PN-ABP-772
84624

WORKING PAPER SERIES

FISHERIES STOCK ASSESSMENT

TITLE XII

Collaborative Research Support Program

Fisheries Stock Assessment CRSP Management Office
International Programs, College of Agriculture
The University of Maryland, College Park, Maryland 20742

In cooperation with the United States Agency for International Development (Grant No. DAN-4146-G-SS-5071-00) the Fisheries Stock Assessment CRSP involves the following participating institutions:

The University of Maryland—Center for Environmental and Estuarine Studies
The University of Rhode Island—International Center for Marine Resource Development
The University of Washington—Center for Quantitative Sciences
The University of Costa Rica—Centro de Investigación en Ciencias del Mar y Limnología
The University of the Philippines—Marine Science Institute (Diliman)--College of Fisheries (Visayas)

In collaboration with The University of Delaware; The University of Maryland—College of Business and Management; The University of Miami; and The International Center for Living Aquatic Resources Management (ICLARM).

WORKING PAPER SERIES

Working Paper No. 32

"The Spawning and Recruitment Patterns of Tropical Marine Fish Stock"

by

Jerald S. Ault
William W. Fox, Jr.
University of Miami

March, 1988

Fisheries Stock Assessment
Title XII
Collaborative Research Support Program

The Fisheries Stock Assessment CRSP (sponsored in part by USAID Grant No. DAN-4146-G-SS-5071-00) is intended to support collaborative research between the U.S. and developing countries' universities and research institutions on fisheries stock assessment and management strategies.

This Working Paper was produced by the University of Maryland-Center for Environmental and Estuarine Studies and the University of Costa Rica-Centro de Investigacion en Ciencias del Mar y Limnologia (CIMAR) in association with the University of Delaware and the University of Miami. Additional copies are available from the CRSP Management Office and from:

Chesapeake Biological Laboratory
Center for Environmental and Estuarine Studies
The University of Maryland
P.O. Box 38
Solomons, Maryland 20688

Fisheries Stock Assessment CRSP

The Spawning and Recruitment Patterns of Tropical Marine Fish Stocks

by

Jerald S. Ault and William W. Fox, Jr.

Division of Biology and Living Resources
Rosenstiel School of Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149
USA

February 1988

To be submitted to the *Bulletin of Marine Science*

Introduction

Tropical fishery systems (TFS) are receiving increased attention for development of rigorous management plans. This is because the fishery resources of tropical seas provide important economic and social benefits to the developing countries adjacent to these regions. Decision makers (DM) in the TFS are mandated to maintain resources at optimum productive levels while concomitantly accommodating a variety of user groups and system objectives. Management must now accurately appraise the risks associated with various policy objectives. Thus, stock assessments are given priority by many developing countries despite the apparent lack of the appropriate fishery institution management infrastructures. Many of these resources are now fully exploited. Exploitation in this context can be viewed following Minsky (1986) as the act of one agency making use of the activity of another agency without the former knowing how the latter works. The situation has intensified with infusion of sophisticated fishing technology into the traditionally artisanal fisheries. The requirement for expert knowledge has intensified. This can only come about with a clear understanding of how the system works. Decision making methodology for tropical regions needs considerable improvements and development. Without expert analysis it is impossible to manage resources optimally or to develop sound public policy (Rothschild, 1980).

There is a paucity of available knowledge regarding fundamental aspects of tropical fish stock demographics and dynamics. The global objective of this research was to develop quantitative techniques and heuristics designed to facilitate optimal benefits acquisition from TFS resources. This paper tests the hypothesis that the life history strategies of tropical fish stocks, particularly with respect to spawning and recruitment patterns, vary from their temperate and boreal counterparts. This paper systematically evaluates the TFS to achieve a better understanding of the way the system works, and determine how it can be effectively analyzed. Thus, the bounds of what can be learned about complex systems are explored. Most tropical fish stocks of economic importance are

thought to spawn, recruit and grow continuously. Continuous demographics contrast sharply with the seasonal life history dogma for fish stocks dwelling in temperate oceans. Continuous rates satisfy more of the theoretical arguments under which the FATs were developed (*vis a vis* continuous distributions and continuous mathematics) and are of far greater interest to the mathematically inclined, but they make traditional methodologies of dubious validity under such dichotomous conditions. Thus, this paper is concerned with the potential for understanding variations in recruitment of fish populations related to seasonally oscillating, but continuously-breeding tropical marine fish stocks. The reason being that preferences between policies may be quite different when variations in cohort strengths, either random or directional, are taken into account versus policies based on constant parameterization.

Patterns of marine fish recruitment are often important determinants of the distribution, abundance and density of stocks. Spawning is the precursor to recruitment and in some cases may largely determine the observed recruitment patterns. There is considerably more information on spawning than recruitment. Adult stock abundances may be directly related to recruit abundances. This paper reviews and consolidates the literature and relevant information for marine fish stocks situated circum-tropically. The objective of this paper was to document and qualitatively analyze the demographics specific to tropical fish stocks, and to evaluate the processes mapping spawning to recruitment. Patterns and periodicities in spawning and recruitment are examined and hypotheses proposed. The objective was motivated by the belief that tropical fisheries can be more effectively managed by systematically evaluating the processes specific to generic fish stocks indigenous to these regions.

Processes Mapping Spawning to Recruitment

The birth strategies of fish species are those complexes of reproductive and behavioral traits that are manifested so as to leave some offspring surviving to reproductive

age. In population biology this usage has lead to the development of the evolutionarily stable strategy (ESS) concept. The ESS embodies a mixture of strategies adopted by a population that are not susceptible to invasion by hypothetical alternatives (Maynard Smith, 1976). A strategy designates a plan so robust that it cannot be upset by competition or environmental fluctuations. The term strategy implies a rational planning or natural selection, but note that it is not required to be an optimal strategy. That a species continues to survive means that the maximal quantity of matter and energy are transformed over from one generation to the subsequent one. To maximize the quantity of surviving biomass between generations means that a species regulates its biomass so that the size of its niche is filled completely by its progeny (Kawasaki, 1983). To regulate the biomass means to regulate the number of organisms. Two problems for mathematical demographers are: (i) to define the specific reproductive strategy in quantifiable terms which have physical and biological meaning, and (ii) to demonstrate how specific reproductive strategies may be adaptive in particular environmental circumstances.

Spawning Patterns for Tropical Marine Fishes

Many tropical and subtropical marine fish tend to have a protracted spawning period, or even continuous breeding throughout the year (Lam, 1983; Bye, 1984). Intense spawning activity in tropical latitudes is periodic with individuals breeding serially throughout the year (Munro et al., 1973; McKaye, 1977; Nzioka, 1979; Hunter & Goldberg, 1980; Bayliff, 1980; Sale, 1982; Munro, 1982; Lam, 1983; Bye, 1984; Grimes, 1986). More than 30 families of economically important tropical and subtropical marine fish and invertebrates are documented to have protracted spawning seasons (Table 1). Whereas intense spawning activity is periodic in tropical latitudes (Bye, 1984), it is clear that small population fractions of many species spawn in a continuum over most of the year. Serial spawning fishes are characteristic of subtropical and tropical seas (Nikolsky, 1963). Qasim (1956) suggested that the breeding cycles of marine fishes have adapted to provide the

optimal conditions of food and temperature for the larvae. The lower the latitude, the longer the season when temperature and food conditions favor the survival of juveniles (Johannes, 1978). During the relatively warm breeding seasons of fish stocks dwelling in the low latitudes of the northern hemisphere sufficient food is available for adults to support the maturation of many successive batches of eggs. Cushing (1982) proposed that in an environment where variability in the timing of the annual production cycle results from a combination of factors a fixed spawning time on the same spawning ground each years is most likely to ensure a match between larvae and food. In the tropics and subtropics the production cycle is relatively continuous and of low amplitude so that precisely timed spawning is apparently not as important and breeding occurs throughout much of the year (Cushing, 1975). Perhaps this is because there is no feeding advantage to be gained by restricting the spawning season, however the effects of predation can be mitigated by spawning over an extended period (Grimes, 1986).

Several species of scombrids including skipjack, bigeye and yellowfin tuna are believed to spawn year-round in the equatorial Pacific Ocean. Yellowfin tuna larvae are found all over the northern tropical Pacific in nearly all seasons (Matsumoto, 1966). Skipjack tuna however are believed to have a spawning period which decreases with increased distance from the equator (Forsbergh, 1980), indicating that some set of conditions favors a continuous dispersal of potential recruits in tropical waters. Grimes (1986) identified two reproductive seasonal patterns for lutjanids: (i) continental populations having a spawning season which is typically centered around summer, while (ii) insular populations associated with oceanic islands reproduce year-round with pulses of activity in the spring and fall. Within the breeding "season" of various reef fishes production of multiple broods is usual. The distribution of spawnings by the population may not be symmetrical (Figure 1). Daily, weekly, biweekly and monthly spawning cycles are all common (Robertson & Warner, 1978; Fischer, 1981; Warner & Robertson, 1978; Sale, 1982; Victor, 1983; Munro & Williams, 1985). Daily spawning is a common

phenomenon among coral reef fishes (Victor, 1983), particularly in wrasses (Labridae), parrotfishes (Scaridae), and the groupers (Serranidae). Some families are reported to spawn once or twice every two weeks (Ross, 1978; McFarland et al., 1985), and others spawn monthly, with perhaps several spawnings occurring over two or three days each month (Lobel, 1978). The queenfish, a sciaenid, is a serial spawner with protracted spawning. Repeated spawning within a season is reflected as characteristic size-frequency distributions of oocytes within mature ovaries where, as well as a batch completing vitellogensis or already ripened, there is also a comparably numerous group at mid-vitellogensis which which generate the next spawning (Hunter & Macewicz, 1985). Many tropical marine fishes exhibit lunar or semilunar spawning periodicity (Johannes, 1978; Lam, 1983). Spawning of the queenfish is asynchronous among females, but has monthly peaks in intensity during the first quarter of the moon (DeMartini & Fountain, 1981). Queenfish spawning activity closely resembles many or most small planktonic spawners of warm temperate regions. Lunar spawning intervals are reported for several littoral fishes that spawn demersal eggs (Hines et al., 1985). Seasonal spawning peaks do occur for estuarine species and are usually associated with seasonal rainfall or floods (Lam, 1983).

Recruitment Patterns for Tropical Marine Fishes

The term *recruitment* for commercially exploited fish populations was generally defined by Beverton and Holt (1957) as the process in which young fish enter the exploited area to become liable to contact fishing gear. Parrish (1978) distinguished two life history stages to recruitment: (1) **prerecruits** ≡ recruitment to a fishable stock, and (2) **recruits** ≡ recruitment to the fishery. Gulland (1983) defined Parrish's recruitment slightly different: (1a) the ***prerecruits*** ≡ (including eggs, larvae, and usually, juveniles), and (2a) the ***post-recruits*** ≡ entered the exploited phase of the population. Cushing (1982) recognized another stage: (3) **reproductive recruits** ≡ those fishes recruiting to the reproductive segment of the fish stock. Survivorship to post-recruitment is apparently very low.

Several recent studies have measured recruitment to monitored sites (Figure 2). Although reproductive activities of marine fishes in these areas often extend over considerable periods, seasonal patterns in reproductive activity of adults, larval abundance and recruitment of fishes have been well documented (Munro et al., 1973; Luckhurst & Luckhurst, 1977; Johannes, 1978; Nzioka, 1979; Bayliff, 1980; Murphy, 1982). The most detailed information on both spatial and temporal variation in recruitment concerns tropical reef species; particularly the pomacentrids of the Indo-Pacific and Caribbean Sea (Luckhurst & Luckhurst, 1977; Victor, 1983; Eckert, 1984) and the haemulids of the Caribbean Sea (McFarland et al., 1985). The plethora of observations from tropical waters may be more related to the researchers abilities to tolerate ambient oceanic conditions. The relative paucity of data for other species groups reflects to a great extent: (1) the low densities in which other species settle, (2) the cryptic behavior of some juveniles, and (3) the inability to sample larval habitats properly (Lasker, 1981). Recruitment during seasonal peaks is apparently not uniform, but tends to occur in pulses (see Figure 2, especially panels n, o, p). Seasonal peaks in larval abundance and recruitment have been observed on the Great Barrier Reef (Sale, 1980; Dougherty, 1983; Williams, 1983), in the Philippines (Pauly & Navaluna, 1983; Ingles & Pauly, 1984), Japan (Yamamoto, 1976). Guam (Kami & Ikehara, 1976), Hawaii (Watson & Leis, 1974; Walsh, 1987), eastern Pacific Ocean (Bayliff, 1980), the Gulf of California (Molles, 1978), and the Caribbean Sea (Luckhurst & Luckhurst, 1977). Spring and fall peaks which seem to be confirmed for the Caribbean Sea and the Gulf of Thailand might converge in more northerly waters and be replaced by a summer peak. Large yearly variations in recruit abundances have been observed in Hawaii (Walsh, 1987) and the Caribbean Sea (Luckhurst & Luckhurst, 1977). Presently, there is no solid evidence that the degree of annual variation in recruitment is any greater, or less, in some species than others (Sale, 1982). For many reef species 3 to 4 fold differences between years in given months in the number of recruits arriving have been demonstrated, and up to 10 fold differences between integer years (Sale, 1982). In some locations (e.g. Philippines,

Hawaii, Jamaica, Panama) seasonal recruitment peaks are multimodal. In other areas there appears to be just one seasonal peak (e.g. Great Barrier Reef, eastern Pacific Ocean, western Atlantic Ocean). Most species in an area tend to recruit during the same season(s), but exceptions do occur.

Characterizations of Spawning and Recruitment Patterns

The processes of natality are important in establishing fish stock structure. A supposed universal reproductive strategy of fish stocks is to maximize the production of surviving progeny relative to the available environmental energy and parental life expectancy (Ware, 1984). The variety of reproductive strategies and tactics found among fishes clearly indicates that no single reproductive pattern is universally adaptive, even for fishes within the same ecological community. Rather there is some combination of life history characteristics where each specific strategy confers the highest fitness to the species utilizing that strategy (Maynard Smith, 1976). For fishes inhabiting environments with pronounced seasonal climatic characteristics the breeding season is invariably confined to a brief and specific period of the year (Cushing, 1969) to provide optimal conditions of food and temperature for the larvae. In these environments large-scale primary production occurs over a short period such that species with the most explosive capabilities to change their numbers corresponding to a change in niche have been the most successful (Kawasaki, 1983). The community structure is relatively simple and the abundance of a few species with large biomass vary in proportion to fluctuations in niche size. Many fishes and invertebrates of the high northern hemisphere latitudes produce a single or few tightly grouped spawning batches in a given year (Qasim, 1956; Ault, 1985). These species are required to make a larger focused energy contributions to reproduction to secure broods, rather than extensive contributions to maintenance and somatic growth. Prerecruits can be considered as a black box with a certain number of adult fish providing the input and the output appearing as a certain number of post-recruits. The processes which occur

within the black box, although presently poorly understood, are very important to optimal fishery management. The translation of restricted spawning is reflected traditionally as a discrete unimodal set of fishes which recruit to the population once annually over a retracted period (Cushing, 1969), and is modeled as a discrete-pulsed *cohort* believed to be normally distributed (e.g. Yong & Skillman, 1975; MacDonald & Pitcher, 1979) (Figure 3a). A "**cohort**" is a set of fish from the same species which is issued at the same spawning event and which recruit to the population at the same instant in time. Recruitment involves well-defined events such as: (i) the substantial movement of cohorts from nursery areas, (ii) a change of habit, or (iii) it may simply involve growing to a size which is of interest to fishermen (Gulland, 1983).

In the tropics the production cycle is continuous and of relatively low amplitude so that precisely timed spawning is apparently not critical. Variation in niche size is small in this poor, efficient and stable environment. Thus, the species need not greatly change their numbers. More energy may be diverted to maintenance and growth. Sufficient food is available for adults to support successive batches of eggs. Theoretically, breeding, spawning and recruitment could occur throughout the year (Cushing, 1975; Lam, 1983). Environmentally adapted population features result in multiple cohort production within a given calendar year (Figure 3b). The tropical community is complex and is composed of many species whose biomasses are relatively small and stable (Kawasaki, 1983). However, interspecific relations are intense. In contrast to the tightly channeled reproductive effort of temperate fishes the extended breeding season for tropical fishes may be because their is no feeding advantage gained by restricting the season. It has been suggested that the ova produced during protracted spawning seasons generally encounter a "*survival window*" (Bakun et al., 1982) that is open during a short restricted period of the year resulting in sharply peaked recruitment pulses. The annual distribution of cohorts is typically asymmetric which sometimes shows several modes (Figure 2). By traditional nomenclature multiple cohorts produced within the same calendar year are considered of the

same singular annual cohort. A dynamical view of tropical fish stocks with continuous cohort production may severely alter parochial perceptions with respect to the features which underlie and drive observed population length frequency distributions.

Periodicity of Reproduction and its Relationship to Physical Parameters in the TFS

Faced with a paucity of annual data points a number of researchers have chosen to investigate within year recruitment variability to identify factors which may affect reproductive success (Johannes, 1978; Barlow, 1981 ; Pauly & Navaluna, 1983; Lobel & Robinson, 1986). There must be some specific explanation for the evolution of a particular set of characteristics. However, little is known of environmental cues for seasonal peaks in reproductive activity (Lam, 1983). The temperature of tropical seas may play a role. In tropical regions (near the equator), photoperiod varies little throughout the year, although temperature may change slightly in accordance with the wet and dry seasons. Temperature can directly affect gametogenesis (Lam, 1983; Ault, 1985). However, little supporting evidence would appear to promote temperature as the controlling variable (Lam, 1983). There have been few correlative studies on the productivity of plankton and the collective spawning intensity of the stocks or larval fish densities. Allen (1975) states that periodic "blooms" may occur in some coral reef fishes in seasons when favorable environmental conditions enhance recruit survival. Nzioka (1979) suggested that peak spawning occurs among continental East African lutjanids at the time of highest productivity during the southeast monsoon, which speeds up the East African current, lowers the thermocline, and promotes vertical mixing. A similar conclusion was professed for Philippine fishes (Pauly & Navaluna, 1983). Wallace (1975) noted that the dominant species in South African estuaries had extended spawning seasons of up to eight months. He supposed that prolonged periods of post-larval and juvenile recruitment to South African estuaries had a buffering effect against recruitment failures resulting from droughts or unseasonable floods. Rainfall might be one of the only exogenous variables that shows a clear annual

rhythm in the tropical environment. A noteworthy example response is that the peak spawning activity for tropical freshwater fishes occurs at the beginning of the rainy season (McKaye, 1977). Unfortunately, there have been no unambiguous examples of this relationship in tropical marine waters. The speed of prevailing currents and winds may play some role. Eddies and other larval fish transport mechanisms are believed to influence temporal and spatial fluctuations in recruitment. Eddies appear to be common features of tropical islands and landfronts (Olson & Backus, 1985; Lobel and Robinson, 1986). Reproductive strategies of tropical marine fish stocks may reflect to some extent these transport mechanisms. There may be an important link to the periodicity of the spawning and recruitment of species taking advantage of such features (Lobel and Robinson, 1986). Numerous examples are given whereby many individual species have common spawning peaks that are occurring at time of the year when prevailing winds or currents are weakest. Synchronization of spawning with periods of reduced current flow would allow development and metamorphosis of the pelagic larvae before they are swept out to sea. This would suggest that the reproductive strategies of some tropical fishes have evolved in part to maximize recruitment of offshore larvae to nearby inshore habitats.

Peak spawning activity in tropical species has often been associated with the lunar cycle (Lam, 1983). Lunar recruitment and settlement cycles in tropical fishes are reported (Shulman et al., 1983; Schmale, 1985; Hines et al., 1985; McFarland et al., 1985). Most of the fish spawn on or around the new or full moon in synchrony with the spring tides. The timing of settlement of potential prey species relative to their predators can be crucial factor in successful settlement into a habitat (Shulman et al., 1985). This may suggest that fishes are spawning at night or near dusk to reduce the likelihood of their spawn being observed directly by predators (Johannes, 1978). The timing of spawning to lunar cycles which coincide with ebbing spring tides may have the adaptive value of maximizing the offshore tidal transport of the eggs (Johannes, 1978; Hines et al., 1985). Endogenous rhythmicity has been suggested, but the rhythm may require some lunar or related factors

for synchronization or entrainment (Lam, 1983). There are also occasional reports which suggest that social factors (i.e. chemical, visual, auditory, or tactile) may influence gametogenesis in fish (Lam, 1983). Factors associated with crowding have been shown to retard or inhibit spawning in several species. Factors associated with the presence of the opposite sex may be important in synchronizing spawning (Robertson & Warner, 1978). Some tropical species have overlapping or identical habitat requirements (Sale, 1982). When space in a given habitat becomes vacant, the species that arrives there first will be the species fortunate enough to colonize the habitat. Thus, to increase population abundance under the oscillating *musical chair* conditions, a species may benefit most by spreading it's reproductive output over extended periods of the year.

Intraspecific and Interspecific Population Pressures

Competition and predation are two population abundance forcing mechanisms which undoubtedly influence the reproductive strategies of tropical marine fishes (Munro & Williams, 1985). Competition from both intraspecific and interspecific cohorts, has been widely recognized in the ecological literature (Fox, 1975; Levine, 1976; Botsford & Wickham, 1979; Caddy & Sharp, 1986). Competition for resources, habitat, etc. have certain but generally unquantified levels of impact on young fish species. Predation is widely recognized in tropical waters and directly impacts the numerical abundance of a given species recruits (Munro & Williams, op cit.). Predation is probably of significant importance in tropical marine waters due to the plethora of species of similar ecological roles which occupy adjacent or contiguous habitats. In tropical regions fish populations are suspected to lose individuals principally through predation. Since predation occurs unpredictably both temporally and spatially it may be beneficial for a certain species to have a permanent pool of recruits ready to buoy population levels. Reproductive strategies may therefore have evolved to maintain a continual source of recruits to buffer losses (Luckhurst & Luckhurst, 1977). Spreading the spawning activities out over a long period of time may

provide assurance that at least some of the eggs and juveniles encounter favorable conditions. Disproportionate biomasses of predaceous reef fish communities have been noted at certain locations (Goldman & Talbot, 1976). Munro (1974) confirmed this notion when he stated that the natural mortality rates of fishes in tropical marine environments are remarkably higher than those in temperate water fishes. Predation may be more important than the availability of specific food resources influencing when, where, and how many species of tropical marine fishes spawn in a given area and where their eggs and larvae are subsequently distributed.

The Dependence of Recruitment on Stock in Tropical Seas

The stock and recruitment relationship (SRR) has been identified as the most serious problem facing those concerned with fishery management (Gulland, 1983). Understanding SRR's involves determining how the interactions of stock growth and survivorship, and the resultant stock structure recursively establishes an expectation for recruitments. Population structure and the potential for exploitation of marine fish stocks may be dependent upon intrinsic recruitment patterns; however, the typical measured correlation between stock and recruitment is always very low. Three roles of stock abundance in governing recruitments to a marine fish populations have been identified: (i) effective independence, (ii) direct proportionality, and (iii) density-dependence. Direct proportionality would increase a population without limit, while complete independence implies that recruits can be obtained from no spawners. Recruitment variation is a significant causal factor in the inter-year variation of the annual catches of many fisheries (Parrish et al., 1986). Several authors have indicated that the recruitment observed for certain fish stocks bears no *obvious* relationship to the abundance or the spawning density of the parent stock, implicating effective independence of the two variables (Cushing, 1982; Gulland, 1983). Environmental conditions may play an important role in determining cohort strength, and in several instances, stock size appears to play a

secondary role (Lett & Kohler, 1976; Nelson et al., 1976; Sissenwine, 1977; Van Winkle et al., 1979; Lasker, 1981). In these cases the strength of the cohort arising out of a given spawning event may be determined mostly by environmental factors at some early stage or stages in prerecruitment. Successful spawning and the production of juveniles requires careful sequencing of the spawning activities with natural production processes (Paulik, 1973; Rothschild, 1986). Natural factors may include: (i) temperature after spawning, (ii) the quantity and quality of food available to the first-feeding larvae at the time yolk-sac absorption, (iii) the physical distribution of the currents, and (iv) the abundance of predators. Recruitment during periods of increased temperature may enhance growth rates and reduce the time spent by individuals in vulnerable early life stages (Walsh, 1987). Density-dependence implies that high endogenous stock levels to some degree damp the expectation of recruits. Local densities of specific predators exogenous to the species of concern with identical or similar food resource requirements can also contribute to the loss of recruits from the system.

Several models have been proposed to examine the relationship between parent stock and recruitment in temperate waters. The minimum features recognized necessary to have a biologically realistic SRR are (Shepherd, 1982; Swartzman et al., 1983; Hightower & Grossman, 1985): (i) low recruitment at very low stock sizes; (ii) widely variable recruitment at intermediate stock sizes, (iii) stable or decreased recruitment at high stock sizes. For the persistence of certain fish stocks, there must be an initial rapid rise in recruitment for stock levels close to zero. The rapidity of the rise, or conversely the speed of the decline in recruitment, and the potential hazards in harvestable yield are critically intertwined. The mechanics whereby recruitment is maintained at lower levels of spawning stock undoubtedly involves changes in the growth and mortality among the eggs, larvae, or young fish. The true relationship between adult stock and the average expectation of recruitment may not be as simple as it has been modeled (e.g. Ricker, 1954; Beverton & Holt, 1957; Cushing, 1971; Walters & Hilborn, 1976). Most of these hypotheses are often

not well supported by data (Cushing, 1982), but it is clear that the curve must pass through the origin.

Little work has been done on the relationships between spawning stock potential and the recruitment of tropical fish stocks (Pauly, 1982). The relationship is still considered vague for the extensively studied temperate and boreal zone fish stocks. Variations in cohort strengths greatly affect catch magnitude and composition. The degree to which recruitment depends on population density (=mass per unit volume) or abundance (=numerical quantity), is currently one of the more important, but certainly one of the more perplexing problems of fishery research and management. The SRR is of great interest because it may be central to the control of fish stocks. Clearly, recruitment is a major factor each year. It often fluctuates widely and is almost always input into the management system as an arbitrary stock-recruitment curve. Fishermen are as concerned with interannual variability in catch as they are in average catch over a planning horizon. This is because it is useful for the fishing industry to have accurate predictions of fluctuations in catch to optimize vessel, employment, processing, inventory, marketing, and distribution channels. Ubiquitous use of fishery models that predict events on the average when optimization of a fishery requires point estimates for each interval of the fishing season has weakened support of fishery management institutions.

There are several marine fish stocks for which recruitment has not been demonstrated to have any trend over quite a wide range of spawning stock sizes. Obviously, progeny cannot be expected without any parents. Predictable recruitment patterns of some coral reef fishes are thought to closely parallel spawning patterns in the adult stock (Victor, 1983; McFarland et al., 1985). The occurrence of ripe fishes or the presence of very young individuals has been considered as evidence of spawning activity. Corresponding recruitment peaks could be expected to be lagged to some degree after peaks in larval abundance (Hunter and Leong, 1981). In Jamaican waters spawning shows two main peaks species within a year for most of the larger commercially desirable reef species,

with maxima occurring around March-April and September-October (Munro et al., 1973). Corresponding recruitment peaks occur after peaks in spawning activity (Luckhurst & Luckhurst, 1977). As has been suggested for many temperate species (e.g. Hunter, 1976) recruit abundances of coral reef fishes may be directly related to adult abundances (Walsh, 1987). Data on spawning are also analyzed since spawning is intimately related to recruitment and, in some cases, may largely determine observed patterns (Walsh, 1987). As illustrated for the central-southern subpopulation of northern anchovy located off Baja California there appears to be a functional response between the spawning activity of the adult stock and the appearance of recruits, lagged by an appropriate period of larval development (Figure 4). The belief that recruitment is completely independent of parent stock is fatuous. Three explanations have been offered for the habitually poor statistical fits for stock-recruit models (Sissenwine & Shepherd, 1987): (i) the models may be too simple biologically, (ii) variability caused by abiotic factors obscures biotic relationships, and (iii) measurement error (Walters & Ludwig, 1981). Undoubtedly all three conditions contribute to the problem. For the northern anchovy: (i) recruitment has been tied to upwelling events which affect the stability of the upper surface microlayers during spawning and development (Lasker, 1981), and (ii) the anchovy spawns over a protracted portion of the year. Poorly correlated observations most probably result from the methods of discretization utilized in measuring the spawning stock's potential in time, and possibly perturbations introduced by exogenous physical oceanographic phenomena (Lobel and Robinson, 1986). Typically, single annual values of recruitment on stock are used to represent the stock's intrinsic SRR, even in continuously spawning fishes. The aggregation of data into annual holistic lumps for both the distributions of stock and recruitment undoubtedly introduces some bias into the determination of the functional response for a fish stock whose spawning and spawning stock potential are protracted and of variable intensity during extended periods of the year. Parent stock determines a set of possible outcomes for recruitment. These continuous distributions may also be influenced

by various abiotic factors (Gulland, 1983) which occur continuously throughout the year. Thus, in serially spawning fishes the determination of the SRR may actually require a large number of intra-annual points that would fully represent the level of quasi-continuousness to *capture* the true functional response. Inter-year variability in stock age/length composition or in abiotic factors associated with individual energy reserves or egg production are likely to alter greatly a stock's reproductive potential. Much of the variance in the SRR for multiple spawning fishes may be due to the fact that spawning biomass is a poor index of the reproductive potential of the stock (Parrish et al., 1986). An understanding of what the relationship is between the stock distribution and it's spawning potential at a given instantaneous interval Δt, and the subsequent recruitment at some life stage aged τ at time $(\tau + \Delta t)$ is of considerable importance for continuously spawning tropical fish stocks. The expected *annual* mean recruitment corresponding to a given adult stock can be an important attribute as are the corresponding variances and the shapes of the distributions. A small adult stock may be less able than a large one to produce a reasonable base recruitment under less than favorable conditions. Reflecting carefully upon the conditions under which it was developed the *Ricker*-type SRR may in fact be produced from *Beverton and Holt*-type recruitment dynamics when variability in expected recruitment is higher at lower stock sizes. The physical environment may play a substantial and more significant role in inducing variability in expected recruits at small parent stock sizes.

Conceptual Structure for Spawning and Recruitment

Most subtropical and tropical fishes are iteroparous (i.e. reproduction occurs on more than one occasion during the life-span). Many of these fishes have seasonally indeterminate annual fecundity (frequently called multiple, partial, serial, or heterochronal spawners) (Hunter et al., 1985). In such fishes the standing stock of yolked eggs, regardless of maturity state, gives no indication of annual fecundity because these fishes continuously mature new spawning batches throughout the *protracted* spawning season.

Such fishes usually spawn many times during a season, and several through a *continuum*. Annual fecundity is a function of batch fecundity and the number of spawnings per years. The most conservative assumption is that seasonal fecundity is determinate for multiple spawning fishes and that estimates of batch fecundity and spawning frequency are required. The documented cases of determinate fecundity appear to be restricted to boreal or cold temperate climates where spawning seasons are short. Thus in most of the world's oceans indeterminate fecundity and multiple spawning are the rule for tropical and epipelagic spawners (Hunter and Macewicz, 1985). *Retracted* spawning/recruitment is typical of the discrete-pulsed spawning/recruitment of temperate zone fishes. These fishes spawn and recruit over a very short interval of the year (≤3 months). In most boreal and temperate species all the eggs to be released in a season develop synchronously prior to spawning and spawning typically takes place over a "retracted" period. In such species, the standing stock of oocytes within a certain range of maturity classes is considered to represent the annual fecundity of the spawner (Hunter et al., 1985). Although some of these fishes may spawn repeatedly during the season, the standing stock of yolked eggs is considered representative of the annual fecundity (Hislop et al., 1978). Heterochronal spawning and recruitment patterns exhibited by iteroparous fishes were classified. The approach allowed the basis for a conceptual framework from which tropical and temperate population types were subsequently numerically modeled. Three classes were assigned to each of the following three categories: (1) spawning/recruitment (S/R) patterns, (2) distribution of annually observed modes, and (3) the observed pattern's affinity to well known statistical distributions. Spawning/recruitment included: (i) retracted, (ii) protracted, and (iii) continuum activities. The S/R patterns included: (i) uniform, (ii) unimodal, and (iii) bimodal forms. Distributions over an annual interval included: (i) normal, (ii) beta, or (iii) trigonometric arrangements. Obviously, overlapped and interconnected breeding and recruitment strategies exist. *Protracted* and *continuum* spawnings and recruitments are characteristic of fishes from tropical environments.

Continuum recruitment refers to an infinite set of recruit-particle emissions such that between any two of them there is a third pulse of recruits. By definition this condition is continuous spawning/recruitment. The *protracted* S/R condition refers to an intermediate process that has an extended duration in time and thus is quasi-continuous.

The S/R conditions delineated for both the tropical and temperate situations above have various modal forms associated with them. Statistically, cohort propagation may be modeled by either a uniform distribution (i.e. time and magnitude constant); or single or multiple normal, log-normal, beta or some other probability density function. Any equation representing a real biological system should be valid irrespective of the units in which we measure the quantities involved in the system. In all cases the magnitude of the recruitment is not particularly revealing other than to provide a scaling constant which allows calculation of potential fishery yields. The form and periodicity of recruitment are critical in establishing the probability distribution of a particular population, and the subsequent impact those particular distributions may have in influencing recruitment.

A spectrum of selected examples of both the spawning and recruitment patterns have been shown. In no case has account been made for any more than two years of interannual variability due to abiotic (i.e., climatological) characteristics. Rather, interest here was directed more towards the apparent distributions of spawning and recruitment observed in these fishes and the causal mechanisms generating these patterns. Clearly some insight is needed into what can happen in the evolution of a fishery system, and in the possible ways the system might be influenced by the initial conditions (Thompson and Stewart, 1986). The time dependence of population phenomenon suggests that variations in the amplitudes of recruitments coupled with intrinsic and extrinsic population interactions and feedbacks may be important in helping to understand whether *attractor spaces* exist in continuous tropical fish stock population cycles.

The TFS and the Promise of Patterns

Fundamental features of the tropical fishery system vary to such a degree that traditionally applied sampling, assessment, and analysis procedures may be of dubious validity in a tropical context. A lack of detailed biological information forces fishery managers to turn to other data sources as a basis for management decisions. Fishery statistical da a in tropical regions are often proportionally more important in the management of fisheries in developing countries than in developed countries (Dudley & Harris, 1987). Conventional methods for analyzing changes in fish stocks use fishery catch and effort statistics. Tropical based fisheries present several problems in the collection and application of catch and effort data such as: (i) the wide variety of gear use causing difficult standardization, (ii) diverse and remote landing sites, and (iii) a stark absence of suitable data sampling frames. Collection of statistics from small-scale fisheries has proved a difficult task. Statistical systems in tropical areas are recognized as being far from reliable. In many cases no infrastructure exists. Most sources of error occur because many of the catches do not pass through even the smallest of processors resulting in underestimates of the total catch. Little attention is paid to the collection of effort statistics in a conventional stock assessment sense. Catch records, usually aggregated by large combinations of species, sometimes have associated effort information but it typically consists of the numbers of fishermen and the number of vessels. Although the system is unreliable alternative approaches are also expensive and labor intensive. Several prominent features of the tropical and temperate fishery systems are contrasted (Table 2). Note however, that despite the obvious advantages of temperate-based fisheries in terms of assessment modeling and management applications, fishery management in the temperate regions *has not and does not* necessarily serve as a paradigm.

Fish from tropical waters are usually difficult to impossible to age because of subtle seasonal variation. The fact suggests that large-scale sampling programs for age distribution are not feasible (Jones 1981, 1984). Furthermore, any indirect ageing methods

for these fishes are complicated by the quasi-continuous, multiple cohort production occurring intra-annually, and continuous growth. Because spawning may be continuous or extended over several months, sometimes more than once a year, tropical fish also pose special problems for growth estimation from modal size progressions. Typically, the catches from fish stocks in temperate seas are aged by an average length key by making assumption that once annual pulse-recruitment distributes itself normally in time. These annual cohorts are assumed to have a parametric distribution about a mean size at age, and this age is annual and integer-valued. Statistical averages are more meaningful when they refer to homogeneous groups (Keyfitz, 1977). Protracted spawning, which can be distributed asymmetrically may induce considerable error in the basic catch-at-length data, the magnitude of which is presently unquantified. Traditional methods may become useless and concepts like following cohorts through time become difficult to grasp because of the inconcise definition of a cohort under this pretext. Traditional age-based stock assessment techniques may be of limited utility in tropical fisheries.

A spectrum of examples of both S/R patterns of tropical marine fishes have been shown. In no case was there account made for any more than two years of interannual abiotic (i.e. climatological) influences. Rather, interest here has been more directed towards the apparent static distributions of S/R observed and the causal mechanisms which contribute to their generation. Clearly, insight is required into what can happen in the time evolution of a fishery system and in the ways the system state can be influenced by the initial conditions and the level of perturbation (Thompson & Stewart, 1986). If one considers a system and its *phase space* (i.e. the space of variables that specify the system) then the initial conditions may be *attracted* to some subset of the phase space as time $\rightarrow\infty$. In attracting system space motions from adjacent starts tend to converge towards stable attracting solutions. However, given a large enough perturbation an entirely new steady state may be observed (May, 1987; Grebogi et al., 1987; Ault, 1988). Different starts of the system may lead to alternative final states. This possibility suggests the concept that a

chaotic or *strange attractor* may capture the solution of a perfectly deterministic equation and place it into a state of steady but perpetual chaos (Thompson & Stewart, 1986). The time dependence of population demographic phenomenon suggests that variations in the periodicity and amplitude of recruitments coupled with intrinsic and extrinsic interactions and feedbacks may be important determinants as to whether *attractor spaces* exist in continuous tropical fish stock population cycles.

Insufficient system resolution may result when traditional assessment methods are tacitly applied to these seemingly simple fisheries which are embedded within complex frameworks. This section has set the stage for the development of a cadre of techniques and methodologies for understanding and assessing the stability and transition among tropical multicohort populations. The study of spawning and recruitment patterns seems very promising. Most probably, recruitment patterns will, among other things, allow for a quantitative evaluation of the relative impact of various environmental factors affecting the recruitment important to exploited fish stocks and the optimization of fishing activities in tropical regions. If studies of subtropical and tropical fish communities are to have the adequate theoretical background essential for a proper understanding of the complex phenomena involved, then a feasible alternative is to develop models according to the properties of the particular systems, rather than attempt to apply any general theory. A *model* here is defined as any structure that a person can use to simulate or anticipate the behavior of something else. Models of the tropical fishery system should emerge as syntheses of knowledge of a range of cases actually observed.

Acknowledgements

This work was partially supported by a subcontract from the University of Maryland under U.S. Agency for International Development Contract No. DAN-4146-G-SS-5071-00 for the Fisheries Stock Assessment Collaborative Research Support Program.

Literature Cited

Allen, G.R. 1975. *Damselfishes of the South Seas.* Tropical Fish Hobbyist. Neptune, New Jersey.

Ault, J.S. 1985. Some quantitative aspects of reproduction and growth of the red abalone, *Haliotis rufescens* Swainson. J. World Maric. Soc. 16:398-425.

Ault, J.S. and G.C. Broadhead. 1980. Status of the Baja California anchovy fishery. Living Marine Resources Rept. San Diego, Calif. 31p.

Bakun, A., J. Bayer, D. Pauly, J.G. Pope and G.D. Sharp. 1982. Ocean science in relation to living resources. Can. J. Fish. Aquat. Sci. 39(7):1059-1070.

Barlow, G.W. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. Env. Biol. Fish. 6:65-85.

Barret, I. and G.V. Howard. 1961. Studies of the age, growth, sexual maturity and spawning of populations of anchoveta (*Cetengraulis mysticetus*) of the coast of the eastern tropical Pacific Ocean. IATTC Bull. V(2):113-216.

Bayliff, W. H. 1980. Synopses of biological data on eight species of scrombrids. Inter-Amer. Trop. Tuna Comm. Spec. Rpt. No. 2. 530 p.

Beverton, R. J. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food UK (Series 2), No. 19:533 p.

Boardman, C. and D. Weiler. 1980. Aspects of the life history of three deepwater snappers around Puerto Rico. Gulf Carib. Fish. Inst. 32:158-172.

Botsford, L.W. and D.E. Wickham. 1979. Population cycles caused by inter-age, density-dependent mortality in young fish and crustaceans. In *Cyclic Phenomena in Marine Plants and Animals*, E. Naylor and R.G. Hartnoll (eds.). pp 73-82. Pergamon Press, New York.

Brouard, F. and R. Grandperrin. 1984. Les poissons profonds de la pinta recifale externe a Vanatu. ORSTOM Notes Doc. D'Oceanogr. 11:71-79.

Bye, V. J. 1984. The role of environmental factors in the timing of reproductive cycles. In *Fish Reproduction: Strategies and Tactics*, G. W. Potts & R. J. Wooten (Eds.) pp. 187-205. Academic Press, New York.

Caddy, J.F. and G.D. Sharp. 1986. An ecological framework for marine fishery investigations. FAO Fish. Tech. Pap., (283):152p.

Collins, M.R.; Waltz, C.W.; Roumillat, W.A. and D.L. Stubbs. 1987. Contribution to the life history and reproductive biology of the gag, *Mycteroperca microlepis* (Serranidae), in the South Atlantic bight. Fish. Bull. 85(3):648-653.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. J. Cons. Int. Explor. Mer 33(1):81-92.

Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33:340-362.

Cushing, D. H. 1975. *Marine Ecology & Fisheries.* Cambridge University Press, Cambridge. 278p.

Cushing, D.H. 1982. *Climate and Fisheries.* Academic Press, New York. 373p.

DeMartini, E. E. and R. K. Fountain. 1981. Ovarian cycling frequency and batch fecundity of the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547-560.

DeVries, D. A. and M. E. Chittenden, Jr. 1982. Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. Fish. Bull. 80(3):487-500.

Dougherty, P. 1983. Diel, lunar, and seasonal rhythms in the reproduction of two tropical damselfishes, *Pomacentrus flavicauda* and *P. wardi*. Mar. Biol. 75:215-224.

Dudley, R.G. and K.C. Harris. 1987. The fisheries statistics system of Java, Indonesia: operational realities in a developing country. Aquaculture and Fisheries Management 18:365-374.

Eckert, C. J. 1984. Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Group, Great Barrier Reef. Marine Biology 78:123-127.

Fischer, E. A. 1981. Sexual allocation in a simultaneously heraphroditic coral reef fish. Amer. Nat. 117(1)64:82.

Forsberg, E. D. 1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean. Inter-Amer. Trop. Tuna Comm. Spec. Rpt. 2:295-360.

Fox, L.R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. Syst. 6:87-106.

Garcia, S. 1985. Reproduction, stock assessment models and population parameters in exploited penaeid shrimp populations. Second Australian National Prawn Seminar. Pages 139-158.

Gilmore, R. C., C. J. Donohue, and D. W. Cooke. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook, *Centropomus undecimalis* (Bloch). Fla. Sci. Spec. Suppl. Issue 45(4) Part 2.

Goldman, B. and F.H. Talbot. 1976. Aspects of the ecology of reef fishes. p. 125-154 in O.A. Jones and R. Endean (eds.) *Biology and Geology of Coral Reefs*. Vol. 3 Biol. 2 Academic Press, New York.

Grebogi, C.; E. Ott and J.A. Yorke. 1987. Chaos, strange attractors, and fractal basin boundaries in nonlinear dynamics. Science 238:632-638.

Grimes, C. B. 1986. Reproductive biology of the Lutjanidae: a review. Snapper-Grouper Workshop, S. Ralston and J. Polovina (eds.), Honolulu, May, 1985, p.239-294.

Gulland, J. A. 1983. *Fish Stock Assessment: A Manual of Basic Methods.* Wiley-Interscience Publ. 223p.

Hightower, J.E. and G.D. Grossman. 1985. Comparison of constant effort harvest policies for fish stocks with variable recruitment. Can. J. Fish. Aquat. Sci. 42:982-988.

Hislop, J. R. G., A. P. Robb, and J. A. Guild. 1978. Observations of the effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus*, in captivity. J. Fish. Biol. 13:85-98.

Hines, A. H., K. E. Osgood, and J. J. Miklas. 1985. Semilunar reproductive cycles in *Fundus heteroclitus* (Pices: Cyprinodontidae) in an area without lunar cycles. Fish. Bull. 83(3)467-472.

Hoar, W.S., D.J. Randall and J.R. Brett (eds). 1979. *Fish Physiology. Vol. IX: Behavior and Fertility Control.* Academic Press, New York. 786p.

Hoar, W.S., D.J. Randall and E.M. Donaldson (eds). 1983. *Fish Physiology. Vol. VIII: Bioenergetics and Growth.* Academic Press, New York. 477p.

Hunter, J.R. (ed.). 1976. Report of a colloquim on larval fish mortality studies and their relation to fishery research. January 1975. NOAA Tech. Res. NMFS Circ-395.

Hunter, J.R. and S.R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. 77(3):641-652.

Hunter, J. R. and R. Leong. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Full. 79(2):215-230.

Hunter, J. R. and B. J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. In R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, pp. 79-94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. In R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, Engraulis mordax, pp. 67-77. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Ingles, J. and D. Pauly. 1984. An atlas of the growth, mortality and recruitment of Philippine fishes. ICLARM Tech. Rpt. 13:127p.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3(1)65-84.

Jones, R. 1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fisheries Circ. No. 734. 55p.

Jones, R. 1984. Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256. 118p.

Kami, H.T. and I.I. Ikehara. 1976. Notes on the annual juvenile siganid harvest in Guam. Micronesia 12:323-325.

Kawasaki, T. 1983. Why do some pelagic fishes have wide fluctuations in their numbers? ---Biological basis of fluctuation from the viewpoint of evolutionary ecology. FAO Fisheries Rept. 291(3): 1065-1080.

Keyfitz, N. 1977. *Applied Mathematical Demography*. John Wiley & Sons. New York. 388p.

Knudsen, P. K. 1977. Spawning of yellowfin tuna and the discrimination of subpopulations. IATTC Bull. 17(2).

Lam, T.J. 1983. Environmental influences on gonadal activity in fish. In *Fish Physiology Vol. IX: Reproduction*. p.65-116. Academic Press, New York.

Lasker, R., editor. 1981. *Marine Fish Larvae*. University of Washington Press. Seattle, Washington. 131p.

Lasker R. and P. E. Smith. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

Lett, P.F. and A.C. Kohler. 1976. Recruitment: a problem of multispecies interaction and environmental perturbations, with special reference to Gulf of St. Lawrence Atlantic herring (*Clupea hargenus harengus*). J. Fish. Res. Bd. Can. 33:1353-1371.

Levine, S.H. 1976. Competitive interactions in ecosystems. Amer. Nat. 110:903-910.

Limbaugh, C. 1961. Life-history and ecological notes on the black croaker. Calif. Fish & Game 47:163-174.

Lindeman, K.C. 1986. Development of larvae of the french grunt, *Haemulon flavolineatum*, and comparative development of twelve species of western Atlantic *Haemulon* (Percoidei, Haemulidae). Bull. Mar. Sci. 39(3):673-716.

Lobel, P. S. 1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the Pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pacific Science 32(2):193-207.

Lobel, P. S. and A. R. Robinson. 1986. Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. J. Deep-Sea Res. 33(4):483-500.

Luckhurst, B. E. and K. Luckhurst. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curacao, Netherlands, Antilles. Can. J. Zool. 55:681-689.

Macdonald, P.D.M. and T.J. Pitcher. 1979. Age-groups from size frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Bd. Can. 36:987-1001.

Madrigal, E. 1985. Dinamica pesquera de tres especies de Sciaenidae (corvinas) en el golfo de Nicoya, Costa Rica Thesis, Universidad de Costa Rica. 65p.

Manickchand-Daas, S. 1987. Reproduction, age and growth of the lane snapper, *Lutjanus synagris*, in Trinidad, West Indies. Bull. Mar. Sci. 40(1):22-28.

Matsumoto, W. M. 1966. Distribution and abundance of tuna larvae in the Pacific Ocean. Proc. Gov. Conf. Centr. Pac. Fish. Res., 221-230, State Hawaii, 1966, 266p.

May, R.M. 1987. Chaos and the dynamics of biological populations. Proc. R. Soc. Lond. A 413(1844):27-44.

Maynard Smith, J. 1976. Evolution and the theory of games. Amer. Sci. 64:41-45.

Minsky, M. L. 1986. *The Society of Mind.* Simon and Schuster, New York. 339p.

Mizenko, D. 1984 The biology of the western Samoan reef-slope snapper populations. M.S. Thesis, Univ. Rhode Island.

Molles, M.C. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. Ecol. Monogr. 48:289-305.

Munro, J.L. 1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. J. Cons. int Explor. Mer 35(3):337-350.

Munro, J. L. 1982. Some advances and developments in coral reef fisheries research: 1973-1982. Gulf & Caribb. Fish. Inst. 35:161-178.

Munro, J. L., V. C. Gaut, R. Thompson and P. H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. J. Fish. Biol. 5:69-84.

Munro, J. L. and D. McB. Williams. 1985. Assessment and management of coral reef fisheries. Fifth International Coral Reef Congress. Tahiti. 35pp.

Murphy, G. I. 1982. Recruitment of tropical fishes. p. 141-148. In Pauly, D. and G. I. Murphy (eds.) *Theory and management of tropical fisherics.* ICLARM Conference Proceedings 9, 360p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronulla, Australia.

McFarland, W. N., E. B. Brothers, J. C. Ogden, M. J. Shulman, E. L. Bermingham, and N. W. Kotchian-Prentiss. 1985. Recruitment patterns in young french grunts, *Haemulon flavolineatum* (Family Haemulidae), at St. Croix, Virgin Islands. Fish. Bull. 83(3):413-426.

McKaye, K. R. 1977. Competition for breeding sites between the cichlid fishes of Lake Jiloa', Nicaragua. Ecology 58:291-302.

Nelson, W.R., M.G. Ingram, and W.P. Schaaf. 1976. Larval transport and yearclass strength of Atlantic menhaden, *Brevoortia tyrannis.* Fish. Bull. 75:23-41.

Nikolsky, G. V. 1963. *The Ecology of Fishes.* Academic Press, N.Y., 352pp.

Nzioka, R. M. 1979. Observations on the spawning seasons of east African reef fishes. J. Fish. Bio. 14:329-342.

Olson, D.B. and R.H. Backus 1985. The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. J. Mar. Res. 43:113-137.

Otsu, T. and R. Uchida. 1959. Sexual maturity and spawning of albacore in the Pacific Ocean. Fishery Bulletin 59:287-305.

Parrish, B.B., editor. 1978. Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164.

Parrish, R.H., D.L. Mallicoate and R.A. Klingbeil. 1986. Age independent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, Engraulis mordax. Fishery Bull. 84(3):503-517.

Paulik, G.J. 1973. Studies of the possible form of the stock-recruitment curve. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:302-315.

Pauly, D. 1982. Studying single-species dyanmics in a tropical multispecies context, p. 33-70. In Pauly, D. and G. I. Murphy (eds.) *Theory and Management of Tropical fisheries.* ICLARM Conference Proceedings 9, 360p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronulla, Australia.

Pauly, D. and N.A. Navaluna. 1983. Monsoon-induced seasonality in the recruitment of Philippine fishes. FAO Fisheries Rept. 291(3):823-833.

Qasim, S. Z. 1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. J. Cons. Int. Explor. Mer 21:144-154.

Qasim, S. Z. 1973. An appraisal of the studies on maturation and spawning in marine teleosts from the Indian waters. Indian J. Fish. 20(1):166-181.

Ralston, S. 1981. Aspects of the reproductive biology and feeding ecology of *Chaetodon miliaris*, a Hawaiian endemic butterflyfish. Env. Biol. Fish. 6:167-176.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11(5):559-623.

Robertson, D. R. and R. R. Warner. 1978. Sexual patterns in the labroid fishes of the western Caribbean, II. The parrotfishes (Scaridae). Smithsonian Contributions to Zoology. Number 255: 26pp.

Ross, R.M. 1978. Reproductive behavior of the anemonefish Amphiprion melanopus on Guam. Copeia 1978:103-107.

Ross, R.M. 1983. Annual, semilunar, and diel reproductive rhythms in the Hawaiian labrid *Thalassoma duperrey*. Mar. Biol. 72:311-318.

Rothschild, B.J. 1980. First annual David H. Wallace memorial lecture on living marine resources. J. Mar. Tech. Soc. 14(5):5-11.

Rothschild, B.J. 1986. *Dynamics of Marine Fish Populations*. Harvard University Press. Cambridge, Mass. 352p.

Russell, B. C., G. R. V. Anderson, and F. H. Talbot. 1977. Seasonality and recruitment of coral reef fishes. Aust. J. Mar. Freshwater Res. 28:521-528.

Sale, P. F. 1980. The ecology of fishes on coral reefs. Oceangr. Mar. Bio. Ann. Rev. 18:367-421.

Sale, P. F. 1982. The structure and dynamics of coral reef fish communities. p. 241-253. In Pauly, D. and G. I. Murphy (eds.) *Theory and Management of Tropical Fisheries*. ICLARM Conference Proceedings 9, 360p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronulla, Australia.

Schmale, M. 1985. Histopathology, distribution and development of a neoplastic disease in the bicolor damselfish (*Pomacentrus partitus*) from Florida reefs. Ph.D. Dissertation, University of Miami, Florida. 186p.

Shepherd, J.G. 1982. A verstaile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40:67-75.

Shulman, M.J., J.C. Ogden, J.P. Ebersole, W.N. McFarland, S.L. Miller and N.G. Wolf. 1983. Priority effects in the recruitment of juvenile coral reef fishes. Ecology 64(6):1508-1513.

Sissenwine, M.P. 1977. A compartmentalized simulation model of the southern New England yellowtail flounder, *Limanda ferruginea* , fishery. Fish. Bull. 75:465-482.

Sissenwine, M.P. and J.G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44:913-918.

Swartzman, G.L., Getz, W.M., R.C. Francis, R.T. Haar, and K. Rose. 1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40:524-539.

Thresher, R. E. 1984. *Reproduction in Reef Fishes*. T.F.H. Publications, Neptune City, New Jersey. 399pp.

Thompson, J.M.T. and H.B. Stewart. 1986. *Nonlinear Dynamics and Chaos: geometrical methods for engineers and scientists*. John Wiley & Sons, New York 376p.

Tillman, M.F. and D. Stadelman. 1976. Development and example application of a simulation model of the northern anchovy fishery. Fish. Bull. 74(1):118-130.

Van Winkle, W., B.L. Kirk, and B.W. Rust. 1979. Periodicities in Atlantic coast striped bass (*Marone saxatilis*) commercial fisheries data. J. Fish. Res. Bd. Can. 36:54-62.

Victor, B. C. 1983. Recruitment and population dynamics of a coral reef fish. Science 219:419-210.

Walker, M. 1975. Aspects of the biology of emperor fishes, family Letherinidae, in North Queensland barrier reef waters. Ph.D. dissertation. James Cook University, Townsville, Australia. 241p.

Wallace, J. H. 1975. Investl. Rep. Oceanogr. Res. Inst., Durban 41:1-51.

Walsh, W.J. 1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Env. Biol. Fish. 18(4):257-276.

Walters, C.J. and R. Hilborn. 1976. Adaptive control of fishing systems. J. Fish. Res. Bd. Can. 33:145-159.

Walters, C.J. and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Can. J. Fish. Aquat. Sci. 38:704-710.

Ward, J. 1986. Reproduction of spiny lobsters in Bermuda. Gulf & Carib. Fish. Inst. 39:(*in press*)

Ware, D. M. 1984. Fitness of different reproductive strategies in teleost fishes. In *Fish Reproduction: Strategies & Tactics*, G. W. Potts & R. J. Wooten (Eds.) pp.349-366. Academic Press, New York.

Warner, R. R. and D. R. Robertson. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I. The wrasses (Labridae). Smithsonian Contributions to Zoology. Number 254:27pp.

Watson, W. and J.M. Leis. 1974. Ichthyoplankton in Kaneohe Bay, Hawaii. A one-year study of fish eggs and larvae. Univ. Hawaii Sea Grant Tech. Rept. TR-75-01. Honolulu. 178p.

Williams, D. McB. 1983. Daily, monthly and yearly variability in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Series 10:231-237.

Willman, R. and S. M. Garcia. 1985. A bio-economic model for the analysis of sequential artisanal and industrial fisheries for tropical shrimp (with a case study of Surinam shrimp fisheries). FAO Fish. Tech. Pap., (270):49p.

Yamamoto, T. 1976. Seasonal variations in abundance, size compositions and distributional patterns of residing damselfishes in Sesoko Island, Okinawa. Sesoko Mar. Sci. Lab. Tech. Rept. 4:19-41.

Yong, M.Y. and R.A. Skillman. 1975. A computer program for analysis of polymodal frequency distributions (ENORMSEP). Fishery Bulletin 73:681-694.

Yoshida, H.O. 1968. Early life history and spawning of the albacore, *Thunnus alalunga*, in Hawaiian waters. Fishery Bulletin 69:205-211.

List of Figures

Figure 1: Selected circum-tropical protracted spawning patterns for five families of marine fishes. Sources of data: Nzioka 1979 (A,B,D), Qasim 1973 (C), Munro 1982 (E), Ault & Broadhead 1980 (F).

Figure 2: Selected circum-tropical protracted and/or continuous recruitment patterns for 16 families of marine fishes and invertebrates. Sources of data: Luckhurst & Luckhurst 1977 (A,D,E,F,G,I,K), Victor 1983 (C), McFarland et al. 1985 (H), Cushing 1969 (B,J), Pauly 1982 (E), Willman & Garcia 1985 (L), Pauly & Navaluna 1983 (M,N,O,P).

Figure 3: Hypothetical population length frequency distributions for the (A) retracted discrete spawning temperate zone, and (B) protracted quasi-continuous spawning tropical zone marine fish life histories.

Figure 4: Observed average from 10 years of data shown over two averaged spawning (closed dot) and the recruitment (open dot) cycles for northern anchovy from the California-Mexico central subpopulation stock. (Data from Cushing, 1969; Tillman & Stadelman, 1976; and Ault & Broadhead, 1980).

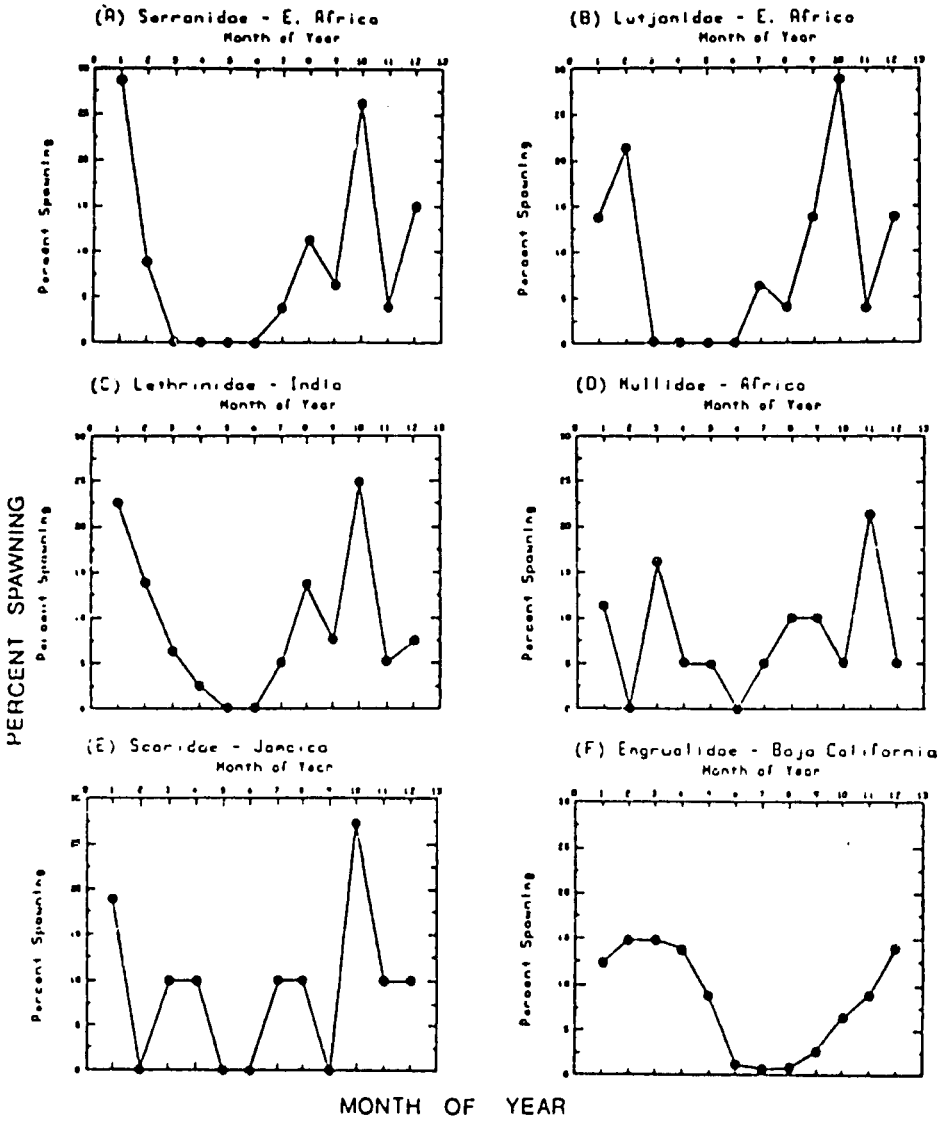

(A) Serranidae - E. Africa
(B) Lutjanidae - E. Africa
(C) Lethrinidae - India
(D) Mullidae - Africa
(E) Scaridae - Jamaica
(F) Engraulidae - Baja California
Month of Year
Percent Spawning
PERCENT SPAWNING
MONTH OF YEAR

Figure 1

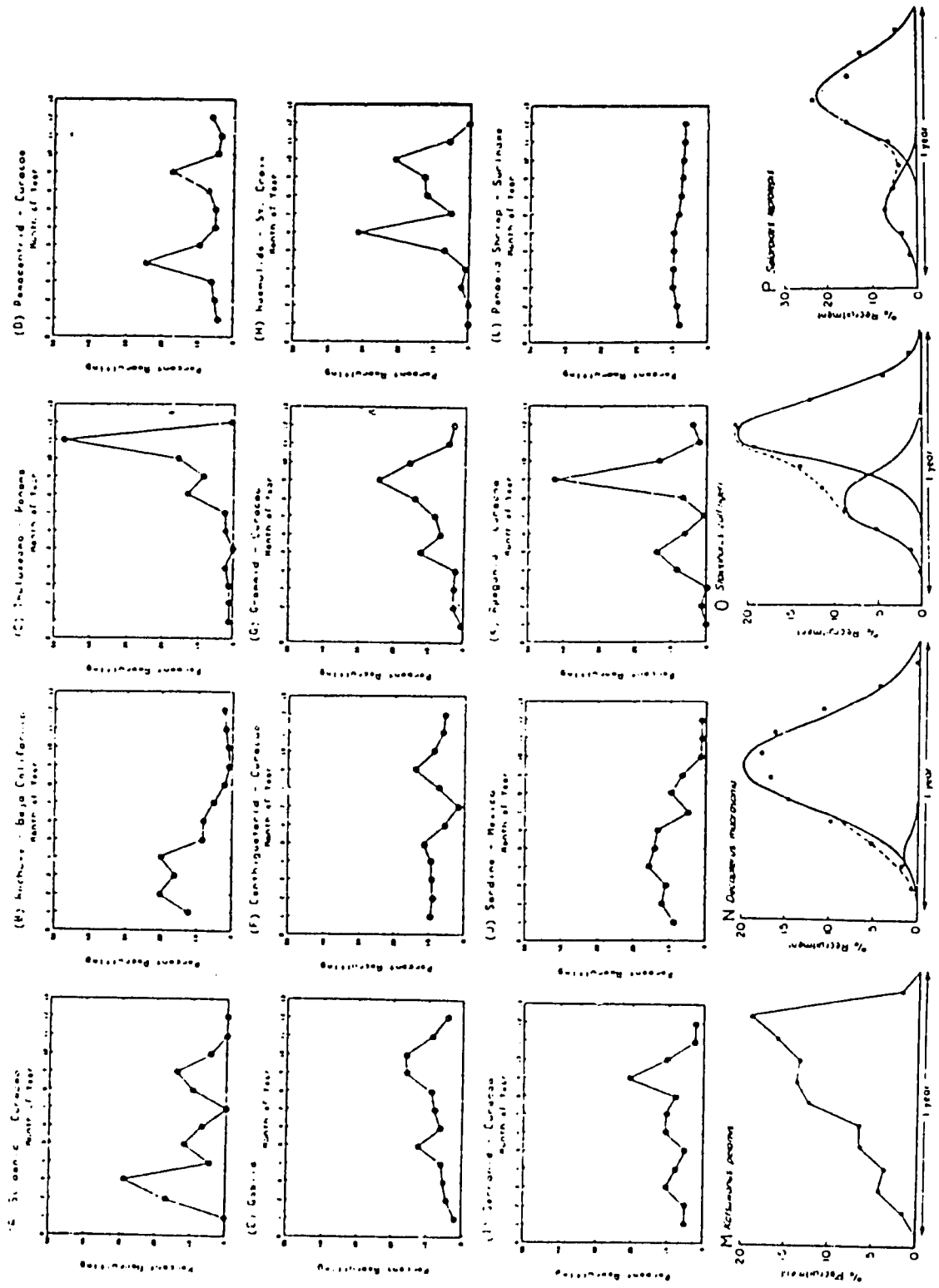
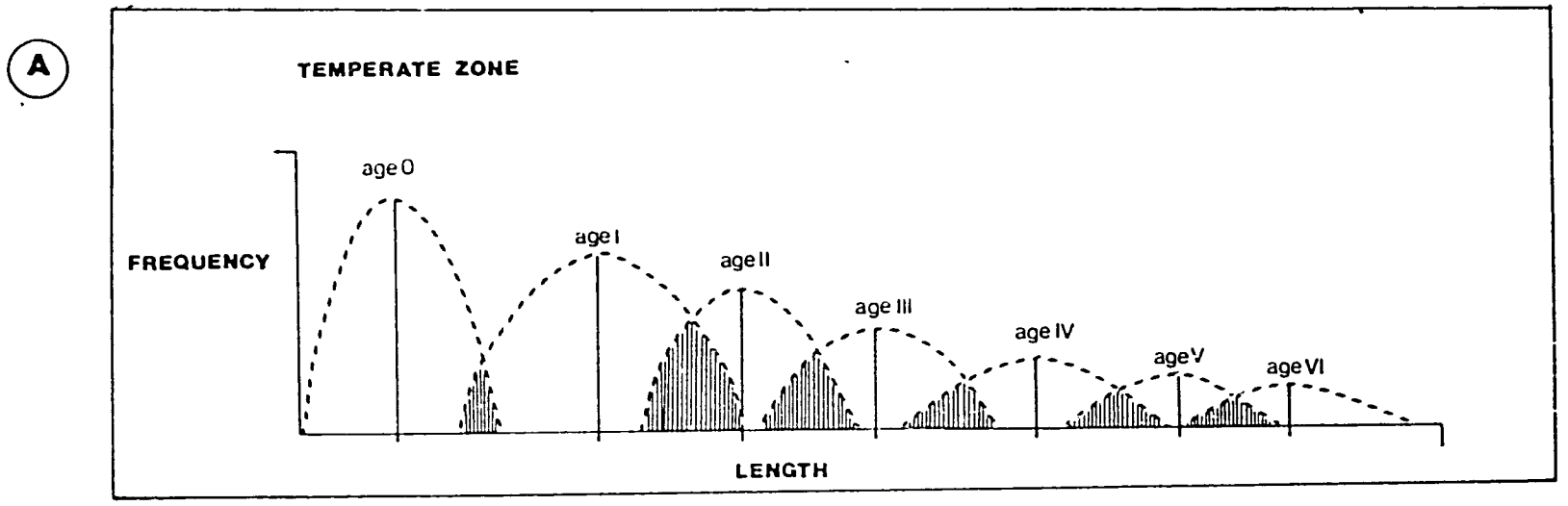


Figure 2


A
TEMPERATE ZONE
FREQUENCY
age 0
age I
age II
age III
age IV
age V
age VI
LENGTH

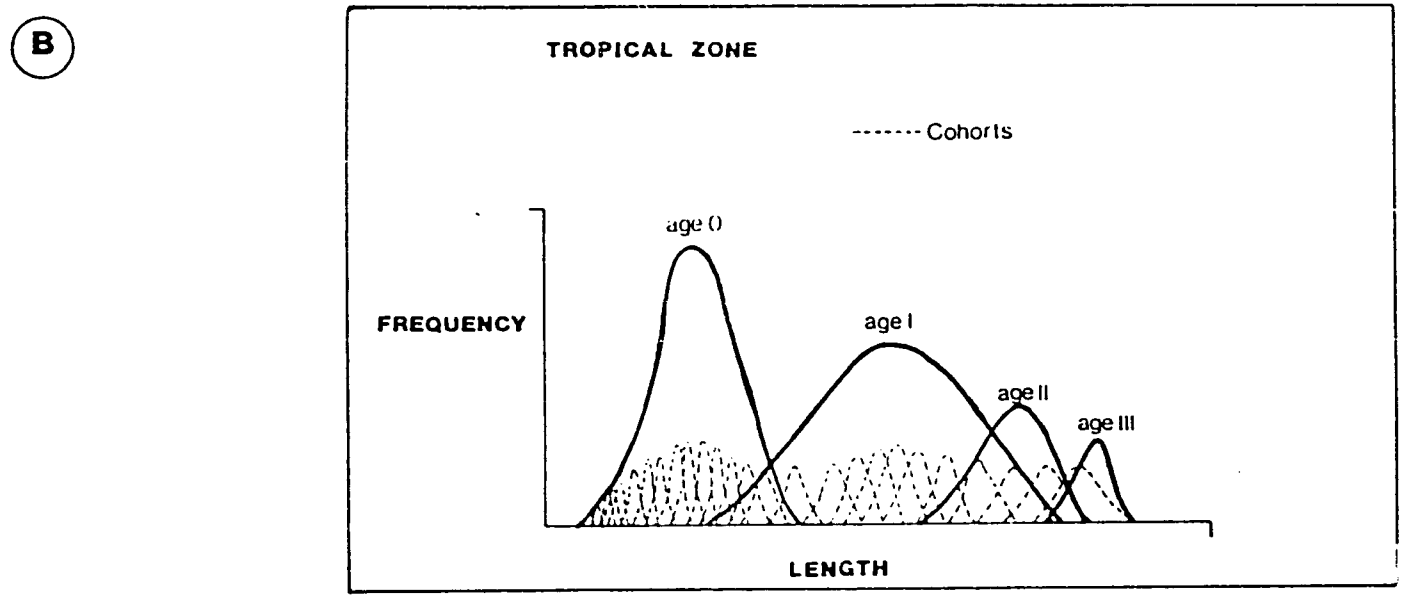

B
TROPICAL ZONE
------- Cohorts
FREQUENCY
age 0
age I
age II
age III
LENGTH

Figure 3

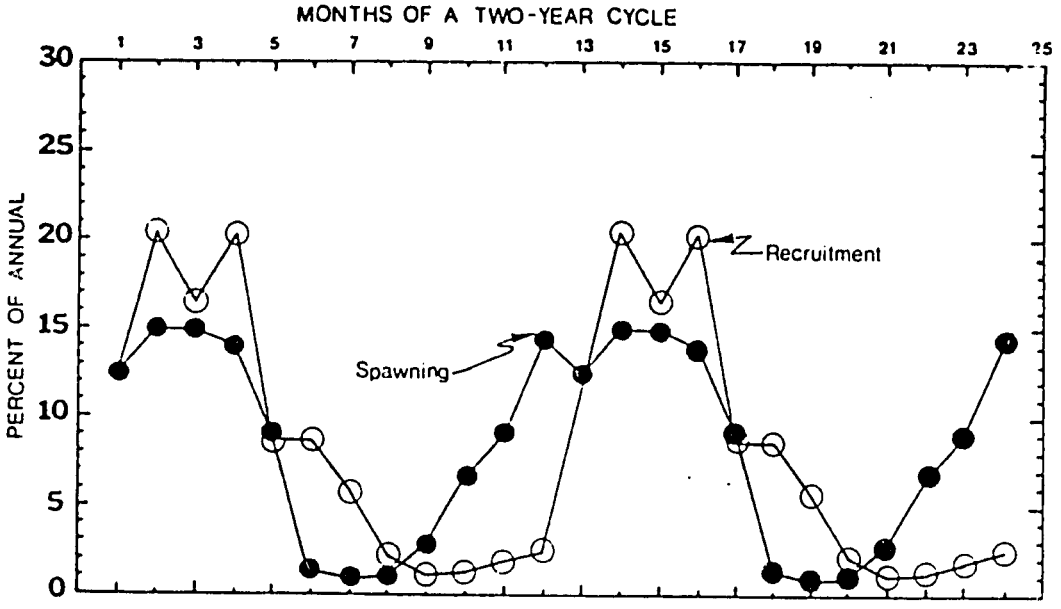

MONTHS OF A TWO-YEAR CYCLE
1
3
5
7
9
11
13
15
17
19
21
23
25
30
25
20
15
10
5
0
PERCENT OF ANNUAL
Recruitment
Spawning

Figure 4

Table 1 List of some families of tropical and subtropical marine fish and invertebrate stocks that are known or suspected to spawn and or recruit continuously or quasi-continuously on the basis of empirical data.

Family	Observation	Spawns	Recruits	Location/Source
Labridae	wrasses	Daily, year-round	Concentrated July-December	Panama/Victor ('83)
	""	year-round semi-lunar	year-round	Hawaii/Ross ('83)
	""	October-May		Australia/Russell et al. ('77)
Scaridae	parrotfishes	Daily, year-round		Panama/Robertson & Warner ('78)
	""	year-round (peaks: January & October		East Africa/Nzioka ('79)
	""	January-June		Jamaica/Munro et al. ('73)
	""	October-May		Australia/Russell et al. ('77)
Serranidae	hamlets	Daily, year-round		Panama/Fischer ('81)
	groupers	January-July (peak: February-March)		Jamaica/Munro ('82)
	""	July-February (two peaks: January & October)		East Africa/Nzioka ('79)
	""	November-January		Australia/Russell et al. ('77)
	""		year-round	Curacao/Luckhurst &
	""		winter & spring peaks	Luckhurst ('77)
	gag	December-May Unimodal		S. Atlantic & Gulf of Mexico Collins et al. ('87)
Lutjanidae	*L. apodus*	year-round (2 peaks: spring & fall)		Jamaica/Munro et al. ('73), Munro ('82)
	Lutjanus	July-February		East Africa/Nzioka ('79)
	L. campechnus	April-December		N.W. Gulf of Mexico/ Bradley & Bryan ('75)

Table 1 (Continued)

Family	Observation	Spawns	Recruits	Location/Source
	L. synagris	year-round		Trinidad/Manickchand-Dass ('87)
Lutjanidae	*L. vivanus*	year-round		Puerto Rico/Boardman & Weiler ('80)
	L. kasmira	March-December		Western Samoa/Mizenico ('84)
	L. filamentosus	March-December		Hawaiian Islands/Ralston ('81)
	L. multidens	year-round		New Hebrides/Brouard & Grandperrin ('84)
	Thunnus albacares	year-round multiple spawning	larvae year-round seasonal density peak	Mexico, Central America, equatorial waters of W. & Central Pacific/ Bayliff ('80), Otsu & Uchida ('59)
	T. alalunga	March-September (peak:March-May)		Hawaii/Yoshida ('68), Foreman in Bayliff ('80)
	skipjack	year-round multiple spawning	period becomes decreased with increased distance from equator	Pacific near 0°/ Forsbergh in Bayliff ('80),
Scombridae	Southern bluefin	September-March (peak:November-December)		Australia/ Olson in Bayliff ('80)
	bigeye	year-round (peak:April-September)	larvae more in W.&E. Pac.	Equator-12°N/ Calkins in Bayliff ('80)
	Northern bluefin	April-July		Between Japan & Philippines/Bayliff ('80)
	Scomber japonicus	March-October (peak:April-August) multiple spawnings		Baja California/ Schaefer in Bayliff ('80)
Sciaenidae	*Cynoscion nothus*	May-November (bimodal)	bimodal	N. Gulf of Mexico/ DeVries & Chittenden ('82)
			bimodal	Curacao/Luckhurst & Luckhurst ('77)

Table 1 (Continued)

Family	Observation	Spawns	Recruits	Location/Source
Sciaenidae	queenfish	year-round		California/DeMartini & Fountain ('81)
		8 months		South Africa/Wallace ('75)
	corvina	year-round	year-round	Costa Rica/Madrigal ('85)
Engraulidae	northern anchovy	year-round (20 batches/year)	year-round (peak:July-Nov)	California/Lasker & Smith ('77), Hunter & Leong ('81)
Clupeidae	sardine	August-February (2 peaks:Aug & Dec)	Nov-Dec Larvae	Baja California/Barret & Howard ('61)
Haemulidae	grunts	year-round	year-round dominant 15-day period	Virgin Islands/ McFarland et al. ('85)
	""	year-round	year-round	Florida/Lindeman ('86)
Pomacentridae	*Pomacentrus wacoi*	year-round	semi-lunar	Australia/Dougherty ('83)
	P. flavicauda	""	sporadic pulses	""
	Chromis		October-March	Australia/Sale ('80)
		year-round	semi-lunar	Hawaii/Lobel ('78)
			year-round bimodal: September & April	Curacao/Luckhurst & Luckhurst ('77)
Lethrinidae	emperor fish		June-November	Australia/Walker ('75)
	""	year-round (2 peaks:Sept. & January)		East Africa/Nzioka ('79)
Gobidae		October-April		Australia/Russell et al. ('77)
			year-round multiple modes	Curacao/Luckhurst & Luckhurst ('77)

Table 1 (Continued)

Family	Observation	Spawns	Recruits	Location/Source
Apogonidae	cardinalfishes	year-round	year-round (peaks:spring & fall)	Curacao/Luckhurst & Luckhurst ('77)
	angelfishes	summer-fall		Gulf of California/ Thresher ('84)
Pomacanthidae	""	year-round		Florida/Thresher ('84)
	""	October-May		Australia/Russell et al. ('77)
Grammidae	fairy basslets		year-round bimodal:Sept & May	Curacao/Luckhurst & Luckhurst ('77)
Canthigastidae	puffer		year-round bimodal	Curacao/Luckhurst & Luckhurst ('77)
Carangidae	jacks	year-round (largest % in coolest months)		Jamaica/Munro et al. ('73), Munro ('82)
Pomadasyidae		year-round		Jamaica/Munro et al. ('73), Munro ('82)
Holocentridae	squirrelfish	July-May		Jamaica/Munro et al. ('73)
Mullidae	mullet	year-round		Jamaica/Munro et al. ('73)
	""	""		East Africa/Nzioka ('79)
Chaetodontidae	butterflyfish	October-February April-August		Jamaica/Munro et al. ('73)
	""	December-June		Hawaii/Lobel ('78), Ralston ('81)
Acanthuridae		year-round December-August		Jamaica/Munro et al. ('73) Hawaii/Walsh ('87)
Balistidae	triggerfish	July-March		Jamaica/Munro et al. ('73)

Table 1 (Continued)

Family	Observation	Spawns	Recruits	Location/Source
Centropomidae	snook	April-December (2 peaks)		South Florida/Gilmore et al. ('83)
Penaeidae	*P. subtilis* Shrimps	year-round	year-round	Suriname/Willman & Garcia ('85), Garcia ('85)
Panuluridae	spiny lobster	year-round	year-round	Bermuda/Ward ('86)

Table 2: Characterizations of the tropical and temperate fishery systems.

Tropical Fisheries	
(1)	Combinations of large and diffuse artisanal operations compounded with semi- or industrial fisheries.
(2)	Fishing effort directed towards selected species (typically the top predators in the system) which are components of multispecies assemblages.
(3)	Gear types are highly variable. Gear more size-specific than species specific. Various targeted species are differentially vulnerable.
(4)	Catch is landed at multiple ports, with multiple species lumped in tl . catch statistics. Catch and effort data, when existing, are incomplete.
(5)	High species diversity for a given area.
(6)	Intense competition among cohorts within a given species.
(7)	High predation among species.
(8)	Continuous growth.
(9)	Continuous or protracted spawning and recruitment activity.
(10)	Alternative reproductive strategies (e.g. hermaphroditism).

Temperate Fisheries	
(1)	Heavy industrialization with a roughly homogeneous fleet structure.
(2)	A less heterogeneous distribution of the stocks for a given area.
(3)	Single or few gear types and fishing effort affecting most age groups equivalently.
(4)	Comparatively improved statistical reporting.
(5)	A reduced number of species.
(6)	Suspected levels of intra-species competition?
(7)	Predation is implicated in several fishery systems?
(8)	Seasonally restricted growth.
(9)	Recruitment restricted to a retracted portion of the year.
(10)	Few incidences of alternative reproductive strategies.