as in trout, the establishment of a feeding territory affording relief from current. Hatchery-raised fish often quickly succumb to capture or starvation as they are unable either to locate vacant sites or to dislodge resident fish from the occupied ones (Miller 1958).

However, Ivlev (1961) reported that *Ameiurus* ingested more food in groups than singly, while the opposite result occurred in goldfish and carp. Welty (1943) found increased feeding in groups in goldfish as well as in *Brachidanio* and *Macropodus.* Such conflicting results could possibly be explained in relation to the degree of acclimation achieved to handling and surroundings before presentation of food. The social effect may in fact relate more to security than to appetite.

The dominance of larger fish over smaller ones during feeding is an important problem in the culture of many species. Either the food must be scattered over the pond or spread over enough time so that the larger dominant fish become satiated, and the smaller get a chance to feed. This effect seems to be responsible for the development of so-called "shoot carp" which skew the length-frequency distribution of carp fry toward a number of exceptionally large individuals. When large individuals are culled, a new set grows rapidly to re-skew the distribution (Wohlfarth 1977)! Blaxter (1975) discussed this effect in comparing reared with wild fish, noting that while common in hatchery conditions, it may be "obscured by the range of spawning time and egg size" in natural conditions. It may also be obscured because, as remarked by Ricker (1969), "few people have taken the trouble to compute the variability in length of the fish they were studying." In any case, the size of hatchery-reared fish in relation to the size of naturally produced residents of the same species may be important in determining whether the hatchery or the wild fish will be most advantaged.

After transfer to the wild, fish must also acclimate to the new food types. Whatever the food supply may have been previously, the most available food in the new habitat may be rather different. Most fish can be readily trained to take new food (Adler 1975). However, Ivlev (1961) found that carp took 15 to 20 days to change their food selection habits when "trained" to a new food. The ease with which this is accomplished seems to depend on a number of factors which relate to the similarity of the new food to accustomed types, and the degree of similarity required to initiate a feeding response does seem to depend on the degree of acclimation of the fish to the surroundings. Nagel (1976) reports training walleye to feed on an Oregon Moist Pellet diet. He noted that every disturbance to the fish "causes stress and interrupts feeding, usually for several hours."

Generalized Recovery Process

From the foregoing it seems possible to generalize the recovery sequence into three steps: an initial "fright" response of short duration, probably rather stereotyped; a transition phase in which wary exploratory behavior predominates but in which feeding may begin if food is readily available, and a final phase in which the fish explores its new environment, familiarizing itself with its new spatial and social frame (Fig. 1). The first and second phases are presumably very similar to recovery from other sorts of fright. The last, however, can occur only in the context of transplantation, including transfer of experimental fish from tank to tank. "Normal" behavior could be said to occur only after all these phases are complete. While the first phase is typically short, there is little

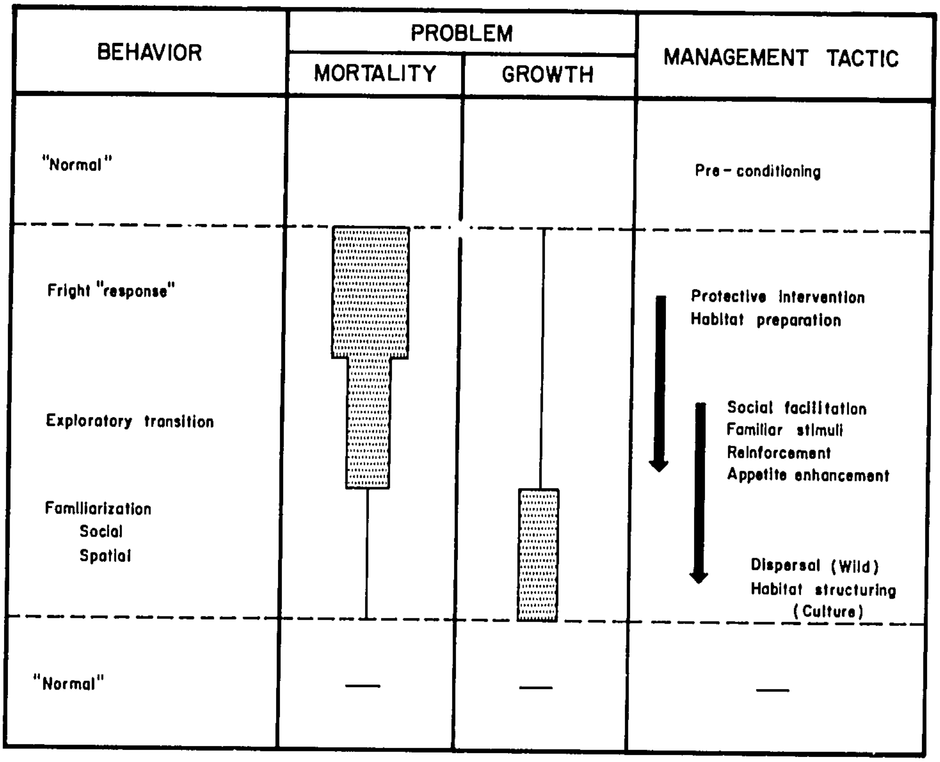

FIG. 1. Summary of behavioral adaptation to transplantation. Adaptation is divided into three sequential phases of behavior (column 1). The relative importance of mortality or growth retardation in transfer of fish to the wild is roughly indicated by the width of the shaded areas in the center columns while the last column indicates pertinent management tactics (see text).

systematic evidence to suggest how long the whole process may take.

As suggested in Fig. 1, mortality, primarily from predation and in transfers to "the wild," is most apt to occur during the first phase. Its risk diminishes with the recovery from the initial fright response. On the other hand, reduced growth through ineffective feeding is most apt to be a problem if the familiarization period is prolonged.

Practical Methods of Reducing Mortality or Stress in Transplantation

The procedures adopted to reduce the behavioral problems of transfer should be considered in relation to these different phases of recovery. Tactics appropriate to each phase have also been suggested on the diagram. The bottom-seeking behavior of perch, effective on a rocky or weedy bottom, would seem less appropriate over sand. Supplementary protection or some other means of direct assistance is likely to be the only effective means of reducing predatory loss when the natural response is insufficient or inappropriate to the location of planting. A temporary barricade is a possible solution, as used in Israel with silver carp. Careful selection of a release site affording appropriate shelter is to be recommended for crevice- or weed-seeking species. Alternatively, one could provide appropriate shelter. Certain times of the day or night could also give better protection than others because of predator visibility or habit. Even a turbidity screen might be effective.

Quite a different approach has sometimes been used. Fish are raised or acclimated in permanent predator-free enclosures from which they are allowed to swim into the new habitat. Such an approach is used in China and in Finland for lake stocking, and in northern Italy in mullet "ranching." In the latter case, use is made of the strongly rheotactic response of the mullet to direct their movements from pond to lake, and to the sea. Such natural transfers may create a "gauntlet" condition in which predators can easily catch the concentrated migrants as they pass. O. Mathiesen (College of Fisheries, University of Washington, Seattle, Washington 98195 USA, personal communication) has noted that survival of young salmon is inversely proportional to the distance they must travel to reach the sea. Here it is highly advantageous to locate salmon hatcheries as close to the sea as possible.

The period of initial fright is generally followed by a period of re-adaptation. It is during this period that the presence of other individuals may increase the rate of adaptation, even in non-schooling fish. For laboratory work, this social effect is reason to consider group testing where such is feasible. In pond or lake stocking the problem is one of ensuring that sufficient numbers of fish are within visual distance to ensure an immediate and effective group response.

If the fish are a schooling species, artificial protection should be considered until the schools are fully formed. If there is much difference in size, the schools first formed may later break up into more evenly-sized groups. Until this happens, the smaller fish are likely to be at a disadvantage, easy prey to predators if present. There is still much to learn about the factors which determine both optimal and actual sizes of schools, information that may be important to determining how many fish to stock at one time and place.

Active feeding may be delayed partly as a result of loss of appetite associated with the stress of transfer. It may also be delayed by lack of familiar food, and, in inshore fishes, by lack of familiarity with the new surroundings. In those circumstances where initial protection has been provided to reduce predatory losses during the "fright" period, it might also be advantageous to provide a familiar food to hasten the onset of feeding. If carried too far, however, such feeding might delay dispersal. Indeed, in some cases it may be desirable to find ways of hastening dispersal to avoid the excessive predation resulting from the concentration of the prey when the protective screen is removed.

Training may also be used to reduce the period of re-adaptation. The objective might be to reduce the severity of the stress produced by handling and change, or it might be to encourage early onset of behavior appropriate to the new habitat. Fraser (1974) was not able to obtain increased survival of brook trout through conditioning to an electrified model loon. However, other types of predators may have been more important in the lake studied. Patten (1977), however, found that conditioning to sculpin decreased the mortality of coho fry. This conditioning was rapid, probably acting to reinforce innate responses.

It is indeed generally assumed that repeated and frequent handling of fish will tame them, reducing the shock of transfer. Nevertheless, I am not aware of any demonstration of the amount of conditioning required to significantly reduce or eliminate initial fright responses. The re-adaptation period that follows can perhaps be more easily affected. Main et al. (1976) have shown, for example, that cobalamin stimulates appetite in wild bluegills transferred to an aquarium, significantly increasing the consumption of food pellets after the first day.

Conclusion

Much of the information which has been published on the behavioral responses of fish to a change in habitat occurs as incidental comment and has not been the result of deliberate study, and much of the above has been found in the methods sections of papers dealing with experimental studies of "normal" behavior. However, there do seem to be some clearly stereotyped responses to transfer which, in their own right, should be of interest to ethologists, not only as indices by which to judge the completion of the adaptation period, but also in relation to the evolution of defensive behavior. Social interactions seem also to play an important role in reducing the stress of these unfamiliar situations, and study of them could perhaps lead to new understanding of the function of groups in fish.

However, it is also important to study these behavioral responses in order to devise better ways of handling fish in the laboratory, the fish farm or in support of wild stocks. The most important application in this regard is to reduce mortalities during the adjustment period and delays in the initiation of feeding. The information cited suggests that such improvements could be obtained.

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Discussion

LILEY

Isn't one of the problems not the avoidance response of fish which are transplanted, but the lack of avoidance? There is an interesting paper by Ginetz and Larkin (J. Fish. Res. Board Can. 33: 19-24, 1976) on survival of sockeye fry when exposed to rainbow trout predation. They found that after the initial attacks by the rainbow trout, the fry which survived were much more able to survive further attacks. It is not clear whether phenotypic or genetic selection (or both) was taking place in those experiments. If the selection in such situations is genetic, then it may be advantageous if the susceptible fish are removed from the population. If the selection is operating mainly on phenotypic variation, then it should be a matter of concern to the fisheries biologist.

HENDERSON

Recently there has been another study of that sort with sculpin and coho salmon with much the same sort of conclusion. But it is not clear how much actual predation is occurring in those experiments and how much is simply reinforcing innate avoidance responses.

LILEY

I think it's very clear in the type of experiment that Ginetz and Larkin did that there is a change in the behavior of the fry which survived. I find it with fish in my tanks. If I expose guppies to predators, then the behavior of those guppies changes dramatically and remains changed for days or weeks thereafter. In other words, they've become much more responsive to any frightening stimulus, especially the one which they associate with attacks upon them. In this case there's no evidence of a fright substance being released.

MURPHY

Did you say you were concerned if that was a phenotypic selection and not if it was genotypic? I don't understand.

LILEY

If there is great range in genetic variability with respect to responses to predators and perhaps other hazards, then it may be beneficial from a fisheries point of view if predators quickly eliminate the more susceptible fish. However, if the genetic variability is low, when you release fish into a stream some get eaten, and others survive the initial attacks and quickly learn to avoid predators. However, in this case, perhaps all fish are potentially equally valuable to the fishery and you may be losing an unnecessarily large proportion of the introduced population on the first encounters with hazardous situations.

MURPHY

What you lose in the first instance might be genetically identical.

LILEY

Yes.

BLAXTER

We have great problems in Britain with plaice. Plaice reared by Shelbourne were put into Loch Ewe and also into some Welsh bays. The result was a disaster; the survival was nil. The first lot were released in the daytime just at the surface and were immediately mopped up by gadoid predators; later they were marked with latex and released on the bottom in darkness. The survival was again negligible. As far as preconditioning is concerned, we have fed salmonids with salt before we put them into sea water to try to stress the osmoregulation system. I think that there is some promise in that.

HENDERSON

Going back to predation, there was an attempt to use an electrified model loon to condition fish to loon predation before planting, which was not particularly successful. And I think there is also a paper in the literature in which they have used bird silhouettes to try to condition trout to bird predators ahead of time. These attempts seem to have been relatively unsuccessful compared to those where real predators were used, perhaps suggesting that actual selection by predation is significant.

LILEY

Dr. R. B. Thompson (Ph. D dissertation, University of Washington, Seattle, 1967) performed experiments in which hatchery fish (juvenile coho and chinook salmon) were conditioned to model predators before release into a natural stream. Recovery of the fish from the stream and from the stomachs of predators indicated that trained fish showed a greater survival than untrained fish released at the same time. I would like to refer again to the paper by Ginetz and Larkin. They showed that an increase in turbidity or a reduction in light intensity resulted in a considerably reduction in predation by trout salmon fry. These results suggest other manipulations which might be used to improve the survival of hatchery reared stock.

MURPHY

An important way of stocking trout fingerlings in the Pacific coast of the U. S. is stocking freefalling from airplanes. How does that fit into your scheme?

HENDERSON

I think we ought to try to find out if improvements can be made. Apparently the program itself works.

FISHELSON

We know that many fish species moved through the Suez Canal from the Red Sea to the Eastern Mediterranean. In the twenties, a lizardfish invaded the Israeli coast and displaced another *Saurida* that was living there and used as a foodfish. Today we are catching the immigrant, but the autochton is not there anymore. In the thirties, we caught on the Israeli-Mediterranean coast the first specimens of *Siganus rivulatus*, another emigrant from the Red Sea, and today it is one of the worst enemies of the net fishermen on the Israeli coast because it sticks in on the gill nets and to take out a *Siganus* from a gill net is painful. So we must be wary of these types of natural or artificial introductions.

HENDERSON

There is another strategy that has been used in China and in Finland. In China they block off coves of reservoirs which are heavily fished to remove the predators. These coves are then used to raise the young fry to a size of 15 cm or so before they are released to the main part of the lake. This means that they can simply open a gate and let the fish swim from the cove to the lake, provided there are no predators that are sitting outside waiting for them to file by. In Finland, they are doing the same thing with trout and char. They dig ponds next to the lake to use for raising the young fry up to a size where they can escape predation, and then let them swim on their own out into the lake.

BARDACH

Wherever care and work with fishes is a tradition, e.g. China, and the cost of labor is not unduly high, it may be easier to do this than where labor costs a lot.

MURPHY

I think one lesson from that paper of Miller's cited is that you certainly don't plant fish where there aren't empty living spaces, and I think that was one problem in those trout streams. The streams themselves were very well populated with wild trout and they just harassed the newcomer out of the picture.

BLAXTER

This points to the problem of using aquarium-reared fish either for transfer to the natural environment later or to interpret environmental events. Aquarium fish are abnormal biochemically and often in their locomotor performance. Quite a number of us are using results from the aquarium to make judgments about the environment, and I think we have to be very cautious about this.

HUNTER

I have a comment on the application of these ideas to breeding fish in captivity if it is stressed. Often it is not obvious except for the fact that the gonads don't develop. It might be useful to develop criteria for stress such that a culturist would know if his animals were being stressed.

HENDERSON

Yes, and I think too that some attention to behavioral aspects of stress and indicators of stress would be useful for evaluating the real well-being of experimental fish.

HUNTER

The trouble with behavior is that every animal is going to be different, while endocrine criteria might have a more general application. For example, we could never get sardines to settle down very well in captivity, whereas we had no problem with anchovies, which regularly spawn in our tanks. Tuna are stressed by small containers, but there may be some other factors besides the container involved.

HENDERSON

The clupeids in Lake Tanganyika can't be held at all. We want to do so in order to calibrate their echos in our sonic biomass estimation procedure. We can't even keep them alive in a holding net.

HASLER

I had some discussions this summer with the French research people who are trying to rehabilitate the salmon runs in French streams, and they raise the question of whether the introduction of the coho would be desirable. There's a good deal of objection to that from the sportsmen's point of view. Do you think it would be wise to get some estimate on what kind of inroads that introduction would make on the food of the native Atlantic salmon in the sea, let alone the possibility of introducing competing fish in the streams?

HENDERSON

Surely such questions should be evaluated before stocking. The problem with such studies is that you are never quite sure what constitutes a satisfactory evaluation before a decision to stock an exotic species is made. Also, a study of food resources in the ocean is complicated by overlapping habitats.

LILEY

I suppose you could use the same argument being used to justify the salmon enhancement program on the west coast of Canada. In that program, an attempt will be made to double the salmon stocks, this on the basis of the fact in 1900 the stocks were twice what they are now, and therefore, it is assumed there must be the space and resources available to support a lot more fish.

HARDEN JONES

There are many rivers in Scotland from which less than 1000 fish are reported as being caught each year. These rivers must have small spawning escapements, and if coho was going to compete, and to compete favorably, it might displace the native stock.

Environmental Preferences and Behavior Patterns of Gulf Menhaden *(Brevoortia patronus)* Inferred from Fishing and Remotely Sensed Data

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KEMMERER, ANDREW J. 1980. Environmental preferences and behavior patterns of gulf menhaden *(Brevoortia patronus)* inferred from fishing and remotely sensed data. p. 345-370. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Environmental preferences and behavior patterns of Gulf menhaden were examined through analyses of fishing and remotely sensed (satellite and aircraft) data collected in the northern Gulf of Mexico from 1972 to 1975. These analyses indicated that water turbidity and color were correlated with menhaden distribution and that the distribution of these fish could be inferred from satellite-acquired ocean color measurements. Movement patterns and school sizes appeared affected by fishing activities, and evidence was presented that school size varied with yield. The fish schools appeared to break into smaller schools, move inshore at night, reform, and move offshore during the day in response to varying light intensities. The fish also appeared to seek out waters with specific optical properties (color and turbidity) to compensate for diurnal changes in light intensity which may explain why their distribution patterns could be inferred from satellite ocean color measurements. An April inshore migration was indicated; however, the period of maximum offshore migration could not be determined.

Introduction

Gulf menhaden *(Brevoortia patronus)* have been the target of two satellite related fishery investigations in the northern Gulf of Mexico. Beginning in 1972, these investigations were designed to evaluate and subsequently demonstrate the feasibility of using remotely acquired data for enhancing the management and utilization of coastal pelagic resources. Menhaden were selected as the target species because the fishery was well developed, the industry was cooperative, and more information existed for these fish than for any other coastal pelagic species in the Gulf of Mexico. Results from the first investigation have been summarized by Kemmerer et al. (1974) and from the second by Kemmerer and Butler (1976), Woods, Kemmerer, and Faller (1976), Vanselous (1977), and Kemmerer, Savastano, and Faller (1978). None of these summaries, however, emphasized environmental preferences or behavior patterns of menhaden and how this type of information could be used for management, the purpose of this paper.

Background

Menhaden support the largest volume fishery in the United States. Two species comprise most of the catch: Atlantic menhaden, *B. tyrannus*, from about the Gulf of Maine to central Florida and Gulf menhaden from southern Florida to the Mexican border (Reintjes and Pacheco 1966). Since 1970, annual yield from the Gulf of Mexico and Atlantic fisheries has averaged 564,600 and 300,900 metric tons, respectively.

The fisheries operate similarly along both coasts, being dependent on the surface schooling nature of the fish. In the Gulf, the fishing season begins about mid-April and extends to October. Fishing normally takes place during daylight hours from Monday through Friday, usually within 16 km of shore. Generally, fish are located by spotter pilots flying small, single engine aircraft. The pilots maintain radio contact with vessel captains to direct the vessels into areas with commercial concentrations of fish and to aid in capture operations. The vessels, referred to as steamers, carry two purse boats which are lowered into the water when the steamers encounter menhaden schools. The purse boats, with a purse seine equally divided between them, are lashed together until they reach the fish where they separate and encircle the school with the net. Surplus net is hauled into the purse boats to concentrate the fish, and pumps are used to remove the fish from the water to the hold of the steamer. Each complete fishing operation is referred to as a set.

Considerable information exists on the biology of Gulf menhaden with most of the published material referenced in bibliographies by Gunter and Christmas (1960), Reintjes, Christmas, and Collins (1960), Reintjes (1964), and Reintjes and Keney (1975), and in a management plan by Christmas and Etzold (1977). Adults are relatively small weighing about 100 g and measuring about 17 cm (fork length). During the fall and winter months, they apparently move offshore to spawn (Roithmayr and Waller 1963) where they depend on water movement to transport their eggs and larvae into estuarine nursery grounds, similar to Atlantic menhaden (Nelson, Ingham, and Schaaf 1977). The juveniles require about 1 yr to mature before being recruited into the fishery. They are relatively short-lived with 1- and 2-yr-olds constituting more than 90% of the commercial catch (Christmas and Etzold 1977).

Effects of environmental factors on the distribution and abundance of menhaden are not well understood. Menhaden occur in waters with wide ranges of temperature (0 to 40°C) and salinity (0 to 60 ppt) although a preference for lower salinity waters, i.e., less than 25 ppt, was noted by Gunter and Christmas (1960) and Kemmerer et al. (1974). Food is believed to be the principal biological factor affecting menhaden in estuaries (Reintjes and Pacheco 1966), although no attempts to correlate abundance and distribution with food supply have been reported. Larval menhaden are selective feeding carnivores but after metamorphosis they become filter feeders, with diatoms and dinoflagellates comprising most of their diets (Darnell 1958, 1961). Some bottom feeding also may occur (Peck 1894; Anderson, Jonas, and Odum 1958).

Data Acquisition

Most of the data considered in this paper were collected from three principal areas in the northern Gulf of Mexico in 1972, 1975, and 1976 (Fig. 1). The Mississippi Sound was the only area sampled in 1972; in 1975, both the Mississippi Sound and a 5,200-km^2 rectangle off Atchafalaya Bay, Louisiana, were used. In 1976, the study area was limited to a 185-km Louisiana coastal region immediately west of the area sampled in 1975. Selection of these areas was predicated by LandSat coverage, logistics, and coverage by the fishing fleet.

The Mississippi Sound and the two areas off Louisiana characterize most menhaden habitats in the Gulf. The Mississippi Sound is approximately 17 km wide by 110 km long with average and maximum depths of about 4 and 6 m, respectively. It is separated from the Gulf proper by a chain of barrier islands situated almost parallel to the coast. The study areas off Louisiana had no such physical separation from the Gulf, being characterized as hydrologic transition zones from estuarine to coastal environments. The seaward limit of the Louisiana areas was 50 km offshore at approximately the 24-m depth contour.

Because the two investigations that incorporated the study areas emphasized different objectives, field operations to support them also differed. However, they had similar basic components designed to establish oceanographic preferences of menhaden for correlation with remotely sensed data. These components included observers aboard selected menhaden vessels to measure oceanographic con-

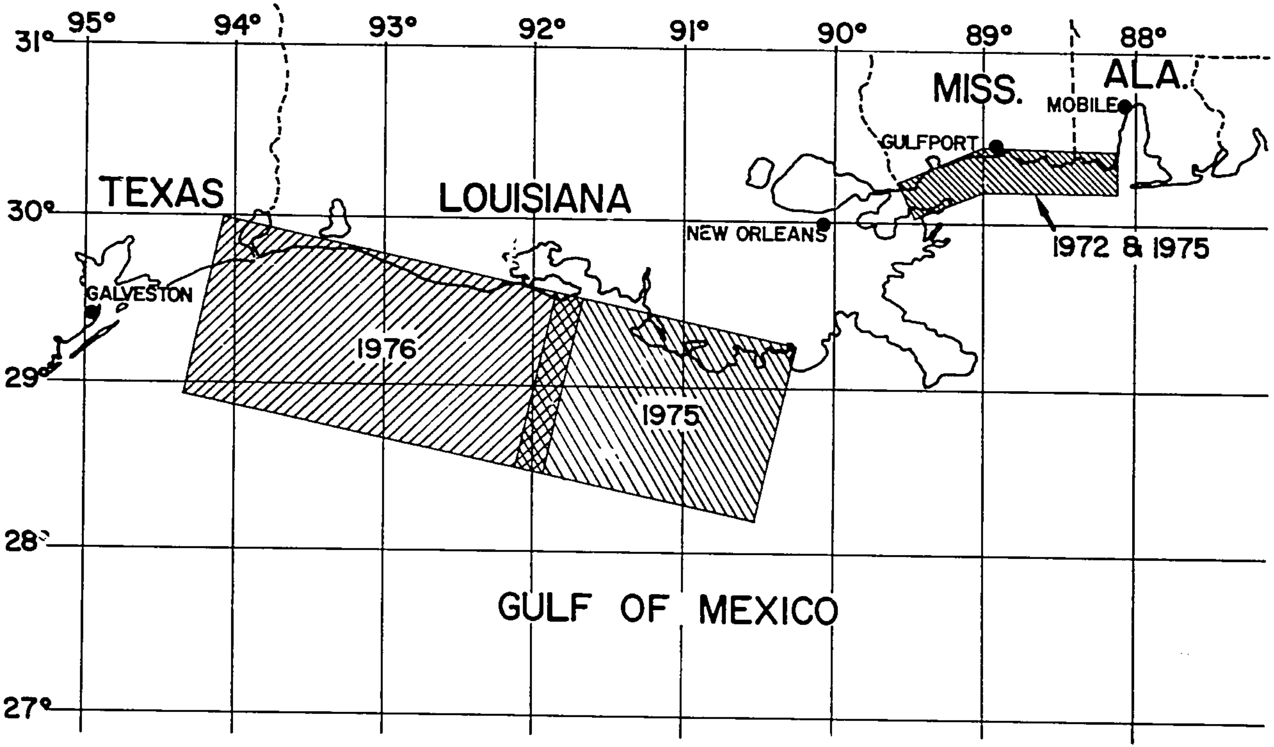


FIG. 1. Study areas for the 1972, 1975 and 1976 satellite investigations of menhaden abundance.

ditions at locations of menhaden capture and to record estimates of set size. The latter estimates were by vessel captains and generally were based on the time required to pump fish. Set size was assumed to reflect school size as all or most of a fish school is captured in a single set. Special logs were used for fishing data from vessels without observers and for selected spotter pilots. In all instances, date, time, location, species composition, and estimates of school size were recorded.

In 1972, aerial photography and a low-light-level imaging television system were used extensively to collect data on menhaden distribution and abundance (number and surface area of schools). In 1975 and 1976, minimal use was made of these systems as the fishing fleet provided data better suited for the purpose of the investigation. Descriptions of the systems and their applications are given by Kemmerer et al. (1974), Benigno and Kemmerer (1973), and Roithmayr and Wittmann (1972).

Oceanographic sampling from selected fishing vessels in 1972 began about mid-June and extended into September. Normally only one or two vessels were manned on the first 3 days of each fishing week. In 1975, the sampling strategy was changed; up to six vessels were manned for the entire fishing week on four separate occasions in each study area. During 1976, observers were on eight vessels for two consecutive weeks in July. Parameters measured normally included surface water temperature, salinity, Secchi disc visibility depth, color (Forel-Ule color scale), surface chlorophyll-*a*, and water depth.

Field operations were designed to take advantage of coverage by LandSat 1 or 2. These two spacecraft are identical in design and application. They operate in circular, sun-synchronous, near-polar orbits at altitudes of approximately 915 km. Each spacecraft circles the earth every 103 min, completing 14 orbits per day and providing repeat coverage of specific areas every 18 days. They carry multispectral scanners (MSS) which provide radiometric measurements in four regions of the electromagnetic spectrum (Freden 1973): 500-600, 600-700, 700-800, and 800-1100 nanometers.

Some oceanographic sampling was done from research vessels during both investigations. Samples were collected only on days of satellite coverage, primarily for calibration of temperature and salinity sensors carried on aircraft, and for development and evaluation of computer algorithms to convert LandSat MSS data into inferred measurements of turbidity and chlorophyll-*a* concentrations. Sampling stations were positioned along predetermined flight lines; procedures followed were identical to those used on the fishing vessels.

Environmental Analyses

Environmental preferences of menhaden were estimated through analyses of oceanographic data collected at sites of menhaden capture. Data from 1975 were emphasized. Ideally, the analysis should have been based on comparisons of oceanographic conditions in areas with and without menhaden. However, that was not possible as only a limited number of samples were collected from areas without menhaden. The alternative was to examine spatial (Louisiana versus Mississippi) and temporal (between sampling periods) variability in the data. The assumption was that if menhaden were caught consistently in the same type of water with respect to one or more parameters, then those parameters were influencing the distribution of these fish. Oceanographic data from the calibration vessels also were compared to the data from the fishing vessels to ensure that consistency was a function of fish preference and not simply a result of a homogeneous environment.

Surface water temperature, salinity, and chlorophyll-*a* concentrations appeared to have little or no effect on menhaden distribution in the two study areas (Fig. 2A and B). Menhaden were caught throughout the range of temperatures encountered during any given sampling period, and as the waters warmed through the summer, the fish were caught in progressively warmer waters. The range of salinities associated with menhaden captures (0-28 ppt) was so broad that any direct effect on distribution seems unlikely, except possibly at concentrations exceeding about 25 ppt. The lack of a consistent relationship between menhaden catch and chlorophyll concentrations was perplexing. Menhaden are filter feeders; therefore, a relationship between the distribution of these fish and their food supply (phytoplankton or the planktonic organisms that feed on phytoplankton) was expected. However, recent food habit studies on Atlantic menhaden suggest that detritus might be important in the diets of these fish which could explain this lack of a relationship (Dr. Walter Nelson. National Marine Fisheries Service, Beaufort Laboratory Beaufort, NC, personal communication).

The consistency of Secchi disc visibility and Forel-Ule color measurements at locations of menhaden capture over time and between study areas indicated a relationship between these parameters and menhaden distribution (Fig. 2A and B). Furthermore, there appeared to be differences between these measurements and those from the calibration vessels. These comparisons suggest concomitance between menhaden distribution and the two parameters.

Effects of oceanic conditions on menhaden schooling behavior were examined by comparing set size to selected oceanographic parameters. Fishermen generally assume that they capture all or most of a school in a set, and as such, set size was used as an indicator of changes in schooling behavior. The comparison was done through regression analyses with results presented in Table 1. It should be noted that in this and many subsequent analyses, data from the Mississippi Sound and Louisiana study areas were pooled into two location categories without regard to the year collected. Some between-year differences were noted, but none significantly affected the results.

TABLE 1. Regression analyses of menhaden set size versus selected oceanographic parameters.

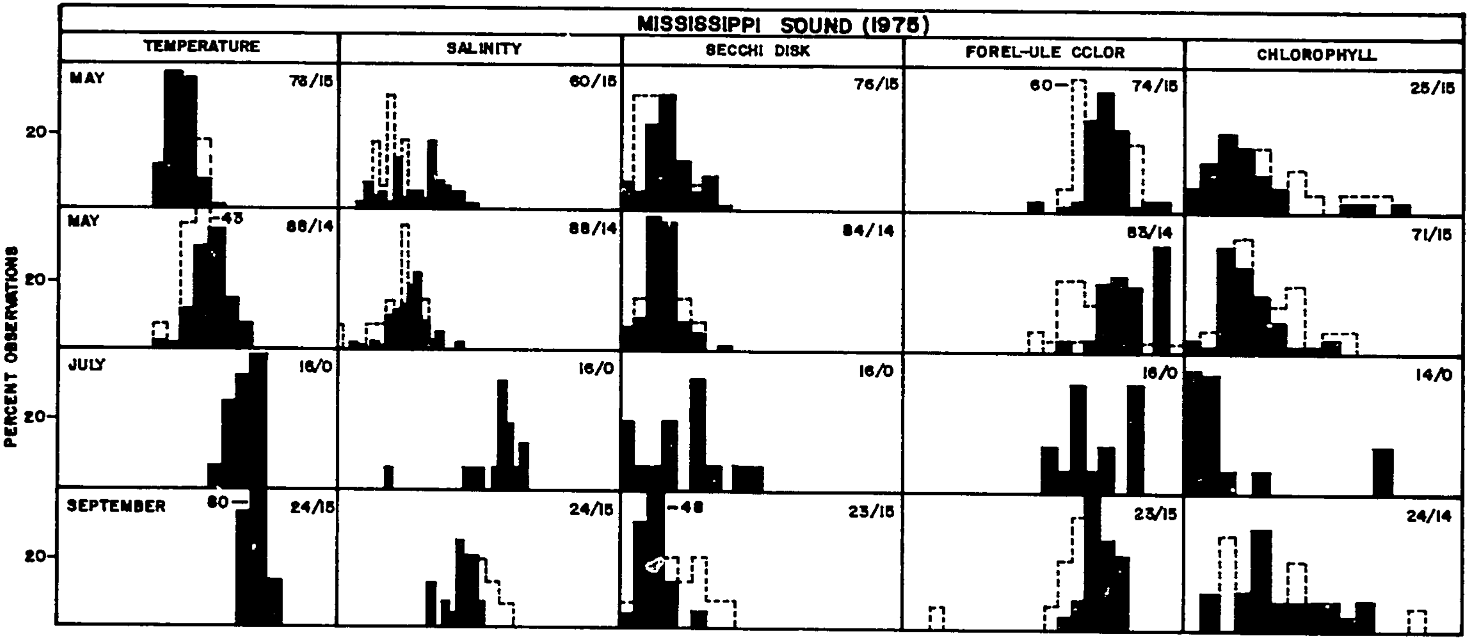
	Mississippi (1972 & 1975)			Louisiana (1975 & 1976)		
Variable	Sample size	Correlation coefficient	Significance level (%)[a]	Sample size	Correlation coefficient	Significance level (%)[a]
Temperature	624	−0.04	50	566	0.18	99
Salinity	587	−0.16	99	553	−0.13	99
Secchi disc	599	0.09	97	554	−0.05	75
Chlorophyll-*a*	212[b]	0.04	25	299	−0.05	50
Color	562	0.08	90	530	−0.05	50
Depth	252[b]	−0.02	10	561	−0.07	90

[a] Test is for a slope significantly different from zero.
[b] Only from 1975.

In general, set size did not appear to be influenced greatly by any of the oceanographic parameters. Salinity was the only parameter seeming to have an effect on set size that was consistent and significant in all study areas. Larger sets (>150,000 fish) generally were made in low salinity waters ($\bar{x}$ = 19.27 ppt for Mississippi and 15.33 ppt for Louisiana). Effects of the other parameters were inconsistent, judging from the signs of the regression coefficients (plus or minus), even though significance levels for some were relatively high (90% or better). A multiple regression analysis with 1975 data from both study areas, where set size was the dependent variable and the six oceanographic parameters were the independent variables, was significant (99% confidence level), but precision was relatively low (r = 0.20).

Satellite Data Analyses

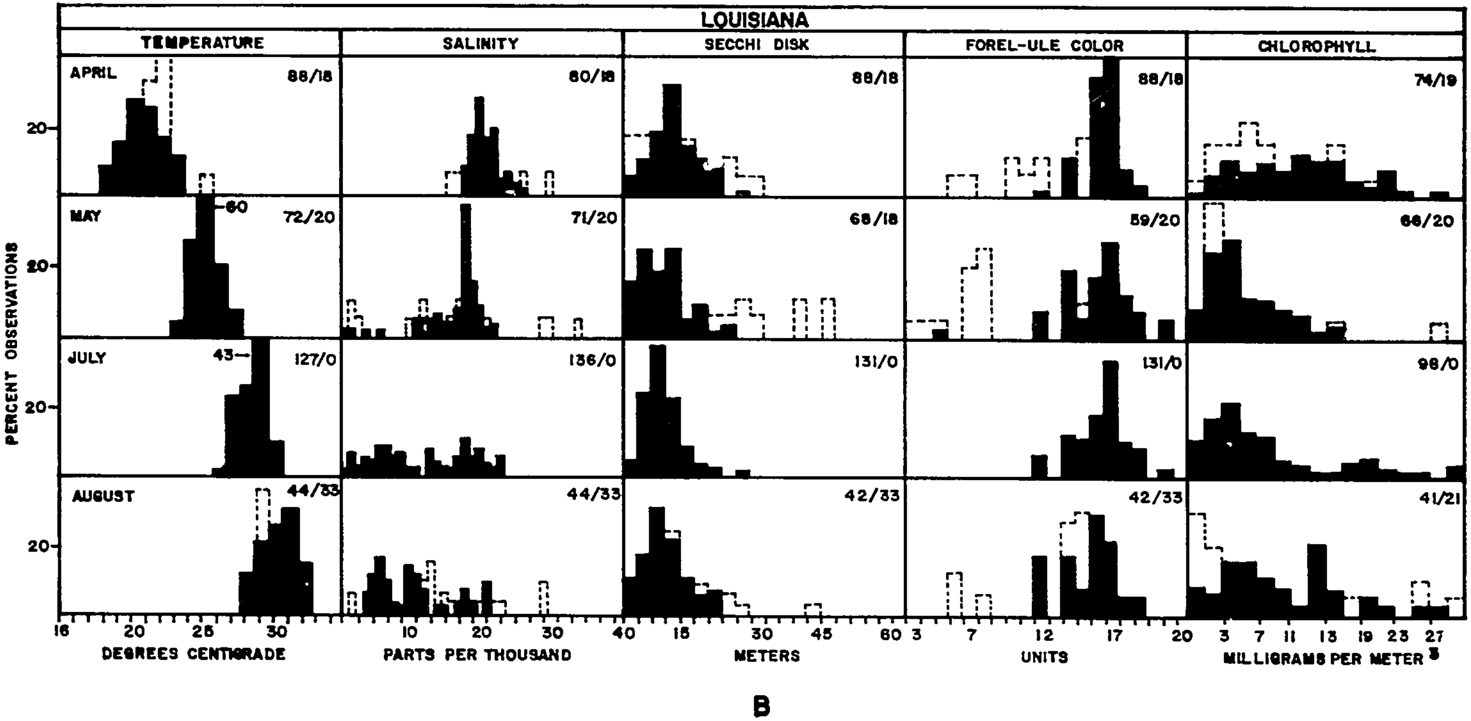
Because of the apparent relationship between menhaden distribution and water color and Secchi disc visibility, an attempt was made to use LandSat MSS data for inferring the distribution of these fish.



A

Fig. 2. A and B. Summary of oceanographic measurements at locations of menhaden capture (solid histograms) and at calibration sampling stations (broken line histograms). Numbers in upper right corners represent sample sizes menhaden calibration.

FIG. 2 (Continued)



Both parameters should be manifest in MSS data although attempts to infer them directly were relatively unsuccessful (Brucks et al. 1977). Correlation coefficients computed from regression analyses of menhaden distribution against radiance values in each spectral band generally were significant at levels exceeding 90% (Table 2). The dependent variable in each analysis was menhaden distribution formed by assigning 1 and 0, respectively, to areas with and without fish.

Several analytical approaches were evaluated for classification of LandSat MSS data into charts of inferred menhaden distribution. These approaches are discussed in detail by Brucks et al. (1977). Essentially, they consisted of first establishing a MSS data training set composed of radiance measurements in each spectral band for 10 to 15 areas with and without reported menhaden observations. These areas selected, plus or minus 2 h of satellite coverage, were used to construct a statistical algorithm composed of radiance value ranges for each spectral band associated with known fish locations. Normally, spectral ranges were established as the mean plus or minus 1 or 2 standard deviations. The final step was to classify portions or all of the LandSat scene into high and low probability menhaden areas by comparing all spectral measurements against the ranges of radiance values established for menhaden locations. Areas satisfying the range criteria, i.e., with radiance measurements falling within the range of values established for known fish locations) were classified as high probability areas; those that failed were classified as low probability areas.

The first classification attempt was with LandSat MSS data from May 20, 1975, covering the eastern portion of the Mississippi Sound (Fig. 3). Most of the reported menhaden school locations fell within

TABLE 2. Correlation coefficients for the relationship of menhaden distribution to LandSat MSS spectral data (1975).

	Mississippi Sound		Louisiana
Spectral range (nm)	May 20	June 25	July 24
500-600	0.65**	0.46*	0.42**
600-700	0.74**	0.82**	0.36*
700-800	0.67**	0.69**	0.28*
800-1100	0.61**	0.30*	0.20
Sample size	36	18	33

*Significant at the 90% confidence level.

**Significant at the 99% confidence level.

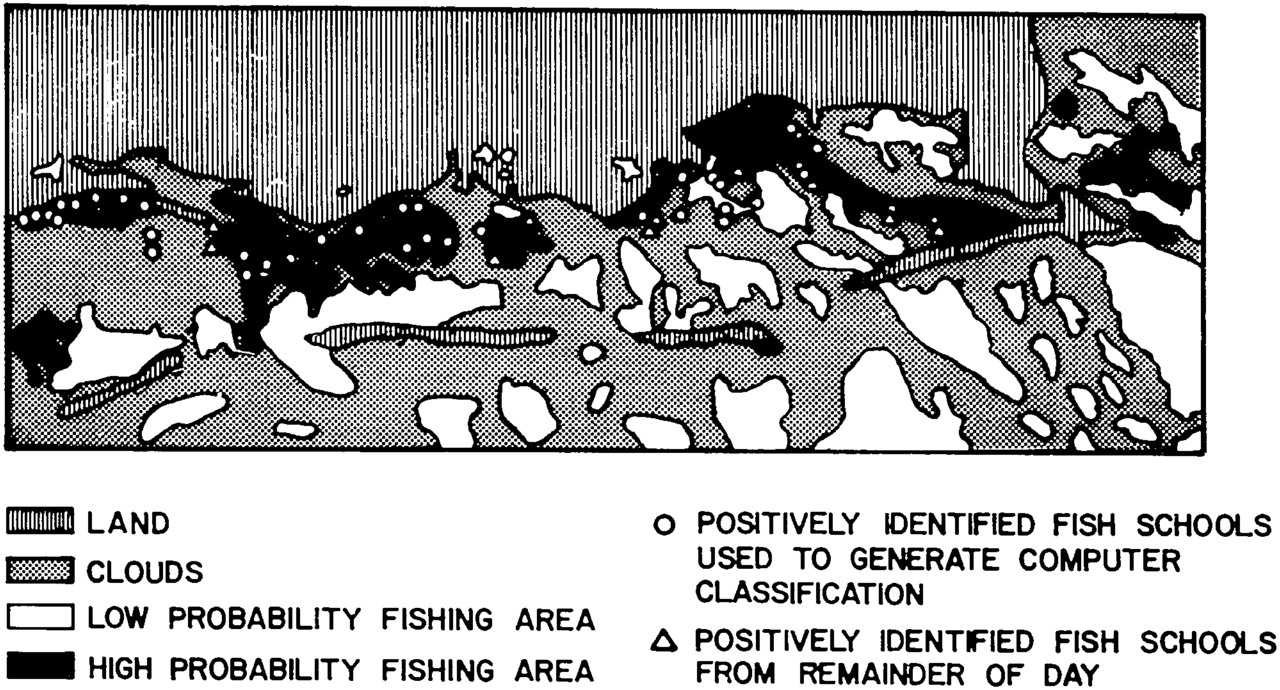


FIG. 3. Classification of LandSat MSS data from May 20, 1975, into high and low probability menhaden fishing areas for the eastern half of the Mississippi Sound.

or immediately adjacent to the inferred high probability areas. The high probability area in the extreme right portion of the figure is in a closed fishing area (Mobile Bay), hence, no fishing reports. The apparent misclassifications in the right-center portion of the image (i.e., school locations outside a high probability area) were probably due to cloud contamination of the MSS data. Close inspection of the LandSat image revealed thin wispy clouds over these school locations which would have caused the misclassifications. Two locations were reported (not shown) under the cloud bank in the extreme lower left portion of figure which may or may not have fallen into the associated high probability area. These results, together with results from two other classification attempts for the Mississippi Sound and off Louisiana, indicated that classification accuracies between 80 and 90% could be expected with LandSat MSS data.

The utility of a satellite-aided fishery harvest and assessment system was demonstrated in 1976 through near-real-time processing of LandSat data into high probability areas for distribution to the fishing fleet. The intent was for the fleet to verify these areas through monitored fishing operations. Since LandSat is an experimental spacecraft system not designed for real-time application, a carefully constructed and tested procedure had to be developed for acquiring, transporting, and processing the data. This procedure required extensive cooperation by numerous Federal agencies and private industries, and resulted in dissemination of the inferred high probability areas to the fleet approximately 21 h after satellite coverage. The lengthy time period was required to allow for commercial air transport of the satellite data from the receiving station in Maryland to Louisiana, data reformat, data reference to geographical coordinates, training field selection, and classification. If the procedure had been fully automated, the time period probably could have been reduced to less than 2 h.

Fig. 4 shows results from the near-real-time demonstration experiment. The probability chart was prepared from LandSat MSS data acquired at 1026 hours on July 19, and the menhaden locations reported by the fishing fleet are from July 20. Most menhaden locations fell within or adjacent to the high probability areas. Some differences, however, should be expected due to period between satellite coverage and fishing verification.

Fishery Analyses

Set size, number of sets per vessel, and set location were used to evaluate effects of fishing activities and other factors on menhaden. In general, there appeared to be a relationship between average set size and fish yield. Between year and study area set size statistics are

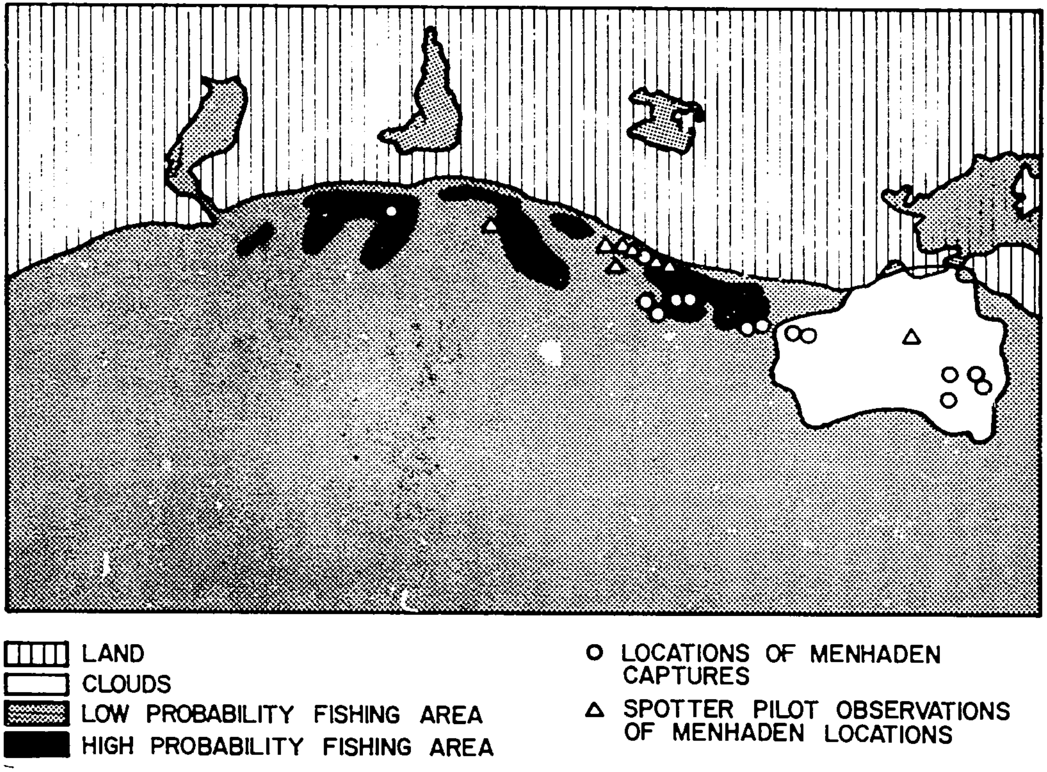


Fig. 4. Predicted high probability fishing areas for July 20, 1976, from July 19, 1976. LandSat MSS data (near real time demonstration test).

presented in Table 3. In 1975, menhaden schools in the Mississippi Sound were significantly larger than in 1972, based on comparisons of geometric means, but not significantly different from those off Louisiana in 1975 or 1976. Total yield for the northern Gulf of Mexico was considerably less in 1972 (501,900 metric tons) than in 1975 (535,600 metric tons) or 1976 (575,800 metric tons) which suggests that set size varied as a function of fish availability.

Effects of fishing activities on menhaden availability were examined by comparing changes in average daily set size and number of vessel sets throughout a fishing week (Monday through Friday). Fishermen claim that menhaden are more available and easier to catch on Monday following little or no pressure over the weekend. Nicholson (1972) suggested that this might be a manifestation of a change in fish behavior due to fishing activity when he found that Chesapeake Bay catches of Atlantic menhaden on Mondays, relative to the rest of the week, increased concomitantly with increases in fishing pressure. He postulated that fishing intensity, or harassment of schools, might be affecting the mechanisms by which small schools coalesce into larger ones or be causing them to sound when approached by fishing vessels.

Off Louisiana, the average fishing vessel made significantly more sets and caught more fish per set on Monday than on any other day of the week (95% confidence level; Fig. 5). In the Mississippi Sound, however, there were no significant differences in number of sets per vessel as a function of week day (Fig. 5). Average set size also varied unpredictably with the larger sets being made on Monday, Tuesday, and Thursday, and the smaller ones on Wednesday and Friday. Significant differences (95% confidence level) were found between average set sizes on Tuesday and Friday, Wednesday and Thursday, and Thursday and Friday.

TABLE 3 Set size statistics (number of fish) for the Mississippi Sound and Louisiana coastal waters.

Location	Year	Sample size	Arithmetic mean	Geometric mean	Geometric 95% C.L.	
					Lower	Upper
Mississippi	1972	395	47,800	35,512	32,837	38,406
	1975	255	70,240	47,778	42,452	53,764
Louisiana	1975	327	78,960	56,736	51,737	62,230
	1976	243	85,810	59,958	53,877	66,742
Mississippi	1972 & 1975	650	56,600	39,895	37,342	42,619
Louisiana	1975 & 1976	570	81,900	58,088	54,038	62,445
Both	1972-1976	1220	68,410	47,550	45,227	50,003

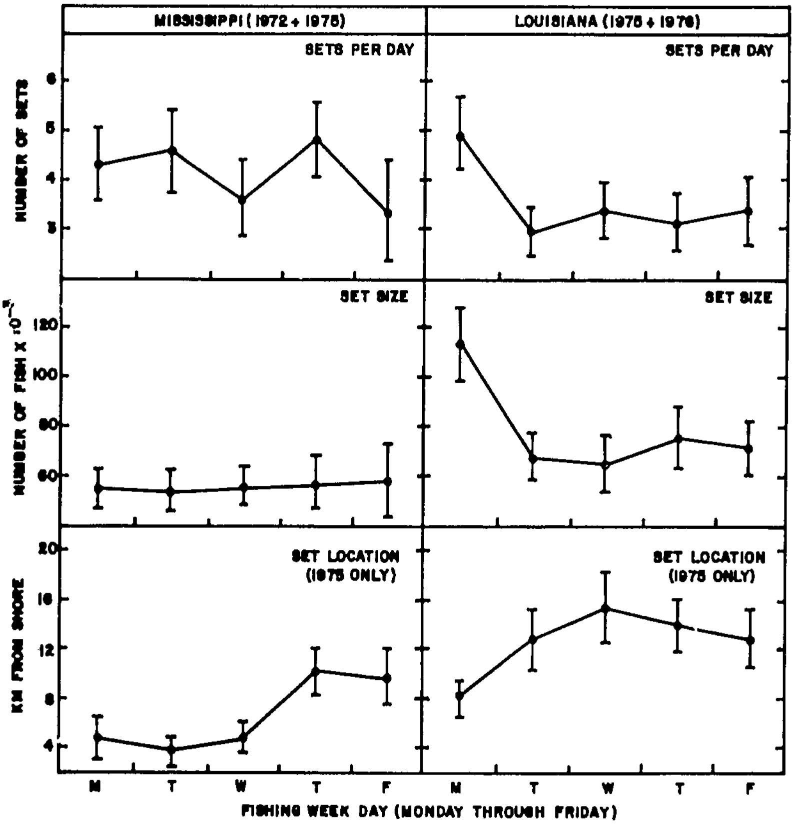


FIG. 5. Pooled fishing statistics for the Mississippi Sound and Louisiana study areas as functions of weekday. Means and 95% confidence intervals are shown as black circles and vertical lines, respectively.

The reason for the lack of similarity between the two areas, insofar as the apparent effect of fishing activity on the availability and behavior of menhaden is concerned, is unclear. The shallower nature of the Mississippi Sound may be part of the reason, as the fish might not have been able to escape pursuing fishing boats as easily. Also, the way the fishery operates in both areas differs slightly as a larger proportion of the vessels fishing the Mississippi Sound make short trips (1 or 2 days); off Louisiana the vessels tend to stay at sea longer.

Another parameter examined to determine if fishing activity was affecting menhaden availability and behavior was distance from shore. Fishermen generally try to fish relatively close to shore where they can quickly find shelter in the event of inclement weather, where they are close to port, and where spotter pilots with their single-engine aircraft prefer to operate. Distance from shore for this analysis was measured from location of menhaden capture to the nearest point of mainland (i.e., islands and political boundaries were ignored).

In both areas, distance from shore varied significantly (95% confidence level) as a function of weekday (Fig. 5). Fish caught in the Mississippi Sound were only about half the distance from shore on Monday, Tuesday and Wednesday as on Thursday and Friday. The differences off Louisiana were not as great with only Monday being significantly different from any of the other weekdays. Thus, there can be little doubt that fishing activity has an effect on menhaden. How this effect influences the fish is unknown, but it is reflected in set size, number of sets per vessel, and in where the sets are made.

Inferred Behavior Patterns

Commonly held assumptions of the Gulf menhaden fishery are that adult fish move offshore in the fall to spawn and return in the spring, and during the fishing season they undergo daily onshore-offshore movement patterns with the schools breaking up at night and reforming during the day. These assumptions were tested with data collected during the satellite investigations.

Annual movement patterns were examined by comparing set locations (i.e., distance from shore) between months. It was assumed that the fish would be caught farther offshore at the beginning and end of the fishing season if indeed they were migrating during these periods. Table 4 shows results from these comparisons.

Menhaden were caught significantly farther offshore during April in both study areas than during any of the other months (95% confidence level). Furthermore, mean distances from shore tended to decrease as the fishing season progressed. However, there was no indication of the fishes' beginning to move offshore near the end of

Table 4. Summary of monthly set locations (distance from shore).

	Mississippi Sound (1975)			Louisiana (1975)		
Month	Sample size	Mean distance (km)	95% Conf. limits (±)	Sample size	Mean distance (km)	95% Conf. limits (±)
April	24	11.51	4.80	86	18.75	2.34
May	158	6.76	1.14	114	11.25	1.94
June	0	–	–	0	–	–
July	23	3.78	1.62	135	10.69	1.30
August	0	–	–	44	7.75	2.11
September	71	4.06	0.65	0	–	–

the season, suggesting that offshore migration may begin later than assumed. Low-light-level television coverage of the Mississippi Sound in November 1972 showed that many menhaden schools remained in the area even though most fishing had ceased.

Daily movement and behavior patterns of menhaden were inferred from fishing data supplemented with data acquired with photographic and low-light-level television sensors. In both areas, significantly more sets per vessel were made after 1500 hours than in any preceding time period (95% confidence level; Fig. 6). Mean set size also tended to be larger after 1500 hours than in any of the preceding periods (Fig. 6).

Remotely sensed data collected in 1972 supported the conclusion derived from fishing data that school size and availability increased in the late afternoon. Surface areas of menhaden schools recorded on photographic film from morning (0800-1000 hours) and afternoon (1500 to 1700 hours) flights were compared. Geometric means for the two periods differed significantly (95% confidence level) with the schools larger in the afternoon ($\bar{x}$ = 140.28 m^2; n = 1199) than in the morning (x = 93.54 m^2; n = 183). Menhaden schools imaged at night averaged 97.05 m^2 (n = 4269) which was significantly different (95% confidence level) from the other two periods. More fish schools also were detected at night than during the day and more in the afternoon than in the morning. Quantification of these differences, however, was not attempted because the flights generally were not flown consecutively. Sensor bias may have affected the results, but the effect probably would have been an overestimation of school size at night and an underestimation during the day.

Besides changes in availability and school size, menhaden appeared to move offshore during the day and onshore at night (Fig. 6). Sets made before 0900 hours were significantly closer to shore than were the sets made after 1500 hours in both study areas (95% confidence level). Low-light-level television imagery also suggested

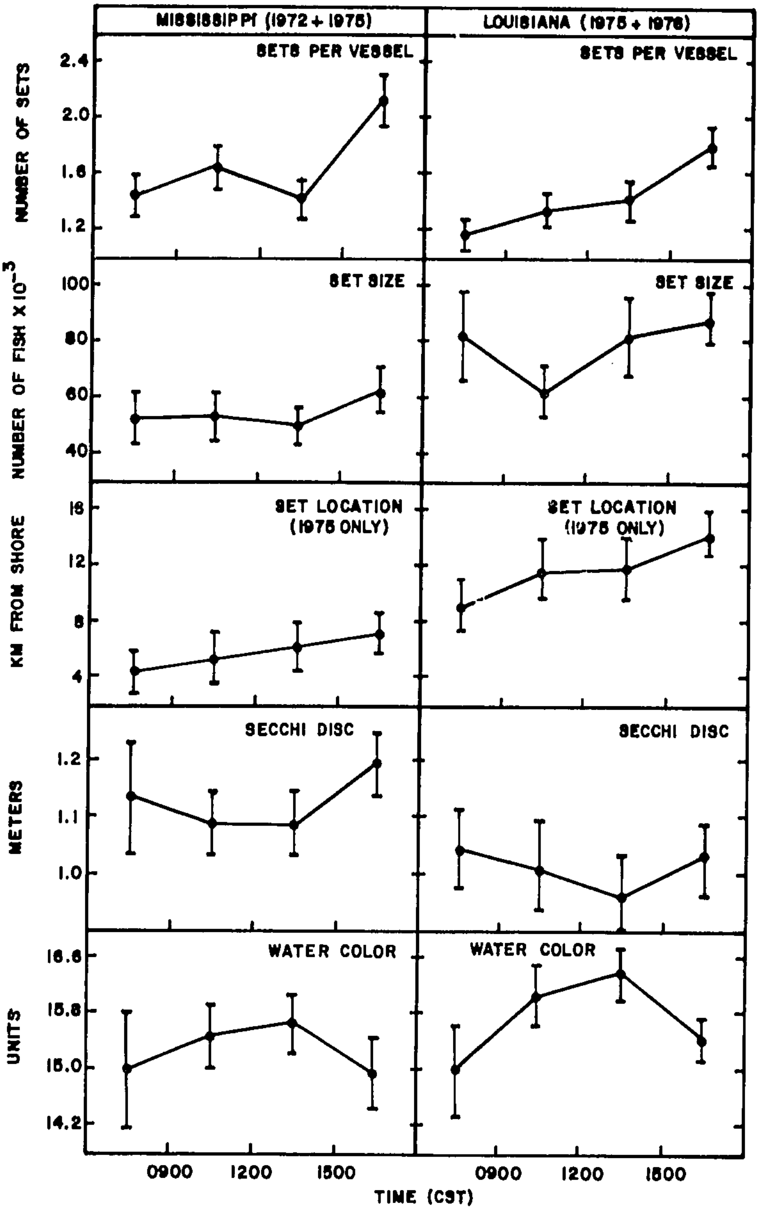


FIG. 6. Pooled fishing statistics and environmental data for the Mississippi Sound and Louisiana study areas as functions of four time periods. Means and 95% confidence intervals are shown as black circles and vertical lines, respectively.

that school aggregations tended to disperse at night followed by aggregation in the morning close to beaches.

The environmental factor or factors responsible for changes in menhaden schooling behavior and movement patterns could not be firmly established based on available information. However, as many fish species have been reported to respond to changes in light intensity (reviewed by Breder 1959, and by Blaxter and Holliday 1963), this seemed to be a logical variable to consider. The movement from shore during the day coupled with larger school sizes in the evening could be due to behavioral responses to differing light intensities. Also, the increased availability of fish after 1500 hours could be due to fish moving into surface waters in response to lowered light intensities where they would be more accessible to the fishermen. The fact that more sets were not made in the early morning hours compared with the middle portion of the day, when average light intensities are roughly the same as those after 1500 hours, neither supports or rejects these assumptions. If, as the data suggest, the fish schools fractionate into smaller schools at night, fishermen would necessarily have to spend more time searching for commercially acceptable schools in the early morning hours compared to the remaining portion of the day. Furthermore, fishermen have reported that in the morning menhaden are often concentrated near beaches in waters too shallow for purse boat operation, or in restricted fishing areas. Both of these factors would tend to decrease the number of sets made in the early morning hours.

An attempt was made to substantiate the hypothesis that light intensity was a major factor controlling menhaden movement and behavior. This was done by comparing changes in the parameters considered previously as functions of three cloud cover conditions: clear, partly cloudy (<50% coverage), and cloudy (>50% coverage). An increase in cloud cover was assumed to represent a decrease in light intensity. Cloud cover estimates were from coastal weather stations (Smith 1978) although differences between cloud cover over the stations and the fishing areas undoubtedly occurred.

Menhaden in the Mississippi Sound were caught significantly farther offshore on cloudy days than on days when the skies were clear or partly cloudy (95% confidence level; Table 5). No significant differences, however, were noted off Louisiana although it should be emphasized that no sets were recorded for clear sky conditions. Effects of cloud cover on number of sets per vessel and average set size were mixed with no significant differences noted for Louisiana, and a reduction in the average number of sets per vessel in the Mississippi Sound with increased cloud cover. Mean set size also tended to decrease in response to increased cloud cover. However, since the fishery depends on spotter aircraft to locate commercially acceptable concentrations of fish and to aid in capture operations, the analyses of set size and number of sets per vessel are probably

TABLE 5. Summary of set locations (distance from shore) under three cloud cover conditions.

	Mississippi Sound (1975)			Louisiana (1975)		
Cloud cover	Sample size	Mean distance (km)	95% Conf. limits (±)	Sample size	Mean distance km)	95% Conf. limits (±)
Clear	64	3.50	0.71	0	–	–
Partly cloudy	88	3.47	0.58	73	11.01	2.72
Cloudy	124	9.60	1.56	306	12.69	1.07

confounded by effects of cloud cover on spotter aircraft operations. Distance from shore, however, should not be affected.

The implication that menhaden are further offshore on cloudy days than on clear ones can be explained several ways. An explanation consistent with the results is that under cloudy skies menhaden move offshore sooner and faster than normal because light intensities approach those experienced in the late afternoon. The movement itself might not be a direct result of varying light intensities, but the mechanism triggering when and how fast the movement occurs could be.

As responses to light intensity also should be manifest in temporal differences in the turbidity and color of water preferred by menhaden, changes in these parameters at set locations were examined as functions of time (Fig. 6). In both study areas, menhaden generally were caught in clearer waters in the early morning and late evening hours than in the middle of the day. These differences, however, were not significantly different for menhaden captured off Louisiana, but in the Mississippi Sound there was a significant difference (95% confidence level) between midday (0900-1200 and 1201-1500 hours) and evening (after 1500 hours) periods. The color of water preferred by menhaden in the four time-periods also differed with the fish seeming to prefer waters closer to the blue end of the Forel-Ule color scale in the morning and evening compared to waters where they were found in the late morning and early afternoon hours (Fig. 6). These differences were significant (95% confidence level) off Louisiana; no significant differences were noted for the Mississippi Sound.

A daily behavior and movement pattern for Gulf menhaden was postulated based on the foregoing analyses (Fig. 7). Light intensity was assumed to be the principal controlling factor. The postulated behavior pattern shows the fish moving offshore during the day with small schools coalescing into larger ones. It also shows them moving into relatively turbid waters shortly after sunrise to compensate for increases in light intensity. The quality of light and hence the type of

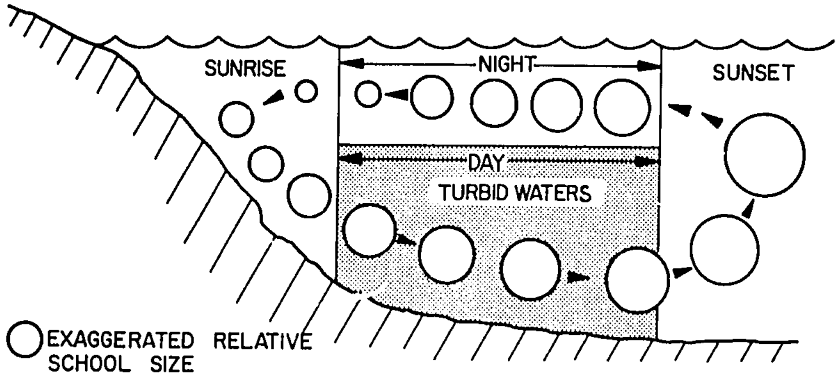


FIG. 7. Postulated menhaden diurnal movement and behavior pattern. Schools break up and move inshore at night. In the morning the schools move into turbid waters to compensate for increased light levels, begin forming larger schools, and move offshore. In both early morning and late afternoon hours, the fish are near the surface and in relatively clear waters, compared to those at midday, because of reduced light levels.

turbidity was assumed to be important, based on the analysis of Forel-Ule color and LandSat MSS data. In the evening concurrent with decreases in light intensity, fish leave the turbid waters and surface where they are available to the fishery. After sunset the fish school aggregations disperse because light intensity no longer limits distribution and the schools begin to break up. The smaller schools gradually begin to move inshore where they concentrate before or shortly after sunrise.

An annual movement or migration pattern also can be postulated. Adult fish apparently move offshore sometime during the fall (after September and possibly not en masse until November or December). In early spring (March to April) they migrate back to coastal areas and by midsummer most are concentrated along the coast. This postulated movement pattern is consistent with the one suggested by Roithmayr and Waller (1963) and monthly catch summaries compiled in unpublished reports by the National Marine Fisheries Service (i.e, peak harvest occurs in midsummer).

Management Implications

Knowledge of environmental preferences and behavior patterns of menhaden and other species can significantly aid management and utilization of coastal fishery resources. Coastal areas often experience major changes in environmental conditions due to natural and man-induced perturbations. These changes can affect fish distribution, availability, and ultimately productivity. Existing management attitudes tend to relate most changes in available stock size to fishing pressure. Poor fish yields general are blamed on overfishing when indeed they could be due to changes in environmental conditions. Reductions in fishing pressure normally are required in either situation to ensure continuance of the fishery; however, if yield reductions are due to environmental changes, fishing pressures probably should be allowed to return to normal levels when these conditions improve.

An ability to infer fish distribution patterns synoptically from environmental data collected by spacecraft would have profound management and utilization implications. From a management viewpoint, it would enable resource investigators to tactically improve sampling designs and resultant analysis for more efficient and accurate stock assessments. Long-term monitoring of these patterns would enable resource managers to detect and subsequently predict effects of natural and man-induced perturbations on the resource. Similar information would enable fishermen to reduce search times for commercial concentrations of fish and could be used in long-range strategic planning. Knowledge of behavior patterns such as those exhibited by menhaden would help to identify optimum periods for assessment surveys such as late in the day or at night when most of the fish are near the surface. The same information could be used by fishermen to improve fishing efficiency and possibly as a means to evaluate gear and fleet performance.

Acknowledgments

I thank all of the people from industry and government agencies who worked so hard to make the satellite investigations successful, and who through our many discussions stimulated preparation of this paper. Special thanks are due Hillman J. Holley who did most of the computer programming for the behavioral portions of the paper.

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Discussion

JOHANNES

Were fishermen using water color to locate menhaden prior to your studies?

KEMMERER

Yes, but we did know they were. In our early meetings with fishermen they were asked for the variables they were using to locate fish. Every fisherman, especially the spotter pilots, seemed to have a different group of variables. Color was mentioned, but never emphasized. After they reviewed our results, several commented that they already knew color was a key variable and indicated some concern about why we had not asked them about it. Obviously, the problem was communication. They were saying one thing and we were thinking something else.

MAGNUSON

I wish we had more data on light preference—both intensity and color preference. Warren Stuntz' preliminary work with the bluegill at our laboratory showed that bright light was one of the only variables that overrode temperature preference. The fish occupied less preferred temperatures at lower light intensities rather than occupy preferred temperatures at higher light intensities.

HARDEN JONES

I am impressed with the amount of information you have obtained from fishermen. Did you have any difficulty securing it?

KEMMERER

Yes, but we avoided many problems by using a single experienced person coordinating our requirements with the industry. Five companies were involved; each one appointed one or more people to represent them during the planning, analytical, and report preparation phases of the investigation. These people were from middle and upper management levels. Frequent meetings were held, especially at the beginning of the investigation. It was amazing how cooperative they were, given the opportunity.

HARDEN JONES

How did you manage confidentiality of information, which reflects profitability and competitiveness with other companies?

KEMMERER

Nothing was recorded about the vessel or company.

JOHANNES

We are doing a small study on coral harvesting in Hawaii. We have interviewed approximately 150 people who either harvest or sell corals. Unfortunately, we have not been able to get much information from them. They are afraid information will get to the Internal Revenue Service, or to their competition, or to the game wardens.

BARDACH

Forgive me for belaboring something for clarification. What is the annual value of the fishery; what was the real cost of the experiment; how much was "for free" because it was in the interest of the government, and can you apply the same techniques in a less expensive way to areas where there is little knowledge of fish distribution?

KEMMERER

That is a good question; let me see if I can respond to all of its parts. The dollar value of the menhaden fishery is about seventh or eighth in the United States. In the Gulf it ranges between 45 and 50 million dollars and in the Atlantic between 25 and 30 million dollars.

The satellite investigations probably cost the Federal Government about $350,000; the fishing industry contributed about $400,000 worth of in-kind services such as aircraft and vessel support, people, etc. Total cost probably approached a million dollars.

ATEMA

Are you including the cost of the satellite?

KEMMERER

No, we paid only for the data.

BARDACH

What did you gain by using the satellite instead of spotter aircraft or aircraft equipped with multispectral scanners?

KEMMERER

The intent of the experiments was to determine if observations from space could be used to define fish distribution patterns. It could have been done from aircraft, but since the satellite already was in orbit, it made sense to use it. I should emphasize that the impetus was not to develop a remote sensing technique for menhaden; rather, it was to demonstrate a capability that might be used for underutilized species. Menhaden comprise only a small percentage of the total biomass in the Gulf of Mexico.

BARDACH

Would you have to repeat the experiment for say, thread herring?

KEMMERER

Portions, yes, but it could be done for considerably less than for menhaden because now we know how to do it.

BLAXTER

It seems to me that a serious disadvantage of satellites is the cloud cover aspect.

KEMMERER

A major disadvantage, yes, but it is a disadvantage that one finds with aircraft also. Temperature and salinity, however, can be measured through clouds. A new satellite scheduled for launch in May 1978—SEASAT-A— will have several sensors operating in the microwave region of the electromagnetic spectrum, a region where clouds essentially are invisible.

FISHELSON

With this potential increase in efficiency, are we not endangering the resources? How does one estimate the percent being harvested so that sufficient resources are left for replenishment?

KEMMERER

They are probably harvesting near the maximum sustainable yield of gulf menhaden and probably more than that in the Atlantic menhaden fishery. If satellite remote sensing were applied to these fisheries and more fish were caught, probably the fisheries would suffer.

BARDACH

I would like to pursue this matter of cost further. Are there not easier, cheaper, and equally good ways of finding the fish?

KEMMERER

Not necessarily. A low-light-level television system costs about $100,000, and an aircraft from which to operate it costs $200 to $500/h. A satellite system would be time shared, as much of its time would be used for other purposes, e.g., pollution monitoring, communications, etc. Thus, the cost associated with fisheries should be relatively small.

Habitat Preferences and Fishery Oceanography

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MAGNUSON, J.J., S.B. BRANDT, and D.J. STEWART. 1980. Habitat preferences and fishery oceanography, p. 371-382. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Fishery oceanography has taken advantage of correlations between the catch of fish and easily measured oceanographic features, usually surface water temperature. Water temperature or other environmental features often provide better information for locating fishes than does geographic position. The response of fish to temperature gradients at the edge of the Gulf Stream near Cape Hatteras and to oxygen gradients in the highland lakes of northern Wisconsin exemplifies the importance and use of physical data in predicting fish distribution. Our inability to judge the perceptual world of fishes or unravel the interactions among the multiple factors determining the distribution of fishes are considered to be major impediments to refining present predictions. Arguments are made for applying laboratory methods to the solution of these problems. Potential applications of habitat preference data include locating desired fishes for harvest, stratifying waters for stock assessment, and setting criteria to screen species to be used for aquaculture.

Fishery oceanography has taken advantage of correlations between the catch of fish and easily measured oceanographic features. Usually catch per unit effort from a commercial fleet is related in time and space to surface water temperature. The results of these efforts have been documented and summarized by scientists from Japan, northern Europe, USSR, and elsewhere (Dietrich et al. 1959; Hela and Laevastu 1962, 1970; Moiseev 1971). More recent efforts continue with good results; for example, Laurs and Lynn (1977) and

Robertson et al. (in press).

Our paper concerns the biological basis for fishery oceanography and is focused on three postulates: (1) temperature or other environmental axes are a better set of coordinates for finding fishes than is geographic space; (2) man's view of fish habitat is often distorted because it is based on our own perceptual abilities and values rather than those of the fish; and (3) an a priori approach to predicting where fish are located, based on laboratory and field experiments on the causal relationships, should be more efficient than simply correlating catches with oceanographic features. These three ideas are interdependent.

Our objectives are to illustrate the importance of these ideas in formulating a conceptual framework for fishery oceanography. Our points of view will be developed with examples of our work on the continental shelf of the Western Atlantic near Cape Hatteras and in temperate lakes of the Highland Lake District in northern Wisconsin. Habitat gradients of temperature and oxygen will be emphasized. Research on the distribution of fishes near Cape Hatteras and in Mystery Lake was supported by the National Science Foundation, Grant #s 770853 and GP18272.

Temperature profoundly affects physiological processes of poikilotherms (Brett 1970; Fry 1947, 1971) and has often been considered to be the primary determinant of pelagic fish distributions (Brett 1971; Fry 1947; Coutant 1974). The biological basis for the importance of temperature to fishes is elaborated upon by Hela and Laevastu (1970), Kinne (1970), and Fry (1971). Aquatic systems exemplify complex heterothermal environments, and sharp thermal gradients are common features.

Insight into factors governing fish distribution and the interplay of temperature and geographic space was gained by an intensive study of an oceanic front between two water masses near Cape Hatteras. An abrupt horizontal gradient in bottom temperature was encountered near 35°31′N latitude on the continental shelf just north of Cape Hatteras. Bottom water temperature taken at the beginning and end of 15-min trawl hauls along the 30-m contour (Fig. 1) illustrates the sharpness of this gradient. Individual bottom trawl hauls spanned up to 8°C in less than 2 km. The entire front spanned about 12°C. Thus, opposite sides of the front are close together in terms of space, but far apart in terms of temperature. The 12°C temperature difference is approximately 1/3 to 1/2 the full range of temperature found in the sea and constitutes a long distance in temperature space.

Similarities in species composition and the abundance of individual species in the trawl hauls suggest that organisms are distributed with respect to temperature space. Changes in the species structure of the fish community are most rapid immediately at the front (Fig. 2 upper) and individual species change in abundance most rapidly at the front (Fig. 2 lower). Distribution of southern species such as 1 and 2 (Fig. 2 lower) do not extend north of the front into cold water; northern species such as 5 and 6 do not extend south of the front into warm water. A third response is exhibited by species (for example, 3 and 4) that reach maximum abundance in the intermediate temperatures of the front but do not extend either north or south of it. Outside of the frontal region the northern and southern species are broadly distributed over space. Our conclusion is that distance between two points is best measured in a habitat dimension (e.g., temperature) rather than in geographic distance when we wish to identify what is important to the animal. Points differing greatly in temperature are conceptually far apart even though they are close together in geographic space.

The frontal region near Cape Hatteras can be used to point out

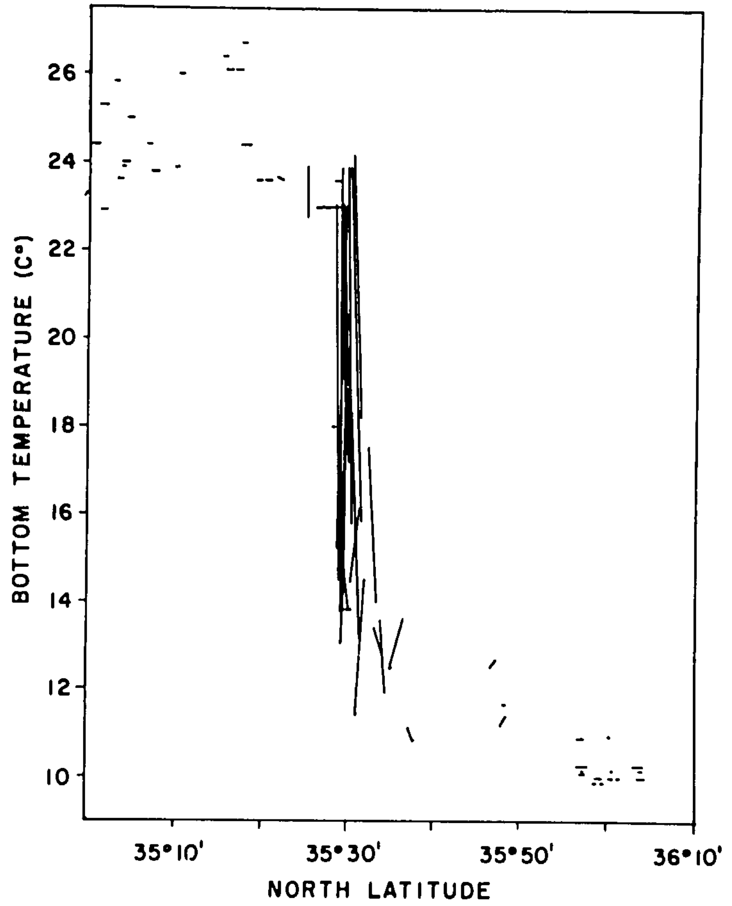

FIG. 1. Bottom temperatures along the 30-m depth contour north of Cape Hatteras in the Western Atlantic in May-June 1975, using a BT at the beginning and end of each 15-min trawl, connected by line segments.

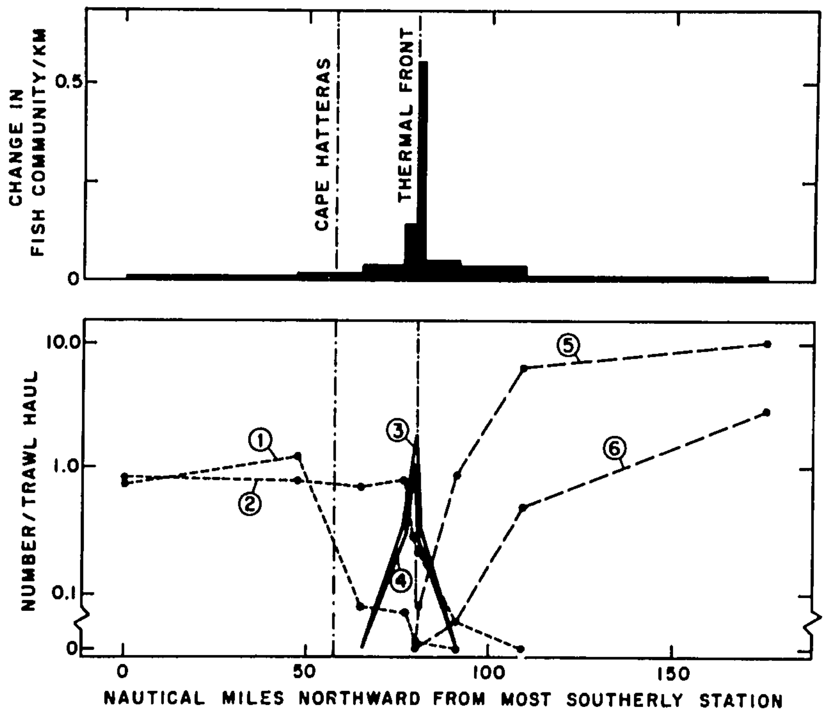

FIG. 2. Changes in the distribution of fishes along the 30-m depth contour on the continental shelf off North Carolina in the Western Atlantic in May-June 1975 based on bottom trawl catches (from Magnuson, Stewart, and Brandt MS). Upper panel is rate of change in species structure of the fish community based on difference in similarity per km between stations. Index is calculated as follows: based on presence-absence data of species, Simpson's similarity index between adjacent stations is calculated. This is converted to an index of dissimilarity by taking the arccosine of the similarity index and expressing it in radians. This is in turn converted to a dissimilarity per unit distance by dividing by km between stations. Ninety species are represented.

Lower panel is the geometric catch per trawl haul of selected species living south of the front (----), in the front (_____), and north of the front (— — —), between Gulf Stream and Virginian waters. The species are (1) offshore lizardfish *Synodus poeyi*, (2) file fish *Monacanthus hispidus* (3) Atlantic croaker *Micropogon undulatus*, (4) spot *Leiostomus xanthurus*, (5) spotted hake *Urophycis regius*, and (6) Gulf Stream flounder *Citharichthys arctifrons*.

another potential problem resulting from our human frame of reference. From our conventional human reference of geographic space, the location of this front is highly variable. We have observed the front move up to 10 km in a day. If we view the situation from the fish's perspective, we may think of the front as stationary and points in geographic space such as Cape Hatteras or the bottom moving. We suspect it is useful at times to view the world from the fishes' frame of reference rather than ours.

This brings us directly to our second premise; we are biased or even limited by our own values and sensory capabilities in attempts to conceptualize the "world of fish." This idea is not new and was well developed more generally by von Uexküll (1909, 1934, 1957) with the idea of "unwelt" or the world as we perceive it (Klopfer and Hailman 1967). More precisely, each species of fish should have a somewhat different perceptual world which can confuse us even further. For example, we know that dissolved oxygen is an important habitat feature for fishes (Doudoroff and Shumway 1970). Thus, in habitats with oxygen gradients including zero we would expect the distribution of a fish to be related in some positive way to the dissolved oxygen concentration of the water. When Mills (1972) related the CPUE of the central mudminnow *Umbra limi* to the distribution of dissolved oxygen beneath the ice of a shallow northern lake in winter, he did not find the expected relationship. In fact, knowing the dissolved oxygen concentration at a particular point did not increase the ability to predict the catch of mudminnows even to the extent of predicting their absence in water with no dissolved oxygen (Fig. 3). Mudminnows were caught as frequently in traps at the lake bottom as at the underside of the ice even though there was less dissolved oxygen at the deeper traps—sometimes <0.1 mg/L. Also, the catch from traps at each depth was not related to horizontal distribution of dissolved oxygen beneath the ice. Further examination revealed the source of these apparent contradictions: Magnuson (unpublished data) showed that the mudminnow filled its gas bladder by gulping gas bubbles that were encountered at the ice-water interface. The gas bubbles contained oxygen and were used by the mudminnow to survive in water with little or no dissolved oxygen. Thus, the prediction of the mudminnow's distribution based on

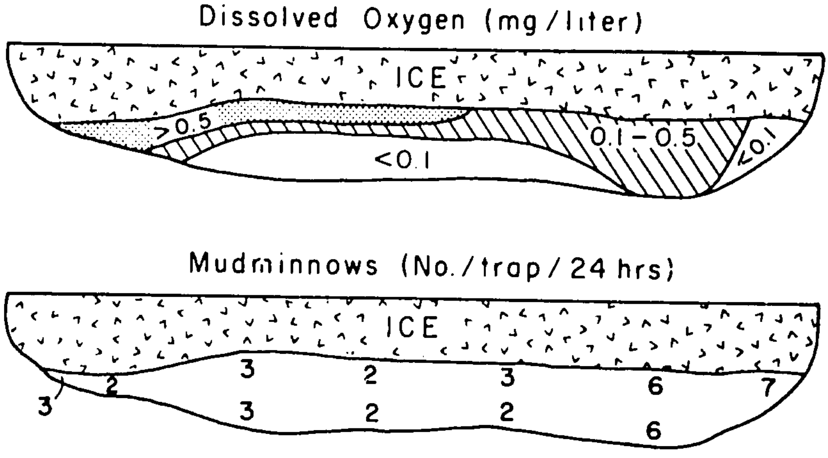

FIG. 3. Central mudminnow catch per minnow trap and the dissolved oxygen concentration beneath the ice in Mystery Lake, Wisconsin on March 5-7, 1971. Dissolved oxygen by Winkler titration. Mudminnows caught in two minnow traps set at each site for 48 h (modified from Mills 1972).

distribution of a needed resource, i.e., dissolved oxygen, was wrong because the fish's biology and habitat were not understood sufficiently.

Hypotheses concerning causal mechanisms of fish distribution need to be tested both in laboratory conditions and in the field. For example, the distribution of fish with respect to temperature in the front north of Cape Hatteras (Figs. 1, 2) does not in itself prove that the fish are responding to temperature. Some evidence that the response is largely to temperature is apparent in Fig. 4. Species in our June 1975 catches were distributed in the study area at temperatures directly proportional to their preferred temperatures reported by Wyllie et al. (1976). Interestingly, all species were caught

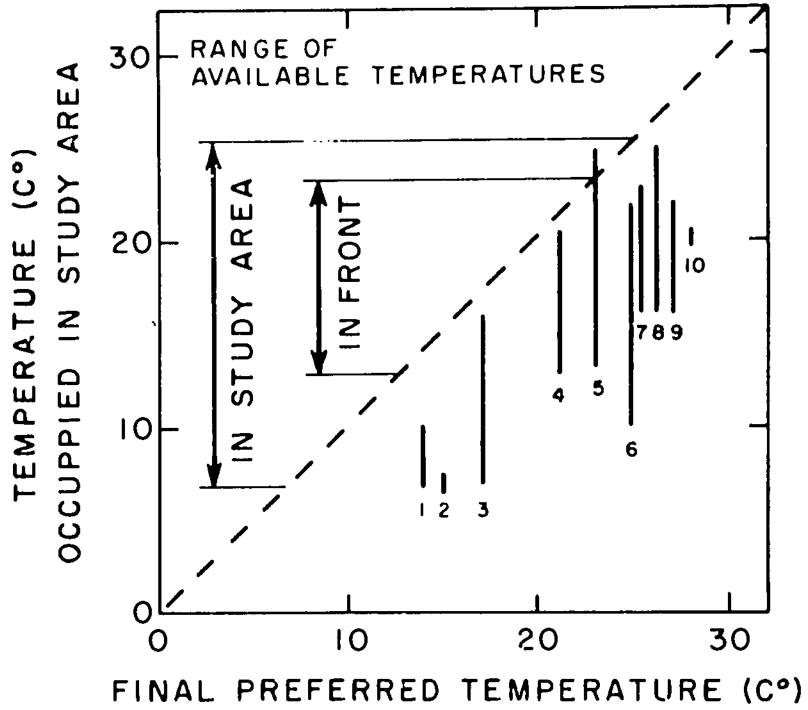

FIG. 4. Relationship between the laboratory preferred temperature of selected fish species (Wyllie et al. 1976) and temperatures occupied along the 30-m depth contour off Cape Hatteras, North Carolina in May-June 1975. Species are (1) red hake; (2) winter flounder *Pseudopleuronectes americanus*; (3) spotted hake; (4) butterfish *Peprilus triacanthus*; (5) scup *Stenotomus chrysops*; (6) black sea bass *Centropristis striata*; (7) spot; (8) round scad *Decapterus punctatus*; (9) bluefish *Pomatomus saltatrix*; and (10) bigeye scad *Selar crumenophthalmus*.

at temperatures that averaged about 6°C below their final preferendum. Avoidance temperatures and preferred temperatures measured by Wyllie et al. (1976) on two species found in the study area (red hake *Urophycis chuss* and spot *Leiostomus xanthurus*) suggest that upper avoidance temperatures are 3-6°C warmer than the preferred temperature. If the same temperature increment were also true for lower avoidance temperature, then the occurrence of fish at sea about 5°C below their preferred temperatures is quite reasonable. Species moving northward in spring perhaps aggregate against the boundary formed by their lower avoidance temperature.

We suspect that the distribution of each species in the front near Cape Hatteras is determined to a great extent by the fish's thermoregulatory behavior and that by orienting to the thermal gradient they can maintain preferred and perhaps optimal body temperature. When given the opportunity to regulate their body temperature, many fishes do so quite precisely in the laboratory (Magnuson and Beitinger 1978). Upper and lower avoidance temperatures of the freshwater sunfishes, the centrarchids, describe a preferred range of temperature that is only 3 or 4°C wide. For centrarchids, temperature shock and acclimation temperature have little influence on final preferred temperature, but biotic factors such as food abundance and social interactions cause fish in laboratory experiments to move out of their preferred temperature range.

Environmental correlates of thermal gradients confound interpretation of causal mechanisms. A fish may be orienting to a preferred temperature, thermal gradients, or to increased food supply at the front. We know fish prefer specific temperatures and that gradients are more likely to contain the preferred temperature of a species than would an area of constant temperature simply because more temperatures are represented. However the gradient itself may influence the behavior of the fish directly. The alternatives are difficult to separate with field data.

Following up field correlations with laboratory and field experiments would, in our view, be a more efficient way to determine where to search for fish than to rely entirely on the field correlations. Laboratory data are usually less expensive to obtain than field data. Also it is easier in the laboratory to isolate variables affecting habitat preference of a fish.

Sometimes the interacting effects of several habitat factors can be seen in field data. We placed bluegill *Lepomis macrochirus* in Mystery Lake, Wisconsin (Fig. 5) in a net enclosure beneath the ice and then used a periscope to observe their vertical distribution in relation to temperature and dissolved oxygen as described in Magnuson and Karlen (1970). In laboratory experiments bluegill prefer temperatures near 30°C and when such temperatures are not available they choose the temperature closest to it, even at winter

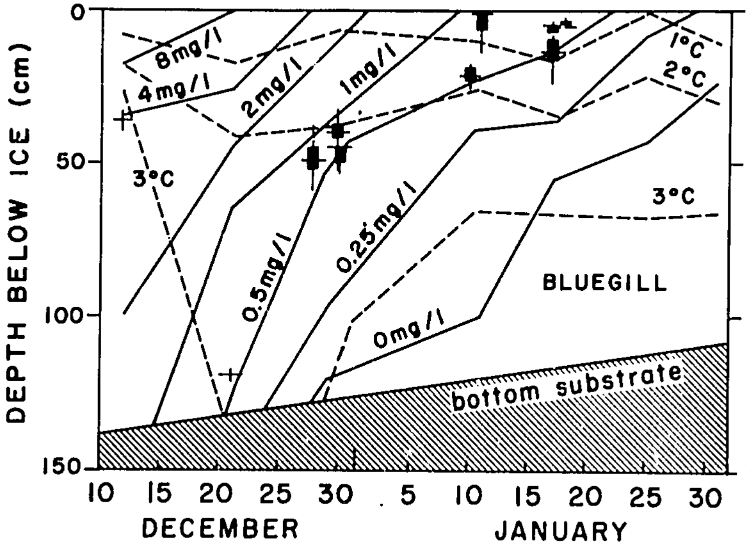

FIG. 5. Vertical distribution of bluegill beneath the ice of Mystery Lake, Wisconsin, in relation to dissolved oxygen (——) and water temperature (— —) during December 1969 and January 1970. Five bluegill (mean total length, 18 cm) were placed in each of two field enclosures. Except for the first two dates when only two fish were sighted, 6-25 sightings (median 15) were made for each enclosure on each date. Range (vertical lines), median (horizontal lines), and quartiles (top and bottom of black rectangles) indicate observed location of fish. Bottom substrate appears to rise because the bottom of the ice was used as a fixed reference and it thickened during the winter (From unpublished manuscript by Magnuson, J. and B. Petrosky).

photoperiods and acclimation temperatures (Beitinger and Magnuson 1976; Beitinger 1977). Thus, in a control lake which did not experience marked oxygen depletion, the bluegill went to the bottom of the net enclosure and remained in the warmest water all winter as expected. However, in Mystery Lake as the oxygen was depleted from the bottom water during winter, bluegill moved toward the surface and occupied colder water, remaining in water with dissolved oxygen concentrations of at least 0.5 mg/L. A behavioral response to the oxygen concentrations maintained the bluegill in a liveable habitat even though the temperature was far from preferred. When dissolved oxygen was depleted under the surface of the ice, all fish in the enclosure died.

A serious problem in evaluating the influence of multiple factors acting simultaneously on a fish's habitat preference is that of determining how the fish weighs the different habitat axes with respect to each other. In the above observation on oxygen and temperature, the fish gave more weight to dissolved oxygen less than 0.5 mg/L than to temperature less than 3°C. How can we scale oxygen and temperature in equivalent units with respect to the fish's behavioral response to them? Ecosystem ecologists, by standardizing the great diversity of food eaten in terms of energy units, i.e., calories, provided a simplification helpful in understanding trophic ecology. Distributional ecology and fishery oceanography also need a way to treat habitat axes in equivalent units. At present, the axes are the traditional "apples and oranges" and have units such as °C for temperature, mg/L for dissolved oxygen, newtons/cm^2 for pressure, etc. We suggest two approaches to this problem of scaling habitat axes.

One approach is to express each variable as a function of the fish's behavior and in the common units of one variable. For example, oxygen levels could be expressed as the number of degrees centigrade a fish will depart from its preferred temperature to avoid, or the food density or ration could be expressed as the number of degrees centigrade a fish will depart from its preferred temperature to obtain. Neill and Magnuson (1974) found that bluegill would expose themselves to temperatures of about 5.5°C below their preferred temperature to obtain a ration equal to 4% of their body weight per day. Thus, the density of food required to produce a 4% ration is equivalent to -5.5°C. There are some serious experimental problems with this approach and it would be easiest to do for a series of abiotic variables. Someone should try it!

A second approach is the scaling used by some psychologists in dealing with human preferences. Organisms are required to choose between alternative stimuli; multivariate statistical approaches not unlike ordination, principal components analysis, and factor analysis are used to weight each factor's influence on preference. Statistical approaches are discussed in Coombs (1964). To our knowledge this approach has not been applied to fish habitat preference.

Problems of scaling multiple axes of habitat preference are not trivial. A general solution or even the development of an acceptable conceptual framework would be a major advance to predicting the distribution of fishes. Perhaps it comes back to our three premises, and in particular the inherent difficulty we have in perceiving the perceptual world of fishes.

We have drifted some distance from the matter of immediate concern, namely the application of information on habitat preference to increased efficiency of capture and culture fisheries. Fishery oceanography, of course, is applied already. Distributions of fishes are predicted from sea surface temperatures and sea surface temperature charts are made available to fishermen for directing their search.

Other applications that seem feasible at present are to locate new concentrations of fishes by searching for the locations of subsurface thermal fronts that would not be visible from satellite imagery or surface temperature records. Towed midwater or bottom thermisters or thermisters attached to trawls could help direct subsurface fishing near the subsurface fronts. The use of selective fishing based on temperature preferences of fishes could help concentrate effort on target species and reduce overexploitation of specific species, or even reduce disoperation between sport and commercial fisheries.

Temperature preference information could be used to stratify the habitat for stock assessment research by fishery agencies. Assessment could be restricted to the preferred habitat or the preferences could be used to help allocate biomass estimates from acoustic assessments to specific species or communities of fishes.

In culture fisheries, laboratory derived preferences could be used to rapidly estimate habitat characteristics that would be expected to be optimum. The approach could be used in screening new species for aquaculture to match them with the temperature, oxygen, and salinity characteristics of specific aquaculture ponds or sites.

In conclusion, fishery oceanography is presently being applied to many fisheries and depends on correlative data. Further applications and increases in efficiency can be expected as methods of predicting fish distribution in complex habitats are developed from laboratory and field experiments on the actual preferences of the fish.

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Discussion

BLAXTER

It is quite common in experimental preference experiments to find preferred conditions which are outside the ecological range, for example a salinity of 40° ‰. It seems dangerous to me to apply such results to the movements and behavior of fish under natural conditions.

MAGNUSON

There are many explanations for fishes living outside their preferred range, but explanations for this can be built into the experiment and the expectations. Bluegill, if given a choice between two temperatures, always choose the one closest to their thermal peferendum. If the final preferred temperature does not happen to be present in nature, our prediction would be that they occupy the closest available temperature to it. The fact that bluegill choose temperatures in the laboratory that are warmer than normally found in the field leads to an expectation for the behavior which actually occurs in a lake. They have a strong tendency to occupy the warmest part of the lake—the littoral—in summer, deep water in winter. Eventually, laboratory-based predictions will have to be multifactored, as I indicated in my presentation, and there must be interactions among factors.

One reason I put my third premise forward—that laboratory-based (experimental) fishery oceanography is more efficient than field-based (survey) fishery oceanography—is the difference between the relative costs of each. One hundred thousand dollars can produce a significant amount of experimental work; certainly it can support one to two professionals and staff for a year, but it can support a major vessel for only a month or two. In area the size of the Pacific it is impossible to survey a significant portion on a regular basis; thus, even reasonable approximations of distribution from laboratory studies could be a big help.

HARDEN JONES

Some care should be taken when interpreting an apparent relation between the distribution of fish and an environmental factor, such as temperature, in terms of preference. The autumn and winter cod fishery at Bear Island provides an example. Following the lead of Canadian work, the temperature-fish (T/F) studies made in the 1950s by the Lowestoft Arctic Team, led by Michael Graham, showed that paying catches of cod were not usually made in water of less than 2°C. There was some suggestion that 2°C was associated with an osmoregulatory failure and that fish avoided the colder water. It now seems clear that the 2°C isotherm usually marked the boundary, or front, between warm Atlantic (4 to 5°C) and cold polar 0 to 1°C) water masses. In winter and in autumn, the best catches of cod, up to several tons for a 1-h tow were made where the thermal change was most pronounced, the 2°C isotherm invariably marking the steepest part of the gradient. The cod were piled up on the warm side of the front, and the front itself appeared to provide the concentrating factor; the behavioral mechanism involved could have been a kinesis or more likely, a klinotaxis, the fish responding to sequential changes in temperature. Personally, I have never found that the concepts of preference or preferendum make it any easier to interpret or understand the relationship between the distribution of fish and the properties of the environment; on the contrary, the concept of preference may mask the underlying behavioral problems.

MAGNUSON

It is difficult from field data to determine whether the fish respond to the gradient or to the absolute temperatures. Even if they do respond to absolute temperatures, there is a higher possibility that they will be in a front because a greater range of temperature is there.

KEMMERER

My experience is that the water on either side of a front differs tremendously in a number of characteristics, such as plankton and turbidity. It might be more appropriate to consider a front as an ecotone rather than simply an area defined by temperature readings.

MAGNUSON

Yes, I agree. There are many ecological hypotheses which should be raised in respect to the ecotones that might explain why fish concentrate there. I used temperature because it is important to heterotherms and easy to measure, but I feel very strongly that we need more multidimensional research.

The Migration of Plaice *(Pleuronectes platessa)* in Relation to the Environment

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HARDEN JONES, F.R. 1980. The migration of plaice *(Pleuronectes platessa)* in relation to the environment, p. 383-399. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Plaice fitted with acoustic transponding tags have been tracked in the southern North Sea using sector scanning sonar. Fish which moved more than 15 km during the period of surveillance used selective tidal stream transport, coming off the bottom at slackwater and staying in midwater for the duration of one tide and returning to the bottom at the next slack. Plaice moved rapidly over the ground when in midwater on one tide and very little, or not at all, when on the bottom on the other tide. Midwater trawling experiments along the lines of the migration routes of plaice in the Southern Bight of the North Sea showed that plaice with ripe gonads were in midwater on the southgoing tides and that spent plaice were in midwater on northgoing tides. These results suggest that selective tidal stream transport is implicated in the migratory movements. The results are discussed in relation to tidal stream paths, the entrainment of semi-diurnal (tidal) activity rhythms, maintaining the link with the transporting tide when on passage, and the recognition of the spawning area or ground. Groundwater seepage is suggested as a local landmark to identify the spawning ground and this new hypothesis is discussed in relation to the nursery and spawning grounds, and the problems of imprinting in marine species with pelagic eggs and larvae.

Introduction

Migrations raise many problems, particularly with regard to the control and timing of the seasonal movements, the behavior of migrants on passage and the recognition of the spawning area or ground which is probably identified by local landmarks: the latter could be fairly described as pilotage. There are good reasons as to why we need to know, and understand, a lot more about such matters. Some knowledge of the migratory movements of a stock is generally needed for the successful management of the fisheries it supports: without this information it may be difficult, if not impossible, to assign catch and effort statistics to a particular unit stock. While the geographical extent of the migration circuits are related to regional current systems, the causal link between the water movements and those of the fish are not yet known. The main ocean currents respond to long- or medium-term climatic changes. For example, the periodic changes in the volume transport of the cold East Greenland current appear to have affected the migratory circuits and perhaps the abundance of the Greenland-Iceland cod and the Atlanto-Scandian herring (Jacobsson 1969; Dickson and Lamb 1972; Dickson and Lee 1972). A better understanding of the role of environmental factors in relation to fish migration might allow a degree of prediction which could, in the medium term, be used to vary fishing strategy to avoid irreparable damage to a stock and to reduce hardships in the industry. Furthermore, environmental changes could affect the identification of the spawning areas or grounds. We know that chemical stimuli are important for home stream recognition by salmonids and this may be true for other species. The chemical signature could be written by the local watershed in fresh water, estuaries, and fjords; and by specific benthic communities, or bottom deposits, in the open sea. The signatures could be disrupted by man-made activities of which deforestation, large-scale water transfers between rivers, chemical discharges and dumping, gravel dredging, and mineral extraction are obvious examples.

My contribution should be set against this background and the need for a greater understanding of the migrations of fish: it is, in part, a summary of recent work carried out at the Fisheries Laboratory, Lowestoft, and an account of our ideas for the future.

Movements of Plaice in the Sea

Hypotheses to account for migration range from random movements—arrival depending on chance—to directional movements involving orientation to temperature gradients at fronts, water currents, geomagnetic fields, or celestial bodies. A factor common to all such hypotheses has been the lack of data on how fish move from one position to another. Some progress is now being made with the use of tracking techniques to follow fish in fresh water and in the open sea. At Lowestoft, plaice *(Pleuronectes platessa)* fitted with 300 kHz acoustic transponding tags have been followed with high resolution sector scanning sonar. Fish released off the East Anglian coast have been tracked for periods up to 54 h and over distances up to 61 km. The tracking technique enabled a fish to be positioned to within ± 2.5 m in range and 1° in bearing from the research ship, whose position was determined by reference to the Decca navigator system with a maximum variable error of ± 45 m by day and ± 90 m by night. A facility for elevation (vertical) scanning allowed the depth of the fish to be determined to within ± 2.0 m. After release a fish was kept under continual surveillance and a complete record of its movements was reconstructed from the sonar data recorded during the track. Plaice which moved more than 15 km usually came off the bottom at slackwater, moved downstream with the tide in midwater, and returned to the bottom at the next slackwater. When on the bottom the fish showed little or no movement during the opposing tide. Full details of this work are given by Greer Walker, Harden Jones and Arnold (1978): one example will be given here.

A plaice released off Southwold was tracked for 26 h during which it moved 43 km to the north. The track chart (Fig. 1) shows that the fish gained ground to the north during the northerly tide and that there was little movement on the southerly tide. The fish came off the bottom just after highwater slack and stayed in midwater during the northerly tide until it returned to the bottom at the next slack (Fig. 2). The semi-diurnal (12-h period) vertical movements were clearly related to the tidal cycle. Many of the plaice tracked moved slowly through the water when off bottom and rarely exceeded speeds of one body length s^{-1}. The regular pattern of behavior, which we have called selective tidal stream transport, could provide an energy-saving transport mechanism for migrating fish on the continental shelf where the tidal streams are relatively strong.

Plaice in the Southern Bight of the North Sea

We have extended this idea to migratory fish in the North Sea, and in particular the plaice, of which there are four stocks which spawn off the Scottish east coast, Flamborough Head, and in the German and Southern Bights, respectively. The Southern Bight stock spawns in winter and in November and December mature plaice move southwards from the Dogger Bank towards a spawning area bounded by latitudes 51°30-52°00'N and longitudes 2°-3°E. Peak egg production is in January and the spent fish return to the northerly feeding area in January, February and March. Meanwhile the pelagic eggs and larvae drift to the north and northeast with the residual current. In late spring and early summer the metamorphosed "postage stamp" size plaice can be found on their nursery areas in the coastal waters of the Southern Bight; some fish reach English waters but many are carried towards the continent by the residual northeasterly current and subsequently enter the Dutch

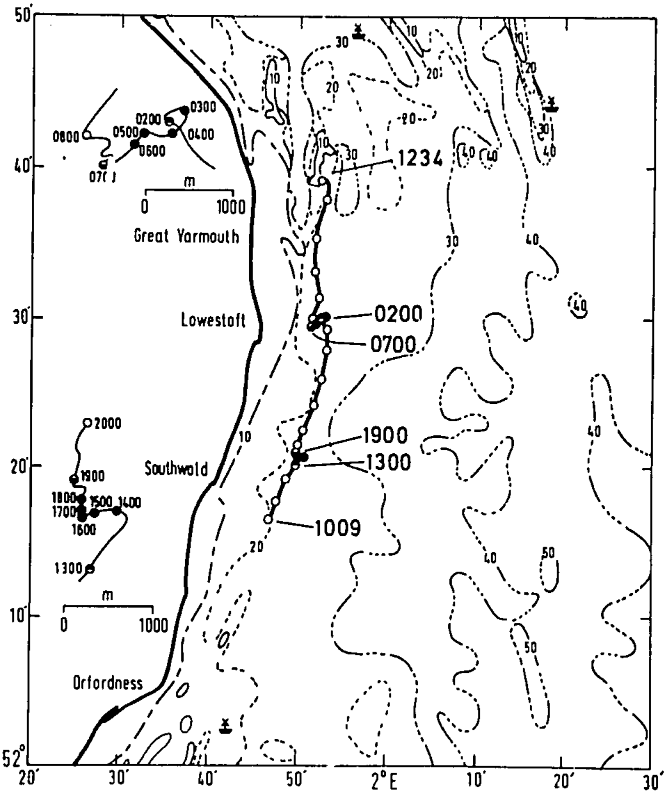

FIG. 1. Track chart of a plaice, 41.0 cm long, released off Southwold at 1009 h GMT on 12 December 1971. Hourly positions of the fish are indicated and the times of slackwater are given. Key: ○, northgoing tide; ●, southgoing tide; ●, low water slack; ○, high water slack. The inset figures show details of the track during the southgoing tides at the scales indicated. Depth contours in meters.

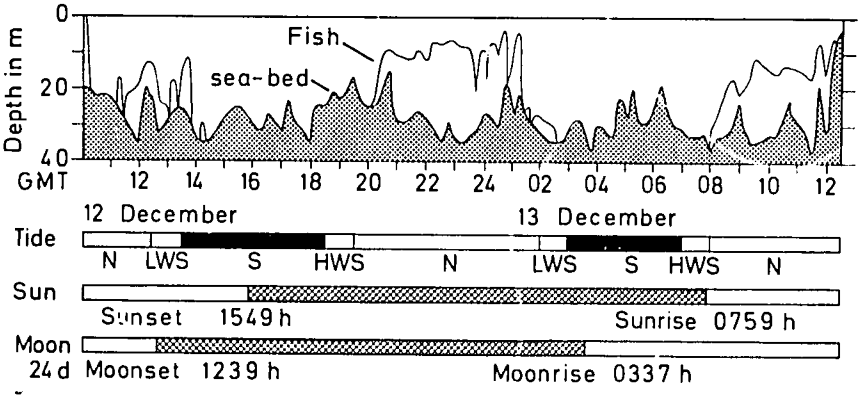

FIG. 2. The depth of the plaice tracked off Southwold in relation to the direction of the tide and other environmental factors.

Waddensee. From summer depths of 2-3 m, the plaice move to deeper water in autumn and return to shallower water the following spring and early summer. There is an overall movement to deeper water in their second and third years of life. Some of the larger plaice, mostly males, come to first maturity in their third year of life, joining the mature fish of earlier year-classes on the spawning grounds towards the end of the season. After spawning, both first-time and repeat spawners migrate to northerly feeding grounds. Most of the remaining immatures spawn for the first time the following year and recruitment to the mature part of the stock in then almost complete. Plaice spawn annually until they die, but with the present levels of exploitation an individual would be fortunate to enjoy 10 consecutive spawnings.

Migration by Selective Tidal Transport

If the Southern Bight plaice use selective tidal stream transport when migration, the mature and ripe fish should be midwater on the southgoing tides when moving towards their spawning area during November and December. By the same token the spent fish, when returning to their feeding area in January and February, should be in midwater on the northgoing tides: there should be a complete reversal of behavior. We tested this prediction by fishing in midwater along the line of the migration route off the East Anglian coast in autumn and in winter. A comparison was made between the catches of plaice taken in pairs of midwater hauls on consecutive north- and southgoing tides. The results, which were surprisingly clear-cut, are summarized in Table 1. Selective tidal stream transport does seem to be implicated in the migratory behavior of plaice in the Southern Bight of the North Sea: a full account of the trawling work will be published later (Harden Jones et al. 1979).

TABLE 1. A comparison between the catches of plaice made in a midwater trawl on consecutive northerly and southerly tides in the Southern Bight of the North Sea from November 1974 to February 1977.

Season	No. of paired hauls	Comparison of catches		
		Greatest on		Equal
		Northerly tides	Southerly tides	
Autumn	39	5	33	1
Winter	22	21	1	0

Tidal Stream Paths in the North Sea

If plaice use the tidal streams for transport when on migration, the distribution of the stocks and their movements might in some way be related to the lines of tidal flow. A tidal stream path chart for British coastal waters can be constructed (Harden Jones, Greer Walker and Arnold 1978) using the data given in chart 3 of the Rostock Atlas (Anon. 1968). The stream paths (Fig. 3) indicate the lines of maximum tidal flow and give the routes along which fish could move round the British Isles by selecting the appropriate tide. The stream paths along the east coast of England clearly link Scottish plaice with those of Flamborough, the Southern Bight and the English Channel: here the expected movement would be north and south. By contrast the plaice of the German Bight would appear to be contained within a separate system where the expected movement would be largely east and west. The tidal stream paths in the North Sea recall the migration patterns for herring which have been deduced from tagging experiments and the movements and catch of the fishing fleets; the fit with the supposed migrations of the Downs

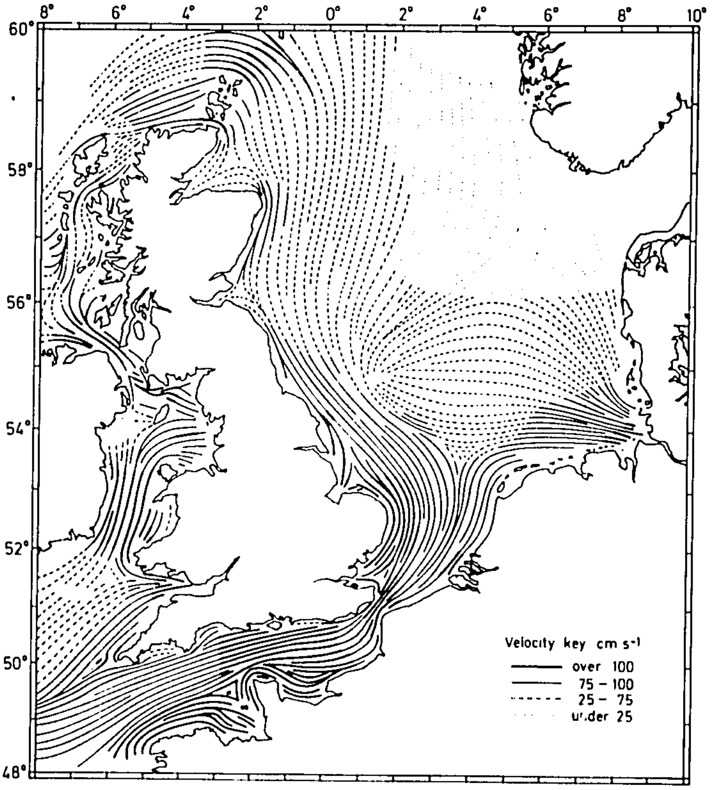

FIG. 3. A tidal streampath for the North Sea and adjacent waters constructed from data given in chart 3 of the Rostock Atlas (Anon. 1968).

herring, which feed in the northern North Sea and spawn in the Channel, is particularly striking (see Harden Jones 1968, Fig. 40). Other aspects of the stream path chart, with particular reference to the directivity of the tidal ellipses and tidal velocity, are discussed elsewhere (Harden Jones, Greer Walker, and Arnold 1978). The tidal stream path chart is of interest when considering the distribution of those stages in a fish's life history whose behavior allows them to select one tide rather than the other: when no choice can be made the relevant chart is that of the residual currents with which the pelagic eggs and early larval stages must surely drift passively.

Problems Raised by Selective Tidal Transport

Weihs (1978) has argued that selective tidal stream transport could save energy on migration: the energy cost to cross a given distance could be reduced by up to 40%. Furthermore, tidal transport could provide a substitute for navigational ability. But migrants will not be able to realize these potential advantages unless they can "lock-on" to the appropriate tide at their initial position, hold the transporting tide during the migration, and leave it on arrival at their destination.

The *initial "lock-on."* To use the transport system, a fish must join the appropriate tide which will take it from the feeding area to the spawning area. For the plaice which spawn in the Southern Bight of the North Sea, the initial "lock-on" to a southgoing tide could arise from the interaction between the diurnal (24-h period) and semidiurnal (12-h period) activity rhythms (Verheijen and de Groot 1967; Gibson 1937, 1976). It is possible that at a certain level of gonad maturation, a diurnal (day-night) activity rhythm—with the fish off the bottom at night—could be entrained to a semidiurnal (tidal) rhythm. But the entraining signal must be unambiguous and there must be a clear distinction between low water slack which is followed by a southgoing tide and high water slack which is followed by a northgoing tide. Intuitively one suspects that the critical period for entrainment would be limited to 2 or at the most 3 d each month when sunset, full moon, and low water slack are in conjunction (for example, see Bolster 1962, Fig. 4). Figure 4 shows the relationship between these three events for a position (53°27.5′N, 02°46.0′E) representative of the feeding area of the Southern Bight plaice. In other areas the coincident slackwater could be high water, and the following tide could carry the fish in other directions. It would be interesting to look at the relationship between sunset, full moon, slackwater, and the direction of the following tide in North Sea and British coastal waters throughout the year. The data could be summarized on 13 "entrainment charts," one for each of the year's full moons. Such charts would show the positions where the co-sunset lines (that is, lines joining positions where sunset occurs at the same

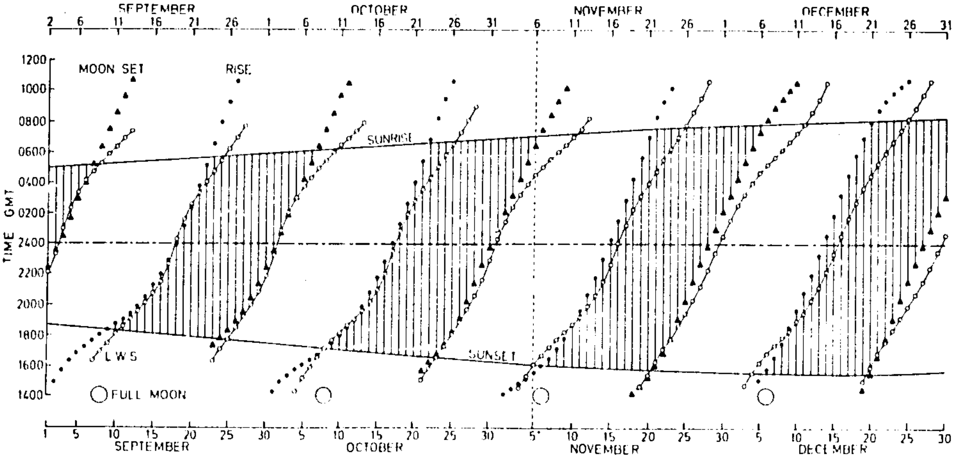

FIG. 4. The relation between sunset, full moon and low water slack for a position representative of the feeding area of the Southern Bight plaice. Key: ○, full moon; ▲, moon set; ●, moon rise; ○, low water slack. The vertical lines indicate the period between sunset and sunrise during which the moon is not visible. Note that sunset, full moon and low water slack are in conjunction at or about 8 September, 8 October, 5 November and 5 December. Data are from a nautical almanac for 1976 for the position 53°27.5′N, 02°46.0′E, and drawn from a figure prepared by Mr. P. Scholes.

time) intersect the relevant co-tidal lines for high or low water slack on the nights of the full moon. Fish so entrained to a semidiurnal pattern of vertical movement will then move or be carried along the tidal stream paths, the direction of migration depending on the direction of tidal flow following the coincident slackwater. How does the "entrainment pattern" fit in with what is known of the timing of the migratory movements, migration routes, and spawning seasons of the fish stocks in different areas?

Maintaining the semidiurnal rhythm. Some behavioral mechanism must maintain the semidiurnal pattern of vertical movement so that the fish repeatedly join and leave the appropriate tide when on migration. Ascents are more closely related to slackwater than descents (Greer Walker et al. 1978), and descents are often preceded by excursions to the bottom. These observations suggest that both a rheotropic response, mediated through sight of or contact with the bottom, and a semidiurnal rhythm of activity entrained to the tidal cycle, are involved in the synchronizing mechanism. Laboratory experiments are being designed to look into these matters.

Leaving the transport system. Plaice must leave the transporting system on arrival at the spawning area or ground and it seems reasonable to suppose that some local landmark is involved. Spawning ground recognition by marine fish has seldom been studied and to stimulate discussion I want to develop the Groundwater Seepage hypothesis. The essential feature of this new hypothesis is that the assembly areas, spawning areas and grounds of marine fish which spawn in coastal waters could be identified by reference to chemicals entering the sea by groundwater seepage.

The hypothesis has some conceptual merit as it could link the anadromous species of some orders with their fully marine counterparts and provide a framework within which to interpret the evolution of migratory behavior on a time scale of the geological history of the North Sea and other basins or areas. According to the Groundwater Seepage hypothesis, plaice, herring, and other species in the North Sea and elsewhere are homing to areas where there is a seepage of groundwater on a rather small scale—for example a cluster of springs with individual flows of about 50 L s^{-1} which might be insufficient to produce more than a very local change in salinity or temperature. Such changes would be restricted to the bottom close to the spring, and if recorded, the anomalies would most likely be rejected as errors. Dr. R.L. Edwards (Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Massachusetts USA, pers. comm.) has told me of reports concerning a relict population of alewives which is said to home to, and spawn on, a particular area of Georges Bank. The Groundwater Seepage hypothesis would suggest that the fish were homing to an area marked by a submarine spring. Fresh groundwater has recently been found below Nantucket Island (Kohout et al. 1976) about 200 km from the Bank. Similarly, groundwater seepage could also be involved in the detection and recognition of island breeding grounds by the green turtle (cf Koch, Carr, and Ehrenfeld 1969).

The geological structure favorable for a submarine spring occurs when a water-bearing stratum, or aquifer (such as chalk), is exposed directly through outcrops or indirectly through faults and fissures in an overlying layer which might otherwise be impervious (such as clay): provided there is a sufficient artesian head in the aquifer to overcome the pressure at the sea floor, groundwater will discharge directly into the sea (Fig. 5). Other things being equal, in a delicately balanced situation the discharge would be greater at, or even limited to, low water slack at spring tides: there would be a connection with lunar periodicity in spawning.

Robert Stephenson, the son of George (Rocket) Stephenson, and also a distinguished railway engineer in his own right, appears to have been the first to suggest that groundwater was discharged from chalk into the sea. A well-known example occurs in the River Humber where a geological fault (Versey 1946) is associated with a number of substantial freshwater springs, the "Hessle Whelps" or "Barton Bulldogs." Boyd Dawkins (1898) mentions foreshore outlets at Flamborough Head, Woolwich, St. Margaret's Dover, Beachy Head, and between Brighton and Rottingdean. More recently freshwater discharges along the foreshore have been located by aerial surveys using infrared techniques (Davies 1973; Brereton

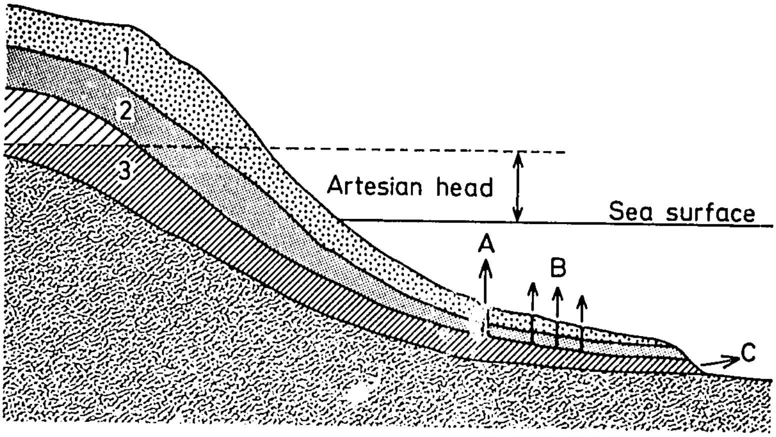

FIG. 5. Diagram to show the conditions under which groundwater could discharge into the sea. 1, superficial permeable deposits; 2, impervious layer (such as clay); 3, aquifer (such as chalk) saturated to indicate level. A, medium discharge through a pit; B, minor discharge through cracks or fissures; C, major discharge through an outcrop. An artesian head of about 3 m would be sufficient to allow fresh groundwater to enter the sea at depths of 100 m (density of sea water 1.026).

and Downing 1975). The success of this method depends on the temperature difference between the groundwater and the sea; the groundwater has a temperature of about 10°C which is more or less constant throughout the year, so the discharge would be warmer than the sea in winter and colder than the sea in summer. But Boyd Dawkins (1898, p. 264) considered that "outlets on the foreshore probably are insignificant compared with those which may reasonably be expected to exist beneath the level of the sea where they cannot be examine." And there the matter appears to have rested.

Under the Southern Bight of the North Sea the chalk is covered by London clay and a layer of superficial deposits. Although there are depressions and tunnel valleys in the area (D'Olier 1975) it is very unlikely that the chalk is exposed as an outcrop. But there may be faults and fissures in the clay which would provide routes for groundwater seepage. While the chalk could be a source of groundwater seepage under the sea in the southern and eastern regions of the British Isles, karstic drainage from limestone is a likely source in other areas, for example in Morecambe Bay (Ashmead 1974) and Galway Bay (Tratman 1969), and off the coast of South Wales. But so far as I know a systematic search for low salinity bottom water has not yet been made in any British coastal waters. But freshwater discharges certainly occur: Mr. G.R. Forster (The Laboratory, Plymouth, pers. comm.) has told me of a freshwater spring he found while diving in the Tor Bay area; and in 1950 Dr. L.H.N. Cooper (The Laboratory, Plymouth, pers. comm.) collected anomalous low salinity bottom samples on the Nymphe Bank (southeast Ireland) which were thought to indicate groundwater seepage. However, groundwater seepage is documented elsewhere (Anon. 1916; Marchand 1928; Kuenen 1955; Emery and Hulsemann 1963; Kohout 1966a,b; Buljan and Zore-Armanda 1976) and in particular in the Atlantic coastal waters of the southern United States (Manheim 1967; Manheim and Sayles 1974). Furthermore, groundwater seepage has long been known to mariners who have used submarine springs to take on board fresh water in the open sea. One such spring occurs off Bahrain in the Persian Gulf and was described in 15th century Sailing Directions by the Arab navigator Ahmad ibn Majid, sometime pilot to Vasco da Gama (Tibbetts 1971, p. 222). A spring used by sloops and schooners occurs off the volcanic island of Saba, 70 km northwest of St Kitts, in the West Indies (Benest 1899, p. 400).

In suggesting groundwater as an attractant for migrants, I am of course following the well-known hypotheseis that chemical stimuli, detected through the nose, are implicated in the return of salmonids to their home rivers. Hasler (1966) is the foremost exponent of this hypothesis which has been confirmed by the recent experiments carried out by his group (Cooper et al. 1976; Hasler and Scholz, this volume). But the naturally occurring chemical attractants have not yet been identified; and the relative contributions of the watershed and resident stream fauna and flora to the chemical signatures of the streams or tributaries have not yet been determined.

There is no evidence that a similar mechanism is involved in the selection of spawning areas or grounds by marine species such as herring, plaice, or cod. But it is likely that some landmark of local origin is implicated if only because fish spawn at one locality rather than another. Herring lay demersal eggs in restricted areas and often on sand or gravel banks free from weed. The pelagic eggs of other species are more widely distributed than those of herring. But recent surveys carried out in the middle and southern North Sea under the direction of Mr. D. Harding (Fisheries Laboratory, Lowestoft) suggest that for some species (plaice, cod, sprat, dab, and gurnard) peak concentrations of eggs only a few days old are often associated with features of bottom topography (ridges, pits, or banks), suggesting that spawning itself may be more localized than has hitherto been supposed. While the spawning grounds of some marine fish could be recognized by chemical substances released from particular benthic communities, there is also the possibility, particularly in coastal waters, that they could be on or close to areas where there is groundwater seepage through the seabed; Hasler's theory would thus be extended to the sea.

There are several ways in which this problem could be pursued: examination of old Sailing Directions and charts; a study of echo sounder records to locate pits, depressions, and other topographical features of the seabed in areas where marine species are known to spawn; a search among hydrographic records for anomalous temperature and salinity observations; and the development of a towed bottom-sampling sledge, or pipe-and-pump apparatus, to give on-line measurements of temperature and salinity—the search is for transient anomalies.

If simple methods such as salinity and temperature determinations provide evidence for groundwater seepage at assembly or spawning areas, more sophisticated analyses could be used to identify the elements or compounds characteristic of the groundwater from local aquifers. Imprinting itself is an interesting problem and I have always found it difficult to understand how the salmonid system of imprinting and homestream recognition could be applied to marine species, particularly those with pelagic eggs and larvae which will be carried quickly away from the spawning ground in the residual current. The young plaice larvae, which hatch from pelagic eggs, must have even less opportunity to become imprinted than the pink salmon which have a short enough period of freshwater residence.

Professor Hasler has made the point that in salmonids, imprinting is still effective in the smolt stage, which is relatively late in the life history. Could the same be true for plaice? Is it possible that groundwater from the same aquifer could be present both on the inshore nursery area and on the spawning area? Some of the areas of foreshore seepage named by Boyd Dawkins have substantial populations of 0-group plaice, and chalk lies under the beaches and the seabed in deeper water offshore. Let us suppose that the imprinting of plaice is delayed until the "postage stamp" stage and that they are sensitized to some substance in the local groundwater which enters the sea close inshore. The 0-group fish leave the shallow waters at the end of their first summer, and it is possible that they would not come across the chemical substance to which they had been originally imprinted until they were carried by the tidal transport system into the immediate vicinity of the spawning area. Spawning area and nursery area would thus be related not only geographically in terms of larval drift and the residual current, but also in terms of geological structure and groundwater.

The first step towards substantiating the Groundwater Seepage hypothesis would be to identify fresh water on the spawning grounds and perhaps on the nursery grounds. If some of you are sceptical about the whole idea, let me say that I, too, have some doubts. But it is a line of approach which could be followed up and there is always a chance of being graced with a moment of serendipity. For example, I was very surprised to learn that the marine coelocanth *Latimeria* is believed to inhabit caves into which there is a seepage of fresh water (Foster 1974).

Acknowledgments

I am grateful to my colleagues at the Fisheries Laboratory, Lowestoft for their comments on this paper, and to all those who have kindly helped me with my inquiries on groundwater seepage and in particular to Mr. Keith Clarke, Chief Engineer, East Anglian Water Company.

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Discussion

LILEY

You suggest that the fish must be reacting to an outflow of fresh water from the seabed. Why do you suggest that in the first place? Why can't they just "recognize" and react to regions of the seabed suitable for spawning?

HARDEN JONES

The groundwater seepage hypothesis allows marine species with pelagic eggs and larvae to recognize the parent spawning area by an imprinting mechanism similar to that of the salmonids; this is probably the main reason why I developed it. Alternatively, the spawning area could be recognized innately, as, for example, elvers respond to inland water which they have never previously experienced.

HASLER

Is there a way to seed an inland aquifer with a tracer flowing seaward?

HARDEN JONES

There may be problems in adding radionuclides to groundwater. In the first instance, anomalous concentrations of naturally occurring heavy metal ions, such as lead and zinc, might provide clues to submarine seepage.

FISHELSON

If there is fresh water, you should find a characteristic bottom fauna and flora around this seepage. For example, in coral reefs, you sometimes find brackish water in cracks with blind shrimps and other organisms in the vicinity. You find a lot of *Valonia,* for instance. I think that *Valonia* is a euryhaline alga that prefers some brackish water. So maybe you should look at the benthic fauna around those breaks, look for indicators of the fresh water.

HARDEN JONES

I agree that pockets of exceptional benthic fauna should become established in the vicinity of submarine springs, and your suggestion of freshwater indicator species is useful.

HASLER

Have you tried tracking fish over the grounds after depriving them of their sense of smell?

HARDEN JONES

No.

MURPHY

I don't know if it is true with plaice, but some fish can detect very, very small changes in salinity.

HARDEN JONES

The threshold level for response to a salinity change, as determined by conditioning experiments, is 0.5°/oo in 30-34°/oo.

HENDERSON

Is there no surface indication of freshwater underneath? The aquifer off the Italian coast that you have marked as a stream of fresh water on the surface that swimmers particularly enjoy.

HARDEN JONES

Apparently not.

REINBOTH

When you are talking about the influence of the tides upon the behavior of the fish, what do you mean? What does it mean for the fish? Is it mainly a question of the currents?

HARDEN JONES

Tide means tidal height and tidal stream means flow. I am talking about flow; but if the fish is responding to the flow, the clue may not be simple. It could be a direct flow over the body of a fish resting on the bottom; a visual or tactile clue such as turbulence or sediment load; or even some form of induced electrical current.

KEMMERER

Do fishermen change fishing tactics to take advantage of the fish's being on the bottom or in the water column?

HARDEN JONES

There are diurnal variations in catch rate that reflect the accessibility of the fish to the gear, day catches often being better than night catches, although the sole is a notable exception. In some sets of data, semi-diurnal (tidal) variations are evident, but the haul-to-haul variance is often too high to allow one to see such effects.

BARDACH

Assuming that fresh water is the indicator of a spawning site, what would be associated with a freshwater spot in the sea to make it such a good spawning site?

JOHANNES

It's hard for me to see why, if these plaice had the time to make a major evolutionary step from anadromy to a strictly marine existence, they wouldn't also have modified their reproductive strategy during that same period unless there was still some selective advantage in migrating to areas of freshwater influence.

HARDEN JONES

The selective advantage could be related to the survival of the young in the first year of life when mortality is the highest. If the nursery area is positioned within a critical range downstream of the spawning area, the fish may have to show a degree of consistency and conservatism with regard to spawning and nursery area, so that the young stages or eggs are positioned so they are swept by the currents into an area where they survive. But it could be advantageous to have greater flexibility with regard to the area over which adults feed, as the food supply must be reflected in both the relative and population fecundities.

MAGNUSON

Certainly young birds are not imprinted on their wintering grounds before they fly south. Why not hypothesize that the location of the site is genetically fixed? If those animals that home back to a certain location have higher reproductive fitness, then you don't need to postulate imprinting.

HARDEN JONES

Your suggestion that the spawning ground clues used by different stocks are recognized innately is surely incompatible with the fact that there are no genetic differences between the North Sea plaice stocks. Baby plaice from the different stocks probably mix (at rates greater than 1%) in the various nursery areas: this is one of the consequences of larval drift. If the young plaice are imprinted at this stage, in their first year of life, stock identity is then established. I would suggest that imprinting at a relatively late stage, on the nursery ground, is the only way to establish stock identity against a background of relatively high mixing rates.

LILEY

Is there any information as to just how localized the spawning areas are? Are we talking about the fish getting back to one square km of area, or are we talking about 50 square km? If we're going to follow this analogy with pink salmon, we're talking about fishes going back to the various streams from which they were derived originally. Are we just talking in this case of a large area that would be suitable for spawning?

HARDEN JONES

The herring has demersal eggs and these can be sampled by grab. The spawning beds are small, perhaps 300 m long and 50 m wide. Delimiting the spawning areas of fish with pelagic eggs, such as cod and plaice, is a more difficult problem. But the areas over which pelagic eggs are spawned may cover several km^2.; in other words they are probably substantial, whereas those of the herring are small.

JOHANNES

Has anyone ever shown that fish eggs, as distinct from larvae, can be imprinted?

HASLER

Nobody. We don't know anything about eggs. I suspect that chum salmon must imprint very early in life if they imprint at all, but all our data are on coho salmon which don't imprint early.

HENDERSON

Given the hypothesis, depletion of these aquifers by use of the water inland could have important consequences for these marine stocks. I wonder if it's also worthwhile thinking of some of the catadromous species that spend part of their life in freshwater, perhaps like the milkfish. We still do not know much about where it chooses to spawn, but it looks as if it might be in areas where there might be subsurface springs of the same water as occurs in their freshwater home.

MURPHY

What do you do with a catadromous fish like *Lates*, that in some cases comes down from freshwater and migrates 112 km on the coast and spawns and the young go back to the stream?

BARDACH

It's possible that there is freshwater seepage there, too.

HENDERSON

Perhaps it is their water that they find 120 km south.

Schooling and the Ecology and Management of Marine Fish

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MURPHY, G.I. 1980. Schooling and the ecology and management of marine fish, p. 400-414. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Schooling can be shown by theory and observation to reduce predation mortality by natural predators. An important element in the protection is satiation of the predators and the optical qualities of sea water which make it nearly as difficult to sight a school as a single prey. Fishing operations nearly negate those advantages as aerial scouting and sonar (water is more transparent to sound than light) provide for efficient location of schools, and fishing vessels particularly as they have good intercommunication, do not satiate readily. In at least one instance (the passenger pigeon) the evolution of large aggregations has been accompanied by adjustments of life history parameters such that the degree of density-dependent reproductive resilience was reduced to the point at which a small population could not persist. Similar phenomena have been proposed for fish populations but the details have not been identified.

Introduction

The purpose of this paper is to review bio-social aggregations rather broadly with particular reference to the significance of aggregations to the management of such species. It is widely appreciated that aggregations, especially schooling, allow the use of very efficient harvest methods, raising the possibility that such fish might be more prone to various types of overfishing. If we assume that schooling has evolved and persisted because it enhances the probability of survival of individuals and hence the species for whatever operational reasons, the corollary of schooling might be a weakening of other mechanisms that operate in a density dependent way to ensure population survival in the face of enhanced mortality. Thus on a priori grounds it can be hypothesized that schooling organisms are peculiarly susceptible to exploitation. It will be shown that this is indeed true.

Bio-social aggregations are widespread throughout the vertebrates. There are schools of fish, flocks of birds, and herds of ungulates. These spectacular phenomena have attracted a great deal of attention from biologists and behaviorists. Unfortunately most of the work has been directed towards understanding the organization of the aggregations, the ways they are formed, and the mechanisms that retain them. That is to say that most of the effort has been directed towards understanding the aggregation itself although Breder's (1967) is an important exception. In contrast, perhaps the more important aspects of aggregation are its evolutionary and ecological implications, for it is these that are of paramount importance to the management of the marine fish. A more general review of schooling is that by Radakov (1973). In the course of the paper I refer to bird flocks, showing that there is quite good reason to believe that the evolutionary advantages of schooling are also applicable to flocking.

Before discussing schools, it would be well to define what is meant by a school. Rather than attempt my own definition, I will simply quote the definition agreed upon at the 11th International Ecological Congress at Rennes, France, as reported in Shaw 1970, p. 476 ". . . a group of students of schooling behavior discussed the designation of the terms 'school' and 'aggregation'. They agreed that the term school should be used to designate any grouping of fish that is a result of bio-social attraction among the fish. To differentiate the way in which the fish are oriented to each other, the term 'polarized school' signifies a group showing parallel orientation. There are gradations in the degree of polarization. Orientation within a school varies during a typical day such that schooling fish may not be polarized continuously.

The word 'aggregation', then, should not be used when referring to fish that are socially attracted to each other. It could still be employed to indicate that fish come together as a direct response to extrinsic conditions or when there is reasonable doubt as to whether or not fish are socially attracted to each other."

The Advantages of Schooling

The very existence of schools is prima facie evidence that they confer a net selective advantage, and as might be expected, some studies have shown the nature of these advantages. This does not, however, explain how schooling originated in the first place. Williams (1964) believes that schooling evolved from aggregation and that the original school was simply the total of the desire of individual animals to seek shelter in an otherwise featureless environment. The featureless environment is, of course, the pelagic open-water realm. Williams holds that the regularities and the properties of schools are those of statistics, not of a functional organization as a whole. Subsequent studies have refuted this latter argument, but so far as I know, Williams' hypothesis is the only reasonable explanation of the beginning of schooling. Once schooling was established, the normal processes of evolution might lead to the development of social responses that would enhance the survival value of the schooling.

Schooling and feeding

With respect to schooling and feeding, the basic observation is that schooling fish are regularly observed to feed while maintaining the integrity of the school, although in many instances its geometry is altered. Conversely I know of no instances where schools have been observed to disintegrate during feeding. However, it has not been shown either experimentally or by observations in the field that schooling generally results in more efficient feeding than non-schooling feeding, except in one instance, and that study involved birds. For this reason many of the feeding phenomena observed with respect to schooling might be adaptations to overcome the feeding disadvantages of schooling rather than as proof of a clear-cut advantage to schooling.

One of the most direct observed advantages of schooling was reported by Hiatt and Brock (1948). They described actual herding of prey and capture by a schooling species of kawakawa *Euthynnus affinis*. Hunter (1966, 1968) has shown that schools spread out while searching. Magnuson (1964) states that skipjack tuna spread out while searching, presumably to increase the swept path of the school and employ a visual signal when prey was sighted. Similar observations have been made on the Pacific bonito *Sarda chiliensis* (Magnuson and Prescott 1966).

Sette (1950) in considering the Atlantic mackerel (*Scomber scombrus*) hypothesized that schooling increased the efficiency of plankton feeders because a prey dodging one predator would fall victim to another. Presumably this would require a rather compact school. Eggers (1976) using the Holling disc equation (Holling 1959) as a basis for a theoretical study showed that planktivorous fish predators should feed less efficiently when schooled. This is an intuitively reasonable suggestion, but its results apply only to particulate feeding and not the presumably more important filter feeding. In any event the result would be important only if it could be shown that schooling fish obtained inadequate rations.

A most stimulating study with respect to feeding is that of Cody (1971). Cody studied finch flocks in the Mohave Desert. His observations led to two hypotheses, the first involving nonrenewable resources, in this case plant seeds which, in the time frame of a season, are nonrenewable. He observed that when the toyon berries were consumed by individual birds, the numbers of berries on the bush were still significant when the density of berries was so low that the food was not available. Hence food was wasted. He then reasoned that flocking observed in the Mohave Desert is a selective response for maintaining as much feeding area as possible untouched by foraging birds; conversely, a flock will completely clear the visited area of food. The same area visited by individual birds would not yield as much food, because as in the case of the toyon berries, at some level the food density would be too low for economic foraging. In support of this hypothesis Cody observed that in years of low food supply, flocking was very pronounced. In addition flocks were larger and more readily found progressively farther from the mountains as food became scarcer. During a subsequent year the food supply was unusually abundant in relation to the numbers of birds; and flocks, as previously observed, simply did not form. The possibility that feeding schools more effectively clear a volume of water was not considered by Eggers (1976).

These observations with respect to flocks are analogous to some human activities. For example in some places, it is more economical to clear-cut a forest area rather than selectively harvest the prime timber. Another example is so-called pulse fishing which has been suggested by some workers as an economical way of harvesting demersal resources. In this type of fishing a fleet of vessels clears the fishing ground of all of the catchable species and moves on with no regard to overfishing or yield per recruit. At some later date when the area or ground has recovered the fleet will return. In this way fishing fleets are always fishing "virgin" grounds.

Schooling and predation

A number of authors have suggested that schools reduce the impact of predation. For example Allee et al. (1949) held that schooling reduces the total area exposed to attack or produces a confusion effect on predators. Presumably this results in reduction of predation.

Some authors assert that schooling or flocking reduces predation by confusing predators in much the same way as a shooter is often confused when confronted by a covey of flying quail. Clarke et al. (1967) directly observed such an effect with respect to predation on anchovies. In this case the confusion was compounded by the nature of the anchovy scales, so that when there was a predator attack, large numbers of shed scales enhanced the confusion effect.

Brock and Riffenburgh (1960) were the first to examine schooling and predation within an algebraic framework. An important element in their argument is the optical quality of seawater. In seawater objects become invisible by contrast attenuation, whereas in the atmosphere they become invisible when the angle subtended is smaller than the resolving power of the eye. The familiar analogy is the disappearance of objects in fog. In such cases the size of the object bears little relation to the visual range. Thus, though a school presents a much larger visual target than an individual fish, the sighting distance of the school is nearly the same as that of an individual fish under normal oceanic conditions. A second element is that the predator, on encountering a school, quickly becomes satiated and breaks contact with the school. Williams (1964) remained unconvinced, stating "It is encumbent on those who believe that schools are protective adaptations to show that the structure and workings of the school are such as to achieve mass protection in a functionally efficient manner." From his discussion it appears to me that Williams did not appreciate the special optical qualities of the seawater.

Brock and Riffenburgh's paper (1960) inspired Olson (1964) to apply operations research theory (Koopman 1956) to the predation problem and the mitigating effects of schooling. Olson's arguments are simpler and more elegant than those of Brock and Riffenburgh and are reproduced as follows. "According to the Koopman Theory of Search, the probability of finding a given object in an area A by a predator swimming at random with constant speed V for a time t is

$$P_a = 1 - \exp(-2rVt/A) \tag{1}$$

where r is the sight range of the predator. If the predator seeks a school of radius r', this equation must be modified somewhat. In search theory $2r$ is regarded as the width of the swept path. Since in the ocean, the visual range to a school is practically the same as to an individual fish, the equivalent swept path is $2(r + r')$. Parenthetically, if r' is several times greater than r, which is often the case, the finding of the school is not so much a matter of vision as it is just "bumping into it." The probability of finding the school is thus

$$P_s = 1 - \exp[-2(r + r')\,Vt/A] \tag{2}$$

These are the two basic equations, but to put reasonable numbers into them is another matter. There is no great difficulty with r and r', and V can be estimated to some degree, but the searched area A is practically impossible to estimate with any assurance of being correct to within an order of magnitude. The precise meaning of search time t in this situation is even more difficult to establish. It is obvious that little is to be gained by direct substitution of numbers into these equations.

But our fish knows that predators do find his school, so that the probability of doing so cannot be very small. If it is 0.5, the exponent in (2) is 0.7, thus $2(r + r')\ Vt/A = 0.7$. Assuming $r = 10$ meters and $r' = 50$ metres, $Vt/A = 0.0058$. From (1), $P_a = 1 - \exp(2 \times 10 \times 0.0058) = 1 - 0.89 = 0.11$. This is the probability of the fish being found and eaten is $p_s\ (m_e/m_f)$ where m_f is the number of fish in the school and m_e is the number of fish eaten by the predator in his attack on the school. If $m_e = 20$ and $m_f = 20{,}000$, the probability of our fish being eaten is $0.5 \times 20/20{,}000 = 0.0005$, which is substantially less than 0.11 when he swims alone."

As Olson (1964) points out, it is especially noteworthy that a simple extension of search theory will show that it is to the predators' benefit to spread out and increase their swept path while hunting. As already noted, there is some evidence that this is what predators do. Superficially this statement might appear to contradict the arguments put forward with respect to bird flocks. However, this is not the case; bird flocks have already located the food-bearing area and are simply increasing the effectiveness of gleaning along the path of the flock. Thus, Williams' (1964) comment that the theory that schooling reduces predation is not supported by quantitative evidence, is at least partially refuted.

The predation protection hypothesis has received powerful support by Major (1977, 1978). In the first paper Major concluded from direct observations of the interaction of silversides and predators that schooling was at least in part a protective response to predation. The second and more elegant study involved a facultative schooling tropical carnivorous carangid and an obligate schooling tropical anchovy. He showed conclusively that schooling reduces predation mortality and that predators when schooled increase their feeding efficiency. The human analogy alluded to by Olson (1964) was the wartime formation of convoys to reduce submarine predation and the development of "wolf pack" tactics to counter the advantage of the convoy.

Seghers (1974) provided evolutionary evidence of the way schooling can develop by studying a series of guppy populations subject to different predation intensities. Those subject to near zero predation did not school at all. Those subject to intense predation had well developed schooling. These differential traits persisted three to four generations in laboratory colonies in the absence of predators. Neill and Cullen (1974) have demonstrated that schooling of prey reduces the efficiency of cephalopod and fish predators under laboratory conditions.

Reproduction

Reproduction is considered primarily to note that a clear-cut function of schooling is ensuring adequate fertilization of eggs during spawning. Generally even species that form large schools tend to occur in smaller schools while reproducing. These schools are not readily observed directly, but from echo traces and trawl catches, appear to be in the order of tens of fish opposed to thousands in many schools.

Effects of Schooling on the Dynamics of the Population

The key assumption in this discussion is that schooling reduces predation mortality. If this is the case, and if school sizes are reduced as the population becomes smaller, then depensatory mortality (Larkin et al. 1964) will set in and the population will collapse. Clark (1974) has developed a theoretical model of this process. Three cases are illustrated in Fig. 1. In case (a) we see the usual assumed stock recruitment curve and the usual nondepensatory yield effort curve. In case (b) which may be the more realistic, there is an inflection in the recruitment curve but up to the maximum population size it is always above the 45° line. This generates what Clark terms non-critical depensation, with the yield falling to zero while the population is still reasonably large. The third case (c) is that of critical depensation because the lower left hand of the stock recruitment curve is below zero. Once the population is reduced past the critical point, it falls away to zero whether or not fishing is altered. A significant criticism of this scheme stems from raising the question of how a population gets started in the first place if its recruitment curve is below the 45° line at low numbers. A possible answer to this criticism is that schooling fishes may have evolved lowered reproduction rates after the population became large so that they are then unable to reproduce themselves at low stock levels owing to enhanced adult mortality. An avian example of this will be considered at the end of this section.

In a later study (Clark and Mangel 1978) it was shown that heavily fished schooling species such as yellowfin tuna may be subject to a catastrophic crash, depending on the schooling strategy of the population. The model that the authors used involved an available population of surface schools and an unavailable reservoir. School size is independent of population size and numbers of schools available are independent of population size. As schools are fished up, animals are quickly drawn from the reservoir so that the availability of the fish to the fishing fleet tends to remain constant. The corollary of this is that catch per unit of effort does not decline as the population declines. At a critical harvest rate the population goes into a crash unless draconian restrictions are imposed on the fishing fleet.

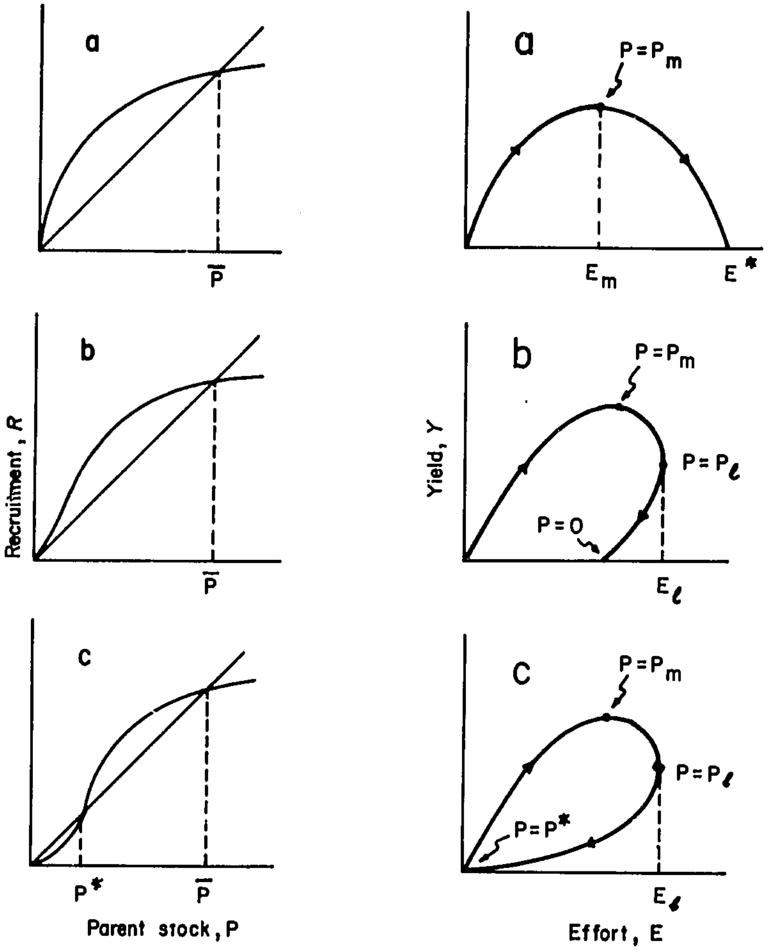

FIG. 1. Stock recruitment curves (left) and the corresponding yield-effort curves (right). (a) Beverton-Holt type; (b) Non-critical depensation type; (c) critical depensation type. $\bar{P}$ = population at stable equilibrium; P^* = population at unstable equilibrium; P_m = population giving largest maximum sustainable yield; E^* = critical effort; E_e = level of effort which, if increased, causes the population to move irreversibly to extinction. Adapted from Clark 1974; reprinted from J. Cons., Cons. Int. Explor. Mer with permission of the publisher, the International Council for the Exploration of the Sea.

The models just described may or may not be realistic, but as discussed in Murphy (1977) there are aspects of the behavior of schooling clupeoids such as contraction of the range and retention of school size as the population declines that, while probably stabilizing natural mortality, tend to maintain catch and catch per unit of effort, thus increasing fishing mortality and leading to crashes.

A summary of world collapses is given in Table 1. The lost production is in the order of 5 million tons and to this must be added 6 million tons of lost Peruvian anchovy production. The great vulnerability of the adults is not the only factor in these collapses. As Cushing and Harris (1973) note, clupeoids generally display weak density dependence in their stock recruitment relationships. This may be related to relatively low fecundity which in turn may be coupled with the protection afforded by schooling. Some of these schooling fish also have very variable reproductive success. These three factors—behavior leading to a high apparent abundance to the last, low fecundity with its attendant imprecise density dependent responses, and variable reproductive success—are additive and it is in hindsight no small wonder that there have been so many collapses in response to heavy fishing.

These same principles can be used to explain the most spectacular avian extinction at the hand of man, that of the passenger pigeon. The key reference to the story of the passenger pigeon is an excellent book by Schorger (1955). This animal was characterized by large flocks and large reproductive aggregations. At the time of the discovery of America the passenger pigeon population may have been as large as five thousand million birds. The last confirmed

TABLE 1. Statistics on clupeoid resources that have collapsed (Murphy 1977).

	Thousands of metric tons		
	1970 catch	Maximum catch	Year of maximum catch
Hokkaido-Sakhalin herring	0	850	1913
Atlanto-Scandian herring	21	1723	1966
Downs herring	0	98	1961
Pacific sardine	36	791	1936
Japanese sardine	17[a]	2320	1939
South African sardine	45	452	1963
Total	119	6234	

[a] 297,000 tons in 1973.

record of the species in the wild was a single specimen in Ohio on March 24, 1900, and the last captive bird died in September 1914.

In the interests of economy I will focus only on the breeding aggregations because it is here that I believe the depensatory mortality (Larkin et al. 1964) which led to their extinction occurred. A typical nesting flock occupied an area approximately 4.8 km wide and 16 km long. A single egg was laid per female. As many as 300 nests would be placed in a large tree. No doubt the single egg was in part an adaptive response to the vast numbers of birds nesting together, for it would probably have been difficult for the parents to obtain food for more than one squab because of competition with other birds. The other compensatory parameter (with respect to low fecundity) is the longevity of the passenger pigeon, well over 20 yr. Schorger thinks this was the result of reduction in predation mortality associated with huge flocks. Another important point is that a nesting site was never occupied for two consecutive years and the flocks appeared to shift around in a random way between nesting seasons. This would prevent entrainment by predator populations. The lack of entrainment would be crucial to the survival of the young, for on leaving the nest, the young flutter along the ground exercising their wings before they are able to fly. During this period predators of course attacked in great numbers, but owing to the vast numbers of young, the few local predators soon became satiated. The periodic cicadas employ analogous tactics in order to circumvent excessive predation (Lloyd 1966).

While the shifting about may have decoupled the natural predators of the passenger pigeon, it had no effect on man, who had access to railway trains and telegraph lines and was able to shift about and follow the birds. The toll was enormous and finally the vast flocks disappeared. However, well after the commercial hunting was ended by legislation, there were still large numbers of passenger pigeons in North America by any standard. But, the flocks were very small. No doubt the natural predation rate on these small flocks was much higher than on the vast flocks that existed formerly. Perhaps even more important, small flocks form small breeding aggregations and the small number of young would be unable to satiate locally available predators, so that reproduction would fall to a very low level. Extinction, once the population declined to a certain level, was then inevitable.

Capture Strategy

Capture strategy is well known and need not be treated in detail here. The theoretical foundation for capture strategy is the converse of the arguments discussed under schooling and predation. If fish tend to be randomly distributed, then clearly the most efficient capture strategy is one that employs a wide-swept path and utilizes methods that are efficient but easily satiated, e.g., trolling. If the fish are schooled, then the relationship of searching time to fishing time will change: the more highly developed the schooling habit is, the more time must be spent searching. This requires an efficient search and/or information system and a capture technique that is not easily saturated. The halfway house in this respect is the pole-and-line fishing that is employed in many tuna fisheries. The method par excellence, however, for schooling fish is the purse seine, developed for such fishes as pilchards, anchovies, mackerel, and tuna. The ideal is to retain the entire school once contact is made. It is indeed this method of fishing that dominated the capture techniques in the several spectacular population collapses discussed earlier.

Management Problems

The theoretical and observational considerations described in this paper together with the sorry historical record in Table 1 rather emphatically suggest that schooling imposes unique restraints on fishery development and management policy, or at least should. Modern scouting techniques and intervessel communication result in good fishing down to the last school. Thus, the built-in economic feedback that tends to depress levels of effort as the population declines is missing, and conversely the fall in the catch per unit of effort which is the classical way of gauging the effect of fishing on a fish population is either not observable or severely damped by the behavior of the populations. In addition there is the possibility of depensatory natural mortality which might cause a population to go to extinction or near extinction even if fishing is curtailed or stopped. Finally schooling fish resources frequently display imprecise density dependent reproduction and erratic reproductive success which compounds the sensitivity of the resource to exploitation.

If these resources are to be used on a sustainable basis, certain things must be done. Management must be in a position to impose draconian reductions in the level of exploitation at the appropriate time. Measures of abundance independent of catch per unit of effort must be developed. Finally and perhaps most important, organizations responsible for the exploitation of schooling fish should support more research aimed at understanding the schooling strategy of the populations under exploitation and the ecological role of schooling. Unless these are understood, managers will not be in a position to forecast the effect of either reduction in school size or reduction in total number of schools. The alternative is to be cautious and to hold the harvest rate far below what it might be if the managers are properly armed with information and authority.

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Discussion

BARDACH

Which schooling species are now under management that appear to satisfy or get close to satisfying the postulates you set? Do you think that the Peruvian anchovy fishery being taken over by the state is being managed for true conservation?

MURPHY

Well, they're trying to get there. They've reduced the power of the fishing fleet to about a third of its peak. Whether they've got the courage to hang on until the anchovy population gets up to a critical size remains to be seen. The population went down to a standing stock of 2 million tons in 1971. They greatly curtailed the fishery and the population started back up, but then they caught more than 4 million tons, and the population dropped again.

BARDACH

Also, I think they had another harmful climatic event.

MURPHY

Yes, but some people also hold that that the first catastrophic decline in the anchovy population was associated with a climatic event. There's no direct evidence of that. There was an El Niño 18 mo after the first bad year-class. It is not clear that that caused it, but at any rate the reproductive environment is variable from year to year. If the population is shakily growing and experiences lower spawning success coupled with more fishing, you destroy the gains you have made. I think that we are too eager to get back into the fishing business. If they had kept fishing down to a very, very low level for another couple of years, they would probably have been in good shape in 1977. The recovery of the British Columbia herring is an example of the results of a draconian measure: no fishing until the population recovered.

LILEY

Can you say anything about the condition of baitfish in these depressed fishery areas? You tell us that there are fewer schools, but they are of the same size as previously. Can you say anything about the growth rates of the fish within those schools?

MURPHY

Yes. The growth rate of these animals and their condition does not change very much as the population sizes change. You can conclude from that that food isn't the resource in short supply.

LILEY

It seems as if by reducing a fishery to a certain point you have done something to the environment in such a way that the fish population cannot recover, at least in the immediate future. You have not destroyed their ability to reproduce because there are still some large schools, and they can reproduce as large schools.

MURPHY

Well, I think that in the instance of the Pacific sardines the schools at some point did become smaller. Now there are a few sardines around but they seem to have forsaken the large schooling habit for hanging around pier pilings in bays. Probably the answer is that the same gene pool does not exist anymore.

KEMMERER

The reason for the smaller schools when the overall population of fish is small may be due to randomness. When large schools fractionate into smaller schools, the small schools are less likely to find another school to combine with. It has nothing to do with the environment, just fewer and fewer fish.

MURPHY

But this is counteracted by contraction of the range of the population. They are occupying a smaller ocean area, so that even though the total population is smaller the chance of reforming a large school is still smaller.

KEMMERER

In the menhaden fishery, on the first day of the fishing week, many large schools are caught, but as the week progresses, the schools tend to get smaller and smaller.

FISHELSON

Are schools mixing? We have some observations on the mackerel *Auxis thazard.* If you enclose two schools in large nets in the open sea, they move between one another but they don't mix. They remain apart and you can fish out one school and the other separately.

MURPHY

I don't know about this.

FISHELSON

Yes, I have seen this in the northern part of the Gulf of Eilat several times.

BLAXTER

Is it true that in a way the fish can't win? Because if in that hypothesis or model the school is keeping the same size and the catch per unit of effort remains the same as the number of schools gets smaller, only predation takes a toll.

MURPHY

Yes, that's right.

ATEMA

I wonder if there's any information that there may be two behavioral traits in the gene pool of a schooling fish, one for very tight schooling. The fishery is a selective predator that takes out the tightest schooling ones, so that eventually if you sustain it for many years and crop out those genes, you end up with fish that don't tightly school, and they might end up around the pilings in La Jolla.

HUNTER

I would like to hear your thoughts on N.V. Lebedev's concept of elementary fish populations, or the aggregates of schools, which I think is a fairly common phenomenon. I've seen in groups of tuna schools in the eastern tropical Pacific a great deal of interchange between fish within the individual schools, but the aggregates seem more stable than the individual school and move as a group. Lebedev in his book, Elementary Populations of Fish, states that these aggregates of schools are the critical biological units.

MURPHY

I would like to point to one biological change in the sardine population that is incontrovertible. The old population used to spawn up to 320 km offshore, and anchovies at that time spawned close to shore: now what sardines remain spawn around pier pilings and not offshore, and so there has been a real change in the population, not just its size.

HUNTER

In the last days of the sardine population when it had retracted to a single locality, the population may have been composed of only one school aggregate in which the school size distribution was behaviorally regulated by the time of day, food, and breeding.

HASLER

I wish I could give you some encouragement from fresh water, but we have had three collapses in Lake Mendota. These involved three different species over 40 yr. One was the cisco, the next was the perch, and this last year the white bass. All are schooling species. Angling by man was modest.

BLAXTER

In the table you showed, what evidence is there for a decrease occurring through overfishing rather than through some natural change? Is it well documented that all collapses have occurred through overfishing?

MURPHY

One of the reasons the collapses occurred was that during the course of the decline there were two schools of thought: one that the fishery played the major role and one that environmental changes were the major cause.

HUNTER

To what extent do you think the biomass has been replaced by other clupeoids or other fishes in your Table ? In other words, was there a loss of fish biomass?

MURPHY

Well, in California, there was replacement to a very large extent, and there's evidence for that in Japan and South Africa. I don't think there's any evidence with respect to the herring populations but I may be wrong.

BLAXTER

Capelin have replaced the Norwegian herring.

MURPHY

The sardine came up in Peru. You can look at it as no loss, but often the replacement isn't as valuable as the thing lost—anchovies in California vs. the pilchards, and so forth. At the minimum, the industry is dislocated and there's a huge loss of income.

Partitioning and Sharing of Space and Food Resources by Fishes

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FISHELSON, LEV. 1980. Partitioning and sharing of space and food resources by fishes, p. 415-445. *In* Bardach, J.E., J.J. Magnuson, R.C. May and J.M. Reinhart (eds.) Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5, 512 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Multispecies fish populations in aquatic habitats evolved in response to two main resources: shelter and food. This is reflected in the fishes behavior patterns which enable optimal use of these resources with the maximal stability and lowest cost.

Shelter or space partitioning and sharing occur in the form of changeover behavior during which fish species occupy the same space but at different times or at various depths. Such developments lead to evolution of specialists that use the same shelter all their lives, and generalists that use different spaces at different ages. Competition is thus decreased, especially between various age-classes and so enables the existence of larger polyspecific populations. Artificially increasing space and shelter heterogeneity, especially for juveniles, enables an increase in survival rates and enlargement of the populations.

Adaptation to food shows similar lines of development, with specialists living on the same food items all their lives, and generalists using various food sources during their development. These facts should be considered when aquaculture ventures are undertaken.

In connection with feeding, the phenomenon of following or mimetic social behavior evolved, during which various fish take advantage of feeding activities of other fish to obtain their food. This pattern develops as fish mature and diversify their diet.

By manipulating space and food, marifarms or aquafarms can raise their yields. The farms can prevent depletion of natural resources and provide enough juveniles for restocking. The fish species to be used should be selected according to their space-shelter preferences and plasticity of their diet at various stages in their development.

Introduction

The question of how many species of animals manage to coexist has been the main object of ecological and socioecological investigations for the last four decades. The proliferation of autecological and synecological studies has enabled the construction of mathematical models for animal populations, as well as the formation of general concepts (Wynne-Edwards 1963; McArthur et al. 1966; Pianka 1972). Most of these works were of profound importance for developing systems of management for mono- and multispecific populations, especially in terrestrial habitats. As knowledge of natural and artificial aquatic ecosystems increased, ecological models began to be applied to aquatic habitats as well. Fish have become the object of such studies only in the last two decades, especially after multispecific fish assemblages in tropical waters were extensively observed. The first summary on this subject was written by Breder (1959). The invention of SCUBA diving triggered studies on fish ecology along tropical coral reefs (for summary see Ehrlich 1975) as well as in African lakes (Lowe-McConnell 1969, 1975; Fryer and Iles 1972) and in South American freshwater bodies. All these studies triggered the rediscovery of fish from the point of view of socioecology. Especially important general works on marine fishes were those of Randall (1963, 1967), Jones (1968), Randall and Hartman (1968), Collette and Talbot (1972), Smith and Tyler (1972, 1973), Munro (1975), Munro et al. (1973), Vivien (1973), Bradbury and Goeden (1974), Sale (1974, 1976), Fishelson et al. (1974), Adey et al. (1977), Fishelson (1977) , Hobson (1975), Smith (1977), Parrish and Zimmerman (1977), and Thresher (1977). Regarding analysis of ecological and sociological phenomena of specific taxa of fish, one should mention the works of Strassburg (1966) on Apogonidae, Jones (1968) on Acanthuridae, Fishelson et al. (1974) on Pomacentridae, Barlow (1974a and b) on Acanthuridae and Cichlidae, and Reese (1975) on Chaetodontidae. In fresh water, the investigations performed by Corbet (1961) on Mormyridae and Siluridae, Greenwood (1965a and b) on Cichlidae, Weizman (1962) on Characidae, and Emery (1973) on fish of Ontario lakes are also important.

Although all the studies were performed by different methods and focused on specific problems, all looked for answers to the following ecological questions: "Which strategies are used by various fish species to fare optimally in any given situation?", and for polyspecific situations, "How do the different species coexist?" With answers to these question, fish biologist and ecologist will be more competent to advise fishermen and aquaculturists on how to manage their production units so as to obtain optimum yields with a minimum energy input, and in nature with maximum conservation of the stock.

My purpose is to present some ideas about strategies of sharing and partitioning of resources by fish, based on examples from marine and fresh waters.

These examples demonstrate that the ability to coexist and to share common food and space resources in a given aquatic habitat optimizes exploitation of various niches and produces interspecific behavioral phenomena that decrease competition. Some of these strategies are innate and persist unchanged during a fish's life, whereas others are "learned", appearing during ontogenesis, and differ in different age classes. Application of these ideas in fishery management and aquaculture will lead toward optimal utilization of resources.

The niche concept and fish populations

According to the classical niche concept (Hutchinson 1965), a niche is a multidimensional hyperspace in a given habitat and consists of a set of values (variables), a part of which are the animals involved. The temporal and spatial distribution of animals in such a niche will be in accordance with their tolerance to those variables. Starting from this point of view we can postulate that:

1. The more variables (diverse) that comprise the habitat, the more users (fishes) will be able to utilize it.
2. The number of animals (fish) able to use a habitat is a function of the variety of ways in which the resources are used.

Postulation 1 represents one part of the habitat—its qualities—whereas postulation 2 represents the second parts of the habitat—the number of species (users). These are two integral parts of one system, but they are not identical.

Whittaker and Woodwell (1972) designated alpha-diversity as the number of species in a community resulting from diversification (specialization of users), and beta-diversity as the habitat-differentiated species occurring along environmental gradients. Alpha-diversity is similar to my second postulation of animal diversity, and beta-diversity to my first one of environmental complexity.

To discuss the kinds of diversity observed in aquatic habitats, we must identify the crucial resources that influence a fish population's growth. For what do fish compete? What factors act to limit their biomass? As a result of many investigations published recently, we know that space and food are the two main factors determining the type of fish assemblage observed in the species-rich habitats, marine or freshwater. I put space first because it acts as a shelter also and includes important anti-predatory qualities. Knowing the importance of these two resources, we are able to try to identify the strategies used by fish to partition them. As stated by Weatherley (1972), in multispecific communities, "differences in behavior, activity patterns, and habitat preference make it unlikely that two or more species persistently clash competitively." More and more people involved in fish production are starting to use this knowledge, and the development of polyculture is the result of it.

Space Partitioning

Most descriptions of marine or freshwater fish populations deal with the problem of the spatial and temporal distribution of individual species. As mentioned by various authors, in crowded aquatic habitats that are in a food-rich environment, space seems to be the main factor that regulates the number of animals (see also Rothstein 1973). Smith and Tyler (1972) also state that "The number of individuals that can live together depends . . . on the extent to which the space can be shared by other individuals." This seems to be true also for lakes in Africa (Lowe-McConnell 1975). On an interor intraspecific level some of the strategies used in space (shelter) selection lead toward socialization and a decrease in competition, whereas others are more individualistic and increase the agonistic drives.

To generalize this question of space-sharing or partitioning we should ask ourselves:

1. How do fish species manage to use the same space and coexist?
2. How do various age groups of the same fish species avoid competing for space?

To answer these questions, most investigators have concentrated on studying space-shelter partitioning by various fish species, including location of the space (shelter), type of shelter used, dimensions of the shelter, and time of utilization. The most extensively investigated types of shelter use are place and type of shelter. As an example, we may use the coral reef, which for many years served as the "battlefield" for marine ecologists dealing with environmental structure and diversity. These investigations, starting with the classic publications of Abel (1960) and Hiatt and Strassburg (1960) on coral reef fish distribution, were recently summarized in part by Ehrlich (1975). Parallel to the investigations in the marine habitats, several research programs of the same type were also performed in freshwater lakes (summary in Lowe-McConnell 1975).

Although some fish, like parrotfish, are able to produce their own shelters (Winn and Bardach 1959), they are exceptions. Today it is more or less obvious that the richer the habitat is in shelters, the more fish species are found in it. This pertains, of course, to stable environments, like large undisturbed lakes and tropical seas.

The ability of fish to exploit various parts of a multidimensional space is well illustrated by the work of Eigenman (as cited by Lowe-McConnell 1975), who collected 54 species of fish in South America from a pool with a diameter of 30 m. We also observed species diversity on a coral reef of Dahlak Archipelago, Red Sea (Lewinsohn and Fishelson 1967). I collected 63 species of fishes from a coral platform of 120 m^2. Among these were 13 species of apogonids, of which 2 species lived among the spines of sea urchins, 3 species formed schools hiding close to the reef wall, and 8 species lived solitarily dispersed in the crevice-rich body of the reef. As all these cardinalfish are planktonivorous, feeding on various prey, they occur together with a very diffuse agonistic interaction among them. Such a multispecific structure could be taken as a model for cultivation of marine fish, provided we are able to manage a habitat in which food-oriented competition does not exist. This again can be overcome by conditioning schools of juvenile fish of closely related species to various diets, a technique now being developed in Japan. Such conditioned "users" can utilize shelters with relatives, not competing with them for food. Of course, I should mention that in natural habitats such sympatry of relatives is not very common, and usually fish are distributed in relation to major environmental features such as depth, light intensity, and wave action. This type of distribution by habitat is the result of adaptation to space during the course of evolution, and as such, prevents competition between relatives.

Specialists Versus Generalists

Some fishes use the same shelter-space throughout their lives, whereas others change during ontogeny. As an example, I shall mention two species of the genus *Dascyllus* (Pomacentridae), both of which have planktonic larval stages.

Juveniles of *Dascyllus aruanus* settle from the plankton at 7-9 mm total length. They find branching colonies of the coral *Stylophora* and *Acropora* and grow and reproduce in them as a small monospecific group. Juveniles of *D. trimaculatus* settle in the same manner but are less specialized and occur among spines of the sea urchin *Diadema setosum*, in crevices of corals, or between the tentacles of giant sea anemones. When 30-40 mm TL, those juveniles leave their symbionts and aggregate in groups of 10-20 individuals above and between coral colonies. When 50-70 mm total length, the young *D. trimaculatus* move to the fore-reef region, school and swim along the coral wall, or hover around coral knolls (Fishelson et al, 1974). This change of shelter location develops during ontogeny. Finally, *D. trimaculatus* forms a part of a multispecific society, a guild, that includes in the Red Sea *Neopomacentrus miryae* (= *Abudefduf azysron*), *Anthias squamipinnis, Chromis dimidiatus,* and *C. caerulaea.* All these species and many additional fish use the coral knoll as a refuge while they collect their food from the surrounding plankton (Popper and Fishelson 1973). While feeding these species spread out in harmony, and dive in unison toward the shelter when danger is spotted (Fig. 1). In this case, the multispecific society shares a common shelter, and as a consequence shows social behavioral patterns of interspecific nature (Fishelson 1977). These "new" elements of sociobehavior that develop during ontogeny are superimposed on the intraspecific behavioral patterns, and seem to be the result of reciprocal stimulation, and in some cases also have elements of maturation and learning.

Measurements I made on coral knolls of various complexity in the Gulf of Aqaba during 1976-1977 showed that the number of fish species and individuals found over them is strongly correlated with the complexity and dimension of the knolls (Fishelson, in preparation). Under favorable conditions a coral knoll of the highest complexity can accommodate more than 35 species of fish and occasionally more than 2000 individuals (Fig. 2). Such a physical shelter could be used in mariculture as will be discussed later.

The sergeant major *(Abudefduf saxatilis)* provides another example of shelter change and use during ontogeny. Juveniles 10-30 mm long always occur in crevices and cracks in shallow-subtidal or sometimes even tidal pools. Here they live solitarily, usually in the shadow of cover. This behavior occasionally brings them together with large groups of other juvenile fishes which hide below various floats and rafts. Hiding beneath floating structures is a phenomenon that could be utilized in mariculture and stock management and will be discussed later. When 40-50 mm long, the fish aggregate around and over the coral colonies and behave like *D. trimaculatus* juveniles. The larger subadults, 100-110 mm TL, move to the fore-reef, form schools of 100-200 individuals, and wander along the coral wall (Fishelson 1970, 1977). At this stage they use shelters in the coral reefs only for refuge at night. During this time the *A. saxatilis* also change their diet. Thus, within one closely related group of fish (even in a single genus) two types of shelter sharing and partitioning have evolved.

One type, as observed in *Dascyllus aruanus,* represents evolutionary specialists that use the same shelter throughout their ontogeny. The initial colonizers are juveniles and as they grow, limited shelter becomes the factor that prevents additional settlers from invading (see also Sale 1976). The intense demand of this resource is accompanied by strong territoriality and competition at specific and interspecific levels.

The second type, exemplified by *D. trimaculatus* and *Abudefduf saxalitis,* shows more complicated space-shelter utilization characterized by ontogenic development in behavior and sociability. These species during their life span, use a variety of shelters, thus decreasing competition between age classes and optimizing their chances for survival, especially during extreme environmental

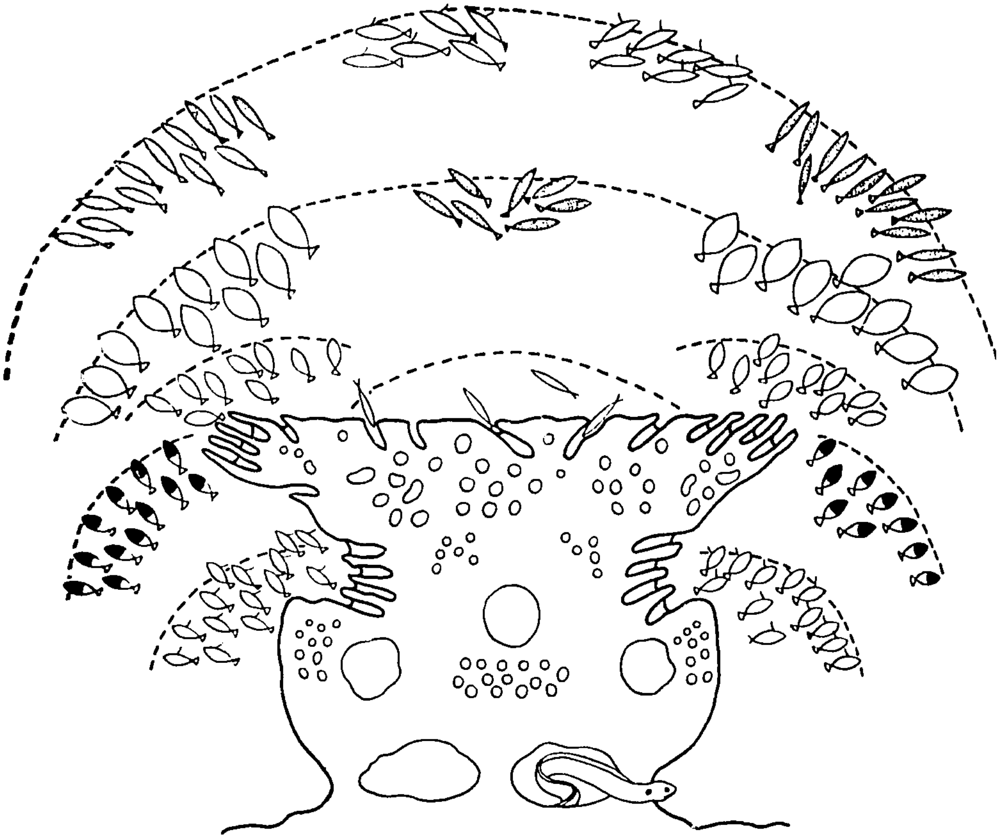

FIG. 1. The multidimensional structure of a coral knoll and assembly of fish found around it during the day: grey-spotted, *Neopomacentrus miryae;* black and white, *Chromis dimidiatus;* with dorsal ray, *Anthias squamipinnis,* upper adults, lower juveniles; large, white fish, *Dascyllus trimaculatus;* small, white fish, *Chromis caerulea;* long, thin fish, *Blennys;* and at bottom, a moray eel. (Drawn by S. Shaeffer).

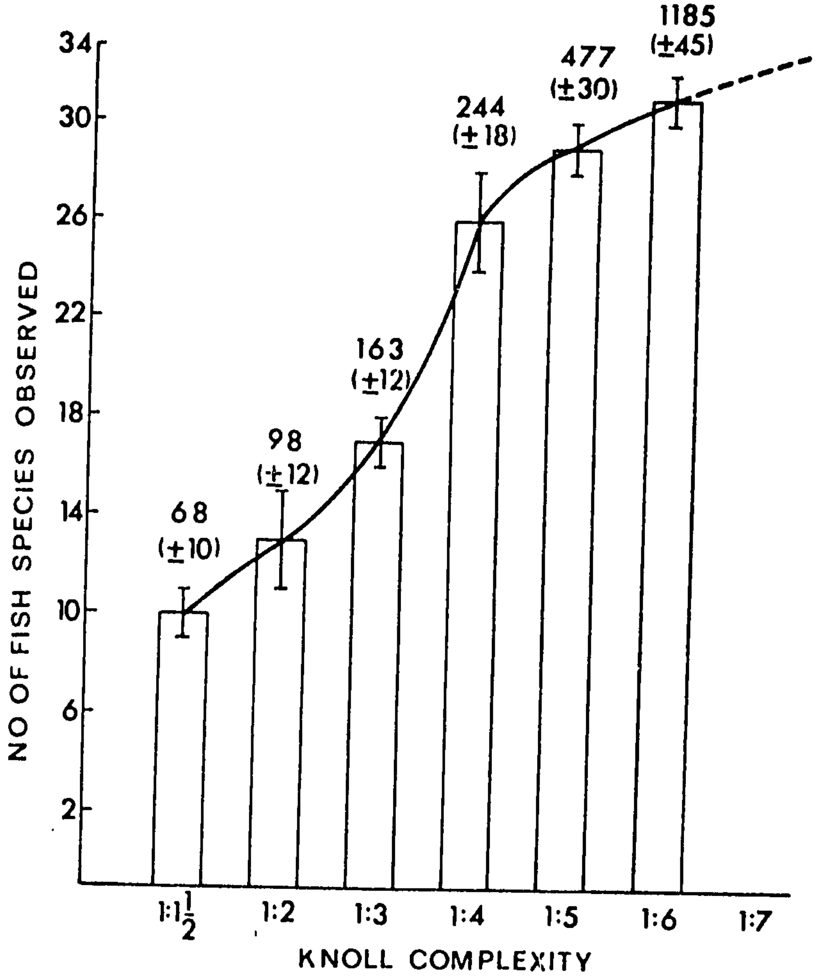

FIG. 2. Correlation between coral knoll complexity and the number of fish species and individuals on them. Each figure represents an average of 3-4 knolls and the ± shows the range in number of individuals. Complexity was measured by comparing the linear length of the knoll wall to its topographic length and by measuring the holes (hiding places) along the line.

events.

Similar types of shelter use also occur among freshwater fishes. For example, in Lake Tiberias (Israel), juveniles of the endemic cichlid *Tristramella sacra* hide in shallow water among *Phragmites* and other grass-like plants, but the adults hover in open water, especially opposite the inflow of rivulets (Fishelson, in preparation). In Lake Tanganyika (Coulter 1967) where 12 species of *Tilapia* live, groups of 2-3 species form specific associations at different sites, while juveniles of the same species occupy entirely different localities in shallow water. Other examples are described by Lowe-McConnell (1975) from American and African basins.

With the first type we are dealing with shelter specialists, and with the second type, with generalists that utilize different spaces during their lives. Thresher (1977) pointed out that there is some advantage to being a specialist, as far as familiarity with shelter and pair formation are concerned, but in a resource-rich environment, this seems to be of minor importance. More importantly intraspecific competition for such specialists begins from the first day the juveniles settle into shelters, and this limits their numbers and triggers energy-consuming, antagonistic behavior.

In a fish like *A. saxatilis,* in which different age classes utilize different shelters, maximal dispersion and decrease of intraspecific competition is achieved, enabling survival and development of larger populations. This is evident if we compare numbers of fish in isolated places. Thus, on an Eilat reef (Red Sea), the number of *D. aruanus* in *Stylophora* corals was 68, whereas on the same reef, *A. saxatilis* was represented by almost 600 individuals and *D. trimaculatus* by 320. Strategies in shelter utilization should be taken into account if we are going to establish artificial fish assemblages for food production.

Specialized requirements are dangerous in changing environments and they act as evolutionary traps and handicaps as do most symbiotic relationships. Any reduction in shelter quantity or quality will have an immediate negative influence on the users, even if all other resources remain unlimited. We know that the strong attachment of *D. aruanus* to *Stylophora* corals caused their disappearance as the coral colonies were killed by pollution. We also know that symbiotic relationships that limit the mobility of fish lead to stenophagy, a specialization that can limit the biopotential of the fish. An example is observed in the Lake Tiberias population of *Sarotherodon galilaeus,* which spawns almost solely on unique rocky areas in shallow water. In contrast *S. aureus* is an extreme generalist, able to spawn and reproduce throughout the lake. Recent changes along the shoreline perturbed the rocky sites and thereby influenced the population growth of *S. galilaeus.* Today there is an increase in the population of *S. aureus* along with a decrease of that of *S. galilaeus.*

Type of Shelter Used

The type of space used by fish species has been described in numerous publications dealing with fish from freshwater and marine environments. For example, in Lake Tiberias *Sarotherodon galilaeus* prefers rocky localities during breeding; *S. aureus*, shallow, well illuminated subtidal waters with soft bottoms; *Tristramella sacra*, places close to shore overshadowed by branching trees; and *Tilapia zillii*, gravel bottoms, especially with slowly flowing water. An interesting example is provided from Lake Malawi by Fryer and Iles (1972). Five sympatric species of the genus *Tilapia* separate along a transect from the shore toward the open water. Many similar examples are found in marine habitats; for example, *Pseudochromis olivaceus* occurs together with *Gobiodon citrinus* and *G. rivulatus* in various types of branching corals, but *Pseudochromis friedmani* occurs in various habitats, hovering along coral walls and caves. In the damselfish family, *Dascyllus aruanus*, *D. marginatus* and *D. reticulatus* are branching-coral users, whereas the *Pomacentrus* use a wide variety of habitats.

As mentioned before, the change of shelter-type used during the fish's ontogeny decreases competition among unequal competitors. This enables juveniles to occupy shelters situated within spaces occupied by adults even during reproduction. Groups of small individuals of *Anthias squamipinnis* and *Neopomacentrus miryae* are found on the same knolls as the adults, but occupy positions on the coral knoll closer to the bottom, and at night settle in very small crevices. In freshwater habitats, as in African lakes (Dunn 1975) or in Lake Tiberias, the small *Haplochromis* species are able to live and breed within territories occupied by large tilapias (personal observation). In Israel, this advantage is used well by *Haplochromis flaviijosephi* which is ignored in the territories of *Tilapia zillii* but prey on the swimming fry of *T. zillii*.

Such interspecific sharing of space should be considered if we wish to establish hatcheries for fish fry. We can also use fry predators to prevent overcrowding in commercial fish ponds. We introduced small *Ophiocephalus striatus* into aquaria with reproducing *Sarotherodon niloticus*, and the small piscivore preyed on most "wild" offspring produced in the aquarium. The euryhaline bass *Morone (Dicentrarchus) labrax* that grows well in fresh water can also be used for such cases in aquaculture. Developing this method of predator-controlled reproduction will make it possible to grow early breeding fish commercially in ponds, especially those from warm water. In Israel, uncontrolled reproduction of cichlid fish in commercial fishponds can cause high losses for the net production of ponds (Fishelson 1966).

Time and Shelter

Time partitioning of shelter utilization has been extensively investigated in marine environments. Especially interesting are those species that change place and space during their circadian behavior. This type of space utilization was called day-night changeover by Collette and Talbot (1972). The simplest case was described by Fishelson et al. (1971) for *Pempheris oualensis.* During the day these fish hover in large groups in shadows of caves and cracks of the fore-reef, and during the night they wander out into the pelagial, collecting macro-zooplankton. In many places the same habitat that hosts a school of *Pempheris* during the day also hides several species of cardinalfish and squirrelfish, which are active at night. At night, this shelter is used by the day-active *Anthias squamipinnis, Neopomacentrus miryae, Chromis dimidiatus,* and occasionally *Abudefduf saxatilis,* as well as by some labrids and chaetodontids. As the night-active group returns, competitive interactions occur between them and the night-users of the shelter. The latter are slowly "pushed" out, so that before sunrise, a mixed population of day- and night-active fish is found in the shelter (see also Hobson 1972). We are dealing here with typical changeover behavior, and during the evening hours, after sunset, the motion occurs in the opposite direction: the day dwellers move out when the day-active fish invade the shelter. Numerous investigations quoted by Ehrlich (1975) describe sharing of shelter by fish of coral reefs. This modus vivendi enables the formation of multispecific populations, even if their components compete for other resources of the environment, for example, food. This is illustrated by the cardinalfish from my investigation in the southern Red Sea.

The cardinalfish are carnivorous; nevertheless 13 species of them were found on a small isolated reef. From among these, *Ostorinchus cyanosoma, O. angustatus,* and *Paramia bipunctata* are partly day-active and occupy large holes in the reef. The second nocturnal group is formed by *Fowleria aurita, Apogonichthoides taeniatus, Ostorinchus nubilis, O. annulatus, O. endeckatenia, O. fowleri, O. flourieu* and *Pristiapogon snyderi.* From among these, *P. snyderi* and *O. fowleri* hide in the reef just below the water surface level, while the others are found in cracks and crevices close to the bottom. The third group of species that includes *Cheilodipterus lineatus, C. caninus,* and *Apogon multitaeniatus* are crepuscular and hide along the shadows of the fore-reef wall (Fishelson 1977). In the example of cardinalfish we are dealing with a group of closely related species that share the same habitat but use different parts of it. As described by Strassburg (1966), in this case as well, the cardinalfish hunt partly at different times, and their hunting spaces are partly separated. An interesting case of changeover behavior was recently described by Edeling and Bray (1976) in tropical fish occurring today in kelp forests of Santa Barbara. These authors regard these as atavistic patterns, remnants from the tropical past of the observed fish.

Changeover behavior was also described in freshwater habitats. American cichlids and characids are active during the day, whereas in the same basins, the silurids and gymnoteids are night-active (Lowe-McConnell 1975). Emery (1973) describes this type of activity in Ontario lakes, and Andersen (1969) mentioned this for various *Cottus* species occurring in Swedish rivers.

Although in most cases of changeover activity and shelter sharing, we are dealing with multispecific populations both at night and during the day, socially there is a profound difference between day- and night-active fish. The groups of day-active fish, merging during their activities, form integrated social units (condominia) with typical interspecific mimetic behavioral patterns as described before. This formation of social, usually large schools of day-active fishes, was discussed in numerous papers, and most authors agree about its antipredatory value. Recently Breder (1976) mentioned an additional advantage of this swimming together: the fish utilize a special type of locomotory efficiency, achieved due to lubricants produced by their skins. Contrary to the day-active, the night-active species are together while in the shelters at their rest time during the day. There they show only diffuse threat postures that maintain individual distances between fish. At night, in most species each fish acts independently, showing no social interaction. These differences seem to have evolved because of the difficulties of visual communication at night.

Shelter and Fishery Management

The fact that fish species utilize different spaces and shelters can be utilized for fish management in mariculture, including stock maintenance and increase of yield. Several recent investigations (e.g., Gundermann and Popper 1975) show that rocky shelters that were artificially denuded of their fish inhabitants are quickly repopulated, and in most cases by the previous inhabitants. It looks as if in stable environments, there is a chronic need for space, and by providing new reatreats, the biomass can easily be raised.

The first steps in increasing the space supply have been taken by the construction of artificial reefs, especially in shelter-poor habitats. Such introduction of a new ecological element into the habitat dramatically increases the environmental complexity and very soon also the habitat or so-called point diversity (Slobodkin and Fishelson 1974) of fishes. As summarized in several publications (Rickards 1973; Steimle and Stone 1973; Colunga and Stone 1974; Russell et al. 1974) and more recently shown by Tsuda et al. (1977), such artificial structures are *terra nova* for fisheries, increasing possibilities for improved yields. But most of these artificial structures did not take into account the variability of shelter need for the various age classes of the same fish species, and the difficulties facing juveniles as they try to populate (settle) structures already occupied by older individuals. Today we know that inadequate shelter limits mostly the juveniles. Thus, the example of a natural coral knoll, with its polymorphic shelters, should be used, and for this purpose modular knoll reef-marifarms should be constructed providing optimal types of shelter for individual age classes. By investigating the many rocky retreats and their fish populations in various geographical regions, we will be able to construct knolls in which competition between invading juveniles and resident older fish can be avoided. Once such modular units are established, we can plan multidimensional reefs constructed from artificial knolls and placed on sandy bottoms near large rocky habitats. Fish can be cropped from such knolls by short standing nets (Fig. 3) as described by Popper and Fishelson (1973) or other techniques specially devised for this type of fishing. As observations show, artificial knolls soon become covered by an algal carpet of the Aufwuchs type, and as this occurs, not only fishes

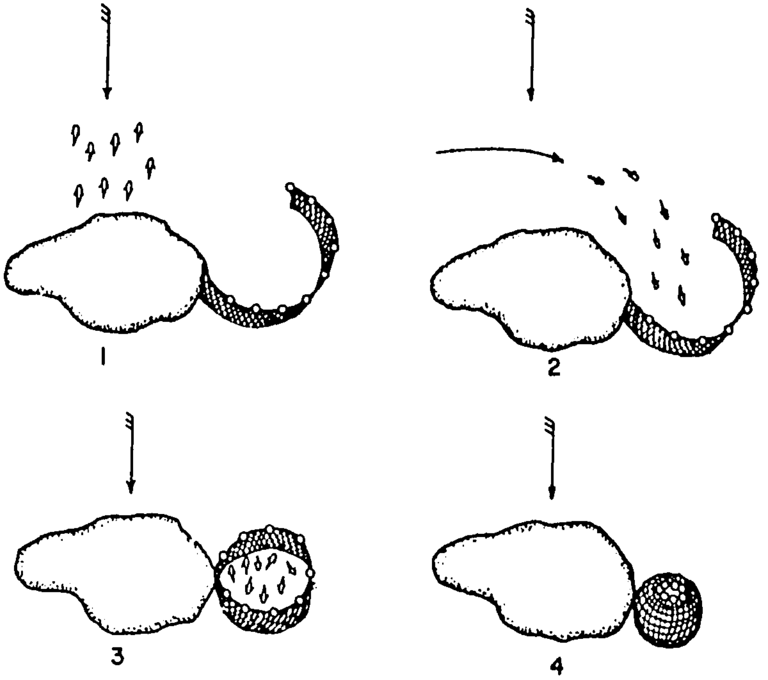

Fig. 3. Schematic diagram showing how the standing net captures fish (from Popper and Fishelson 1973). Reprinted from the Journal of Experimental Zoology with permission from the Wistar Press.

looking for shelter are attracted, but also schools of food-fishes, like sparids, mullids, and siganids, browsing on the algae. Floating rafts can also be used as attractants for juvenile fish looking for shelter. As mentioned before, juveniles of several species show a tendency to aggregate in large number below different types of rafts, using the shadows as protection [see also summaries of Gooding and Magnuson (1967) and Wickham and Russell (1974)].

Under such a raft opposite the Marine Biological Laboratory at Eilat, on one occasion I counted about 600 juvenile fish belonging to 7 species, of which several were food-fishes. Experiments performed with floating rafts in fresh water (Dahomey) also contribute to the yield of commercial fish. Also Swingle (1968) recorded increased yield in fish ponds after the introduction of shelters. This technique should be used more extensively, and it seems that such rafts, providing security for juvenile fish, will be more protective if provided with an artificial "grass" carpet hanging down (Fig.4). The fish will hide among these grasses and most of them will feed on the Aufwuchs. For cropping the population a hanging net should be constructed attached to the float which could be dropped down for collection. These rafts, coupled with artificial or natural rocky environments, can provide assessments of localities denuded by overfishing or natural and artificial extreme events.

It seems that for the maximal utilization of such marifarms, we should understand their biodynamics, namely the energy flow through the system and behavior of fishes within it. This can be achieved by integrated research programs like that proposed by Sachet and Dahl (1974) for tropical reef ecosystems.

Food Sharing and Partitioning

Food availability is one of the major factors regulating population structure and density, and includes formation of characteristics typical for fish of a given habitat (Nursall 1975; Rounsefell 1975; Hobson and Chess 1976). As in shelter utilization, the type of food utilization also profoundly influences the diversity of fishes.

Numerous investigations on food and feeding of tropical marine fish have been summarized by Ehrlich (1975) and tropical freshwater fish populations by Lowe-McConnell (1969, 1975). Of special interest are the recent papers of Gibson (1968) on feeding behavior of blennies in the Mediterranean Sea, Barlow (1974a) on Acanthuridae, Vivien and Peyrot-Clausade (1974) on food specialization of Holocentridae, and Reese (1975) on Chaetondontidae. Problems of feeding strategies were also discussed by Fishelson (1977) and during the last Symposium on Coral Reefs (Smith 1977; Parish and Zimmerman 1977).

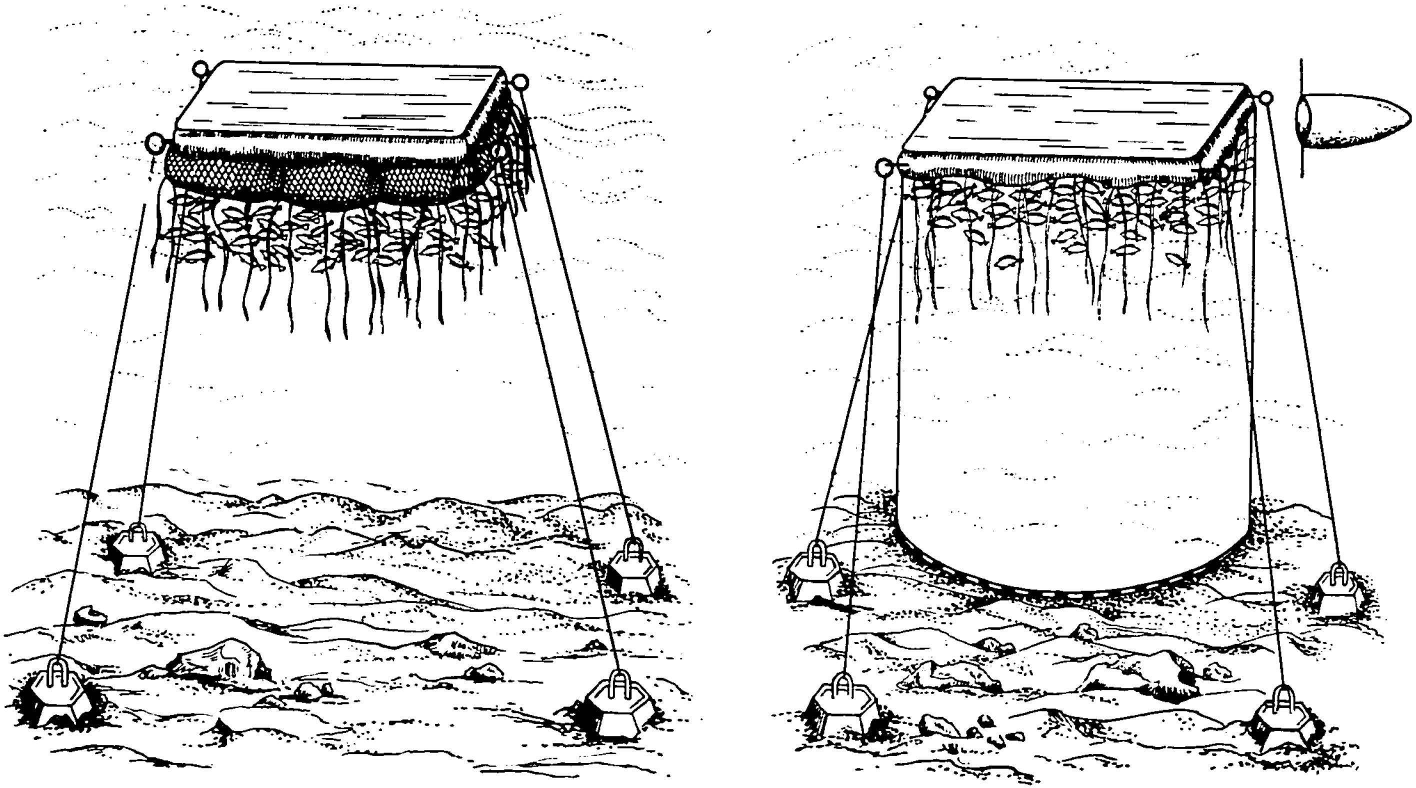

FIG. 4. A floating raft with artificial seagrass before (left) and after (right) the net is lowered. (Drawn by S. Shaeffer).

Food sharing and partitioning in freshwater habitats were discussed in the papers of Nilsson (1955), Larkin (1956), Corbet (1961), Weizman (1962), Greenwood (1965a), Welch and Ball (1966) and Lowe-McConnell (1969). Extensive material in this field is summarized in the books of Fryer and Iles (1972) and Lowe-McConnell (1975). Briggs (1966) also discusses problems involving food preference and specialization in freshwater basins. From the point of view of artificial freshwater fish management, food utilization seems today to be more crucial than space or shelter for two major reasons:

1. Most of the freshwater fish-producing establishments known today use habitats with minimal shelter. This is done to reduce expense of harvest.
2. Fish-producing units in most cases require high-energy foods, the high cost of which can limit production. Because we are dealing with energy balances, the amount and quality of food required can produce limits for fish management.

Thus, after studying the strategy of food sharing and partitioning in natural, multispecific fish communities, we will be more competent to discuss problems connected with fish polyculture in artificial habitats.

According to how fish utilize available food resources, they can roughly be separated into two large groups, specialists and generalists. Each group includes carnivores and herbivores and is represented in most natural habitats.

Some years ago, a strong tendency existed among the ichthyologists to draw a sharp line between herbivores, omnivores, and carnivores, and to analyze the composition of particular fish fauna according to these categories. In the last decade, with more thoughtful analyses of feeding and associated behavior, it seems that these sharp divisions cannot be used anymore, because today many species are known to function as herbivores in one instance and as carnivores in another; there are species of fish that are able to act as specialists in some circumstances, generalists in others. For example, the species of the cleaner-wrasse genus *Labroides* are typical specialists, making a living by cleaning numerous other fish visiting their cleaning stations (Slobodkin and Fishelson 1974). But in time of need, they may feed on various other sources: *L. dimidiatus* will feed on small animals and floating particles, whereas *L. quadrilineatus* will feed on polyps of various corals (personal observation). Randall and Hartman (1968) described sponge-devouring damselfish, but noted that they did not feed exclusively on this food. Of course, numerous fish are stenophagous at one time during their lives and omnivorous at another time. We know that the fry of many *Tilapia* species are carnivorous, whereas the adults feed on a variety of food. The fry of the silver carp, widely used in Israeli ponds, feed on small crustaceans and insect larvae, whereas the adults forage on phytoplankton. Corbet (1961) also mentioned that in Lake Victoria mormyrid fish change their diet with age. As shown by Bowmaker (1969) the juveniles of *Alestes macrophthalmus* from Africa feed on zooplankton; subadults up to 140 mm TL are found inshore feeding on insects; and large adult fish prey on *Engraulicypris.* From the point of view of intraspecific relationships, such change of diet limits the competition for food among age classes and enables the species to optimally utilize the habitat. Weatherley (1972) also states that for many fish we will be able to describe the food requirements only after determining the full feeding pattern over the species entire size range. Together with this we should keep in mind that as part of evolutionary divergence that occurs in populations of widely distributed fish species, permanent changes in diet may occur, sometimes of a very important nature. Thus, for example, *Abudefduf saxatilis,* described from the Marshall Islands as a browsing herbivore (Hiatt and Strassburg 1960), is a planktonivorous fish in the Gulf of Eilat (Fishelson 1970). The African *Alestes macrophthalmus* is a herbivore in Malagasi swamps, and carnivore in Lake Mweru. Such displacement as observed for sympatric coregonid species (Nursall 1972) and for *Haplochromis* (Lowe-McConnell 1975) leads toward adaptive changes in morphological structures and again enables better utilization of diverse food resources.

Food partitioning in populations of herbivorous and carnivorous species takes two different forms. One is the utilization of various types of food within the same habitat; we may call this food-niche preference. Thus, for example, in many freshwater lakes several herbivorous fish species occur together feeding on different plant material. In Lake Malawi, five species of *Tilapia* are found together, each with its own plant diet (Lowe-McConnell 1975). Of those, *T. squamipinnis* and *T. lidole* feed on phytoplankton, but at various depths. In Lake Victoria, *T. esculenta* feeds on phytoplankton from suspension while *T. variabilis* feeds from the sediment.

The last two examples point toward a feeding strategy used by most of the herbivorous multispecies fish populations that are usually day-active. Partitioning among them occurs on a topographical basis, where different species forage in different parts of the habitat. This causes the spacing of species in the habitat, as described by Barlow (1974a), Fishelson et al. (1974), Reese (1975), and Fishelson (1977). As mentioned by Reese (1975), in chaetodontids the highest agonistic tendencies occur between species with similar feeding habits, and in such a way that the sympatry of relatives is decreased. As a consequence, in various places of the habitat groups of fish belonging to different taxa are found that forage on the same food source. In such instances, as in the case of shelter utilization, we are also witnessing the development of guilds, in which interspecific behavioral phenomena connected with feeding emerge. One of these is social feeding of multispecies assemblies (Fishelson 1977). For example, such assemblies browsing on coral platforms in the Red Sea include the surgeonfishes *Acanthurus fuscoguttatus* and *Ctenochaetus strigosus* as the leading and most numerous ones. These are joined by *Chaetodon chrysurus, C. auriga, Rhinecanthus verrucosus, Scarus caeruleus, Coris angulatus, C. variegatus, Acanthopagrus bifasciatus* and *Diplodus noct.* Such groups move back and forth along the platform, feeding on the algal cover. In such groups each animal goes where the group goes, and according to Wilson (1975), in such instances we are witnessing a type of imitative foraging supported by social facilitation. Different types of herbivorous, foraging assemblies are formed over sand flats and in these the leading species seem to be the siganids.

Assemblies like this are also temporarily formed when huge masses of plankton drift into the littoral zone. On such occasions the planktonivorous fish schools like those of *Abudefduf saxatilis, Caesio lunaris,* and *Atherina forskali,* are joined by groups of herbivorous *Diplodus noct, Siganus rivulatus, Acanthopagrus bifasciatus,* and *Scolopsis ghanam,* as well as by such typical reef-dwellers as *Paraglyphododon melas, Abudefduf leucogaster,* and various species of the genus *Pomacentrus.*

In all these groups there are almost no agonistic interactions, and as they stop to feed, each of the monospecific groups departs toward its "home." As soon as one small group starts to feed again, it attracts other groups, and so again a new foraging assembly is formed. This type of social feeding facilitation proves to be a very important device that, in habitats rich in food, enables maximum food utilization with minimum energy expenditure in searching for it. Special guilds of juvenile fish form on shallow, subtidal grass beds, especially during low tides, as those shallow waters are protected from large piscivorous predators. Such guilds include several species of goatfish, numerous siganid and sparid juveniles, and several species of wrasses, damselfish and triggerfish. These species wandering among the grasses are joined by the subtidal sessile blennies, all of them feeding on the Aufwuchs. The adults of some of these fishes (siganids, sparids and some wrasses) are found on grass beds like this but in deeper waters, and it seems that the shallow-water foraging arena serves as an important source of individuals for the deeper-living population.

This interspecific transfer of information has also been observed in Israeli multispecies fish ponds, in which pelletized food is added automatically from mechanical devices. In such ponds, the first to discover the food are the common carps and they rush toward the food source. The next to come are the grey mullets and tilapias, and the silver carps form an outer circle around the foragers. Experimenting with artificial feeding stations in the Gulf of Eilat, Fishelson (1977) observed similar behavior: around each of the temporary, newly introduced food sources, assemblies of fish gathered, usually a mixture of open-water and coral-dwelling species. What was interesting to note was that after experiments were repeatedly conducted in one place, the fish started to gather as soon as they spotted the experimenter, a phenomenon well known from aquaria. It was also observed that individual fish started to swim toward a food source as soon as they spotted another fish rushing in this direction, even if the food itself was not visible to them. Such "learned" behavior was observed only with experienced fish. Naive fish in new localities did not show such capability.

It appears that we are dealing with several evolutionary adaptations that enable much better utilization of existing food resources at the lowest energy cost. This is of great importance from the ecological point of view, for the following reasons:

1. Swimming toward a temporal focal point for foraging, fish frequently leave their "innate" original niche. Thus, they extend their food resources. This is of crucial importance in case the original source vanishes or is insufficient to maintain the population.
2. The lack of aggression and merging into large foraging groups serves as an anti-predator system. According to many authors (see Wilson 1975) single fish in larger groups are much better protected than in small ones.
3. The high learning and memorizing ability (at least for a short time) of fish enables them to change diets (and shelters) and so to survive under severe conditions.

An interesting phenomenon connected with food sharing was recently described by Ogden and Buckman (1974) and Fishelson (1977), and named "following behavior." It was observed that certain foraging fish provoke other fish to approach and try to use the feeding fishes' activity to collect their share. In the Red Sea, the most important attractants are goatfish *Pseudopeneus plerospilus* and *P. macronema.* As they dig with their barbs in the soft bottom and raise clouds of sediment looking for prey, various fish converge on them and catch their food from the cloud. Such a group may move along long paths, and all the time wrasses, surgeonfish, triggerfish and butterflyfish will follow the diggers catching food. Along the Caribbean coast of Panama, such behavior is provoked by *Scarus croicensis,* and in the Red Sea also by the bathoid *Taeniura lymma.* A special type of attraction is produced by wrasses of the genus *Coris,* especially *Coris gaimardi.* When looking for food, these fishes approach small stones or dead corals on the soft bottom and pushing with their noses, while stroking strongly with their tails, push them upside down. Once the hidden part of the rock is exposed, they start to pick up their food. They are joined by other fish species, and all of them feed together (personal observation).

These aggregations of carnivorous and omnivorous fish, as the formerly described assemblies of herbivorous and planktonivorous fish, display food-sharing patterns that are complicated and are probably more highly evolved. This idea is supported by observation of shelter change and of following behavior which develops as the fish matures. Juvenile fish living solitarily or in small hiding groups do not follow and do not react to passing fish assemblies. This was evident from the behavior of juvenile *A. saxatilis,* small wrasses such as *Thalassoma ruppeli* and *Coris angulatus,* and small *Acanthurus* spp. and *Ctenochaetus strigosus.*

Very few papers have been published about food-sharing behavior among carnivorous fish. Most of the planktonivorous species live in schools, especially if they hunt during the day. Individuals in such groups are usually uniformly colored, lack prominent patterns, and show typical schooling characters as described by Shaw (1962). A few such schooling fish hunt for plankton at night, for example *Pempheris* spp. and *Parapriacanthus* spp., and these disperse widely during food collection. During the daytime, these species rest in holes and crevices of the shallow subtidal. As mentioned earlier, these feeding schools of planktonivorous fish are often joined during the day by omnivorous or herbivorous species, and in this way mixed multispecies herds are formed.

A typical food-sharing behavior was recently described by Fishelson (1975) from the Gulf of Eilat. In this case, during the early evening *Pterois volitans,* which usually preys close to the bottom, moves up toward the water surface and takes part in hunting of *Atherina* and *Hepsetia* schools, together with belonid and hemirhamphid fish. During this hunt, the lionfish uses a special technique of "luring." It remains motionless below the water surface, with its head up, waiting for the schools of small fish that in a rush escape from the chasing predators.

Food partitioning is much more common and more often described than is food sharing in carnivorous fish. This is also common in terrestrial ecosystems and it seems to be a more economical way for a predator to meet its food requirements. Territoriality is one type of hunting-space partitioning in piscivorous fish species. When fish populations of coral knolls are observed in the northern Red Sea, it becomes evident that each knoll has its hunter, normally *Cephalopholis argus, Variola lothi,* or *Epinephelus* spp. During the day, these fish control their territories, swimming slowly around and chasing away conspecifics. It is of interest to note that during this cruising of the predator, its prey population on the knoll remains undisturbed. But at dawn as the predators move out for the hunt, any of their approaches toward prey groups elicits escape behavior. This phenomenon, which has been intensively investigated in terrestrial situations, has almost never been studied in aquatic systems.

A type of prey partitioning was recently described for the lionfish by Fishelson (1975). Three species of lionfish occur on the Eilat (Red Sea) coral reefs, of which *Dendrochirus brachypterus* feeds mostly on benthic invertebrates, especially over sandy bottoms surrounding their nest rocks; *Pterois radiata* hunts invertebrates on and along the coral reef surfaces, from time to time also taking fish; and *Pterois volitans* usually hunts fish, chasing them into holes in the reef of taking them in the open water. Thus, these typical coral reef predators do not compete for their food resources. The most ecologically important partitioning of food occurs between age classes of the same species, a phenomenon extensively described in numerous publications. In many cases, with a change in the prey diet, the general behavior of the fish changes also. A striking example is that of the striped catfish *Plotosus lineatus*, a night-active carnivore observed in the Red Sea (Fishelson, unpublished). The adults of this fish live solitarily under cover on the bottom and feed on fish. The fry are social animals, forming schools of 100-150 individuals which are active during the daytime and feed on floating fish fry and crustaceans. When disturbed, these fry do not disperse, but instead they gather into a compact ball, their heads and poisonous pectoral spines directed outwards. Such a "balloon" remains together till the danger passes. This behavior disappears as the juveniles attain 7-8 cm total length.

Feeding Strategies of Fish and Management

In mariculture the artificial reefs and in aquaculture the multispecies fish ponds are the first steps toward the goal of optimal utilization of available resources, namely water, food, space, and fertilizer, at minimal cost. Fish managers should choose fish assemblies with the greatest adaptability to food changes. In Israel, for example, common carp, silver carp, grass carp, grey mullets and *Sarotherodon (Tilapia)* hybrids are raised together. All these are herbivorous fish, but they utilize plant food of different qualities. As a result the yields range from an average of 1000 kg/ha annually to 4000 and even 10,000 kg/ha annually.

If we could add two factors to such herbivorous assemblies in warmwater ponds on all continents the yield could rise again. First of all, we should add prey fish, for example, *Dicentrarchus labrax* or the freshwater *Ophiocephalus striatus*. Introduced at the right time, these fish will prevent overcrowding from natural reproduction and they themselves will be welcome addition to the catch. Secondly, different age classes of the same fish have different diets. By knowing this we are able to stock ponds with fish of different sizes, and using selective capture, to increase the net production. We tested this with *Tilapia* hybrids (Fishelson and Loya 1968), and even in ponds without additional feeding, the results were encouraging.

It seems that to renew and establish assemblies of fish in artificial habitats, we should look for species with the most plastic food utilization strategies. Such a group should include bottom feeders, suspension feeders (day- and night-active), grazers on higher plants, omnivores living on detritus and carnivores preying on fish fry, or as the sparids, on molluscs. As grazers in marine or brackish waters, the siganids seem to be the best adapted (Lam 1974, Wasternhage 1976). In all these groups it is important to look for species with delayed reproduction, thus having optimal growth rate, and diets differing with age classes. These characteristics are typical of pioneer communities in nature, and fishponds should be regarded as being of the same type.

In the marine environment, fish species management should be focused on increasing the survival rates of the juveniles, and this may be achieved by providing a food supply for young fish in localities where they will not compete with older ones. Thus, for example, it is possible to establish feeding stations in nature, with an aim of conditioning local fish populations to a certain diet. Pioneering work in this direction has been performed by Japanese ichthyologists. In the future, the use of such feeding focal points, coupled with adequate catch techniques, will possibly raise the yields and lower the energy input per effort by training fish to feed on food with a low protein level.

As mentioned earlier, subtidal grass beds are foraging grounds for many commercially important fish species. It seems that such niches can be artificially produced, and so raise the survivorship of the juveniles. Such artificial grass beds can be produced from inexpensive or recycled polymeric materials, and anchored on the bottom at optimal sites. As recently observed on the Sinai coast of the Red Sea, such materials are very soon covered by Aufwuchs and various fouling organisms, and are invaded by invertebrates, thus forming good feeding grounds for assemblies of juvenile fish of the same species that form interspecific cohorts in deeper waters. These grass beds would serve as harvesting sites, as well as a supply of individuals for repopulation of extensively fished habitats. It is also possible to establish microhabitats in the natural habitats (Fig. 5) in which large numbers of juvenile fish can be grown until they attain a size that promises better survival.

Conclusions

1. The evolutionary development of multispecies communities has been molded by space and food. In aquatic, food-rich habitats, space was the main factor and several important behavioral and developmental patterns observed in fish are expressions of strategies leading to optimal utilization of this resource. Space partitioning and social-assembly formation are the main characteristics of such co-

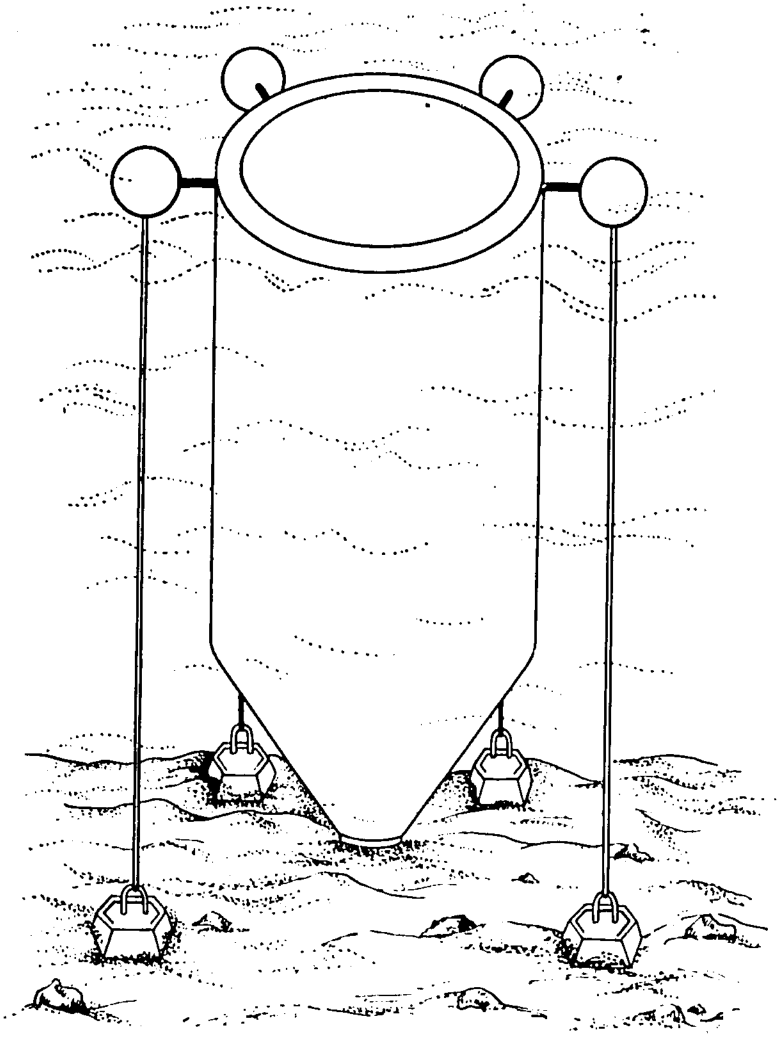

FIG. 5. A microhabitat for raising fish larvae in nature, constructed from a sac attached to a float and anchored in a lagoon. The sac is constructed from plankton netting whose mesh size is determined by dimensions of larvae being raised. (Drawn by S. Shaeffer).

utilization.

2. Changeover behavior of freshwater and marine fishes is one strategy that enables different fish species to use the same space (shelters) at different times. The variety and biomass of species that use such a shelter is controlled by the dimensions and geometrical diversity of the shelter. By introducing artificial shelters and fish assemblies able to use them, this strategy can also be used for fish

management in natural waters as well as in fish ponds.

3. Space utilization and distribution in relation to topographical gradients is the second type of strategy that enables multispecies populations of fishes to disperse in a given habitat and forage on the same food without competition. This, together with the ability of fish to change diet and temporarily space, produces effective general utilizers of the resources.

4. Specialization for specific shelter is the third type of space utilization that enables fauna enrichment. Microhabitat-users normally form a minority group of species in natural multispecies habitats compared to the generalists, but in some predator-prey systems their presence could be of great importance. Until the present these species have been neglected in aquaculture, but it seems that their introduction will significantly improve yields.

5. Space-change with ontogenetic development is an additional trend observed in many fish species. This type of change seems to be the most important strategy for preventing intraspecific competition. As the shelter-seekers are in most cases the juvenile fish, it seems that by improving the absorption ability of spaces, we could immensely increase the survival of replacement stocks for utilized fish populations. By moving from one niche to another during their development, many fish species enlarge the scope of resources they use. Improvement of shelter qualities could be visualized also for polyculture fish ponds by changing the pond complexity from a simple, aquarium-like structure to a multidimensional one. But in such cases new harvesting techniques should be utilized, especially those based on stimulative olfactory, acoustical, or visual attractants.

6. Marifarms or aquafarms with modular units adopted for use by various age classes of fish will facilitate fish production. The units can also be used in naturally existing habitats. Aquafarms using such structures, central feeding stations, and special fishing techniques should also be aware of behavioral patterns and developmental biology of the fish to be harvested.

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fish and then moved the heads closer and closer until they were separated by less than 1/2 m, a part of one population moved over to the other coral. Then we moved the corals apart and we got two coral heads populated. So by constructing artificial biota you will increase the biomass, because food is not the problem there.

BARDACH

And now to the ponds in which we partition space for polyculture.

FISHELSON

Yes. You see, if you are producing a polyculture pond you must decide a priori if it is going to be self-sustaining from the point of food. If so, you will look for an assembly of species feeding on plant matter. To stimulate plant growth you will fertilize the ponds. Today we use only 2 or 3 species of *Tilapia*. There are 12 species of *Tilapia* in Malawi that feed on different plants and diatoms—diatoms from suspension and diatoms from the bottom and so on. In the future, we could put these species together in ponds, and then we would have beautiful growth without adding any food. Food for feeding fish is becoming more and more expensive.

BARDACH

As an example from another continent, Eigenmann's harvest out of a small pond in Brazil was mentioned. I also looked at the feeding types of those fishes: there is a tremendous ramification of feeding types—fruit eaters, plankton feeders, plant eaters, leftover feeders, etc. The South American fish fauna thus presents a great opportunity for developing further polyculture complexes. Fruit eaters, especially, grow to a very nice size in Brazil and are among the best fishes that I've ever eaten.

MYRBERG

Do you believe that resources are being partitioned on the reef?

FISHELSON

No. I suppose the opposite. Concerning feeding, we are dealing more with generalists than specialists, because being a specialist is an evolutionary trap. All the symbiotic relations are traps for evolution.

MYRBERG

If they are generalists from the standpoint of feeding, do you believe that they are also generalists from the standpoint of space?

FISHELSON

Yes, there are many generalists of space and of feeding.

MYRBERG

The cichlids of the rift lakes in Africa are well known as specialists in regard to food. On the reef, although there are many omnivores, there are also many specialists.

FISHELSON

I know this has been mentioned in many papers, but numerous experiments have shown that many of the fish described as specialists are in fact generalists, using various food sources.

MYRBERG

But do you believe that there are many specialists out on the reef?

FISHELSON

Of course there are many specialists, together with many generalists, but the specialists are all small fishes, and their biomass is minute compared to that of the generalists.

MAGNUSON

I'm puzzled. Much of the data you presented and many of the manipulations that have been made were in regard to animals that have particular requirements. For example, you talked of vertical hiding spaces' encouraging more different kinds of species than side hiding spaces.

FISHELSON

Those are the fish specialized for different types of habitats.

MAGNUSON

The goatfish and their followers—are those specialists?

FISHELSON

No, because if in this assembly the goatfish stop moving along, then the acanthurids will feed by browsing, scarids will bite on coral surfaces, chaetodontids will feed among coral, and so forth. At such times this coral fish assembly is dispersing but at the moment that the group forms again, all of them gather to forage on food produced by digging of the goatfish. So this is really a general behavior pattern without narrow specializations. In the life histories of all the investigated species, you have on the one hand specialists like *Dascyllus aruanus,* and you have generalists—or multidomic species as I call them—such as *Abudefduf* spp. and a lot of others, changing their spaces during their life history. The juvenile stages of some pomacentrid fishes are living in an entirely different habitat than the adults.

BARDACH

The danger here is that by selecting only generalists you are not able to make up a good coral reef and you cannot fine-tune that system.

REINBOTH

I had many difficulties when I heard your paper. Just one example. Take the *Dascyllus.* You told us what happens when you move a coral. I do not doubt that a part of the *Dascyllus* population will move out of that coral and colonize the other one. You take a third one and you have the same success. But did you look at the effects which an increase in the number of *Dascyllus* will have on related species? This increase also affects invertebrate fauna, it will affect the plankton, and so on. You neglect all this. I can see your point if you take your experience from the open reef in order to apply it for setting up an artisanal pond. But when you are doing the same thing in the open sea, then I am afraid that something is happening as Dr. Bardach described: you are just moving around a little bit without having an actual increase of the total biomass. You yourself gave an example in an earlier discussion of what may happen when you don't pay attention to interspecific interactions. You mentioned that spear fishermen shooting the big *Epinephelus* will favor an increase in the number of *Pterois.* When you are manipulating a particular species in the sea, what do you know about the side effects of your manipulations on other species that live in the same habitat?

FISHELSON

I know areas in which these population of *Dascyllus aruanus* are much higher. All the reef population feeding on plankton receives the food from the open sea. I cannot manipulate the open sea. But I'm sure if I will establish more optimal situations for *Dascyllus aruanus*, we will have more *Dascyllus aruanus*. And this will not destroy the invertebrate or other populations. Those populations may also rise, because if we talk about coral reefs that are inhabited by fishes, then there are more possibilities. Those reefs are also penetrated by various invertebrates, the larvae of which form an important part of the near-reef plankton.

Influence of Fish Behavior on Use and Design of Setnets

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Fish behavior has a profound influence on use and design of setnets. The depth contours over which the leader net is set are perhaps the most important consideration in the location of a large scale setnet. Movements and aggregation of fishes in relation to the depth contours, possible shelters, and other oceanographic features are important behavioral data for determining effective locations for setnets. Visibility and audibility of the leader net are important in turning and guiding fishes toward the bag. Contrast of the twine with background, illumination, mesh size, and twine diameter all influence visibility. Interspecific differences greatly influence selection of mesh size, not only because their body size differs, but also because propensity of each species to approach the net and swim through the meshes differs greatly. The design characteristics of the bag nets depend greatly on whether the species has a tendency to swim close to the webbing or at a distance from it and on whether the fish tend to enter the net during day or during dusk and at night. The use of the slender bag trap is especially important for fish that approach the webbing closely if good catches are to be obtained.

Introduction

Setnets are anchored along the coasts of Japan where they intercept migrating pelagic fishes and local populations of midwater and demersal fishes. Catches from 12,300 setnets constitute about 3% of our total landings or 300,000 tons of fishes such as yellowtail *(Seriola quinqueradiata)*, bluefin tuna *(Thunnus orientalio)*, mackerel *(Scomber japonicus)* and chum salmon *(Oncorhynchus keta)*.

Considerable attention is being directed towards the improvement of the trapnet in Japanese fisheries. Trapnet fisheries are coastal and more attractive to fishermen than distant water high seas fisheries. In addition, trapnet fisheries have economic and energy-related advantages over active search and active capture fisheries. My purposes are to point out the advantages of trapnets over other types of fishing gear, to describe the design and use of several Japanese trapnets, and point out the relation between fish behavior and the design and deployment of trapnets.

Economic and Energy Considerations

There are large differences among fisheries in the weight and value of fishes caught per unit of fuel consumed (Table 1). Pelagic distant water fisheries are less efficient in regard to fuel than are nearshore fisheries on the same groups of fishes. Demersal bottom trawl fisheries tend to be more fuel efficient than surface and midwater fisheries, but large-scale trapnet fisheries are an order of magnitude more fuel efficient than any other Japanese fishery listed in Table 1, whether measured in terms of yen or biomass per unit fuel consumption.

Fuel efficiency is becoming increasingly more significant as the price of fuel is increasing so rapidly. Since the sudden increase in oil prices in 1973, fuel costs have doubled from 10% to 20% of the operating costs of Japanese fishing boats and profits before depreciation have halved from 40 to 18% of gross income. Wages and interest costs have also increased significantly. Thus, fuel efficiency is becoming more important to the economic vitality of fisheries.

Setnet fisheries have obvious advantages since they do not require distant water vessels and long trips. In addition, setnets are passive gear which depend on the fishes' inherent movement. For example, it is not necessary to use fuel to pull a trawl as is required with active fishing gear. Setnets fish continually day and night and require only periodic tending so that fish can be removed, and damaged or deteriorating nets repaired. In addition to saving energy, I believe the setnet fishery has advantages in preserving resources, developing marine ranching, improving safety of fishermen, minimizing capital investments, and providing a more pleasant life at home for fishermen. Examples of the Japanese bluefin tuna and Hokkaido chum salmon fisheries suffice to emphasize my point. Since the development of the purse seine and drift net fishery for bluefin tuna, the schools do not approach the shore, whereas prior to the Second World War we had a profitable, large setnet fishery. If the energy put into fuel and ships for the offshore fishery were put into artificial spawning, for example, we could again conceivably use

Table 1. Ship size, fuel consumption, weight and value of catch per kL of fuel, and price of fish for 1975 in Japan. (Fisheries ordered from lowest to highest catch (kg) per kL of fuel oil consumed).

Fishery	Ship size (tons)	Fuel oil consumption (kL/year)	Catch relative to fuel consumption		
			Weight (kg/kL)	Value[a] (yen/kL)	Price of fish (yen/kg)
Tuna longline (far sea)	192 229 344	600b 960 1050	270	118,000 208,000 175,000	740
Tuna longline (offshore)	69	390	430	233,000	540
Salmon drift net (mother boat type)	96	220	530	430,000	810
Squid angling (far sea)	300	660	820	172,000	209
Salmon drift net (catcher boat)	65	260	822	374,000	450
Skipjack pole and line (far sea)	284 374	1500 1200	860	130,000 178,000	206
Skipjack pole and line (offshore)	59	400	—	186,000	—

Demersal fish trawl (East China Sea)	114	1200	960	190,000	197
Squid angling (offshore)	99	322	1800	256,000	320
Pelagic fish purse seine (1 unit fleet)	111	3100	3600	218,000	60
Alaska pollack trawl (North Pacific)	349	2800	4800	146,000	30
Setnet large-scale 250 tons of catch per year	—	20	12500	2,500,000	200

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[a] In April, 1975 1,000 yen = 341 U.S. dollars.
[b] Two voyages.

setnets and maintain the stocks at the same time. This has been accomplished with the Hokkaido chum salmon fishery where recently 500 million fish have been produced and released from a hatchery to yield 3 to 4 yr later a catch of 32,000 metric tons valued at 20 billion yen per year from a trapnet fishery.

Increasing the effectiveness of setnets requires detailed information on the behavior of fishes and in particular, their distribution and movements in the coastal waters and their behavioral response to the setnet itself. Any increase in effectiveness would further improve the fuel efficiency of the catches, but requires that the maintenance or even the enhancement of the stocks be given high priority at the same time.

Construction of the Setnet

A large-scale setnet (Fig. 1) is a passive fishing gear capturing fishes that in their movements encounter a lead which directs their swimming through the mouth toward a playground which acts as a

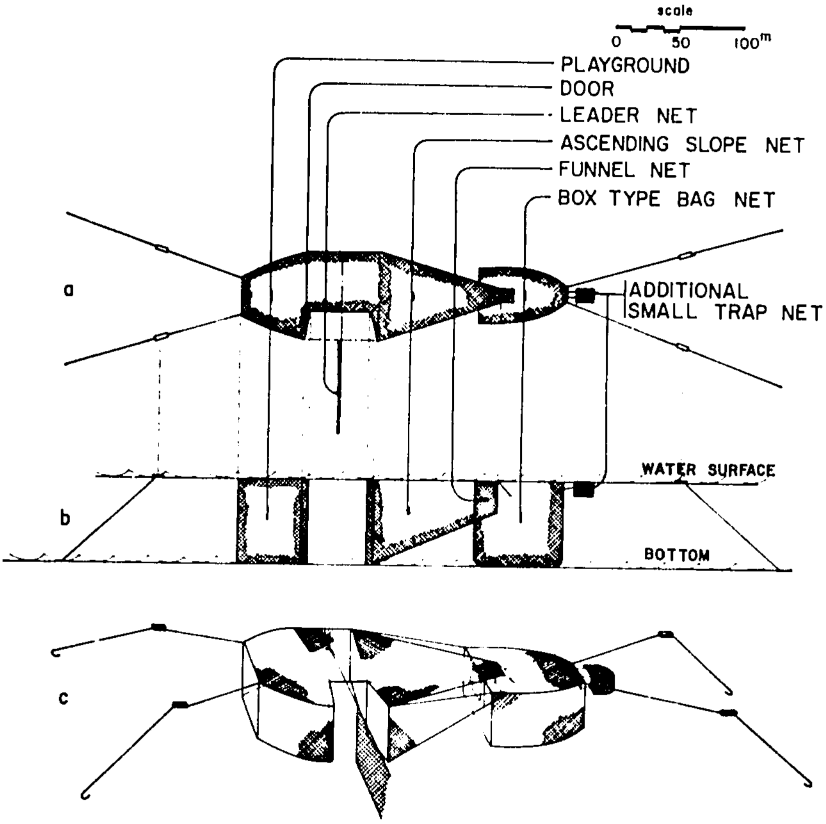


Fig. 1. Structure of a large-scale setnet "Otoshi-ami"; a, top view; b, side view; c, perspective view.

retaining area. An ascending slope net directs the fish into the smaller "bags" where they are finally caught. In water 45 m deep or greater there are at present about 250 of these large-scale setnets fished in Japan. In addition, about 500 medium-scale setnets of somewhat different design are fished in waters 25 to 45 m deep and 12,000 small-scale setnets in waters less than 25 m deep.

Setnets are also classified by how they are fished and set, and they occur in great variety of designs. The design problems usually relate to the material in the leader net, how the leader net is set, construction of the mouth and the door net, the size of the playground, the inclination of the slope net, and size and shape of the funnel net, bag net, and slender bag nets. In many of the smaller nets there may be only a lead and a bag net. Small-scale nets often have a lead and a playground with small funnel traps attached. The large-scale setnet (Fig. 1) is the most important type of setnet and its construction is more complex than that of smaller nets.

Location of the Setnet

Bottom topography, water mass distribution, and coastal circulation patterns are all important in selection of an optimum site for a setnet. Good sites for a large-scale setnet for yellowtail are ones with closely spaced depth contours that have a large area in front of the net (Fig. 2a). The fish tend to enter the bay from deeper water and are caught as they leave the bay. Setting the net across submerged valleys or near natural fish shelters (Fig. 2b) is also effective.

The closely spaced depth contours are important because it is possible to have the net extend to deeper waters. Acoustic surveys by Kawada and Tawara (1958), Tawara (1966) and Inoue (1976) show that yellowtail usually travel along the 30- to 60-m depth contours. Thus, the net can extend deeply enough to encounter the yellowtail and shallow enough so that they do not go around the inshore side of the net.

Fish apparently aggregate around artificial fish shelters (Nozawa 1971). At Shimakatsu (Fig. 2b) the nets are set on each side of several natural fish shelters. Observers have noted that fish move along the shelters one by one and change course and swim along the depth contour toward the setnets. Kuwatani (1962) points out that many factors influence the effectiveness of shelters but experimental verification required for design of the best shelters in relation to environmental conditions is wanting.

We have data on fish distribution from acoustic surveys in relation to setnets at Fukuura and at Enoura (Inoue 1976, 1977). At Fukuura the summer distribution of small, medium, and large schools are compared with each other and with the catch in a small-scale setnet

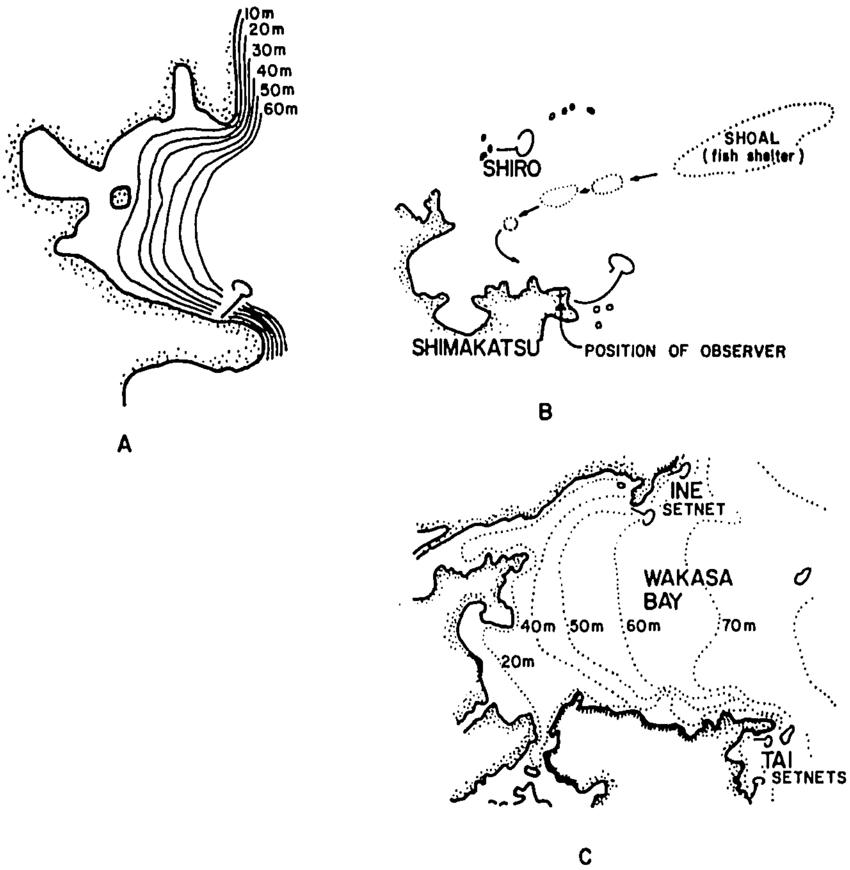


FIG. 2. Examples of good sites for large-scale setnets. A, an area with closely spaced depth contours and a large fishing area (Miyamoto 1962); B, near fish shelters; C, lead set obliquely to depth contours.

at 15 m and a large-scale setnet at 15 m out to 50 m. Small schools occurred primarily near the 10- to 20-m depth contour and large schools near the 20- to 50-m depth contours (Fig. 3). Mackerel and jack mackerel *(Trachurus japonicus)* were the most abundant groups in both nets but a greater number of species made up the catch of the large-scale setnet (Table 2) including significant proportions of squid *(Ommastrephes sloani pacifica)*, frigate mackerel *(Auxishira)*, filefish *(Cantherinus modestus)*, grunts *(Parapristipoma trilineatum)*, hairtails *(Trichiurus haumela)*, flying fish *(Cypeelurus agoo)*, and yellowtails. The large-scale setnet thus caught the same species as the small-scale setnet in shallow water but also caught animals from the larger schools in deeper water.

Similar data from Enoura show that when winter and summer distributions of midwater schools and schools near shoals (reefs or

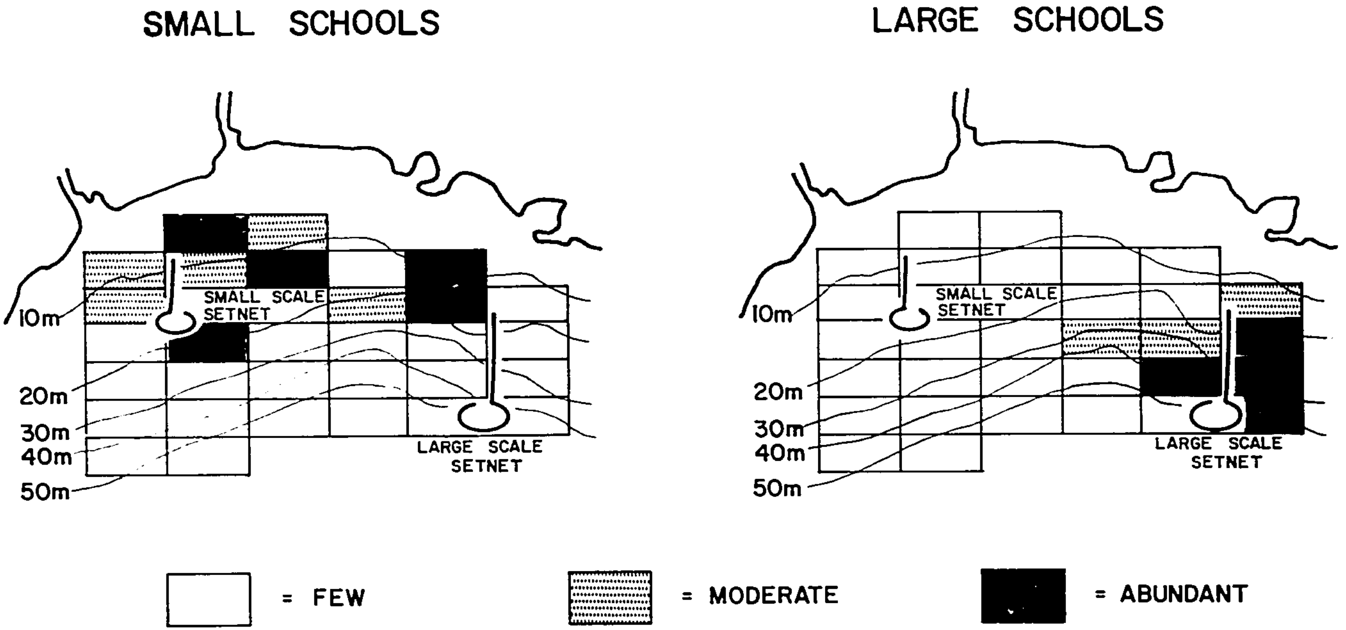


FIG. 3. Distribution of small and large schools in relation to the depth contours and the position of a large and a small-scale setnet at Fukuura Fishing Grounds. Data from acoustic survey in summer.

bottom) are compared, one finds that large schools in midwater were in shallow water (20-30 m) in winter and the fishes were not distributed uniformly in space or time. Large and small schools around shoals were in relatively shallow water (20-70 m) in both summer and winter.

TABLE 2. Frequency (percent) of fish emergence in a large-scale setnet and a small-scale setnet at Fukuura in summer.

	Percent of catch	
Species	Large-scale setnet	Small-scale setnet
Mackerel	31	40
Jack mackerel	15	36
Barracuda	6	12
Squid	11	0
Frigate mackerel	9	0
Round herring	0	7
Filefish	6	0
Grunt	5	0
Hairtail	5	0
Flying fish	4	0
Yellowtail	2	0
Other	7	5

In addition to the depth and location of the setnet, the direction at which the leader net is set is important. Usually the leader net is set perpendicular to the coast to reach deeper waters and ranges from 500 to 5,000 m long. When set perpendicular to the coast, more fish encounter it than if it were set obliquely, but in addition, fish are more likely to swim through the lead and schools are more likely to disperse. According to fishermen's experience the most effective setting angle θ is 130 to 140 degrees from the depth contour so that the migrating fish have to change course by only 40 or 50 degrees when they encounter the lead (Fig. 4). In laboratory experiments with schools of smaller fish the number of fish moving along a barrier increases as the angle θ is increased (Tauti 1929 a,b,c). If the bottom of the tank is sloped, more of the fish move smoothly along the barrier if they approach from the shallow side of the tank than if they encounter the barrier from the deeper side (Tauti et al. 1933).

Tracking fishes with acoustic transmitters may help to provide useful information on the location and orientation of the net. Kuroki (1971) tracked the movement of sea bream (*Plectorhinchus cinctus)* near a setnet. The onshore and offshore movements as well as the alongshore movements were observed. In 28 min the fish ranged to waters as deep as 60 m and moved about 400 m along the coast,

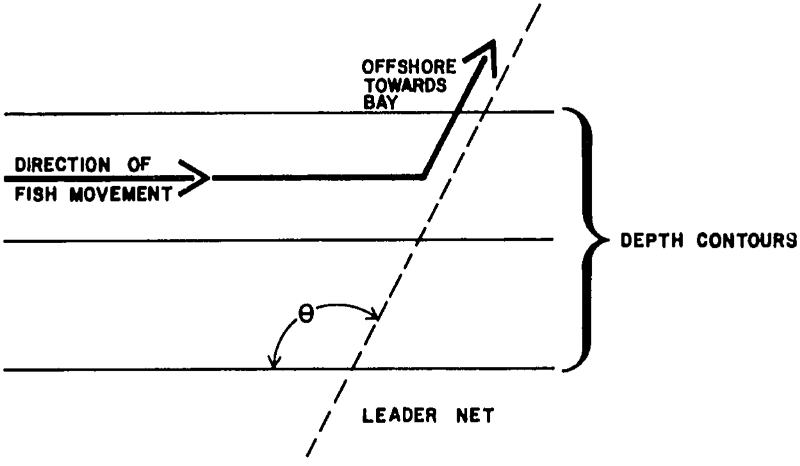


FIG. 4. Optimum angle between the leader net and depth contour is $\theta = 130\text{-}140°$.

making numerous excursions perpendicular to the depth contours.

A few experiments have been conducted to lead, lure, or drive fish into a setnet. Sasaki (1953) used a path of underwater lights that were turned on and off in sequence. Hashimoto et al. (1964) and Maniwa (1976) attempted to lure or drive fish with underwater sound. Feeding sounds apparently attracted several pelagic species from the playground to the bag net (Sagami Branch Station of Kanagawa Prefectural Fisheries Experimental Station, 1972). None of these methods has been considered sufficiently for commercial application to date.

Behavioral Response to the Leader Net

The function of the leader net is to guide the fish to the playground or bag nets. The proportion of schools that lead along the net is quite low, 10-20% (Miura 1924 a,b), based on direct observation in the sea. Depending on the conditions, fish will swim along the leader net, through it, and into it, and be gilled or leave the area. Fish tend to pass through if they are frightened, if a very large school approaches the net perpendicularly, or if there are schools of the same species on the other side of the net. If one species moves through, others may follow. Distances at which fishes swim along the net are 6-7 m for barracuda (*Sphyraena pinguis* Gunther, 5-20 m for jack mackerel, and 10-15 m for yellowtail. Smaller schools will sometimes swim back and forth through the meshes.

Visual and acoustic characteristics of the leader net seem to be significant in leading the fish. Vibrations of the cords of the leader net in a typical current are about 100 Hz, and fish are sensitive to these low frequencies especially from a lateral aspect (Kuroki 1958). While such stimuli perhaps guide the fish along the leader net even at night, most design variations seem to be related to visual aspects of the net, for example, alterations in the construction materials, twine size, color, brightness, and mesh size. These features and others determine whether the fish will be gilled in the leader net, swim through it, swim at too great a distance from it, or change course and swim smoothly to the door of the net for distances up to 5 km.

Originally leader nets were constructed of straw cord. Now leader twines are typically straw cord (0.9 cm diameter), manila twine (0.28 cm diameter) or white nylon twine (0.09 cm diameter). Generally, the straw twine is more effective in leading the fish than is manila twine or white nylon twine, and at mesh sizes of 86 to 112 cm the white nylon twine is inferior to the manila twine based on experiments by Suzuki (1971). When the net becomes dirty after being set too long, its effectiveness in leading declines and catches are poor. To the human eye visibility depends on contrast of brightness with the background rather than the color itself. The yellow coloration of straw twine may be significant in enhancing contrast. Fishermen say that chum salmon are enmeshed in small mesh leaders if the twine is manila or cotton but not if it is straw cord (cord, 6-8 mm in diameter; mesh, 33 cm). Tsuda et al. (1973) observed the visibility of yellow twine was greatest in clear water but decreased in more turbid waters. They also found that transparent twines were less visible than opaque twines. Apparently the more visible the leader net, the more effective it is in leading the fish.

Mesh size and the orientation of the twine influence the effectiveness of the leader net as well. For mackerel, leader nets made only from vertical twine are more effective than those made from horizontal twine (Suzuki 1971). In early setnets meshes of straw cord were usually 35-45 cm longer than the girth of the fish. Mesh size differs greatly depending upon the species and size of fish. For bluefin tuna meshes are 1-3 m because the fish swim too far from the leader net if mesh size is smaller. Chum salmon, on the other hand, tend to pass through the net if the four sides of the mesh are only a little larger than their girth. The ratio between mesh size of the leader net and a gill net used to catch the same species shows that different fishes respond quite differently to the leader net. Mesh size of the leader net is 18 times bigger than mesh size in gill nets for sardine (*Sardinia melanosticta),* 13 times bigger for mackerel, 4 for jack mackerel, 2.3 for yellowtail, 1.9 for Pacific herring *(Clupea harengus pallasi),* 1.3 for chum salmon and trout *(Oncorhynchus masou),* 1.1 for atka mackerel *(Pleurogrammus azonus)* and gizzard shad *(Clupanodon punctatus),* 0.9 for sea bass *(Lateolabrax japonicus),* 0.8 for sea bream, and 0.4 for flounder *(Paralichthys oblivaceus).* Typical mesh sizes for setnets are small scale, 13.4 cm;

medium scale, 23.6 cm; and large scale 32.1 cm (Yoza and Miyamoto 1976) and the diameter of the twine is usually 0.015 times the mesh size. Mesh size can, in general, be larger for species that form large, dense schools.

Behavioral Response of Fish in the Net

When fish first enter the playground (Fig. 1) of the setnet, they may turn around and leave again. Data from acoustic sounders at the door of the playground suggest that 30% of the schools were entering, 20% were leaving, and the direction of the other 50% could not be determined. Speeds of fish entering averaged 0.3 m/sec (range = 0.1-0.6 m/sec) and were similar to those leaving, mean = 0.2 m/sec (range = 0.1-0.4 m/sec). The schools leaving were generally smaller than the schools that entered.

Once in the playground (Hiramoto 1967) mackerel and barracuda take many hours to enter the bag net, yellowtail make a large excursion within the playground and soon enter the bag net, and sea bass and sea bream swim along the walls of the playground and enter the bag net. Jack mackerel enter during dusk, and by dawn half have entered the bag but the other half are still swimming in the playground. Those species that approach the walls more closely are easier to lead into the box type bag net (Suzuki 1971).

The ascending slope net (Fig. 1) is to lead the fish to the funnel net and into the box type bag net. Surface species are more easily led at this point than are demersal species (Hiyama et al. 1954). Carp *(Cyprinus carpio)* and goldfish *(Carassius auratus)* in laboratory experiments by Inoue (1968) can distinguish inclination of 10 degrees primarily with visual senses. The ascending slope of large-scale trapnets usually rises from the bottom to mid-depths in the water column. The slope of nets on the coast of the Sea of Japan differ from those on the Pacific coast even though the same species are caught. The explanation of the differences in slope are not apparent but perhaps they are related to differences in transparency and water temperature.

Once in the bag net (Fig. 5) fishes may still escape; the addition of slender bag nets with nonreturn cones at their entrance will retain fish that would escape from the box type bag net (Dotsu 1957; Nozawa 1967) (Fig. 6). These differences are related to the behavior of the fishes (Suzuki 1971). Those species that will approach the net closely when in the bag tend to be easily led either out of the box type bag or into the slender bag net. Examples of the "approaching" species are yellowtail, black sea bream *(Sparus awinhonis)*, seabass, gizzard shad, grunt, cod *(Gadus macrocephalus)*, flounder, atka mackerel, and plaice *(Limanda herzensteini)*. Those that do not

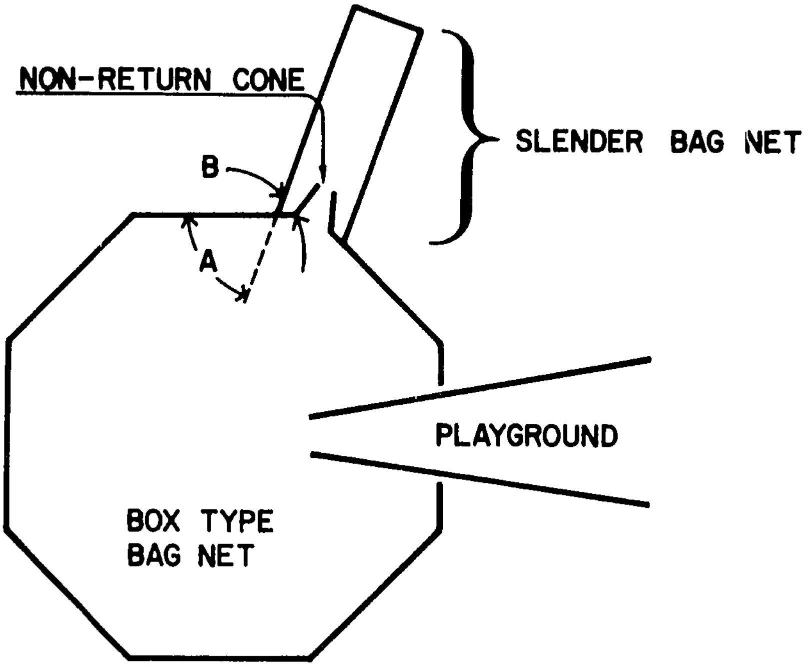


FIG. 5. Box type bag net with slender bag net attached. Entrance angles to slender bag net are indicated by A and B.

approach the webbing but stay at a distance are difficult to lead into the bag nets, especially a small one like the slender bag net, but these species are also more easily retained in a box type bag net. Examples of "non-approaching" type are mackerel, jack mackerel, scad *(Decapterus muroadsi)*, skipjack *(Katsuwonus vagans)*, tuna, saury *(Cololabis saira)*, and Spanish mackerel *(Sawara niphonia)*. These conclusions are additionally supported by tagging yellowtail and jack mackerel and releasing them into a box type bag net and the playground (Hiramoto 1970); some yellowtail released in the box type bag returned to the playground, and almost all released in the playground escaped from the net. A greater portion of jack mackerel remained in the box type bag.

To catch species that approach the webbing closely and those that do not, a combination of box and slender bag nets should be used. The entrance to the box type bag should be designed for those that do not approach the webbing closely and the slender bag traps should be designed for those that do. Slender bag nets should thus be attached to the walls of the box type bag.

Guiding fishes into the slender bag trap is influenced by the angles A and B in Fig. 5, the size of the inner mouth, and the brightness (color) and materials of the webbing. More fish enter the slender bag net as the angle A is decreased (Suzuki 1971; Miyamoto et al. 1954 a,b,c; Miyazaki 1960). Decreasing the angle A from 60 degrees to 30 degrees in Suzuki's experiments increased the number of fish

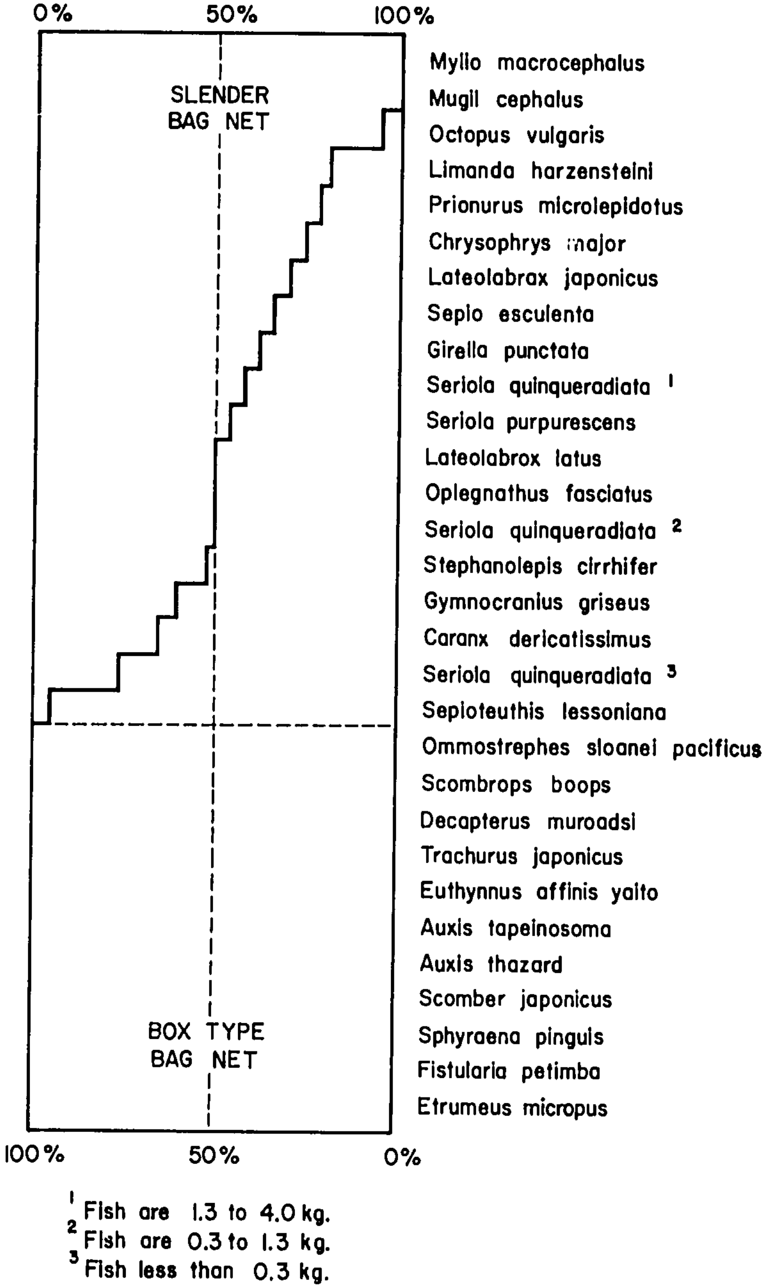


FIG. 6. The proportion of catch taken from the box type bag net and slender bag net in a pound net of medium size (Nozawa 1967).

entering by a factor of 1.3 for sea bass which approach the net closely. "Non-approaching" species such as jack mackerel enter less frequently but decreasing the angle A from 60 degrees to 30 degrees increased the number entering by a factor of 2 or to a greater extent than it did with the seabass. For the angle B (Fig. 5), more fish enter as the angle is decreased from 90 to 60, to 45, to 30 degrees when the inner mouth diameter is held constant (Suzuki 1971). Changes in the mouth size between 10 to 100 cm with a constant angle for B resulted in more fish of the "approaching" type being caught when the mouth was only slightly larger than the cross section of the fish, but for the "non-approaching" type much larger mouths were needed—60-80 cm for mackerel.

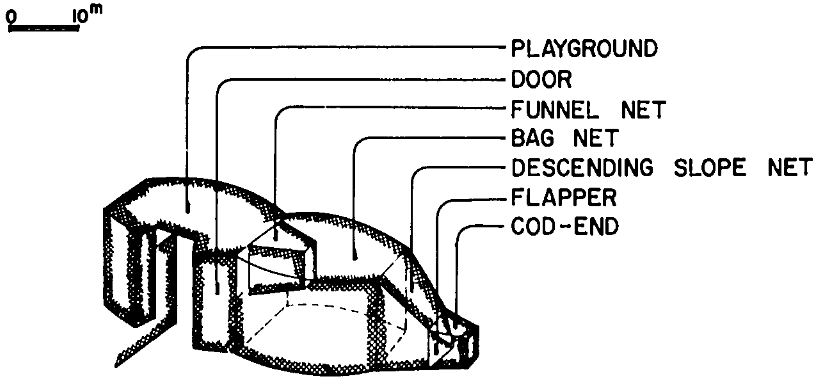
Effects of changing brightness (color) and materials of the slender bag net were studied by Koike (1968) and Miyamoto et al. (1954 a,b,c). Some species appeared to be influenced by the brightness (color) and others were not. Species that tended to enter at night were more affected by net color than those that enter during the day (Koike 1968). Blue appeared good for seabass; green for black sea bream, flatfish, and cuttlefish *(Sepiella maindroni)*; and red for conger-eel *(Lumpenus anguillaris)*, and greenling *(Hexagrammos octogrammus)*. Miyamoto's studies suggest that diurnal coastal fishes such as sea bream, black sea bream, shad, yellowtail, and flatfish were caught more readily by light colored nets, while nocturnal species such as eel and sharptoothed eel *(Synaphobranchus takedae)* were caught more readily in dark nets. Crab and shrimp were not affected. Nylon appeared better than cralon which appeared better than cotton.

Conclusion

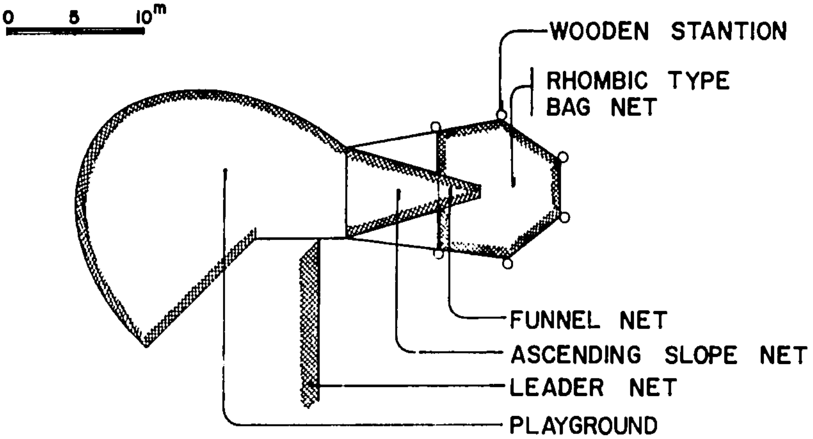
Setnets are fuel efficient, can be designed to increase catches of various species, and can be applied to new areas or species for fishery development. Promising areas for future development of large-scale setnet fisheries include yellowtail near New Zealand and Mexico, and skipjack in the Philippines and other locations. In Japan, decreasing pollution and supplementing reproduction from fish farming are essential to developing fisheries. A combination of ocean ranching and capture by setnet seems especially promising. An appendix (Tokunaga 1977) follows with examples of Japanese setnets (medium- and small-scale) whose designs have been improved by experiments or by the fishermen.

Appendix

I. Small-scale setnets. Floatlines are at the surface and sinkerlines are on the bottom.



PERSPECTIVE VIEW



TOP VIEW

FIG. 1. Upper: Setnet (Komuro type) used locally in Kanagawa Prefecture to catch midwater and bottom "approaching type" fish. Lower: Setnet ("Suisho-ami") used locally in Miyagi Prefecture. Construction of the rhombic type bag not has been improved to reduce manpower needed to operate it.

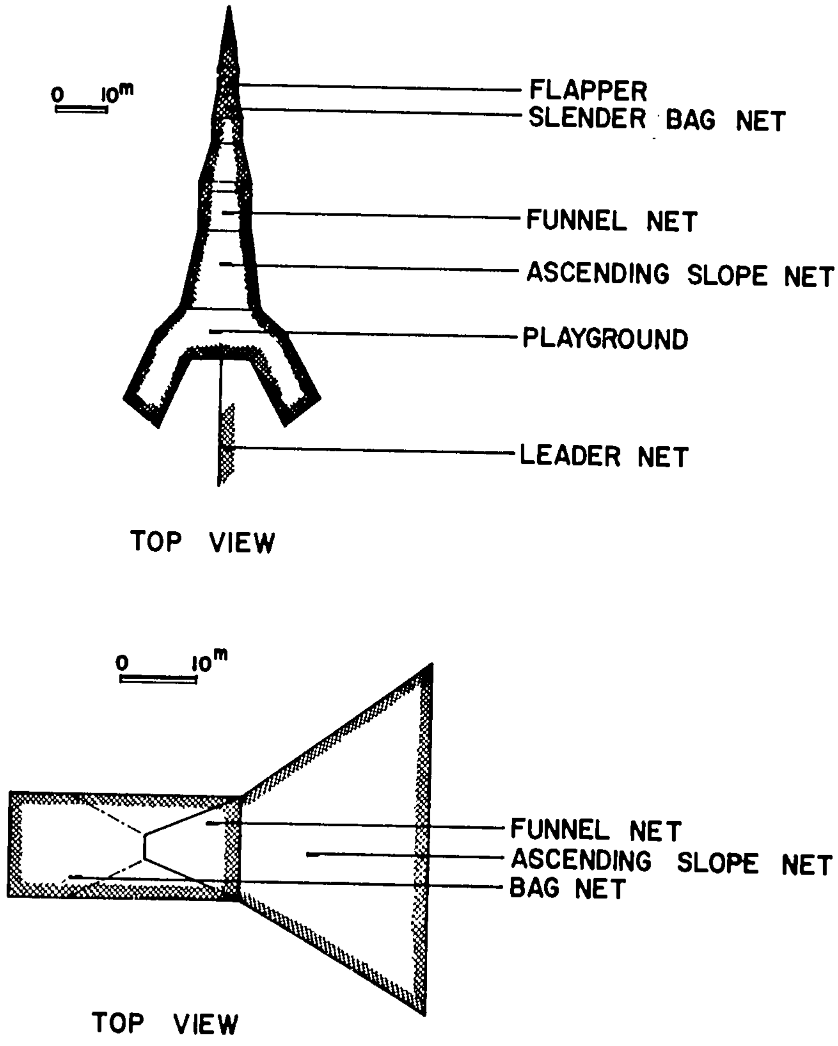
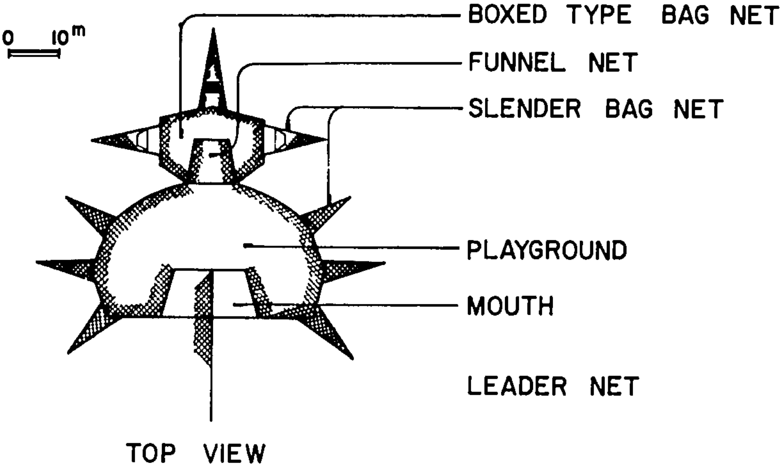


Fig. 2. Upper: Setnet (Yamazaki type) used locally in Nagasaki Prefecture. Long slender net reduces manpower requirement for operation (Tokunaga 1974). Lower: Setnet currently used for squid, with ascending slope net but lacking playground and leader net.



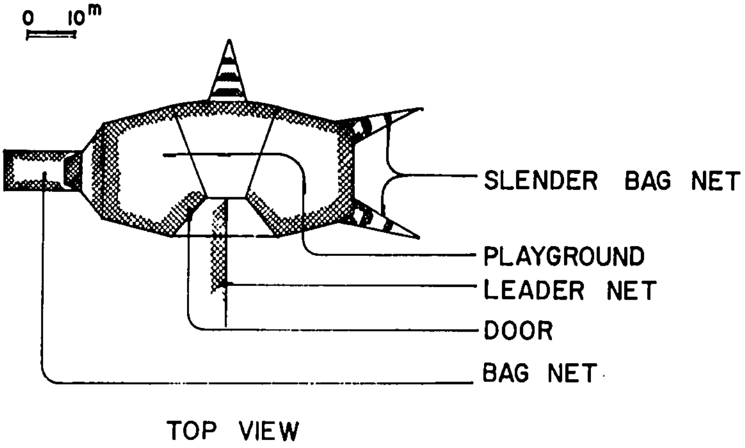


Fig. 3. Setnet ("Nezumitori-ami") currently used in Seto Marine Inland Sea. Boxed type bag net in center replaces one slender bag net, resulting in more fish caught. Lower: Setnet (Nobo type) used in Nagasaki Prefecture similar to net above, having boxed type bag net instead of a slender bag net on the left side of the net.

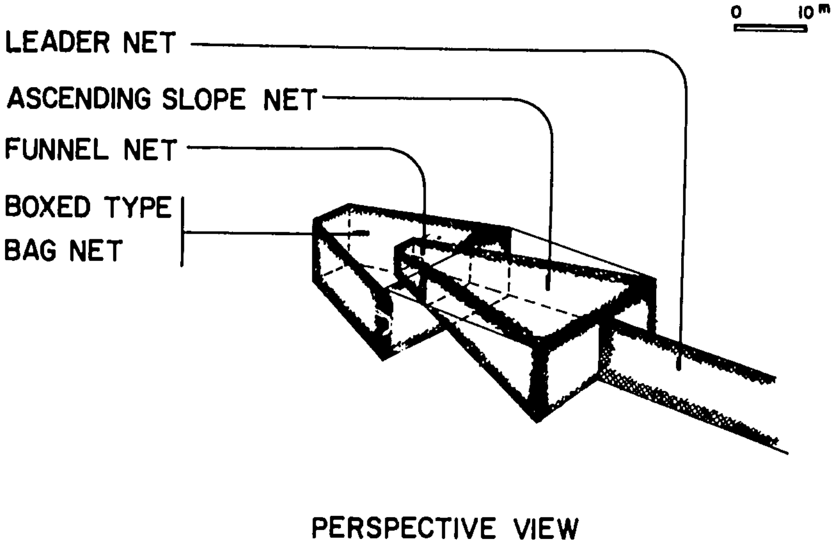


Fig. 4. Setnet for atka mackerel used in Aomori and Akita Prefectures. The combined use of bag net and ascending slope net offers an improvement over previous net designs.

II. Medium-scale setnets.

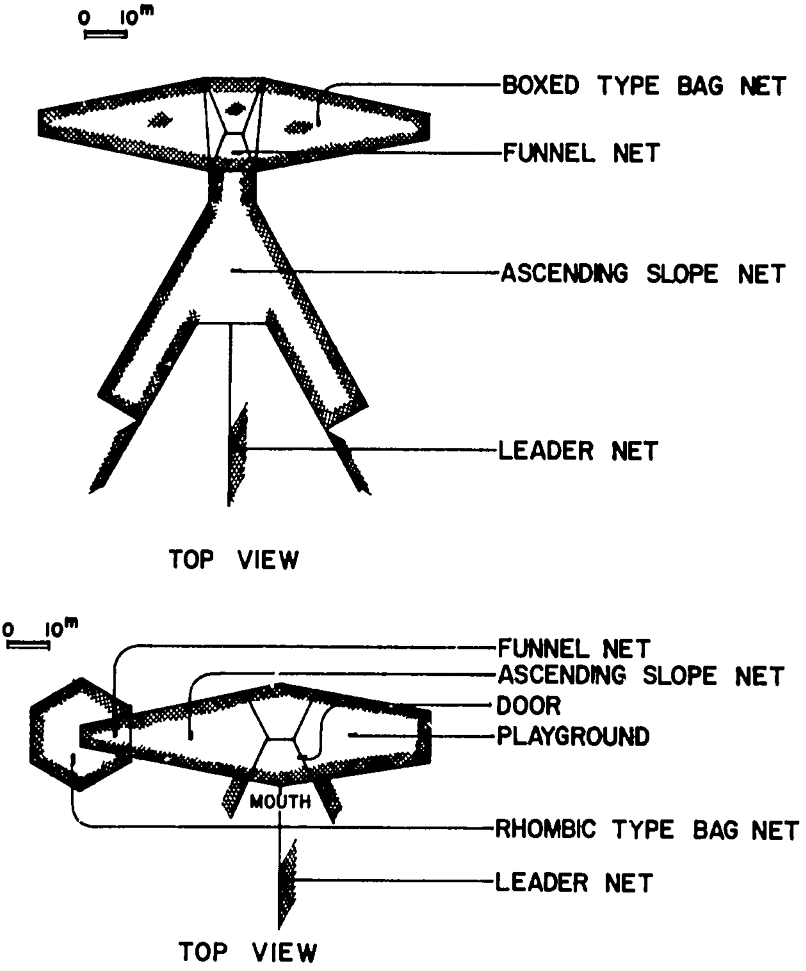


FIG. 5. Upper: "Chuko-ami" currently used throughout Japan for pelagic fish such as sardine. Lower: Setnet for chum salmon used in Hokkaido. Rhombic bag net now replaces previously used boxed type bag net.

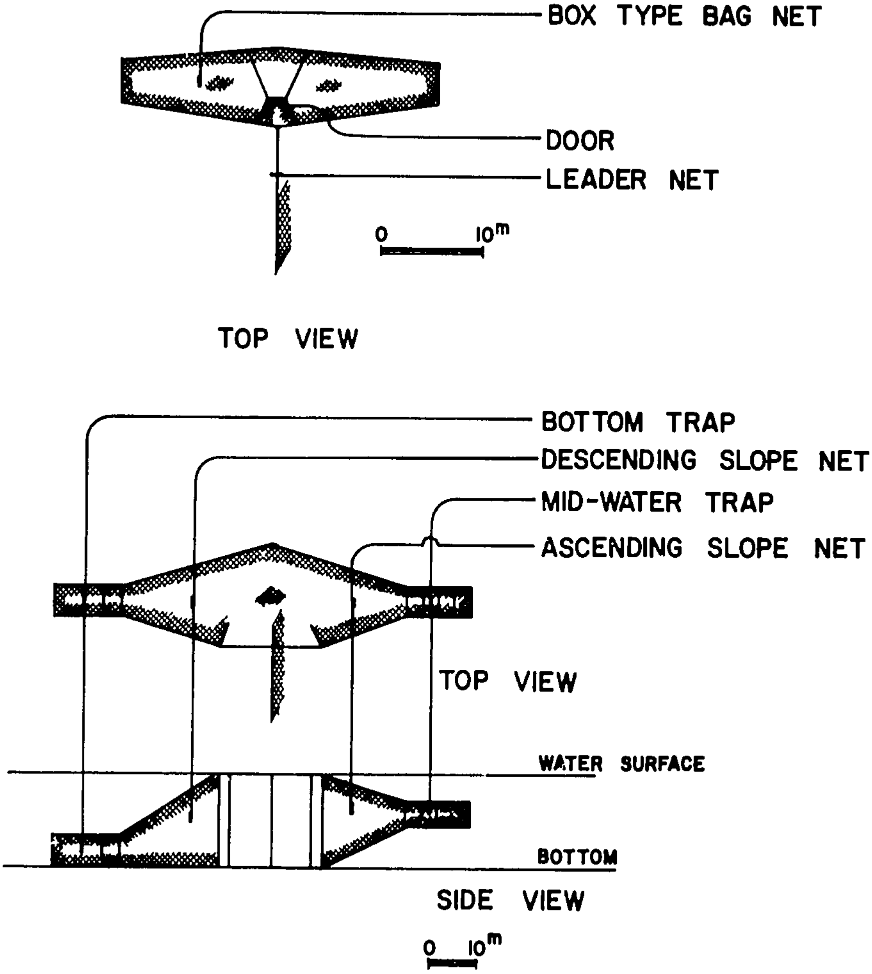
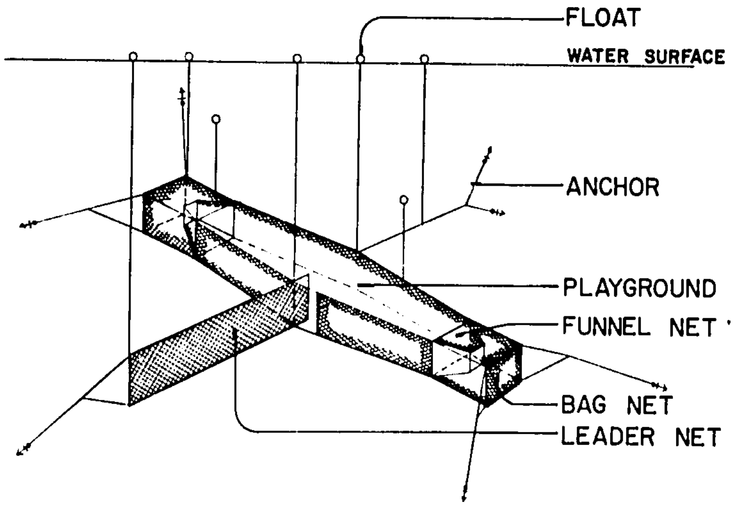
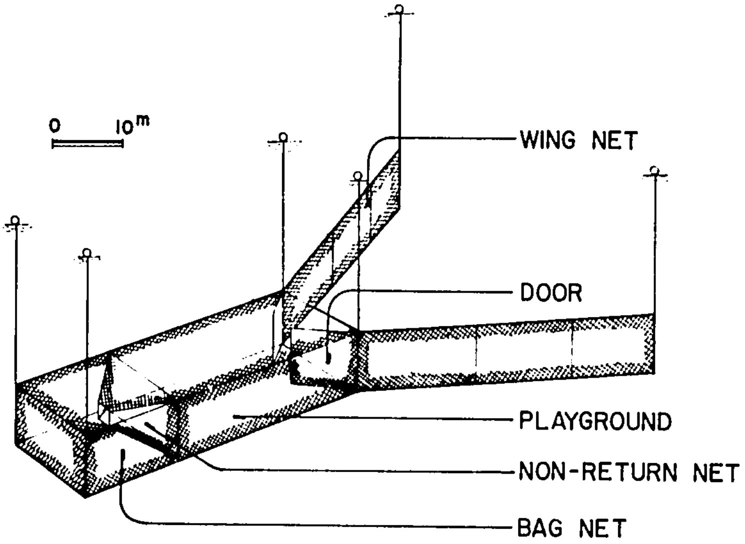


FIG. 6. Upper: Setnet for herring used in Hokkaido. No wing net is attached. Lower: Midwater and bottom trap setnet used in experiment to catch both demersal and pelagic fish (Nomura 1964).

III. Bottom setnets.



PERSPECTIVE VIEW



PERSPECTIVE VIEW

FIG. 7. Setnet for bottom fishes with one small boxed bag net on each end; currently used along the Japanese coast. Lower: Setnet used in Hokkaido catches fish coming mainly from one side of the current.

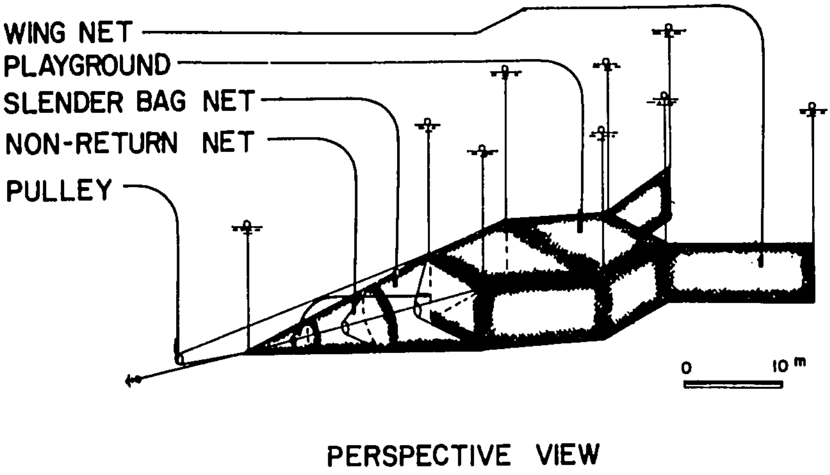


FIG. 8. Setnet for bottom fishes used in northern part of Japan. A long conical net is connected to playground.

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Discussion

BARDACH

In your paper you have related fish behavior to a very developed fishery—a fishery in which there are many units of many different kinds—and you have raised the problem of control of fishermen. You propose introduction of setnets into developing countries and you made a clear case of setnets to be developed according to type of fishing ground, according to fish behavior, and so on. If you want to develop setnets in developing countries, assuming that the intensity/efficiency of fishing is to be increased, you said this is best done by fishery cooperatives. However, fishery cooperatives in many developing countries don't work well. What is your recipe?

NOMURA

Before answering your question, I would like to give some examples. For instance, in the Gulf of Thailand, 1963 was the initial year for making an experimental trawl fishing survey. This was done by the government of Thailand and involved conducting research every year in the same location, in the same season, using the same design of trawl nets. And they calculated and compared the catch per effort every year, and according to these data in 1963 the figure was 232 kg per boat per hour but by 1976 it had dropped to 57 kg. If in the developing countries the fishery cooperatives can demonstrate the small-scale setnet, which is of simple construction, can be operated by one or two fishermen, is easily moved, and has a price of less than $1,000, the net will become increasingly popular in the future. For this purpose some nets whose designs are suited to the various natural sea conditions and the behaviors of different fish species should be studied in tropical waters.

MAGNUSON

It seems to me that another advantage of setnet gear is that it is not lethal gear. At least conceptually it is possible to selectively remove and release animals from these nets, and they might be operated more selectively than many other types of gear which are lethal at the time of capture. An important behavioral factor with setnet gear is the locomotor activity of the fish. The most susceptible species are those with high levels of spontaneous locomotor activity. Data on activity would be essential to an accurate prospectus. It seems that for the use of setnet gear, one should consider not only migratory activity along shorelines, but also spontaneous levels of activity. The most active fishes are high seas pelagic species like the skipjack tuna, which has the most rapid basal level of locomotor activity among fishes. This would make them most susceptible to floating trapnets. Have you had any experience with drifting trapnets that might be used for high seas pelagic fishes?

NOMURA

I once proposed a design for such a net and conducted a pilot test in a tank. This involved drifting trap nets pulled by a boat for the purpose of catching salmon, in the construction of which a number of small trapnets were serially set in a line in combination with draft nets. But it was not considered practical by big fishing companies, mainly for economic reasons.

FISHELSON

I think that by fishing with these standing nets we are dealing with a kind of dilemma between overfishing to produce the desired quantity of fish and not overfishing. Can you produce the same quantum of fishes by standing nets as by trawl nets?

NOMURA

Table 1 of my paper shows the economical efficiency with respect to saving energy, but not the fishing efficiency itself. Setnets also have advantages from the viewpoint of the social life of fishermen. In the tuna longline fishery, for instance, the fishermen must stay on board the boat nearly 1 yr continuously. On the other hand, for the setnet fishery, the fishermen need to work only 3 or 4 h per day on the average. Also, a major advantage is the matter of saving energy, which means not only fuel for boats but also long durability of materials used in the sea, safe operation of gears, light labor by mechanization, guaranteed freshness of fish, etc. In the coastal fishery we could expect more protein by increasing the number of setnets of appropriate design in proper positions.

MYRBERG

Have the various setnet designs been brought about because of the unique behavior of the fish, or is the design of the nets based on tradition?

NOMURA

Basically, the design of setnets is based on the species of fishes. Small-scale setnets capture many kinds of coastal fishes, so their design is mostly based on local traditions, but the large-scale setnets depend mainly on the species of fish.

ATEMA

I was wondering if anybody has ever tried to chemically attract or incite the fish to go into the nets. I can see two uses of such an approach. One is that the fish that is normally wary of the leader nets will get excited and lose sight of that and be led into the nets. The other is that fish might be attracted from various points to the vicinity of the net and led into it.

NOMURA

There have been trials using lamps which are turned off one by one to lead fish into the net body. No effective chemicals have been tried yet.

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General Index

Fish mentioned in the text by their common name are included in this index but the main body of entries for a particular species is included in the specific name index to which a cross reference is made under the appropriate latin name. The specific names of other animals and plants are included in the General Index.

Specific Name Index

This index only includes the specific names, and a few generic names, of the fish referred to in the text. Common names are included in the General Index where they are cross referenced to the appropriate specific name entry.