

Simulation of the Effects of Spawning and Recruitment Patterns in Tropical and Subtropical Fish Stocks on Traditional Management Assessments

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ABSTRACT

Many subtropical and tropical fish stocks are believed to spawn, recruit and grow quasi-continuously. Typically, traditional yield models, derived for seasonally (discrete) spawning and growing temperate zone fishes, are utilized to assess fish stocks and provide management advice in subtropical and tropical marine environments. Population processes specific to fishes in these regions are believed to impair conclusions derived from traditional fishery modeling. No one has investigated the effects of continuous spawning and recruitment in exploited populations in a generalized and comprehensive manner. In this study classes of spawning and recruitment were determined. A continuous-time computer simulation model which accommodates variable recruitment strategies and creates the respective population structures, with facility for seasonally variable growth, is described. Results of a simulation study are utilized to:

1. Compare discrete-versus continuous-recruiting cases.
2. Determine the efficacy of traditional stock assessment techniques under both cases.
3. Identify and evaluate sources and effects of bias.

The effects on management advice produced by standard yield models are discussed.

INTRODUCTION

Fisheries in tropical seas are under pressure for rigorous management policy due to competing interests for available finite resources. Concurrently, with the Law of the Sea and the advent of nationalized 200 mile limits for marine resources, increased attention is being given to fishery management, particularly in productive tropical seas such as those bounded and fished by developing countries.

Combinations of species richness and the abundance of individuals in tropical seas has contributed to a myriad of problems in understanding fishery demographics. Due primarily to the paucity of adequate and appropriate fishery data, simple, single-species equilibrium models with minimal data requirements, are touted as the supporting mechanisms for the development of fishery management policy in tropical regions (Pauly, 1982). These methods are operated in light of the fact that virtually no exploited fish population is in a steady state yet, as a first approximation in modeling a fish population, a steady state is usually assumed (Gulland, 1983).

Traditional exploited fish stock assessment techniques developed specifically for advanced fisheries in temperate waters rely primarily on information concerning the distribution of the ages of fish in the catch.

Temperate region fisheries are characterized by:

1. Single species.
2. Single or few gear types.
3. Heavy industrialization (with good statistical reporting).
4. Well-defined seasonal growth.
5. Homogeneous stock distribution for a given area.
6. Fishing effort affecting all age groups equivalently.

Note that management in temperate regions has not necessarily served as a paradigm.

In contrast, because of subtle seasonal variation in tropical waters and the remoteness of many productive fishing areas, large-scale sampling programs for age distribution are usually not feasible (Jones, 1981, 1984). This is because aging of these fishes is quite difficult due to multiple cohort production and the continuous growth conditions occurring intra-annually. Typically, the catches from fish stocks are aged by an average-length key. Statistical averages are more meaningful when they refer to homogeneous groups (Keyfitz, 1977). Protracted spawning which is distributed asymmetrically induces considerable error in the basic catch-at-age data, the magnitude of which is not known. Thus, age-based stock assessment techniques may be of limited utility in tropical fisheries.

Tropical, multigear, multispecies fisheries are hard to understand. Tropical fisheries are combinations of large and diffuse artisanal operations and/or recreational fisheries that are compounded with developed or developing fisheries. They attempt to operate on selected species from multiple assemblages which are frequently estuarine or coral reef based. Catch is landed at multiple ports (with species lumping in statistics), and catch and effort data, when existing, are incomplete by areas. Tropical species life history characteristics include:

1. Continuous or protracted spawning activity.
2. Alternative reproductive strategies (*i.e.* hermaphroditism).
3. Continuous growth.
4. High predation.
5. Intense competition among and between cohorts.
6. High species richness and diversity.

Fisheries associated with tropical reef systems tend to center on stocks which are top predators in the system. Gear is more size-specific than species specific. The differential fishing mortality strategies by sex, age, and spawning aggregations can damage the stock's reproductive potential. Additionally, simultaneous harvesting of a large number of species in multispecies systems will often manifest complex "catastrophic" behavior, whereby the system is discontinuously transformed to different equilibrium states (bifurcating multiple stable or chaotic points) as the harvest rates increase, or environmental circumstances alter.

Traditional, single-species stock assessments applied to tropical situations most likely fail because the species under study are embedded in complex communities. The dynamics, as well as the equilibrium densities, of the species of interest undoubtedly reflect the embedding. A "paradox of the tropics" results when assessment methods are tacitly applied to these seemingly simple fisheries which are embedded within complex frameworks. 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. Models should emerge as syntheses of knowledge of a range of actual cases. Simulation models are the current vogue in practically all branches of science, fisheries science is no exception. A simulation model is constructed in the hope that it will successfully mimic a real world system. The model may, as a consequence, become very complicated and involved. Numerical models provide the most realistic representation of complex problems of any quantitative technique because they allow characterization of large sets of differential equations with feedback mechanisms from both deterministic and stochastic perspectives.

STATEMENT OF THE PROBLEM

Fishery management programs require estimates of stock size; a function of recruitment, growth, and mortality. These variables are governed by time dependent and spatial mechanisms such as competition, predation, and mesoscale environmental processes. The stock and recruitment problem has been identified as the most serious scientific problem facing those concerned with fishery management (Gulland, 1983). Many subtropical and tropical fish and invertebrate stocks are believed to spawn, recruit, and grow quasi-continuously. Notable among these families are the economically important serranids, scombrids, engraulids, clupeids, lutjanids, and penaeid shrimps. These types of life history strategies can have profound effects on our perceptions of stock response to exploitation. Current stock assessment techniques, developed specifically for temperate, discrete spawning, single-species fisheries, are basically elaborate methods of fitting curves to data. These model's simplifying assumptions may have an insidious nature when applied to tropical situations. To date, no one has adequately quantified or evaluated continuous recruitment, nor its effects on traditional fishery models. Furthermore, there is a paucity of competent technology to deal with these specific conditions. Population structure and the exploitation potential of marine fish stocks are dependent upon intrinsic recruitment patterns. Failure to adequately address indigenous recruitment patterns may have deleterious effects on specific analysis procedures, and impair management advice.

We believe that tropical and subtropical fishery systems can be more effectively managed by systematically evaluating the population processes specific to the fish stocks in these regions. Therefore, the objectives of this study were:

1. To determine and describe classes of spawning and recruitment.
2. To develop a quasi-continuous time simulation model which mimics observed tropical and subtropical fish recruitment patterns and satisfactorily models the respective population structures.
3. To compare parochial, discrete-time recruiting populations with the dynamic, quasi-continuous cases.
4. Perform sensitivity analyses to determine the efficacy of traditional stock assessments techniques under both the quasi-continuous and discrete cases.
5. To determine and identify sources of bias.

Our overall research goal is the construction of widely applicable mathematical algorithms with the ability to model the variability and scale of the

continuous spawning and multiple cohort recruitment processes which presently are believed to impact resource assessments of tropical and subtropical marine species, and which alleviate the problem of having to investigate the full factorial design numerically.

SPAWNING AND RECRUITMENT PATTERNS IN TROPICAL MARINE WATERS

A supposed universal reproductive strategy in fish stocks is to maximize the production of surviving progeny in relation to available energy and parental life expectancy (Ware, 1984). However, the variety of reproductive strategies and tactics in fishes clearly indicate that no single reproductive pattern is universally adaptive, even within the same ecological community. Rather there is some combination of life history characteristics where each specific strategy confers the highest fitness. Nataly processes are critically implicated in establishing fish stock structure. Some remaining questions are:

1. How is recruitment disturbed temporally?
2. What is the magnitude of it's variation relative to transitional fishing strategies?

To date, most theoretical studies of alternative reproduction and survival patterns have concentrated on the evolutionary implications of the equilibrium state, and have largely ignored transient dynamics, which are an important concern of management agencies (Ware, 1984).

For fishes inhabiting an environment with pronounced seasonal climatic variability the breeding season is almost invariably confined to a brief and specific period of the year. At high latitudes many fishes produce a single spawning batch per year (Qasim, 1956). This is reflected in a discrete, unimodal pulse of recruits entering the population annually as a single population cohort (Figure 1A). A cohort here is defined as a set of fish from the same species entering the population at the same instant. Conversely, the less variable environmental fluctuations in tropical latitudes may produce a relatively constant environment in which breeding, spawning, and hence recruitment, can theoretically occur throughout the year. This can result in multiple cohort production within any one calendar year (Figure 1B). By our present nomenclature these multi-cohort yearclass members are considered of the same annual cohort. Furthermore, 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 should therefore have evolved to maintain a continual source of recruits to buffer losses (Luckhurst and Luckhurst, 1977).

Spawning

Many tropical and subtropical marine fish have protracted breeding seasons, with different individuals breeding at different times throughout the year (Sale, 1980, 1982; Munro *et al.*, 1973; McKaye, 1977; Nzioka, 1979; Bayliff, 1980; Munro, 1982; Bye, 1984; Grimes, 1986). Most of these fishes are believed to grow quasi-continuously. At least 27 families of economically important tropical and subtropical marine fishes and invertebrates spawn year-round (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

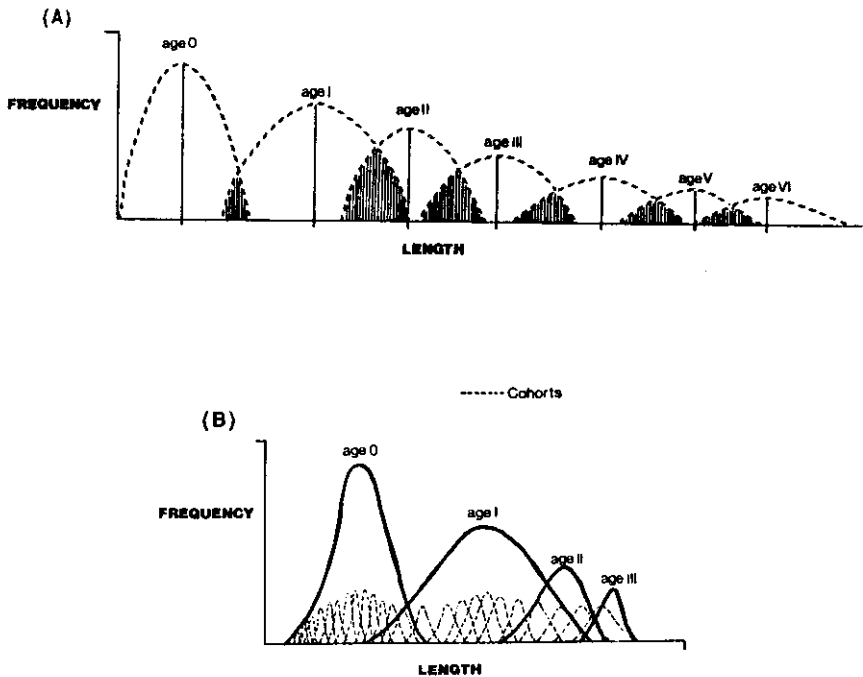


Figure 1. Hypothetical population length frequency distributions for the : (A) Retracted discrete spawning temperate zone, and (B) Protracted quasi-continuous spawning tropical zone marine fish life histories.

a continuum over much longer portions of the year. Qasim (1956) suggested that the breeding cycles of marine fishes are adapted to provide optimum 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 most southern fish stocks, sufficient food is available for adults to support the maturation of successive batches of eggs. Cushing (1970) 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 year is most likely to ensure a match between larvae and food. In the subtropics and tropics 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 predation can be avoided by spawning over an extended period (Grimes, 1986).

Serial spawning fishes are characteristic of subtropical and tropical seas (Nikolsky, 1963). "Repeat spawning" within a season is reflected in

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

Family	Spawns	Recruits	Location/Source
Labridae (Wrasses)	1. Daily-year-round	Concentrated July-Dec year-round	Panama; Victor ('83)
	2. year-round; semi lunar		Hawaii; Ross ('83)
	3. Oct-May		Australia; Russell <i>et al.</i> ('77)
Scaridae (Parrotfishes)	1. year-round (daily)	Panama; Robertson & Warner ('78) East Africa; Nzioka ('79) Jamaica; Munro <i>et al.</i> ('73) Australia; Russell <i>et al.</i> ('77)	
	2. year-round (peaks: Jan, Oct)		
	3. Jan-June		
	4. Oct-May		
Serranidae	1. Hamlets	year-round (daily)	Panama; Fischer ('81)
	2. Groupers		Jamaica; Munro ('82)
	3. July-July (peak: Feb-Mar)		East Africa; Nzioka ('79)
	4. July-Feb (peaks: Jan, Oct)		Australia; Russell <i>et al.</i> ('77)
	5. Nov-Jan		Curacao; Luckhurst & Luckhurst ('77)
Lutjanidae	1. <i>L. apodus</i>	year-round; common winter & spring	Jamaica; Munro <i>et al.</i> ('73), Munro ('82)
	2. <i>L. campechanus</i>		East Africa; Nzioka ('79)
	3. Lane Snapper		N.W. Gulf of Mexico; Bradley & Bryan ('75)
	4. <i>L. vivanus</i>		Trinidad; Manickchand-Dass ('87)
	5. <i>L. kasmira</i>		Puerto Rico; Boardman & Weiler ('80)
	6. <i>L. filamentosus</i>		Western Samoa; Mizenico ('84)
	7. <i>L. multidentis</i>		Hawaiian Islands; Ralston ('81)
	8. <i>L. multidentis</i>		New Hebrides; Brouard & Grandperrin ('84)

Table 1 (continued).

Family	Spawns	Recruits	Location/Source
Scombridae			
1. Yellowfin <i>T. albacares</i>	year-round multiple spawning	larvae year round seasonal density; year-round (2 peaks) 2 cohorts	Mexico, Central America Equatorial waters of W. & Central Pacific; Bayliff ('80), Otsu & Uchida ('59), Knudsen ('77)
2. Albacore <i>T. alalunga</i>	Mar-Sep (peak: Mar-May)		Hawaii; Yoshida ('68), Foreman in Bayliff ('80)
3. Skipjack	year-round multiple spawning	period becomes with increased distance from equator	Pacific near 0°; Forsberg in Bayliff ('80)
4. So. Bluefin	Sep-Mar (peak: Nov-Dec)		
5. Bigeye	year-round (peak: Apr-Sep)	larvae more numerous in W & E Pac. (30°N-20°S)	Australia; Olson in Bayliff ('80) Equator - 12°N;
6. No. Bluefin	Apr-July		Calkins in Bayliff ('80)
7. Pacific Mackerel <i>Scomber japonicus</i>	Mar-Oct (peak: Apr-Aug) multiple spawnings (batches)		Betw. Japan & Philippines; Bayliff ('80) Baja California; Schaefer in Bayliff ('80)
Sciaenidae			
1. <i>C. Nothus</i>	May-Nov (bimodal)	bimodal	N. Gulf of Mexico; DeVries & Chittenden ('82)
2.		bimodal	Curaçao; Luckhurst & Luckhurst ('77)
3.			California; De Marini & Fountain ('81)
4.	8 months		S. Africa; Wallace ('75)
Engraulidae			
	year-round (20 batches/year)	year-round (peak: July-Nov)	California; Lasker & Smith ('77); Hunter & Leong ('81)

Table 1 (continued).

Family	Spawns	Recruits	Location/Source
Clupeidae	Aug-Feb (2 peaks: Aug-Sep & Dec-Jan)	Nov-Dec Larvae	Baja California; Barret & Howard ('61)
Haemulidae	year-round	year-round dominant 15 day period	Virgin Islands; McFarland et al. ('85)
Pomacentridae	year-round	semi-lunar; sporadic pulses-wave fronts	Australia; Dougherty ('83)
(Damsel-fishes)		Oct-Mar	Australia; Sale ('82)
1. <i>P. waco</i>		semi-lunar	Hawaii; Lobel ('78)
2. <i>P. flavicauda</i>		year-round	Curaçao; Luckhurst & Luckhurst ('77)
3. Chromis			
4.			
Lethrinidae	year-round (2 peaks: Sep-Oct & Jan-Feb)	mid-winter; June-Aug	Australia; Walker ('75)
(Emperor fish)			East Africa; Nzioka ('79)
Gobiidae	Oct-Apr	year-round bimodal-mult. modes	Australia; Russell et al. ('77)
1.			Curaçao; Luckhurst & Luckhurst ('77)
2.			
Apogonidae	year-round	year-round peaks: spring & fall	Curaçao; Luckhurst & Luckhurst ('77)
(Cardinal-fishes)			
Pomacanthidae	summer-fall year-round Oct-May		Gulf of California; Thresher ('84)
1.			Florida; Thresher ('84)
2.			Australia; Russell et al. ('77)
3.			

Table 1 (continued).

Family	Spawns	Recruits	Location/Source
Grammidae (Fairy Basslets)		year-round bimodal: Sep & May	Curaçao; Luckhurst & Luckhurst ('77)
Canthigaster (Puffer)		year-round bimodal	Curaçao; Luckhurst & Luckhurst ('77)
Carangidae	year-round (largest % in coolest months)		Jamaica; Munro <i>et al.</i> ('73), Munro ('82)
Pomadasyidae	year-round (peak: Feb-Apr)		Jamaica; Munro <i>et al.</i> ('73), Munro ('82)
Holocentridae	July-May		Jamaica; Munro <i>et al.</i> ('73)
Mullidae	1. year-round 2. year-round (2 peaks: Mar, Nov)		Jamaica; Munro <i>et al.</i> ('73) East Africa; Nzioka ('79)
Chaetodontidae	Oct Feb, Apr-Aug		Jamaica; Munro <i>et al.</i> ('73)
Acanthuridae	year-round		Jamaica; Munro <i>et al.</i> ('73)
Balistidae	July-Mar		Jamaica; Munro <i>et al.</i> ('73)
Centropomidae 1. Common Snook	Apr-Dec (2 peaks: June-July, Aug-Oct)		S. Florida; Gilmore <i>et al.</i> ('83); Garcia & LeReste ('81)
Penaeid Shrimps	1. <i>Penaeus subtilis</i> Brasiliensis	year-round (2 peaks: Feb-June, Oct)	Suriname; Willmann & Garcia ('85); Garcia & LeReste ('81)
Panuliridae	1. Spiny Lobster		Bermuda; Ward (1989)

characteristic size-frequency distribution of oocytes within mature ovaries where, as well as a batch completing vitellogenesis or already ripened, there is also a comparably numerous group at mid-vitellogenesis which will provide the next spawning (Hunter and Macewicz, 1985). This pattern has been documented *inter alia* for queenfish (DeMartini and Fountain, 1981), anchovies (Hunter and Leong, 1981), and snappers (Grimes, 1986). Protracted spawning is characteristic of serial spawners (Nikolsky, 1963; DeMartini and Fountain, 1981). Conversely, northern forms spawn at a season which is not very favorable for feeding, so that the females put all their reserves into a single batch. For example, skipjack tuna, bigeye tuna, and yellowfin tuna are believed to spawn year-round in the equatorial Pacific Ocean. Tuna larvae are found all over the northern subtropical Pacific at nearly all seasons (Matsumoto, 1966). Skipjack tuna, however, are believed to have a spawning period which decreases with increased distance from the equator (Forsberg, 1980). Grimes (1986) identifies two patterns of reproductive seasonality for the lutjanids:

1. Continental populations have a spawning season which is typically centered around summer.
2. 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. Daily, weekly, biweekly, and monthly spawning cycles are all common (Robertson and Warner, 1978; Fischer, 1981; Warner and Robertson, 1978; Sale, 1982; Victor, 1983; Dougherty, 1983). Daily spawning is a common phenomenon among coral reef fishes (Victor, 1983), particularly in wrasses (Labridae), parrotfishes (Scaridae), and the basses (Serranidae). Other 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 a protracted spawning season. Spawning of the queenfish is asynchronous among females, but has monthly peaks in intensity during the first quarter of the moon (DeMartini and Fountain, 1981). The queenfish closely resembles many or most small, planktonic spawners of warm temperate regions. Lunar spawning intervals are also known for several littoral fishes that spawn demersal eggs (Hines *et al.*, 1985).

Recruitment

The term "recruitment" for commercially exploited fish populations has been defined by Beverton and Holt (1957) as the process in which young fish enter the exploited area and become liable to contact with fishing gear. Parrish (1978) distinguishes two life history stages to the recruitment process:

1. Prerecruit — recruitment to the fishable stock.
2. Recruits — recruitment to the fishery.

Cushing recognizes a third stage:

3. Reproductive recruit — recruitment to the mature stock.

Survivorship to the recruit phase is apparently very low. The numbers of recruits are substantially less than the number of eggs produced each season. Several recent studies have measured recruitment to monitored sites. Although reproductive activities of marine fishes in these areas often extends over considerable periods, seasonal patterns in reproductive activity of adults, and larval abundance and recruitment of these fishes have been well documented

(Johannes, 1978; Munro *et al.*, 1973; Nzioka, 1979; Luckhurst and Luckhurst, 1977; Bayliff, 1980; Murphy, 1982). The most detailed information on both spatial and temporal variation in recruitment concerns the more abundant reef species; particularly pomacentrids in the Indo-Pacific and the Caribbean (Eckert, 1984; Victor, 1983; Luckhurst and Luckhurst, 1977) and haemulids in the Caribbean (McFarland *et al.*, 1985). 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.
3. The inability to sample larval habitats properly (Lasker, 1981).

Recruitment during seasonal peaks is apparently not uniform, but tends to occur in pulses. Seasonal peaks in larval abundance and recruitment have been observed on the Great Barrier Reef (Dougherty, 1983; Williams, 1983; Sale, 1980), in the Philippines (Pauly and Navaluna, 1983), Japan (Yamamoto, 1976), Guam (Kami and Ikehara, 1976), Hawaii (Watson and Leis, 1974), the eastern Pacific Ocean (Bayliff, 1980), the Gulf of California (Molles, 1978), and the Caribbean sea (Luckhurst and Luckhurst, 1977). Spring and fall peaks which seem to be confirmed for the Caribbean (Munro *et al.*, 1973; Luckhurst and Luckhurst, 1977), might converge in more northern waters and be replaced by a single summer peak. Presently, there is no 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 have been demonstrated, and up to 10 fold differences between integer years in the number of recruits arriving (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.

Predictable recruitment patterns of coral reef fishes closely parallel spawning patterns (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 (see Hunter and Leong, 1981). For example, spawning in Jamaican waters shows two main periods for most of the larger species of reef fishes with maxima around March to April and September to October (Munro *et al.*, 1973). Corresponding recruitment peaks occur after peak larval abundance (Parrish's prerecruitment) (Luckhurst and Luckhurst, 1977). 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. Wallace (1975) noted that the dominant species in South African estuaries had extended spawning seasons of up to eight months. Prolonged periods of post-larval and juvenile recruitment to South African estuaries was thought to provide a buffer against recruitment failures resulting from droughts or unseasonal floods (Wallace, 1975). Lunar settlement cycles in subtropical and tropical fishes are reported (Shulman *et al.*, 1983; Hines *et al.*, 1985; McFarland *et al.*, 1985). The

timing of settlement of potential prey species relative to their predators can be a crucial factor in successful settlement into a habitat (Shulman *et al.*, 1983). Also, 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 and Backus, 1985; Lobel and Robinson, 1986). Reproductive strategies of marine animals 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).

CONCEPTUAL MODEL

The reproductive strategy of a species of fish is that complex of reproductive and behavioral traits that fish manifest so as to leave some offspring. In population biology, this usage has led to the development of the concept of evolutionary stable strategies (ESS), that is a mixture of strategies adopted by a population that is not susceptible to invasion by a hypothetical alternative (Maynard Smith, 1976). A strategy designates a plan so complete that it cannot be upset by enemy action or nature. The terms strategy and tactic imply rational planning or "natural selection" but note that it does not have to be an optimal strategy. Thus, a major problem for population biologists is to show how particular reproductive strategies and tactics are adaptive in particular environmental circumstances.

The spawning and recruitment patterns exhibited by temperate and tropical marine fishes have been classified within the context of a 3 x 3 matrix arrangement (Table 2). Three classes were assigned to each of the following three categories:

1. The spawning/recruitment patterns.
2. The distribution of modes observed annually.
3. The affinity to well known statistical distributions.

Obviously, overlapped and interconnected breeding and recruiting strategies exist. Our approach allows a basis for conceptual framework from which we will subsequently numerically model these fish populations. The "continuum" and "protracted" spawning and recruitment states are characteristic of tropical environs. The "continuum" recruitment condition refers to an infinite set of recruit particle emissions such that between any two of them there is a third pulse of recruits. This condition is by definition continuous spawning/recruitment. The "protracted" condition refers to an intermediate process where spawning/recruitment has an extended duration in time and thus is quasi-continuous. Most subtropical and tropical fishes are iteroparous (*i.e.*,

Table 2. Classes of heterochronal annual spawning/recruitment patterns for tropical and subtropical iteroparous marine fishes.

	I	Class II	III
Spawning/Recruitment	Retracted	Protracted	Continuum
Forms	Uniform	Unimodal	Multimodal
Distribution	Normal	Gamma	Other

reproduction occurs on more than one occasion during the life-span). Annual fecundity is seasonally indeterminate in many of these fishes (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 year. 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 epipelagic spawners (Hunter and Macewicz, 1985). "Retracted" spawning/recruitment is typical of discrete-pulsed 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). The spawning/recruitment conditions delineated 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, gamma or some other probability distribution. 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 allow calculation of potential fishery yields. The form and periodicity of recruitment are critical in establishing the probability of a particular size/age population distribution, and the subsequent impact those particular distributions may have in influencing recruitment.

A spectrum of selected examples of both the spawning and recruitment patterns are shown in Figures 2 and 3, respectively. In no case have we accounted for any more than two years of interannual variability due to abiotic (*i.e.*, climatological) characteristics. Rather, we are more interested in the apparent patterns and forms of spawning and recruitment in these fishes. Our approach is to model specific observed spawning and recruitment patterns in our investigations and examine the influence these conditions have on our interpretations when standard stock assessment methodology is applied. The time dependence of these events suggests that variations in the amplitudes of sinusoidal recruitment functions may be important in understanding whether attractor spaces exist in continuous population cycles.

MATHEMATICAL SIMULATION MODEL & EXPERIMENTAL APPROACH

In addition to the numbers of recruits produced within a given time interval (*e.g.*, a year), an important aspect of recruitment is its structure within that

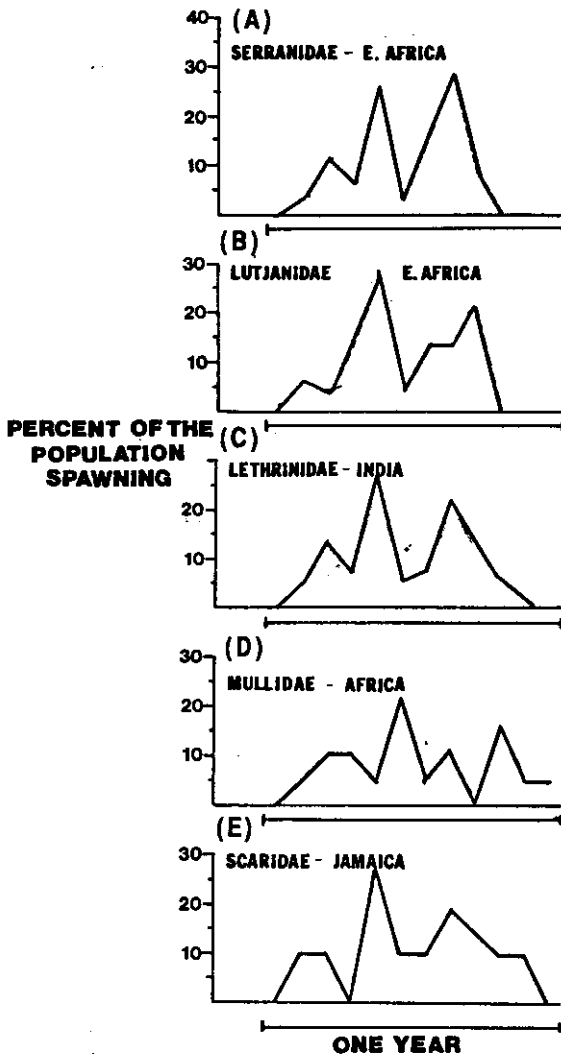


Figure 2. Selected circum-tropical protracted spawning patterns for five families of marine fishes. Sources of data: Nzioka, 1979 (A,B,D); Qasim, 1973 (C); Munro, 1982 (E).

interval, viz. whether recruitment is discrete or continuous. Very little work has been done on stock-spawner-recruitment relationships for tropical fishes (Pauly, 1982). Tropical fishes have been reported by many authors to have "protracted" spawning seasons (op. cit.). In natural fish populations the number of recruits entering the system will vary substantially. Thus, an understanding of the

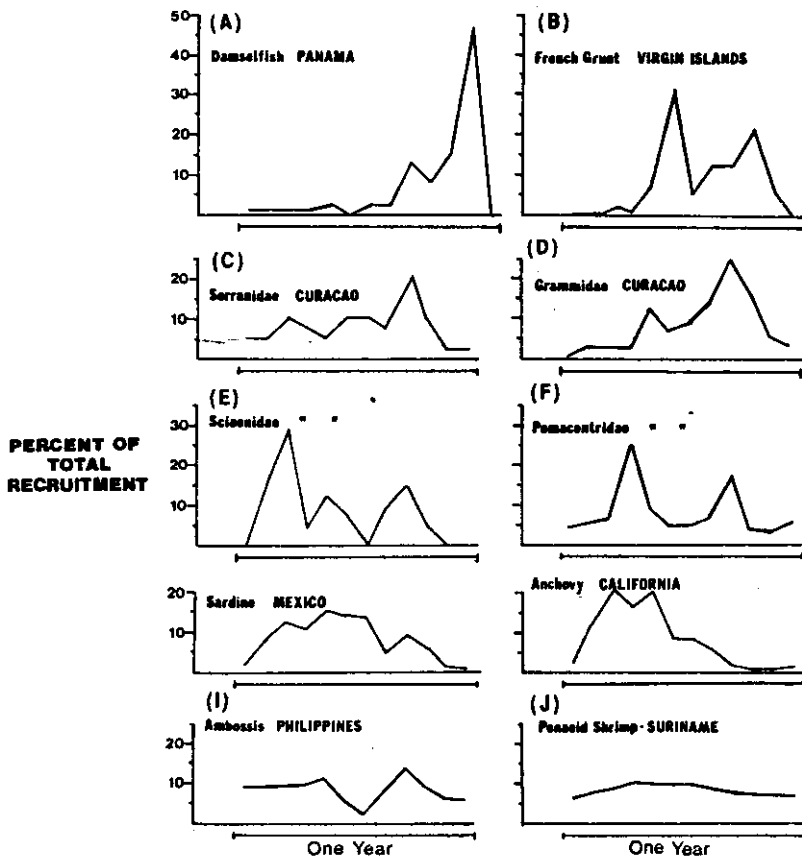


Figure 3. Selected circum-tropical protracted and/or continuous recruitment patterns for ten families of marine fishes and invertebrates. Sources of data: Victor, 1983 (A); McFarland *et al.*, 1985 (B); Luckhurst & Luckhurst, 1977 (C,D,E,F); Cushing, 1977 (G,H); Pauly, 1982 (I); Willman & Garcia, 1985 (J).

growth and decay properties of population cohorts is fundamental to many fishery management decisions as well as to population modeling (Alverson and Carney, 1975).

One technique for analyzing the probable adaptive significance of reproductive strategies or tactics is the use of mathematical models. If continuously recruiting populations do respond differently to exploitation than discrete-pulsed recruiting populations, then use of temperate-based modeling and decision-making to determine optimal management strategy will likely be influenced. If the relationships are simple enough, then the application of closed

solution analytical models might be possible. However, real systems are generally far too complex for smoothed-over analytical evaluation. Therefore, the system must be studied utilizing numerical models. Because of the strong differences between population reproductive behavior in the temperate zones versus the tropical zones with regard to discrete versus continuous response, an alternative approach utilizing continuous mathematical processes was developed. Functions of continuous variables are the principal means of looking more deeply into demographic matters (Keyfitz, 1977). A simulation model, CORECS (CONTinuous-time RECRUITment Simulation), was developed (Figure 4). Specialized model features include the ability to divide the time stream up into as many finite intervals as desired, and allow the introduction of cohorts among any and/or every finite time step. Since "cohorts" in tropical latitudes are produced more or less in a continuum relative to the discrete, once annual, recruitment of temperate based fishes, population structure is simulated numerically by multiple production of cohorts by species group within any one year, and allowed to be constant or variable among years. Because of this scaling feature then, probability density functions peculiar to the various aforementioned classes of multiple-annual recruitment, growth and mortality may be introduced. Thus, simulated populations with varying lengths of protracted spawning and variable density-dependent recruitment rates, but with known catches-at-ages (or sizes) can be parametrized in the algorithm. This allows simulations to be conducted which contrast discrete-event versus continuous-event approaches. We have investigated the outcomes of the two classes of results on predictions rendered by traditional yield models (*i.e.*, analytical and dynamic pool) with special reference to whether the advice derived from these predictions is conservative or nonconservative relative to risk to the resource.

The Simulation

The mathematical description of continuous recruitment in marine fish populations has an affinity to periodic functions. The magnitudes of these functions are generally not known, but inferred. The magnitude can simply be viewed as a scaling feature. The pure form of the function is desired in order to establish its effects on population structure at size under various recruitment hypotheses. Three such plausible annual recruitment structures are presented here:

1. A uniform time-step-constant recruitment.
2. A unimodal-annual recruitment.
3. A bimodal-annual recruitment (Figure 5).

For a simulated Grouperoid (=grouper-like) population characterized by low natural mortality, slow growth, and thirteen year-classes, the population length-frequency distribution is shown for the deterministic uniform and unimodal recruitment hypotheses (Figure 6). Note the fundamental differences in expectation of individuals at size (or age) under the two hypotheses. The pooled length frequency distributions for two recruitment hypotheses and two different pooling schemes, one by 20 mm increments, and two by 40 mm increments, are shown (Figure 7). Note the roughly constant exponential decline for the constant uniform hypothesis (Panel A), with no apparent discernment of age structure. Clearly, recruitment even in tropical fishes must oscillate seasonally, since year-round constant recruitment would generate size

CORECS - Continuous-Time Recruitment Simulation Model

	$i = \underline{1}$	$\underline{2}$	$\underline{3}$	$\underline{4}$. . .	\underline{N}	
$j = 1$	1,1	2,1	3,1	4,1	. . .	N,1	$\equiv R_{ij}$
2		1,2	2,2	3,2	. . .	N-1,2	
3			1,3	2,3	. . .	N-3,3	
4				1,4	. . .	N-4,5	
5					
.					
.					
N						1,N	

where, $N =$ (oldest age in the catch) \times (division of time stream)
 $i =$ time stream
 $j =$ length (or time) class

and

$R_{ij} =$ recruitment in time stream i for length class $j = 1$
 $i = 1, \dots, \infty$

Figure 4. General structure of the continuous-time simulation model, CORECS, showing n-dimensional upper triangular structure.

frequency distributions lacking peaks and troughs. Note that for the unimodal annual recruitment models, (Figure 7, Panels B and C) modes are obvious at smaller sizes, but these become obliterated with increased size (=age), and/or increased pooling. This suggests that estimation procedures can be biased by improper pooling and/or disproportional temporal or areal sampling. Potential yield surfaces for the grouperoids under :

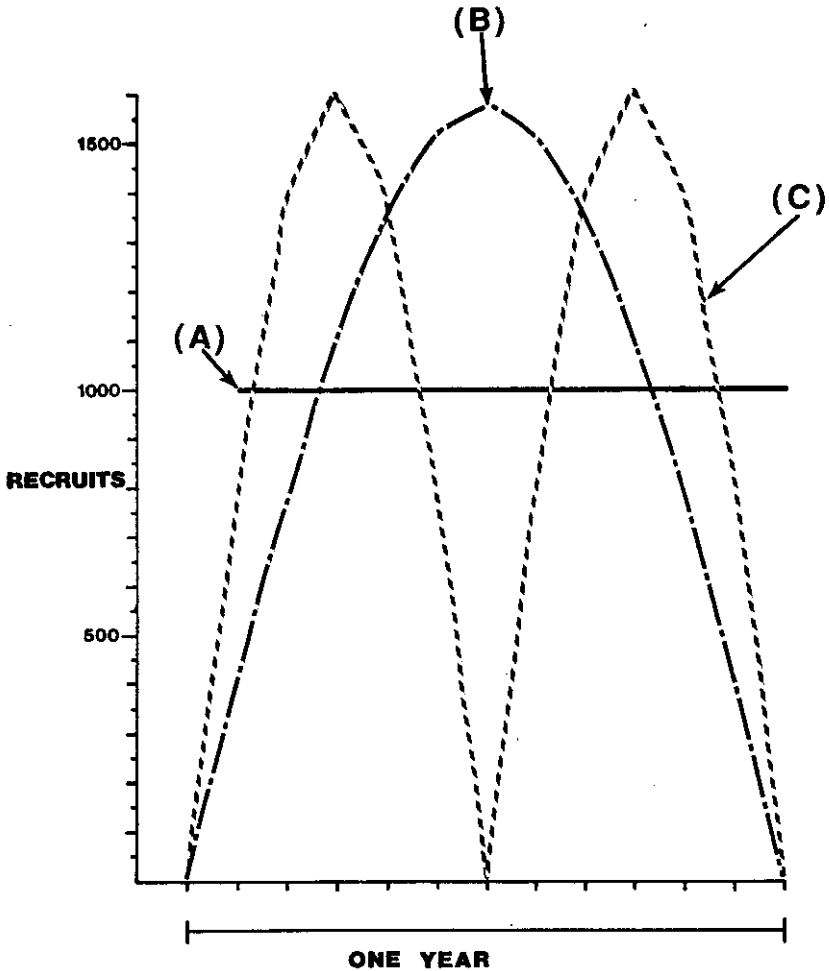


Figure 5. Three plausible annual recruitment structures of tropical and subtropical marine fishes: (A) uniform, (B) unimodal, and (C) bimodal.

1. Constant recruitment.

2. Density-dependent recruitment are shown (Figure 8).

The constant recruitment hypothesis suggests that recruitment remains static regardless of the level of population abundance (Figure 8, Panel A). The density-dependent recruitment, on the other hand, suggests that yields are constrained by a plane that cuts the surface obliquely at high levels of fishing mortality and/or size of capture. Additionally, the global maximum potential yield shifts to lower levels of fishing mortality and higher levels of age of

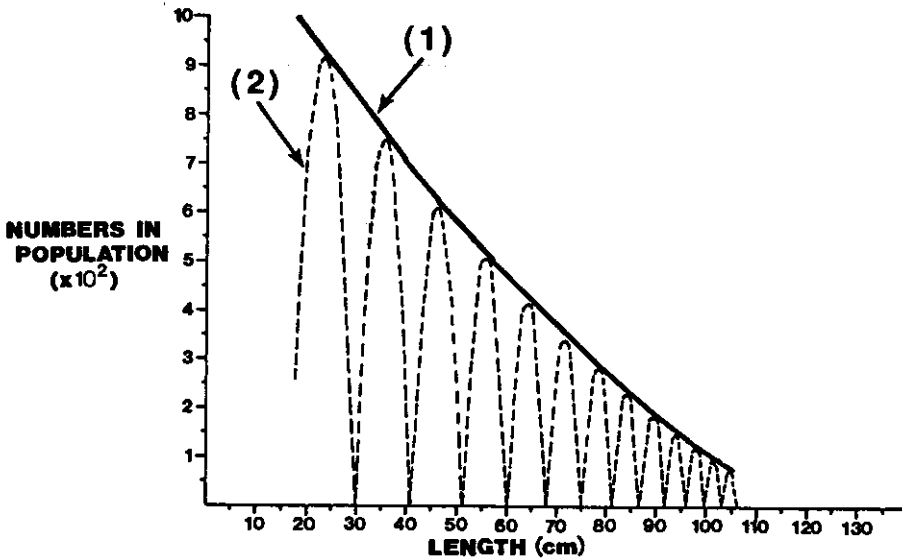


Figure 6. Simulated population length frequency structure for a Grouperoid stock with an instantaneous natural mortality rate of $M = 0.2$, von Bertalanffy growth coefficient of $K = 0.122$, and the oldest age in the catch of $t_{\lambda} = 13$ years for two hypothetical recruitment patterns: (1) uniform constant distributed monthly, and (2) unimodal with an annual period.

capture. When we cut through a plane parallel to the age of first capture corresponding to $tp^1=7$ under the density-dependent hypothesis, the stationary and the dynamic trends in yield and profit are shown (Figure 8, Panel B). Note that trends in increased fishing mortality cause the yield and profit to exceed the equilibrium surface, and subsequently excessive levels of fishing mortality cause both yield and profit to fall below the stationary surface. Statistical fits of the dynamic trends have potential for overestimating sustainable yields, profits, and fishing effort. This condition can be exaggerated by continuous, but seasonally periodic recruitment. If the integrated area under the three recruitment functions is identical, the fishing mortality operates at a constant level on the stationary population throughout the year, and the sampling of the catch is absolute, then the annual yield per annual recruits is identical under all three cases. However, if fishing mortality, growth, and/or natural mortality is seasonal, or varies through the year, then the resulting estimates can be significantly biased.

If we examine the potential yield surface of a Pelagoid population (high natural mortality, high growth coefficient, ten year-classes), then we note quite a different, somewhat pinnacle-shaped surface under a constant recruitment hypothesis (Figure 9, Panel A). This suggests a more critical balance between the optimization of yield through size of capture and the respective fishing mortality, disregarding abiotic influences. For a simulated population structure

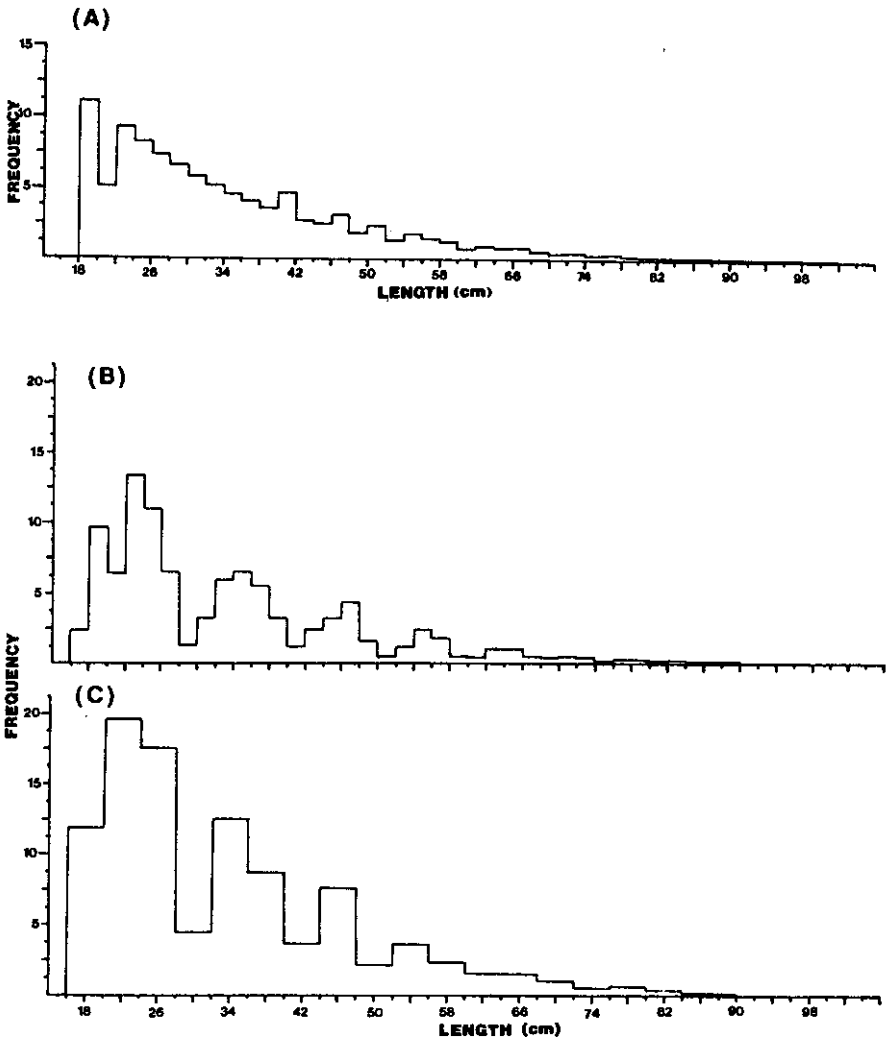


Figure 7. Grouperoid population length frequency distributional structure under several recruitment and pooling hypotheses: (A) uniform constant monthly recruitments pooled by 20 mm size class increments; (B) unimodal annual recruitment pooled by 20 mm size class increments; and (C) unimodal annual recruitment pooled by 40 mm size class increments.

under the three annual recruitment hypotheses, we note that the rate of decline of population numbers is much greater than that in the grouperoids, and that the modal distribution corresponding to "annual lumped cohorts" are stretched out along the abscissa, their discernment diminishes rapidly with increased size or age (Figure 9, Panel B). This suggests that seasonal mortality and sub-optimal

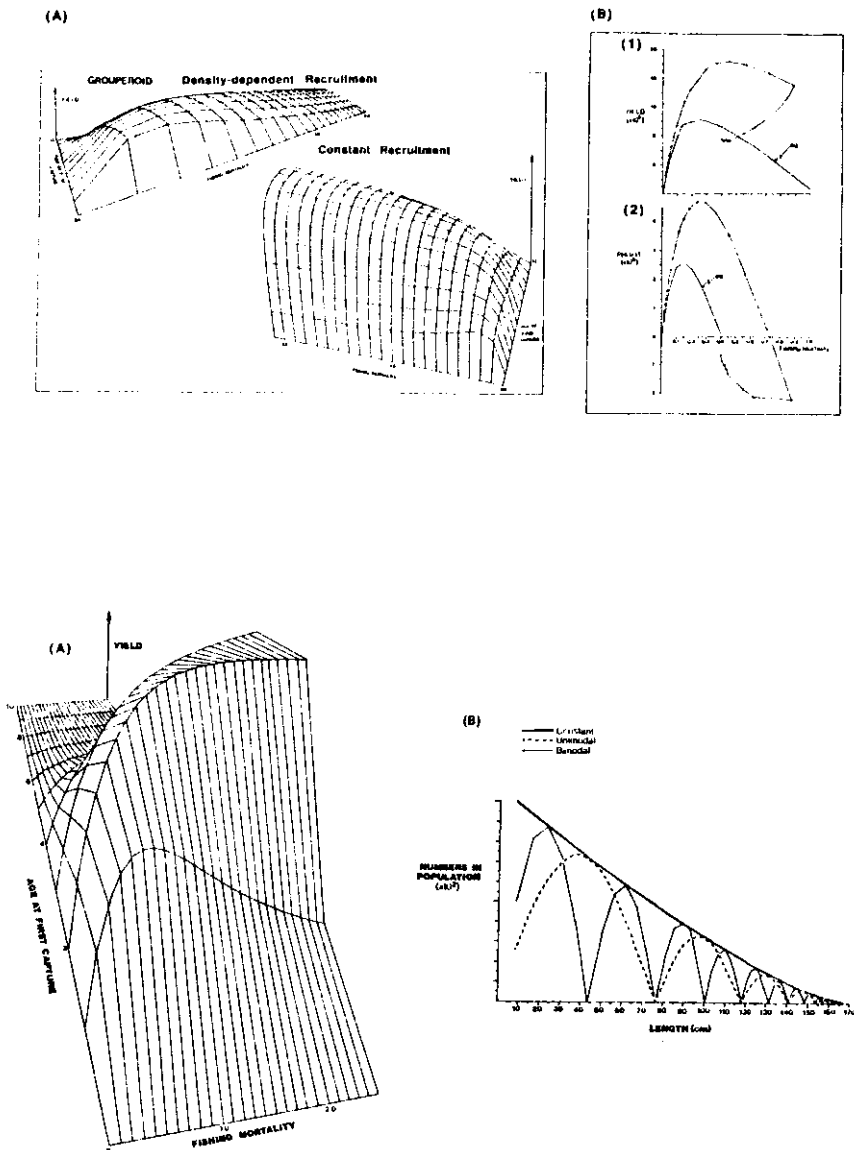


Figure 8. Simulated Grouperoid population: (A) Three dimensional potential yield surfaces using the (1) constant and (2) density-dependent recruitment hypotheses; and (B) The relationships between (1) stationary (eq.) and dynamic yields and fishing mortality, and (2) stationary (eq.) and transitional profit and fishing mortality.

catch sampling can induce significant bias into the estimation of stock dynamics and potential. Additionally, there may be a critical balance of stock numbers in the older size groups to ensure sufficient reproductive input to the stock.

Several estimators have been proposed for total instantaneous mortality estimation from information on average length in the catch (Beverton and Holt, 1956; Ssentongo and Larkin, 1973). Both Beverton and Holt (1956) and the Ssentongo and Larkin (1973) estimators assume an infinite life-span, and both are biased, even at equilibrium (Figure 10, Panel A). We introduce a modified formulation which utilizes a distribution truncated to the oldest age observed in the catch and which significantly reduces bias at low to intermediate levels of Z in a stationary population.

Our formulation solves as:

$$\left[\frac{L_{\infty} - L_{\lambda}}{L_{\infty} - L_c} \right] Z/K = \frac{Z(L_c - \bar{L}) + K(L_{\infty} - \bar{L})}{Z(L_{\lambda} - \bar{L}) + K(L_{\infty} - \bar{L})}$$

where

Z = total instantaneous mortality rate

L_c = smallest size in the catch

\bar{L} = average size in the catch

L_{λ} = largest size in the catch

and L_{∞} , K are parameters of the von Bertalanffy growth equation.

If various rates of increased fishing mortality are applied to these populations initially in equilibrium, the induced perturbations cause a significant propagation of bias (Figure 10, Panel B). This is particularly exacerbated when the dimension of continuous or protracted recruitment is operated in a seasonally based fishery. Thus, attention should be focused on methodology that accounts for the particular features of the life history in question, and for transitional dynamics in fishing effort and life history phenomena.

SUMMARY

Presently it is not possible to predict population fluctuations in single or multispecies assemblages of fishes. Without such an understanding it is generally impossible for us to tell whether a decline in a fish population results from intrinsic population pressure, environmental change, fishing, or some combination of these events. The study of recruitment patterns, such as briefly sketched here, 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 of commercial and recreationally important tropical marine fish and the optimization of fishing activities in these regions.

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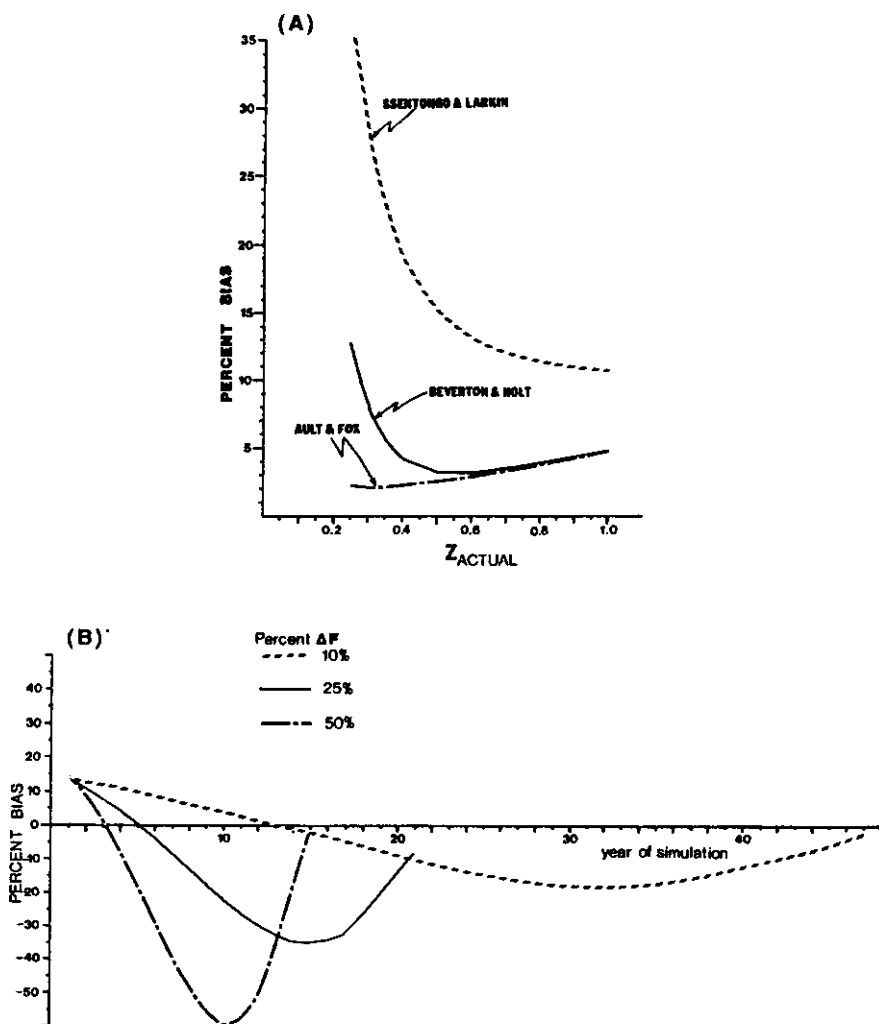


Figure 10. Performance of total instantaneous mortality rate estimators from average size of fish in the catch under: (A) stationary, and (B) transitional conditions.

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