NOAA Technical Memorandum

NMFS-SEFC-80

THE BIOLOGICAL BASES FOR REEF FISHERY MANAGEMENT

PROCEEDINGS OF A WORKSHOP HELD OCTOBER 7-10, 1980 AT ST. THOMAS, VIRGIN ISLANDS OF THE UNITED STATES.

Sponsored by the Southeast Fisheries Center
and the Caribbean Fishery Management Council

Edited by Gene R. Huntsman, William R.
Nicholson, and William W. Fox, Jr.

March 1982

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Beaufort Laboratory
Beaufort, North Carolina 28516

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U. S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
John V. Byrne, Administrator
National Marine Fisheries Service
William G. Gordon, Assistant Administrator
for Fisheries

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Session 1 - Aging of Reef Fishes

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Foreword

Gene R. Huntsman
Workshop Chairman

This workshop was sired by necessity and mothered by the separation of reef scientists. Information demands generated by the Fishery Conservation and Management Act brought the realization that clear channels of communication had to be opened between reef researchers greatly divided by geography and discipline. The purpose of this workshop was to enhance the needed communication.

In our workshop, we brought together academic and government scientists, and workers from the Atlantic with their counterparts from the Pacific. Through the workshop NMFS reef researchers at the Southeast Fisheries Center became more aware of fellow workers with similar problems at the Southwest Fisheries Center and vice versa, although budget constraints prevented attendance of representatives of the Honolulu Laboratory. Even relationships within the Southeast Fisheries Center were strengthened as face to face interchange replaced telephone conversations and memoranda.

Equally important as the bridging of geographic gaps was dialog between disciplines. Ichthyoplankton specialists talked to behaviorists, students of growth with population modellers, and ecologists with assessment biologists. The workshop achieved the cross-fertilization of ideas that is so essential to the research necessary for successful fishery management.

Two definitions are needed to allow us to fully understand SEFC reef research and the discussions at this workshop. First, we need a definition of reef, and hence, secondly a definition of reef fish. To the Southeast Fishery Center the term reef includes not only the shallow high relief coral areas of South Florida and the Caribbean, but also the deeper, (to 70 m), less spectacular but extremely abundant, live-bottom reefs in the South Atlantic and Gulf of Mexico, and the socalled deep-reef areas (70-300 m) along both the continental and insular shelf edges throughout the region. To a great extent we define reefs faunistically, since all the habitats mentioned are occupied principally by snappers, groupers, porgies, grunts, and other groups of tropical affinity. We include live bottom and deep-reef are as in our reef definition even though they are distributed to high latitudes (35°N) and even though water temperatures on the deeper sites may never be extremely warm. Under our inclusive definition of reef, the term reef fish includes many animals not ordinarily associated with shallow coral reefs, such as gray tilefishes, (*Caulolatilus* spp.). Our broad definition is important to understanding the research problems of the SEFC, because deep reefs are immensely more difficult to study than shallow reefs. Deep reefs are at such depths that divers can work only the shallowest portions, and, even then, have little time for observation. Because deep reefs are often far from land, research support vessels must be large and consequently expensive.

We further need a definition of reef fish user. In most fishery contexts, the term user implies consumption and indicates commercial and recreational fishermen. At the SEFC we realize that extremely important users of reefs are nonconsumers. Fish watchers, who employ snorkel or scuba gear, are numerous and their needs must be considered in research and management schemes.

We also want to describe the rationale for the organization of the workshop. In general we used the production equation (i.e. biomass in year 2 equals biomass in year 1 plus growth, plus recruitment minus mortality) as our guide to structuring the meeting. Of six sessions one was on growth; one each on reproduction and recruitment processes, both of which bore on recruitment; and one on stock assessment, or the measuring of biomass. Two other sessions, one on ecological interactions and their implications to management, and one on modelling of reef fisheries, dealt with synthesizing information on intra- and interspecies effects of fishing and predicting the behavior of reef fisheries.

Despite our desire to achieve a mix of ideas, we wanted to keep the meeting small enough so that coherent and fluid discussions were possible. Therefore, we were forced to choose only a few scientists to represent each discipline. Unfortunately many distinguished reef scientists could not be invited. We wish that we could have accomodated more, and hope that those who were not invited understand our problem.

One significant omission from our workshop was the subject of ciguatera. The omission was intentional, not because we felt ciguatera was unimportant, but because it is a subject so large that we could not do it justice in our crowded schedule. Moreover, we felt ciguatera to be more a problem of fishery usage than of production, our main interest.

Finally as chairman of the steering committee, I want to thank many people: Richard Uchida, whose request for information on SEFC research prompted our initiation of a workshop; Bill Richards, Chuck Manooch, and Pete Parker, who were invaluable in planning the workshop and corresponding with speakers and attendees; and Jack Damman, who handled all the local arrangements, and who made our meeting congenial as well as scientific. Thanks also go to Bill Fox, Omar Munoz, Ted Rice and Hector Vega, who provided the necessary institutional, moral, and financial support. And finally, great thanks to the speakers and audience, who made our discussions so stimulating and fruitful.

OVERVIEW COMMENTS

by

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Our research center has the responsibility to provide scientific advice for the management of fisheries in the Southeast Region of the United States. This region includes the South Atlantic Bight, Gulf of Mexico and Caribbean Sea. Reef-related resources in this region are extremely important to commercial fishing enterprises, subsistence fishing, and recreational fishing activities. I define reef-related resources in the sense of resources which appear to be aggregated by sea bottom relief, be it soft corals and sponges, hard corals or rocky areas--in the tropics all three substrate types exist. There are 10 fishery management plans dealing with reef-related resources out of 23 under development by the three Regional Fishery Management Councils in the southeast, underscoring the importance of developing scientific advice on those resources. This week we are focussing on vertebrate fishes associated with reefs. Five of the fishery management plans deal with them. We will not directly consider important invertebrates like lobsters, crabs, or the corals and sponges themselves, but only in the sense of their interactions with the vertebrate fishes that have significant influences on the scientific advice for managing those fishes.

Generally speaking, to provide adequate scientific advice in managing a living resource, one must be able to (1) characterize its status so that managers can decide what, if anything, needs to be done, (2) predict the impacts on the resource and its fishery of alternative management measures, and then (3) monitor and assess the effectiveness of those measures and confirm or restructure the predicted impacts in an empirical manner. In developing the appropriate scientific advice we find significant shortcomings in the data on reef fisheries and in the knowledge of reef fish dynamics. For virtually all southeastern reef fisheries we do not even know the magnitude of the biomass being extracted, much less its species composition or age composition. There is no time series of biomass assessment which would provide the trajectory of the reef resources under exploitation; further there is no generally-accepted routine technology for doing so in an adequate manner. Finally, we find that knowledge of the biological factors critical to developing predictions of impacts simply is not adequately developed.

One of the critical bits of knowledge is delineation of unit stocks, i.e. what constitutes a unit stock of reef fish populations? This is related to answering the question of recruitment in forming the reef aggregations: Are recruits from adult fish that inhabit the reefs or from a spawning in a common location which drifts to various reef communiities? How do the oddities of reef fish life history strategy like protogynic hermaphroditism and a strong dependance on piscivous predator-prey relations affect our advice? Tropical reef communities have very diverse speciation with many species being relatively short lived so that energy and lebensraum are transferred or turned over very rapidly, yet most reef fisheries tend to target on species that are the largest among reef inhabitants and are relatively long lived; does this provide for stability or does it indicate fragility in fisheries for specific species? We need to understand these mechanisms well enough to develop mathematical models which can then be reduced to proximal, understandable management criteria. We need to know what to sample in monitoring the reef system to determine the impacts (or lack thereof) of management measures.

The results of this workshop will provide the fundamental base for launching our research program to develop a theory of fishing for tropical reef fish communities and to develop an appropriate monitoring and assessment program. We hope to determine the current state of the art and to air the research problems that I and others of you will identify. From this we will, with your help, formulate our research directions.

SESSION 1

Aging of Reef Fishes

Chairman

Charles S. Manooch, III

AGING REEF FISHES

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INTRODUCTION

Information on the age and growth of fishes is a central element in fishery management analysis. Unfortunately, age determination methodology is far from standardized and serious difficulties arise in attempting to attain the high levels of precision and accuracy needed for many detailed studies. In a recent review, I have dealt with the general subject of aging tropical fishes (Brothers 1980a). The following is a slightly modified version of that paper with additional emphasis on otolith microstructure studies on reef fishes.

Common biological characteristics of tropical fishes, such as weakly expressed annual or seasonal growth and reproductive cycles and their population structure consequences, have made age and growth rate determination difficult for many species. Knowledge and experience gained from anatomical and statistical studies on temperate fishes can sometimes be successfully adapted to the tropics. However, due to the complexity of interpreting the significance of time markers in calcareous structures, or of unraveling population dynamics, this has proven to be a challenging and sometimes imprecise science. A second factor contributing to the problems of age and growth rate determination of tropical fishes is the greater difficulty in obtaining large, representative samples and statistics for what are typically small-scale or artisanal fisheries.

The purposes of this contribution are first to briefly characterize and review approaches and general results of past studies on reef fishes and other tropical species. Second, major emphasis is placed on recent investigations utilizing analysis of otolith microstructure to obtain extremely detailed growth history information. This approach represents a long-awaited breakthrough in the aging of tropical fishes. Appropriately it is reviewed and discussed in greater detail, with some brief examples of current applications.

There are three basic approaches to the determination of age and growth of fishes: (1) direct measurement of growth in certain individuals and extrapolation to the population, e.g. mark-recapture studies or growth in confinement; (2) statistical approaches based on measurements of large samples, e.g. modal progression in a time series of length-frequency histograms; (3) aging individuals on the basis of regular periodic markers in hard structures (usually calcified) such as scales, otoliths and bones (anatomical method). Reviews of various aging techniques can be found in Graham (1929), Menon (1953), Chugunova (1959), Tesch (1971), Weatherley (1972), and Ricker (1979). Several authors have specifically dealt with tropical fishes (Menon 1953;

DeBont 1967; Fryer and Iles 1972; Lowe-McConnell 1975). Evaluation of the numerous examples cited in these papers plus many other specific studies on tropical fishes reveals that the popularity of traditional anatomical methods so successfully applied for temperate fisheries, is not really justified by the results obtained in the tropics. There have been no substantial improvements in the preparation and viewing methods first developed around the turn of the century. For the vast majority of studies there is only very feeble proof of validation. And finally, the weak or complex expression of age marks in many tropical species makes what in temperate fish is often a subjective discrimination problem an even worse situation with little hope for reproducibility between workers.

The major difficulty of directly aging tropical fishes (anatomical methods) is the apparent equitability of growth processes throughout the year, at least in comparison with most temperate fishes. A growing body of evidence is demonstrating that although this is true in a general sense, there are still clearly observable annual, seasonal, and shorter term rhythms of somatic and gonadal growth and development, feeding intensity, and movements in tropical fishes (Chevey 1933; Menon 1953; Randall 1961; Munro et al. 1973; Talbot, Russell, and Anderson 1978). In a number of examples these rhythms have at least been correlated with the appearance of marks in various calcified structures (Pantulu 1962; Poinsard and Troadec 1966; LeGuen 1976; and several studies on tropical freshwater species). More detailed analyses of hard tissues are needed to determine whether they contain records of such rhythms. Otoliths of many of the species have an overabundance of potentially decipherable marks; discovering their significance is a major challenge for the future.

The perplexing nature of marks in the otoliths, scales and bones of tropical fishes is exacerbated by the equally great problems encountered in statistical approaches used either as verifying criteria or alternate aging methods. The most significant of these complicating circumstances is that recruitment is typically extended over a long period in the year in many species. As noted above, this is made more problematical by the often irregular and incomplete sampling programs available to small-scale fisheries. Thus a major method of analysis, the examination of length-frequency histograms, can be greatly weakened due to the broad overlap of age classes, even in the youngest categories. Further discussion of these statistical approaches is included in the following section.

REVIEW AND DISCUSSION OF METHODS

TIME MARKERS IN CALCIFIED STRUCTURES

For information on this well established and widely practiced method see the general reviews referred to earlier as well as those on otoliths by Blacker (1974) and Williams and Bedford (1974), and on bones by Menon (1950). Time markers of very short periodicity, e.g. daily marks in otoliths, will be discussed separately below. A wide variety of structures are involved in this method, typically scales, otoliths and various bones such as fin spines, vertebral centra, cleithra, hypurals, and skull bones. The basic premise of this approach is that periodic changes in the growth of these structures (both in form, e.g. circuli spacing on scales, and/or composition, e.g. hyaline and opaque zones of bones and otoliths) are reflections of changes in growth of the fish. More specifically the fish may be experiencing endogenous and/or exogenously induced cycles of somatic growth rate, or perhaps just protein and calcium metabolism (the major constituents of these structures). The nature of the causative relationship between the ecology, behavior, and physiology of the fish, and the observed marks is an important and continuing area of investigation. Experimental approaches combined with detailed structural and chemical analyses will potentially yield the greatest insights (e.g. references in Blacker 1974; Simkiss 1974; Bilton 1974).

With due respect for a substantial amount of contradictory results in the literature (only part of which is an artifact of terminology and methods), there still are generally observable patterns in the calcified structures of temperate fishes. To briefly summarize, in bones and otoliths, fast or accelerating growth zones usually appear as broad opaque (optically dense) zones, while slow growth zones are narrower and hyaline (more translucent). As pointed out by Mina (1968) and others, the terms hyaline and opaque are relative terms which refer to optical comparisons of adjacent material. Even under relatively low magnifications, these major zones, which are often demonstrated to be seasonal in occurrence (i.e. one or two each per year), are seen to consist of a gradient of optical densities and are composed of a number of less distinct discontinuities defining "minor" hyaline or opaque areas. The significance of these minor zones is being elucidated in microstructural studies (see below). In scales, slow growth zones are represented by more closely spaced circuli or sclerities, or in some cases by irregular circuli and evidence of resorption.

The highly seasonal nature of growth and reproduction is accepted to be related in some way to the appearance of these marks. In many cases this relation has been clearly demonstrated and the marks are confidently used for age determination. Well-executed,recent studies involving subtropical or temperate families also having representatives in the tropics include McErlean 1963; Moe 1969; Johnson 1972; Tong and Vooren 1972; Cambell and Collins 1975; Powell 1975; Van der Waal and Schoonbee 1975; Warner 1975; Gregory and Jow 1976; Davis 1977.

There are a number of advantages of this widely used method. It affords a relatively simple way to age individual fish, thereby gaining information on intra-populational variation, as well as establishing population parameters from representative samples. A powerful application is the ability to retrieve historical data from the growth records of individuals by back-calculation. This enables investigators to extend their growth studies into periods when population and environmental conditions may have been different, allowing, for example, for the analysis of growth trends with respect to different fishing pressure. Finally, this method of age and growth determination is not as dependent upon extensive representative sampling as some of the techniques that follow.

Age determination by time markers on calcareous structures is clearly the preferred method; the only substantial disadvantage is the sometime difficulty of its application and the extreme care and extensive study that may be necessary to establish its validity in a particular situation. Once established, the amount of technical skill and elaborate equipment necessary can usually be kept to a minimum. In many species marks are observed which are referred to as false annuli or accessory checks. These are features which may be mistaken for true annual or other periodic marks without careful scrutiny. They correspond to the "minor" hyaline and opaque zones referred to above. These accessory marks may or may not be useful for aging purposes, but this can only be determined once causative factors or patterns are established. In many temperate and tropical fishes it is noted that either bones, scales, or otoliths are much more readable. It is not uncommon to find inconsistencies between counts from different structures, particularly concerning the few annual or seasonal marks. Often, even the best of these structures require painstaking preparation in order to enhance the visibility of the marks. Finally there can be a substantial amount of subjectivity involved in discriminating what are considered to be the "true" time markers. For a number of reasons mentioned in the introduction, these problems are exaggerated in most tropical fishes. Many authors simply note that calcareous structures either have no discernible marks or that they do not show any decipherable pattern. Therefore it becomes extremely important to take great care to validate the periodicity of observed marks. The early works of Graham (1929) and van Oosten (1929) were the first to clearly state a procedure for validating age marks. These criteria have been further elaborated and used by many researchers. Too many studies, however, particularly in the tropics, have not followed the criteria in a rigorous manner.

A revised list and brief discussion of types of validating criteria follows. Not all are applicable in every case and some are better than others. The first three are alternate aging methods with which scale, bone or otolith-derived ages and growth rates can be compared. These will be discussed separately.

1. Length-frequency analyses of population samples; Peterson method.
2. Modal-progression analysis in a time series of population samples.
3. Comparison with growth rates derived from tag-recapture data or growth in captivity.
4. Determination of the period and timing of mark formation. This is usually carried out by a qualitative and quantitative examination of the margin of the scales, bones, or otoliths in samples taken at different times of the year. This may require special collecting efforts.
5. Determination of the proportionality of growth of the aging structure and the length or weight of the fish. Once a relationship is established and mathematically or graphically described, measurements to earlier formed time marks

can be used to back-calculate the growth history of individuals. A growth curve constructed from these data should approximately conform to the curve derived from ages of fish at the time of capture.

6. Comparison of ages derived from different structures, e.g. scales vs. otoliths.
7. Tag and recapture studies where the calcified structure itself is also marked using chemicals such as ^{45}Ca (Irie 1960), lead (Ichikawa and Hiyama 1954) or tetracycline (Weber and Ridgeway 1967; Jones and Bedford 1968; Wild and Foreman 1980). Here the number of marks between the chemical tag and the margin is compared to the known elapsed time period. This is a powerful tool, but it requires a large effort in time, energy, and money. An easier, but related method simply compares the number of annual or seasonal zones on fish of known age. This may be accomplished by tag and release where age is known (e.g. for young of the year) or by holding fish in captivity of some sort. All of these techniques require relatively long periods of time before results are meaningful and are also subject to the various biases introduced by tagging and/or artificial confinement. Williams and Bedford (1974), and Poinsard and Troadec (1966) point out an analogous validating technique which relies upon recognition of unusual zones formed in particular years. These marks may be used as a reference point for subsequent counts.
8. Comparison of the empirically derived growth curve to mathematical formulations such as the von Bertalanffy growth curve. This is only one of several possible comparisons (Ricker 1979). All have different biological and non-biological assumptions and a particular one will usually fit the data better than others; however, wildly deviant empirical patterns should be suspect.
9. Correlation of the time of mark formation with various exogenous and endogenous cycles such as temperature, salinity, rainfall, feeding intensity, condition or reproductive activity. Correlation will not establish a causative relation; however, this method will at least help to establish a biological basis for the observed periodically marked structures.
10. Establishment of objective criteria to discriminate marks; avoidance of bias by aging coded samples; and comparisons between readers for consistency.

Criterion 4 is very important, quite straightforward, and it gives unambiguous results when it can be properly applied. Complications arise when the marks are found to be formed over a large part of the year or when different age or size classes form them at different times (e.g. Moe 1969; Williams and Bedford 1974). The apparently extended period of mark formation in tropical fishes can lead to ambiguous results, especially with small samples. Negative results by this test, i.e. determining that marks may be formed at any time of the year, do not necessarily eliminate the possibility of them being regular periodic markers. If it can be shown that the presence of the marks is related to some regular event in the life of an individual fish, such as spawning every four months, then these marks can be used for aging almost as well as if all fish in the population were synchronized.

The studies on subtropical fishes referred to earlier provide excellent examples of the practical application of many of the above criteria. A few case studies involving tropical fishes include those by LeRoux (1961), Pantulu (1962), Krishnayya (1963), and Kutty (1961).

LENGTH FREQUENCY ANALYSIS

Under this heading are included at least three closely related methods which depend upon large, relatively representative population samples as their data base. As the size structure of a sample is plotted as a length or weight frequency histogram, various peaks usually emerge which are taken to represent modal lengths of age classes, usually yearly, but sometimes of shorter intervals. There are statistical and computer techniques to help discriminate the modes by assuming that the total distribution is composed of a series of overlapping normal distributions (Harding 1949; Cassie 1954; Mathews 1974; Skillman and Yong 1976; McNew and Summerfelt 1978). When a single or combined sample is used the technique is usually called the Peterson method. Here assumptions are made on the time interval which separates different peaks assumed to represent age groups (Pauly 1978). A modification involves serially sampling the same population and then noting the growth of fishes as reflected in modal class progression with respect to time. Assumptions in this method involve decisions on which peaks should be interconnected, i.e. represent the same age class. Finally, in species where modes are not well developed, occasionally a dominant or scarce year class may act as a marker which can then be followed as they grow with time. Here one has to be concerned with the possibility that this age class of fish may also exhibit somewhat abnormally fast or slow growth.

There are a number of assumptions and conditions which generally apply to the usefulness of the above method. It works best when recruitment is restricted in time, and when growth is relatively rapid throughout life with a minimum of variability between individuals and age classes. Samples must be representative and unbiased with respect to the population in question; gear selectivity and fish movements altering availability will strongly affect the results.

The major advantage of length frequency analysis is that it can be a relatively simple matter to obtain size data from many fisheries. Thus the catch statistics themselves can, under the right circumstances, form the basis for the age and growth analysis. This makes it easy and cheap, requiring no highly skilled technical personnel. There are several limitations, however, which arise as a result of the fish biology and sampling schemes not conforming to the assumptions and conditions stated above. This is particularly true for tropical species.

1. Breeding seasons tend to be prolonged over several months

or more, thus even the youngest age classes are not easily separable from one another. Short life cycles complicate and telescope the distributions even further.

2. Older age classes tend to crowd and overlap as growth typically decelerates and variability within classes increases.
3. Individual variation, especially differences between the sexes, may obscure modes if not taken into account.
4. Dominant or variable age classes may introduce statistical problems.
5. The lower number available of older fishes due to mortality makes discrimination of their modes difficult.
6. Due to environmental or population changes, current age or size specific growth rates determined from length frequency analysis may not conform with back calculated lengths from anatomically based aging.
7. The method only allows a statistical characterization of a large sample; it does not work for individuals or small samples.
8. Samples are easily biased by gear and site selectivity and fish movements which may cause size or age classes to appear and disappear with, for example, reproductive migrations.

Despite all of these potentially complicating factors, length frequency methods are widely applied, commonly with good results, but also often with statistically unsubstantiated conclusions. A few examples of the use of these techniques for tropical fishes includes studies by Sarojini (1957), Bennett (1961), Pantulu (1962), Longhurst (1965), Fryer and Iles (1972), and LeGuen and Sakagawa (1973). Olsen (1954) used length frequency analysis and tagging data to age subtropical sharks in which no direct aging methods worked. Many fishes, particularly in the tropics, are demonstrated to have a lunar or semi-lunar spawning and juvenile recruitment periodicity (Johannes 1978). Thus the minor peaks in recruitment may be followed to gain information at least on early growth. These cycles are probably the cause for at least some of the "minor modes" noted by several researchers (e.g. Randall 1961; Feddern 1965).

TAG-RECAPTURE STUDIES

Fish can be marked in a variety of ways such as fin clipping, tattooing, attaching a variety of external and internal tags and by chemical exposure (usually injection) which causes a mark to form on calcareous structures (see above). The measurement of fish length and/or weight at the time of release and then at recapture can provide direct information on the growth rate of individuals. These can later be applied to a mathematical growth description to provide estimates of age as well. The most important assumption in the method is that the presence of the tag or perhaps the tagging and capture procedure themselves do not affect growth rate. This may or may not be true, depending on the species, type of tag, and other circumstances (e.g. Bardach and Menzel 1957; Fryer and Iles 1972). In some cases the method of capture, such as trapping may bias results because of the amount of time certain fish spend in the gear and whether or not the fish can feed while enclosed (Randall

1962). Some other examples of tag-recapture studies on the growth of tropical or subtropical fishes include Olsen (1954), Randall (1961), and Joseph and Calkins (1969). As mentioned earlier, tagging studies incorporating a chemical marker on scales, bones, or otoliths are very valuable for verifying the time period of natural mark formation.

There are a number of significant disadvantages to tag-recapture studies. These include the uncertainty of the affect of tagging on growth; the common occurrence of large measurement errors, especially due to the difficult and usually different measuring conditions at release and recapture, sometimes resulting in "negative growth"; the need to mark large numbers of fish to have sufficient returns (more necessary and more difficult for older fish); the need for intensive efforts, usually at great expense since long-term returns may be necessary to show measurable growth; and the difficulty of individually tagging small and delicate fishes, including young of the year of larger species. In some cases, this latter problem has been circumvented by direct diver observation and measurement of sedentary fish (Allen 1975). Gunderman and Popper (1975) took advantage of an accidental fish kill which destroyed the fish fauna of a small reef in the Gulf of Aqaba. Natural resettlement occurred soon afterwards during the normal seasonal spawning peak. Censusing over the following year established early growth rates for several of the more sedentary species. Similar experimental studies may be carried out with natural or artificial reefs. Although no tagging is necessary in such methods, there is still a strong possibility of "abnormal" growth rates in these altered environments.

Fragmentary data from tagging studies or other growth studies can be used to establish more complete growth curves and age estimates. Growth data such as length at t and t + 1 are fit to a theoretical growth formula such as the von Bertalanffy using Walford plots (e.g. Weatherley 1972). In this case a straight line is usually fit to the points and the growth parameters are calculated. The method forces a particular form of growth curve on the data which may or may not be realistic.

LABORATORY AND FIELD REARING EXPERIMENTS

It is partially possible to rear some species under semi-natural conditions, either in the laboratory or some sort of enclosure in the field. The introduction of fish to natural or man-made bodies of water also falls into this category. In this manner fishes of known age can be monitored to establish growth rates and to look for marks on calcareous structures. As in the above preceding case, under such conditions there is an almost certain departure from growth exhibited by fish in their natural, undisturbed environment.

IN VITRO DETERMINATION OF RELATIVE "INSTANTANEOUS" GROWTH RATES

Ottaway and Simkiss (1977) and Ottaway (1978) describe a radically different method which measures the rate of ^{14}C glycine incorporation by cells associated with isolated fish scales. This is a new technique which requires further refinement (Adelam 1980) and rather sophisticated procedures and equipment. Furthermore, as yet this method appears to offer a way to determine only relative growth rate, and is perhaps applicable solely within a species. There has not been any attempt to transform results into absolute growth rates. This work is mentioned here not only for the promise it holds for determining growth rates, but more importantly because of its potential usefulness in experimentation on the factors controlling scale growth.

OTOLITH MICROSTRUCTURE

In 1971 Giorgio Pannella reported on his reexamination of the microstructure of fish otoliths and came to the remarkable conclusion that the finest lamellae of which they are composed are formed with daily periodicity. The structures he described had been seen by a number of earlier workers (most notably Hickling, 1931), but Pannella's careful analysis of recurrent groupings or patterns of the fine growth increments strongly suggested their true temporal significance. A number of papers have since followed, reconfirming the presence of daily growth units by a variety of other means in a wide sampling of species from many different habitats (Pannella 1974; Brothers, Mathews and Lasker 1976; LeGuen 1976; Ralston 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Methot and Kramer 1979; Brothers and McFarland 1980; Wild and Foreman 1980). Many of the species involved are represented by larvae and juveniles and are tropical in distribution. The reason for the interest in these types of fishes is simple; the analysis of otolith microstructure offers the only way to directly age individuals in these categories, since they usually offer no other type of readily visible time marker in their otoliths or other calcareous structures.

The method of preparation for viewing daily growth units varies with the size of the otolith and its structural peculiarities. Unlike traditional otolith studies which almost always utilize the sagitta or saccular otolith, microstructure studies may often best be carried out on the other otoliths, particularly the utricular pair or lapilli (Brothers and McFarland 1980). Specimens may be viewed whole, ground and polished, or also etched (for acetate replication and SEM). The basic and most generally useful technique involves direct viewing of ground otoliths with a high quality compound light microscope at magnifications of about 250 to 1500x. Very helpful and often necessary accessories are television viewing systems and polarizing filters. These can greatly enhance image quality to make otherwise indiscernible features visible. Semi-automated counting and measuring systems are also currently being developed (Methot 1980).

Fundamental research on the occurrence and mechanisms of daily growth unit formation has revealed that they are essentially universally present in the otoliths of all bony fishes, at least during the early life history (i.e. through the juvenile phase). In ontogeny, daily growth units may begin to form as early as the pre-hatching, "embryonic" phase, or as late as yolk absorption in free-swimming larvae, depending upon the species. The daily growth units themselves are usually simple bipartite structures (increments, 0.25 to well over 25 µm thick) each composed of a protein-rich and a protein-poor layer. Research in my laboratory indicates that in temperate stream fishes, the protein-rich layer is deposited at night, under the direct influence of falling water temperatures. Daily growth units are more complex in some species or life stages, being composed of two to several subdaily growth increments formed over a 24-hour period. In temperate stream fishes, temperature is the predominant factor in determining the time of formation, thickness, and overall protein content of growth increments, with food and light cycles having subordinate roles. Taubert and Coble (1977) have also implicated the importance of endogenous rhythms.

Two classes of information are available from the study of otolith microstructure; one is based on counts of daily growth units, the other depends upon detailed examination of the characteristics of each unit (Brothers 1980b). Count data yield ages in days. The method is based upon validating the existence of daily growth units, knowing the age at which growth units begin to form, and also determining that a complete time record is preserved in the otolith. The latter condition appears to hold for larvae and juveniles of most fishes, and may include the adults of some. In the majority of fishes, however, once growth rates (both of the fish and otolith) begin to decelerate, daily growth units become proportionately thinner and are also seem to be interspersed between growth interruptions of varying duration (see also Pannella 1971, 1974). Only under special conditions can the duration of the interruptions be determined. The presence of growth interruptions therefore poses a serious problem to age determination by daily growth unit counts. For fishes which have strongly periodic growth, the growth interruptions are usually clustered in the slow growth (hyaline) zones of the otolith, but clear exceptions occur. As a generalization, complete daily growth records in tropical fishes are usually present for at least the first 150 to 200 days, thereafter the completeness and readability of the record depends upon the physical properties of the otolith and the biological characteristics of the species. In some tropical fishes, continuous daily growth records of two or more years apparently are present (e.g. some damselfishes, wrasses, parrotfishes, snappers, lizardfishes, angelfishes, and several others). Beyond this point other types of longer period otolith growth rhythms which may also be apparent in the microstructure, such as lunar or spawning cycles, perhaps could be used for aging (Pannella 1974). More research, however, is required to evaluate this potential.

The second type of microstructure study involves the thickness, protein content, and subdaily structure of individual daily growth units. Such analysis yields additional information on the day-to-day ("instantaneous") growth, environmental conditions, and changes in the life history experienced by a fish. Daily growth rates and back-calculations of growth history are determined in a manner analogous to back calculations using the traditional annual or semiannual zones.

Validation of correct identification of daily growth units, and demonstration of the existence of complete records are necessary due to the presence of complicating factors such as subdaily growth increments and growth interruptions. Another assumption inherent in calculating instantaneous growth and back-calculations is that there is a precisely definable fish growth-otolith growth relationship, not only on a relatively coarse time and size scale as done for traditional otolith studies, but also on a daily basis. The following procedures are found to be useful in increasing the reliability of microstructure studies.

1. Determining the age at which daily growth unit formation commences is usually established by laboratory rearing of eggs and larvae under close to natural conditions. Such studies are not essential for most applications since the majority of tropical fishes have fairly rapid development times and daily growth units probably first appear within a week of fertilization. Thus, errors that may be introduced by not knowing the absolute age are going to be small relative to the total counts of juveniles or adults.

2. Validation of the daily nature of the increments or units and the completeness of the record can be ascertained by a variety of approaches analogous to those used for validating seasonal or annual marks. Any other method that can be used to approximate age and growth; e.g. length frequency analysis of new recruits; mark-recapture, lab rearing, known time of spawing, etc., can be helpful. Modifications of several earlier presented methods require additional discussion.
    a. Marginal Increment. Under optimal circumstances of rapid growth, large, easily visible growth increments, and availability of fish, specimens can be collected over a 24 hour period and the condition of the margin can be noted; i.e. whether the protein-rich or protein-poor layer is being formed, and quantified. Although this has been accomplished for a few tropical and temperate species (Brothers, pers. obs.) it is very difficult and not possible or worthwhile for a routine aging study.
    b. Otoliths can be marked in vivo in various ways, typically by chemical injection such as with tetracycline. The fish are then either held in the laboratory or externally tagged and released in the wild. Subsequent examination of the otoliths after a known period can be compared to increment counts.
    c. In some cases "natural" marks appear in the otoliths, usually as a result of physical variation in the environment, e.g. sharp temperature fluctuations or tidal cycles. Counting back from the margin to such marks can confirm the daily nature of growth units. This can work if the date of the "disturbance" is known, or one could simply look for consistency between individuals, which would be evidence for regularity of growth

unit formation, but not necessarily the period or the completeness of the record. Pannella (1971) used a modification of this method by counting increments between periodic marks (actually patterns of increment intensity and spacing) and then relating these counts to the duration of expected environmentals cycles, e.g. lunar, seasonal, and annual.

d. Struhsaker and Uchiyama (1976) utilized a statistical approach by sampling a population, calculating a mean otolith age and then resampling the same population to determine if the mean otolith age increase agreed with the known elapsed time period. This method requires that there are no significant changes in the population composition between samples.

POTENTIAL OF THE MICROSTRUCTURAL METHOD AND SOME EXAMPLES

In the course of my own studies on tropical marine fishes I have examined the otoliths of approximately 200 species from over 60 families (see appendix). Most of these were juveniles, but many were adults. Validation was not rigorous for most of the species in this preliminary survey. There is very good evidence, however, that confirmed daily growth units were present and correctly discriminated in several species. The otoliths of all species had analogous microstructural elements assumed to be daily pending further investigation. Given this assumption, a general conclusion of the survey is that tropical fishes, both marine and freshwater, can be accurately aged by means of counts of daily growth units, from the larval at least through part of the juvenile stage. On the average, aging beyond 200 days is often difficult; success is dependent upon the species involved, and further development of preparation techniques is required for many. Pannella (1974) has suggested the use of higher order patterns (e.g. lunar rhythms) to help in age determination of adults. Although such patterns are sometimes visible, in my experience their appearance if often very irregular, inconsistent and difficult to critically demonstrate. Thus I find them to be of very limited usefulness for aging the majority of tropical species.

A recent study by Brothers and McFarland (1980) illustrates the potential power of microstructure analysis. Juvenile French grunts (Haemulon flavolineatum) were aged and a growth curve was established for the first 100 days (other studies have extended it to over 300 days). Furthermore, examination of daily growth unit spacing and structure revealed discontinuities at certain ages that when back-calculated to fish length were found to correspond to observed size ranges undergoing ecobehavioral transitions in habitat, social behavior, feeding ecology, and diet. Continuing work on this project includes back-calculating spawning and settlement dates for new recruits, establishing evidence for a lunar periodicity in these activities.

Thus far the most extensive completed or nearly completed studies on tropical species by other workers have centered on the families Cichlidae (Fagade 1976; Taubert and Coble 1977), Scombridae (Wild and Foreman 1980), Engraulidae (Strushaker and Uchiyama 1976), Chaetodontidae (Ralston 1976), Lutjanidae, Centropomidae, Carangidae, Haemulidae and Holocentridae (Pannella 1974), and Sciaenidae (Pannella 1974; LeGuen 1976). A number of other laboratories around the world have initiated otolith microstructure investigations as a routine procedure. There should be many studies on tropical fishes forthcoming in the near future.

APPLICATIONS OF OTOLITH MICROSTRUCTURE DATA

The technique is most easily applied to accurately detemining the age and growth rate of young fishes. The only data needed to accomplish this are fish size and daily growth unit counts. As mentioned earlier, given the proper validation precautions, the method can be extended to older individuals in a number of species. Where fisheries utilize juvenile fishes, these data are of direct interest for production estimates. Most fisheries analysis, however, requires age and growth information on the entire life history of a species. Even where a complete adult microstructure (i.e. daily) record is not obtainable, growth patterns up to the point when the record is unreliable may be useful to project an expected adult growth rate and longevity.

A procedure that has been tried with success on several reef fishes has as its first step the careful aging of juveniles and young adults by otolith microstructure techniques. These data are then plotted by the method of Walford (with suitably short time intervals) to get an estimate of $L\infty$. In most cases, particularly if the otolith data do not extend to an age when the growth rate is substantially decelerating, the estimate of $L\infty$ will have little value. An alternative is to simply estimate $L\infty$ as the largest size recorded for the species. If the Walford estimate of $L\infty$ is of about the same value as the empirical estimate, then this is a good indication that the microstructure aging has at least extended into ages and sizes where the growth pattern can be projected to much older ages, i.e. early growth inflections have been passed and the otolith ages are on the asymptotic part of the growth curve. Once a trial value of $L\infty$ is arrived at, the age data are graphed according to Beverton (1954) with t (age) plotted versus $\ln (L\infty - lt)$. The equation for the straight line fit to the points can be used to calculate K and t_0 for the Brody-Bertalanffy curve (see Ricker 1979). Better straight line fits can be attempted by modifying $L\infty$ and then replotting the data to calculate new values of K and t_0. The end result is a reasonably good representation of the average growth rate of the species in question, also allowing for estimates of maximum age. The Brody-Bertalanffy curve is only one of several possible mathematical descriptions of fish growth. Sigmoid curves may be more appropriate, especially for the very early phases in the growth pattern. Nevertheless, all such curves should be considered as tools or first approximations which can be utilized for badly needed fishery statistics and evaluation.

The most important consideration in the use of the technique outlined above is that accurate age determination has to be achieved through the period when growth is slowing down, i.e. asymptotic. The assumption of asymptotic growth may not be valid in all cases, but as Ricker (1979) points out, "asymptotic formulas are a convenient way of modeling many observed growth series, and we may expect them to be used into the indefinite future."

Complete, detailed age data may be used to determine spawning times and to reveal the presence of seasonality or periodicity in recruitment. With the proper sampling scheme and knowledge of microstructural patterns corresponding to life history changes, the duration of the larval, planktonic and/or pelagic phases of nearshore tropical fishes can be determined. This is of great importance in understanding the recruitment dynamics of reef fishes and particularly in evaluating whether local stocks are potentially self-sustaining or perhaps receiving substantial input from other areas due to larval drift and water movements. Island fisheries would be especially interested in such information. Given a sufficient knowledge of local current patterns, information on the ages of newly settling fish could even help to locate sites of spawning activity if this is unknown for certain species (especially migratory ones).

Back-calculations of growth history and instantaneous growth rates from daily growth unit measurements can contribute substantial information on the ecology, behavior, and physiology of tropical fishes. The certain identification of spawning marks is also a potentially valuable tool. Published accounts of such marks have not been rigorously verified (Pannella 1974; Fagade Unpubl. ms.1/). Once we have a clear understanding of the exogenous and endogenous factors involved in determining otolith microstructure we should have a remarkably sensitive method to reconstruct the growth history of individual fish as well as environmental changes. For example, my work on temperate stream fishes has demonstrated that the otoliths of some species act as daily (even subdaily) recorders of water temperature and are responsive in different ways to the mean rate of change and range of water temperature. The day-to-day variation seen in the otoliths of some reef fishes is potentially interpretable in a similar fashion, although the exogenous and endogenous influences are certain to be somewhat different.

1/ Fagade, S. O. unpubl. ms. "Analysis of growth markings on the otoliths of three cichlids from Asijire Dam, Ibadan, Nigeria." Presented Otolith Workshop, LaJolla, Calif. July 1976.

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APPENDIX

Families of tropical reef fishes in which otolith microstructure has been examined and found to be suitable for aging investigations.

Acanthuridae
Albulidae
Anomalopidae
Antennariidae
Apogonidae
Atherinidae
Aulostomidae
Balistidae
Batrachoididae
Blenniidae
Bothidae
Carangidae
Carapidae
Centropomidae
Chaenopsidae
Chaetodontidae
Clinidae
Clupeidae
Congridae
Congrogadidae
Coryphaenidae
Cottidae
Cynoglossidae
Diodontidae
Engraulidae
Exocoetidae
Gerreidae
Gobiidae
Gobiosocidae
Grammistidae
Haemulidae
Holocentridae
Labridae
Latimeriidae
Leiognathidae
Lophiidae
Lutjanidae
Merlucciidae
Mullidae
Nemipteridae
Nomeidae
Ophichthidae
Opistognathidae
Ostraciontidae
Pempheridae
Plotosidae
Polynemidae
Pomacentridae
Pomatomidae
Scaridae
Scombridae
Serranidae
Sciaenidae
Scorpaenidae
Siganidae
Sparidae
Sphyraenidae
Syngnathidae
Synodontidae
Tetraodontidae
Xiphiidae
Zeidae

AGING REEF FISHES
IN THE SOUTHEAST FISHERIES CENTER

BY

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INTRODUCTION

For eight years scientists at the Beaufort Laboratory of the National Marine Fisheries Service, Southeast Fisheries Center have been studying western Atlantic reef fishes. This research is conducted within the SEFC Reef Fish Program supported by various Center Tasks, including Bioprofiles.

The collecting and analysis of life history samples (age structures, stomachs, gonads, etc.) continues to be an essential component of this Program and involves people at state, federal, and university levels in the Southeast Region. Of all the specific life history projects, age, growth, and mortality have been assigned the highest priority and therefore have received the most effort.

Results of these aging studies have been substantial. Fish have been aged, growth has been measured, mortality has been estimated, and yield/recruit models have been constructed for a few species. Although this information will be used by Regional Fishery Management Councils to develop Management Plans, many questions remain unanswered. The purpose of this paper is to present the results of reef fish aging in hopes of encouraging constructive discussions which will benefit fishery scientists, managers, and reef fishery constituencies.

Research on reef fish in the Southeast Region has undergone a geographic change over the past eight years. The Program has enlarged from a North Carolina-South Carolina study from 1972 to 1976 to include all the east coast from North Carolina through the Florida Keys. Data are also collected from the Gulf of Mexico and Caribbean. It is understandable that for the first few years, age and growth studies were directed at species economically and sociologically important off the Carolinas. Recently more emphasis has been placed on fishes which are important to Gulf of Mexico and Caribbean fisheries.

We have completed, or are completing, studies on 14 species: red porgy, *Pagrus pagrus*; knobbed porgy, *Calamus nodosus*; white grunt, *Haemulon plumieri*; tomtate, *H. aurolineatum*; gray tilefish, *Caulolatilus microps*; snowy grouper, *Epinephelus niveatus*; speckled hind, *E.*

drummondhayi; scamp, Mycteroperca phenax; gag M. microlepis; vermilion snapper Rhomboplites aurorubens; red snapper Lutjanus campechanus; gray snapper L. griseus; yellowtail snapper Ocyurus chrysurus, and gray triggerfish Balistes capriscus. This work has been aided by graduate students enrolled in degree programs at nearby universities. Manuscripts resulting from research on eight of these species have been or will be submitted as partial fulfillment of degrees (two Ph.D and four M.S.) at North Carolina State University, University of North Carolina at Chapel Hill, College of William and Mary (VIMS), and Rutgers University. Several staff members at the Beaufort Laboratory serve as adjunct faculty at these institutions and direct student research.

METHODS

COLLECTION OF FISH

Most fish were obtained from hook and line fisheries; recreational head boats, and commercial handline vessels. Young-of-year and yearlings were collected from a variety of sources - experimental and commercial trawling, seining, and from power plant intake screens and were used to verify the time of annulus formation and the position of the first annulus on the aging structure. For all fish, total lengths were recorded in millimeters and weights in grams or kilograms.

REMOVAL AND PREPARATION OF AGING STRUCTURES

Four types of structures have been evaluated for aging reef fish: otoliths, vertebrae, scales, and spines. Scales were removed from beneath the tip of the posteriorly extended pectoral fin, soaked in a one-tenth aqueous solution of phenol and were mounted dry between two glass slides. Four to six mounted scales for each sample were viewed at 20 to 41 X magnification on a scale projector. Power of magnification was dictated by the size of scales which varied between species. Measurements were made in the anterior field along a line from the focus to the scale margin. Distances in mm from the focus to each ring and to the margin were recorded (Figure 1a).

Otoliths (sagittae) were removed either by making a cross cut in the cranium with a hacksaw thus exposing the earbones, or by opening the otic bulla with a wood chisel and entering the cranium from under the operculum. The latter was used to avoid disfiguring fish which were to be sold. Otoliths were read intact or after sectioning and were then stored dry in vials or envelopes. Whole otoliths were placed in a blackened-bottom watch glass containing clove oil and viewed under a dissecting microscope with the aid of reflected light. Measurements were made from the core to each ring and to the otolith radius (Figure 1b). The selected field of measurement varied between species. For sectioning, representative otoliths of each species were examined microscopically to identify the area where rings were most legible and

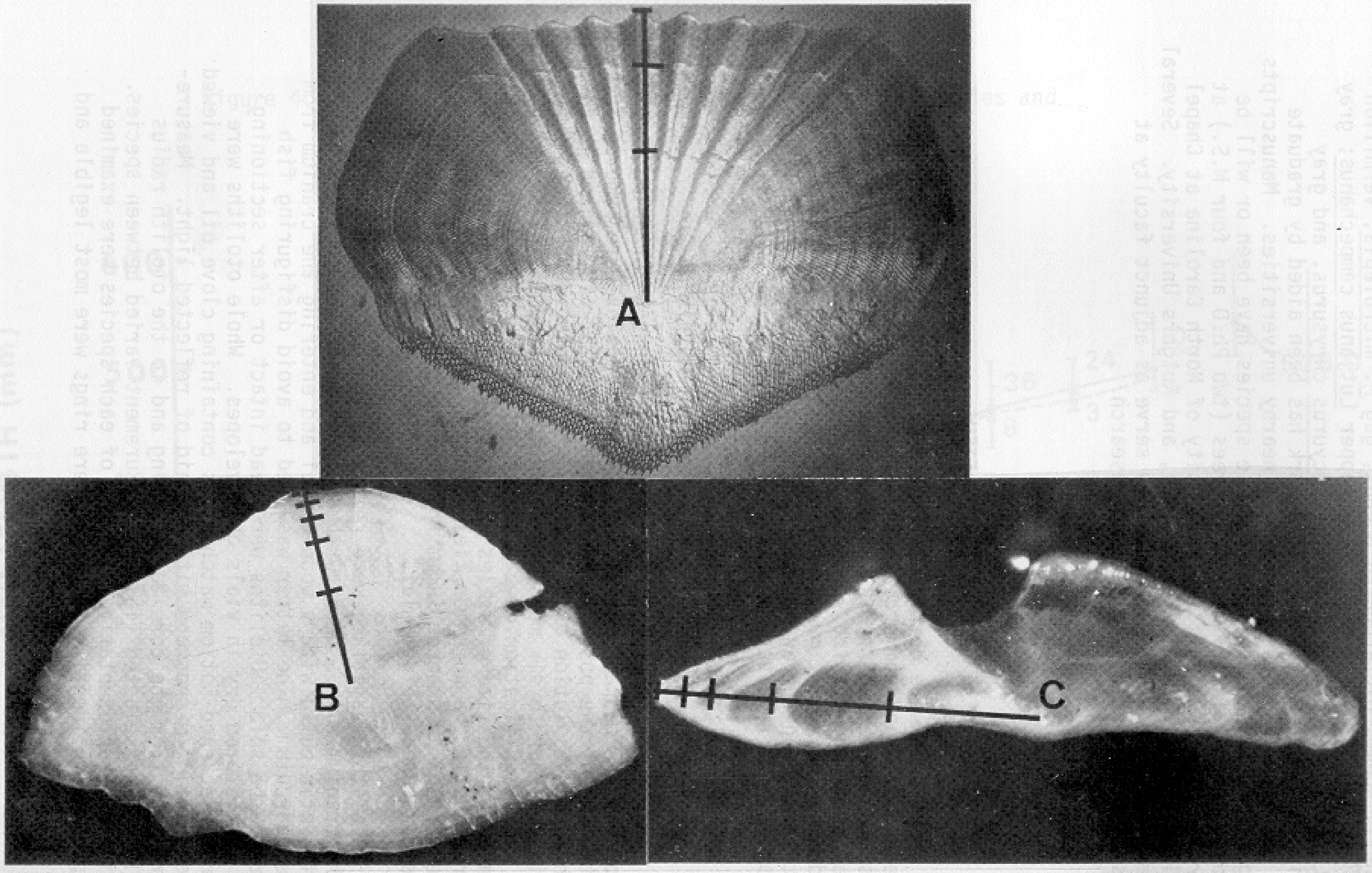

Figure 1. Scale (a); whole otolith (b); and sectioned otolith (c), all from gray snapper.

where erosion of the edge was minimal. Otoliths were then aligned and mounted in a chuck to prevent lateral movement, and sectioned with a Buehler[1], Isomet 11-1180 low speed saw yielding three, 0.18 mm sections (Figure 1c). The sections were read and measured in the same manner as described above for whole otoliths.

Three or four caudal vertebrate were dissected from the fish, cleaned with a 7% sodium hypochlorite solution, rinsed in water and stained with 0.01% crystal violet solution. After drying, the stained vertebrae were cut in half along the lateral plane with a Dremel[1] saw. The distance from the centrum to each ring or ridge, and the centrum depth were measured with the aid of a binocular microscope.

Using dorsal spines to age gray triggerfish and related species looks promising (Allyn Johnson, personal communication). The first dorsal spine is removed by cutting at the spine base with metal or bone shears.

EVALUATION OF AGING STRUCTURES

OTOLITHS

Otoliths were preferred for aging most reef fish. Sagittae alone were used to determine age and growth of all groupers, gray tilefish, gray and yellowtail snappers. Otoliths were selected when scales were too small, and therefore not practical, as with groupers and tilefish, or had a very high percentage of regeneration and nonlegibility, as with the gray and yellowtail snappers.

Both otoliths and scales were analyzed together to age red porgy, vermilion snapper, red snapper, tomtate, white grunt, and knobbed porgy. When used with scales, otoliths were read to validate the scale aging technique.

Sectioned otoliths, although more difficult to prepare, were more easily read and measured than whole otoliths. Johnson (unpubl. ms[2]) found 9% of the yellowtail snapper otoliths had more bands when cross-sectioned than on the surface of the unsectioned otolith. The discrepancy in number of rings identified on whole and sectioned earbones is expected to be even greater for species that live longer than yellowtail snapper, such as Ephinephelus groupers.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] Johnson, A. Unpublished manuscript. An evaluation of yellowtail snapper hardparts for age determination. National Marine Fisheries Service, Panama City Laboratory, Panama City, Florida. 32407.

A disadvantage of otoliths is that annular markings are much wider on otoliths than the "no growth" annuli on scales, forcing the reader to decide exactly where measurements should be made. Also, the subject of otolith annuli formation - causes, what time of year, and chemical composition of bands - is controversial.

SCALES

Scales were easier to collect and prepare than otoliths or vertebrae, and therefore were sometimes selected over otoliths as the primary structure for determining age. Even then a limited number of otoliths were used to validate scale readings. Scales were successful for aging red porgy, vermilion snapper, red snapper, tomtate, and white grunt, but were useless for gray and yellowtail snappers.

VERTEBRAE

Caudal vertebrae were unacceptable for aging red porgy and yellowtail snapper. Since both scales and otoliths were satisfactory for aging red porgy, vertebrae were not used because they were difficult to remove. Johnson (unpubl. ms[2/]) found yellowtail snapper vertebrae also difficult to prepare, and that agreement between two readers for the same vertebrae was only 26%.

VALIDATION OF RINGS AS ANNULI

Regardless of which structure is used, validation of the rings as annuli is important. Three different methods were used: marginal increment analysis, plotting the length frequencies of the distance from the focus or core to each ring for each age group, and by comparing mean lengths for each age determined from otoliths to those obtained by reading scales. In many instances all three techniques were used in a study.

Marginal increment analysis involves calculating for each month the mean distance from the last ring to the edge. The resulting distribution should be unimodal if one ring per annum is formed (Figure 2). Smaller, younger, fish are preferred for this work since rings are more distinct and measurements more precise.

Frequency distributions of focus-to-ring distances (Figure 3) should reveal occurrence of one mode for each ring, and a consistent location of a specific mode on the X-axis for fish of different ages. Plotting focus to ring distance frequencies generally works well for the first ten years of life, afterwards excessive overlapping obscures the modes.

Another method of validation is to examine two different types of aging structures from the same fish to see if the number of rings counted is the same. In most instances scales and otoliths were not

Figure 2. Monthly margininal increment analysis of red snapper scales with two, three and four rings. The fish were collected from the northern Gulf of Mexico (from Nelson 1980).

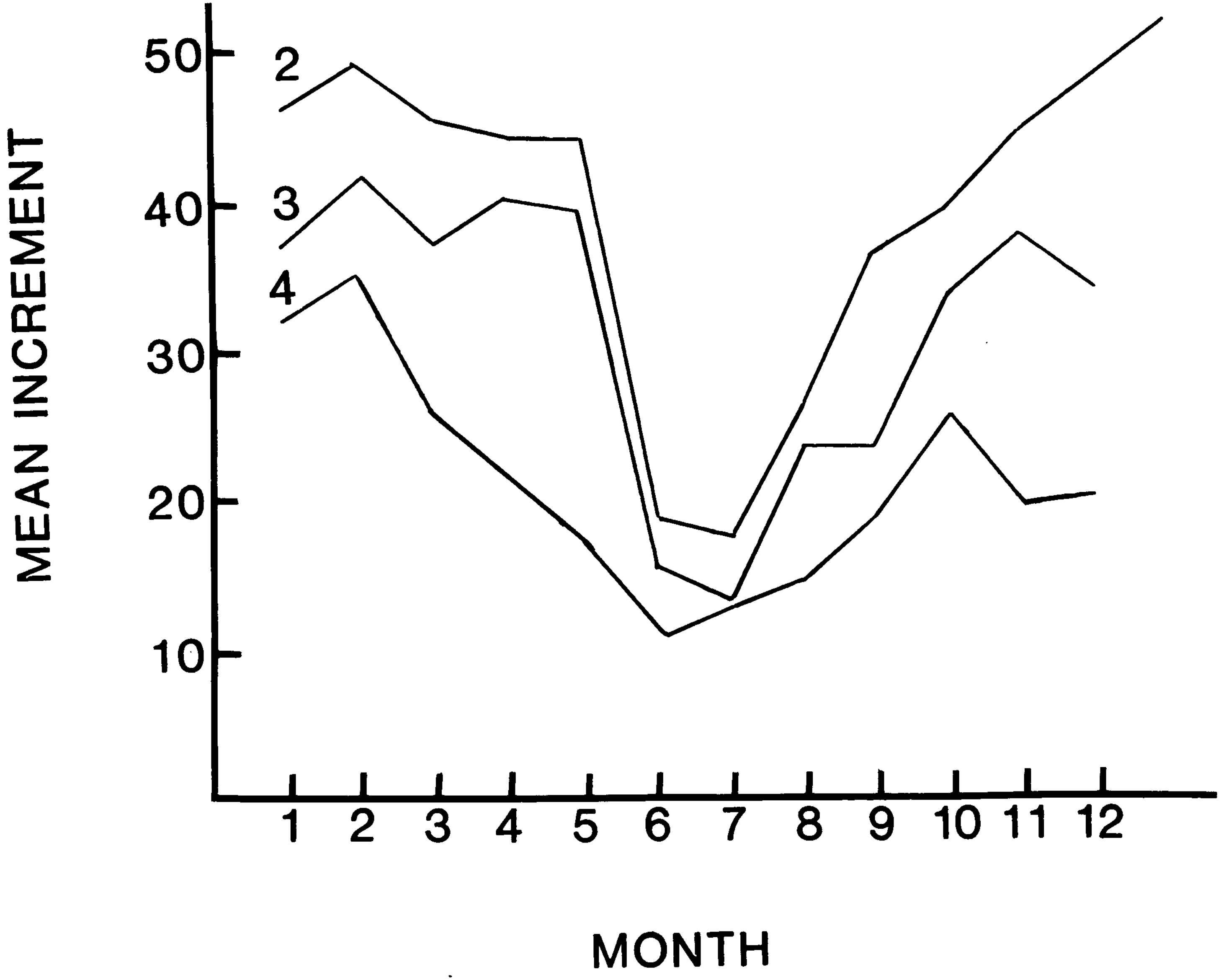
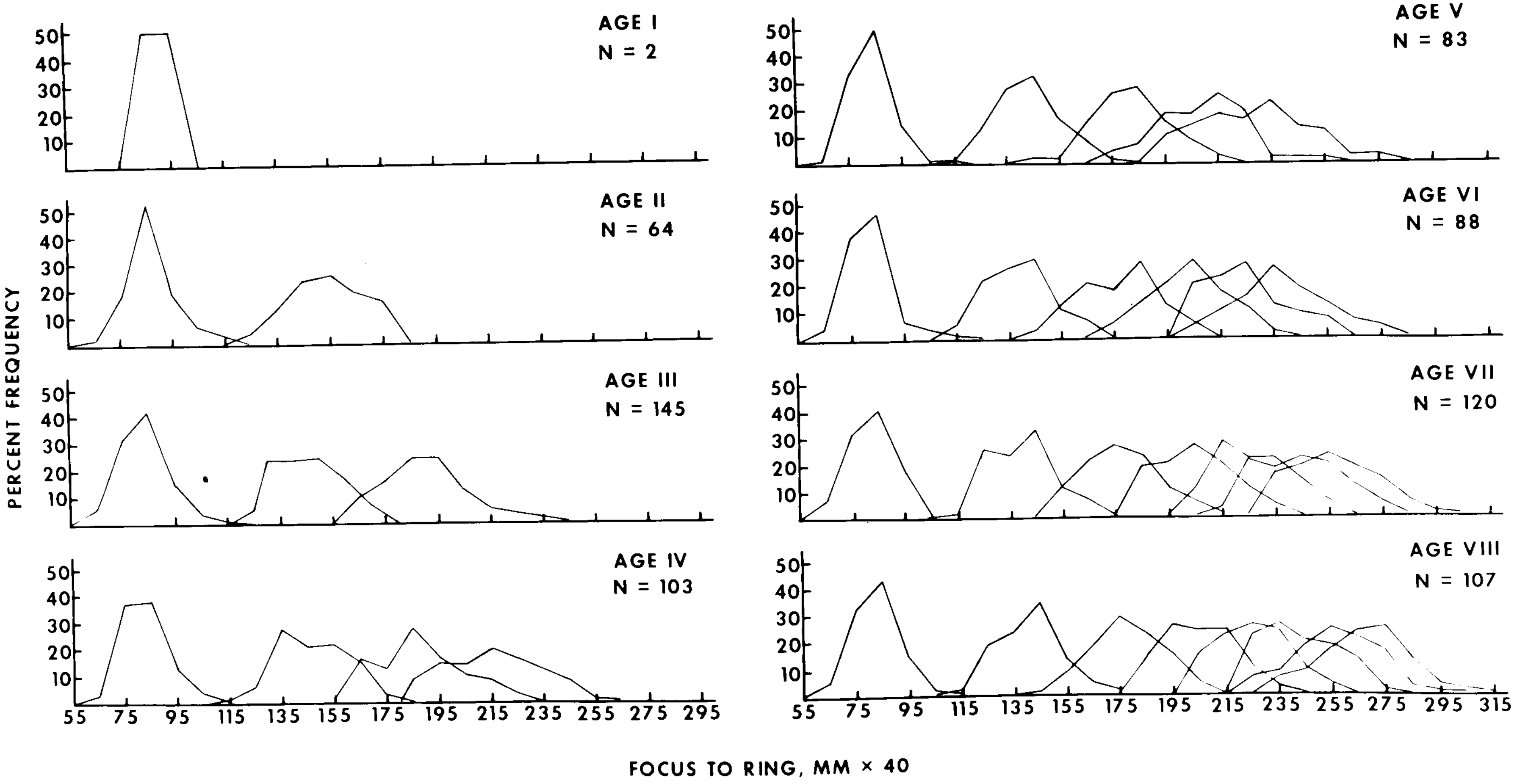


Figure 3. Frequency distributions of white grunt scale focus-to-ring distances (from Manooch 1976).



available from the same fish, therefore comparisons were made between mean lengths for ages from otolith-aged and scale-aged samples of a given species (Figure 4).

Two errors frequently made in aging reef fish have been the ommission of the first annulus or the inclusion of the focus as an annulus. This results, for example, in calling a two year old fish one year old, or a one year old fish, two years old. These errors are particularly common when examining whole otoliths, but also occur while reading sectioned otoliths and scales. The only sure way we had to verify the relative position of the first annulus and the time of its formation was to collect fish which were known to be young-of-year. We then measured the otolith core radius or scale focus radius, thereby eliminating it as an annulus candidate, and then sampled monthly to observe where the first annulus was formed on the structure.

GROWTH

After the aging method is validated the next step is to determine the relationship of body size to aging structure size and subsequently the change in length or weight of the fish over time. We usually describe observed, back-calculated, and theoretical growth patterns.

Observed growth is the change in length from the date of annulus formation to the time of capture. Fish size for a particular age therefore is greater for observed age than for back-calculated age. Observed age and growth information is useful to fishermen who wish to know the age of the fish they have caught, and also for the construction of catch curves.

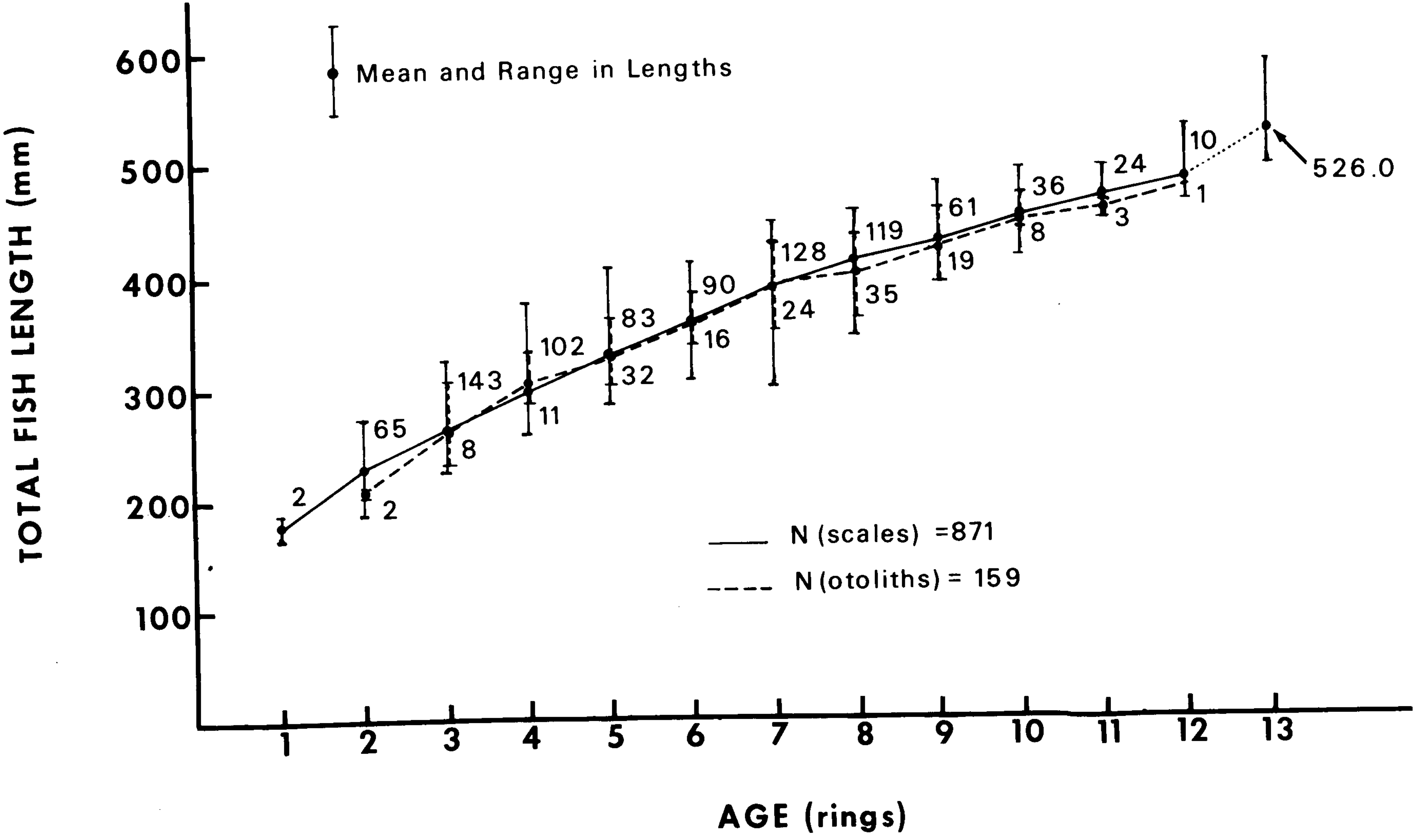
Growth is the increase in length from one annulus to the next and is reported as length at the time of annulus formation back-calculated from length at time of capture. Calculated lengths are used to derive theoretical growth equations and to make comparisons between species, areas, sexes, etc. To obtain back-calculated length at a specific age, we first determined the relation between fish length and the radius of the aging structures by plotting magnified scale or otolith radius of fish length. Usually most fish lengths were concentrated around a relatively narrow size range because of gear selectivity. To reduce this bias subsamples were taken after grouping fish into 25 mm size intervals. The resulting equation usually took the form:

$TL = a+b(R)$, where TL = total fish length, R = otolith or scale radius, a = intercept and b = slope. Occasionally we used log - log regression:

$$\log TL = a+b(\log R) \text{ or}$$

$$TL = aR^b.$$

Figure 4. Observed lengths at age for white grunt aged by scales and by otoliths (from Manooch 1976).



To obtain length at a particular age we substituted the means of the distances from the focus to each annulus for R in the above equations, calculated the mean fish length at the time of each annulus, and then calculated mean growth increment for each age group (Table 1).

Theoretical growth models are useful in estimating yields of fish. Growth parameters such as theoretical maximum attainable size ($L\infty$), growth coefficient (K), and theoretical origin of the growth curve when growth is fully developed (t_0), may be used in constructing population models. Perhaps the most popular theoretical growth curve is the von Bertalanffy ($\ell_t = L\infty(1-e^{-K(t-t_0)})$) and is fitted to back-calculated length at age data (Everhart et al. 1976; Ricker 1975). This particular equation also allowed us to make comparisons with results obtained by other researchers.

The growth parameter, $L\infty$, was first derived by fitting a Walford (1946) line: $\ell_{t+1}=L\infty(1-k) + k\ell_t$ to back-calculated data where ℓ_t = total length at age t, and k = slope of the Walford line. An initial equation $\ell_{t+1} = a + k\ \ell_t$ is developed. The slope (k) is equal to e^k, thus $K = \ell_n k$. A preliminary value of $L\infty$ can be obtained by solving the equation:

$$L\infty = \frac{\text{y-intercept}}{(1-k)} .$$

A second estimate of $L\infty$ may be obtained by regression annual growth increment (X) against fish length at the beginning of the incremental period (Y) (Jones 1976). The intercept is an estimate of $L\infty$. To evaluate the two estimates of $L\infty$, we frequently plotted $\log_e (L\infty - \ell_t)$ against t; the straightness of the resulting line is dependent upon the value of $L\infty$. Using trial values of $L\infty$ ranging from the lowest estimate to one exceeding the highest, we were able to determine the best $L\infty$, that is the one with the straightest line. The K resulting from the equation was used to determine t_0:

$$t_0 = \frac{\text{y - intercept of natural log line} - \log_e L\infty}{K} .$$

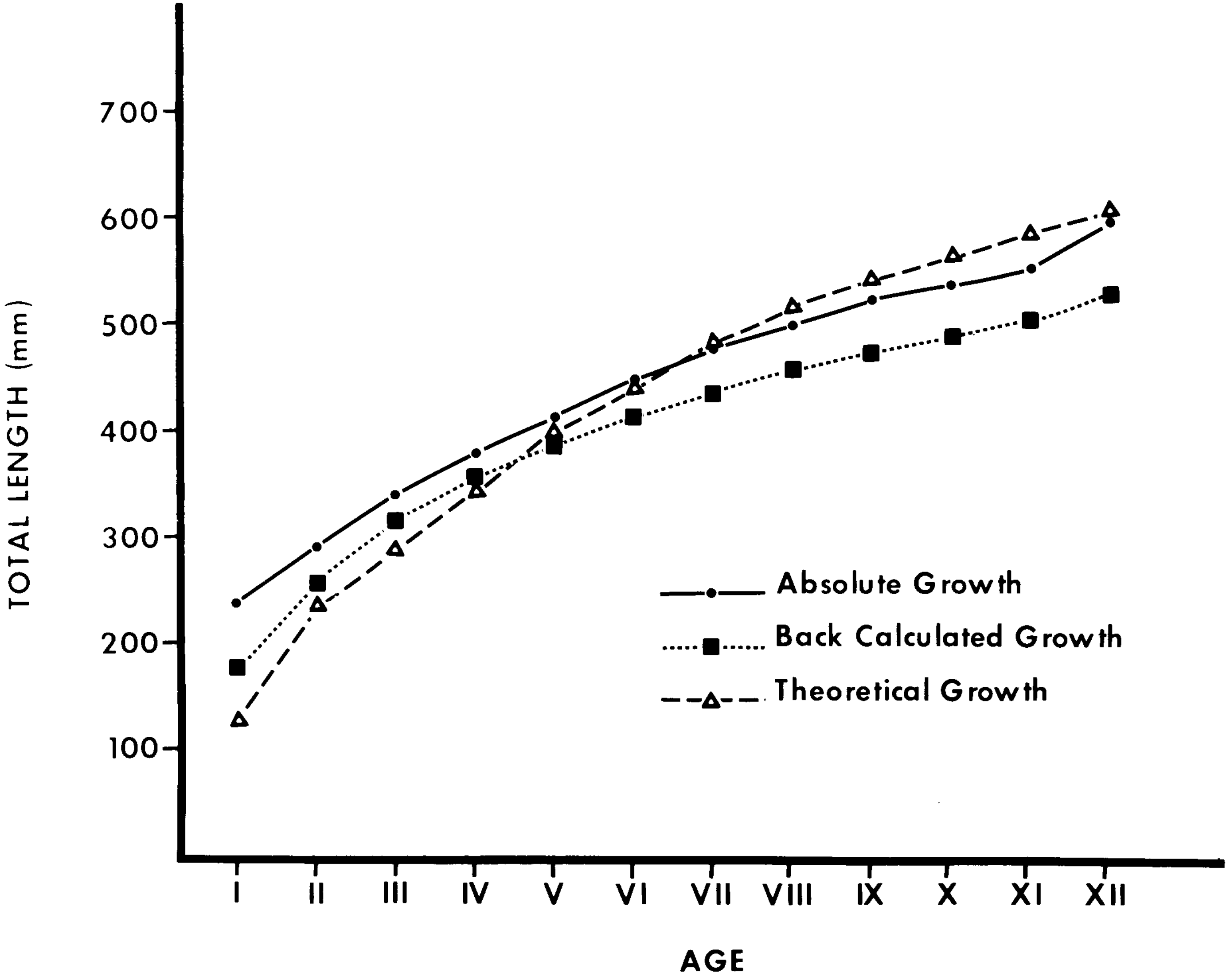
We checked the t_0 value to see if it was biased toward younger or older fish by using the equation $t_0 = t(1/K)\ \ell n\ (1-\ell_t/L\infty)$ for separate ages (Jones 1976). Observed, back-calculated, and theoretical lengths at age for red porgy are presented in Figure 5.

Computer programs are being evaluated to facilitate the derivation of theoretical growth parameters. We have used SAS Proc NLIN to fit age and length data for red snapper to the von Bertalanffy parameters (Nelson 1980). This program, as well as others, (BMDX 85, SPSS NONLINEAR), uses modified Gauss-Newton, steepest-descent, or Marquardt methods in regressing the residuals on the partial derivatives of the model with respect to the relevant parameters. The iterations converge at the smallest possible error sum of squares. The advantages of the non-linear curve fitting approach are that the procedures are completely reproducible and estimates of the variance assoicated with parameter estimates are available for testing differences in growth curves. Additionally, back-calculated lengths at every year of life from each fish are used in the regressions. This reduces the bias induced by using average lengths at age with unequal sample sizes in the various age classes.

Table 1. Back-calculated total lengths (mm) for snowy grouper collected from the South Atlantic Bight (from Matheson, In press).

		Length at time of Annulus Formation																
Age	Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	5	191																
2	41	206	329															
3	52	203	324	400														
4	79	214	332	405	463													
5	81	211	328	402	462	515												
6	56	214	326	398	459	512	560											
7	45	210	326	401	459	511	556	596										
8	35	214	324	400	458	510	558	601	641									
9	22	199	326	406	462	514	562	605	644	680								
10	17	210	320	404	463	510	555	598	635	669	700							
11	11	214	344	416	475	524	572	613	651	688	722	756						
12	10	206	334	408	466	520	576	621	660	698	730	760	791					
13	9	227	329	404	462	515	563	605	645	678	714	749	778	811				
14	3	243	349	429	495	543	588	632	676	712	752	787	818	854	885			
15	7	202	324	406	475	531	583	632	672	705	734	765	814	842	871	902		
16	3	216	340	416	482	539	588	628	672	712	752	782	814	841	867	894	920	
17	2	207	333	419	466	512	572	632	659	698	738	778	811	894	878	904	931	958
Number of calculations		478	473	432	380	301	220	164	119	84	62	45	34	24	15	12	5	2
Weighted means		210	328	403	462	514	562	605	647	686	721	762	798	832	874	900	924	958
Increment		210	118	75	59	52	47	43	42	39	35	41	32	34	42	26	24	34

Figure 5. Observed, back-calculated, and theoretical growth curves for red porgy (from Manooch and Huntsman 1977).



MORTALITY ESTIMATES

Mortality estimates may be obtained after fish have been aged and if the size or age distribution in the catch is known. Reef fish along the southeastern United States and from the Gulf of Mexico are not fully recruited to hook and line fisheries until at least age two and sometimes as late as age seven (Figure 6). Annual total mortality estimates from catch curves, therefore, were based on fish age two or older. If the $\log_e$ of the age frequency in the catch is plotted on age, the slope of the linear descending right limb of the curve estimates the mean instantaneous total mortality. To calculate mortality rates, we first needed to assign ages to the unaged fish whose lengths had been recorded. We grouped fish of known age by 25 mm length intervals, calculated the percentage of fish of each observed age in each group and used these percentages to estimate the number of fish of each age for the unaged group (Ricker 1975). We estimated the annual total mortality rate for areas and years by species using the regression method, (Beverton and Holt 1957).

REEF FISH GROWTH CHARACTERISTICS

Results of our age and growth research on reef fish have been very predictable. Species studied to date are long-lived, their rates of growth are slow, and their natural mortalities are low. These shared growth-related characteristics (Table 2) are important because they allow one to consider management in a generic sense, based at the community level. An exogenous stress on the fishable reef fish stocks, such as fishing, tends to effect each species similarly whether it is a porgy, grunt, snapper, or grouper (Huntsman and Manooch 1979; Huntsman et al unpubl. MS[3/]).

PROBLEMS AND APPROACHES

Considering the previous discussions it should be obvious that some tropical marine fishes may be aged by annular growth rings on hard parts. There are several problems, however, which we have encountered and deserve further discussion. These difficulties may be grouped into three categories: collection of fish, preparation and examination of hardparts, and interpretation of markings.

Most of the fish referred to in this paper were collected from recreational and commercial hook and line fisheries. There are two problems with these collections, size of fish and season of catch. Young-of-the-year, even one year olds, are excluded from hook and line landings, although these

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[3/] Huntsman, G. R., C. S. Manooch, III, L. L. Massey and C. B. Grimes. Unpublished Manuscript. Yield-per-recruit models of some reef fishes of the U.S. South Atlantic Bight. National Marine Fisheries Service, Beaufort Laboratory, Beaufort, NC 28516.

Figure 6. Catch curves for red snapper caught by hook and line (from Nelson 1980).

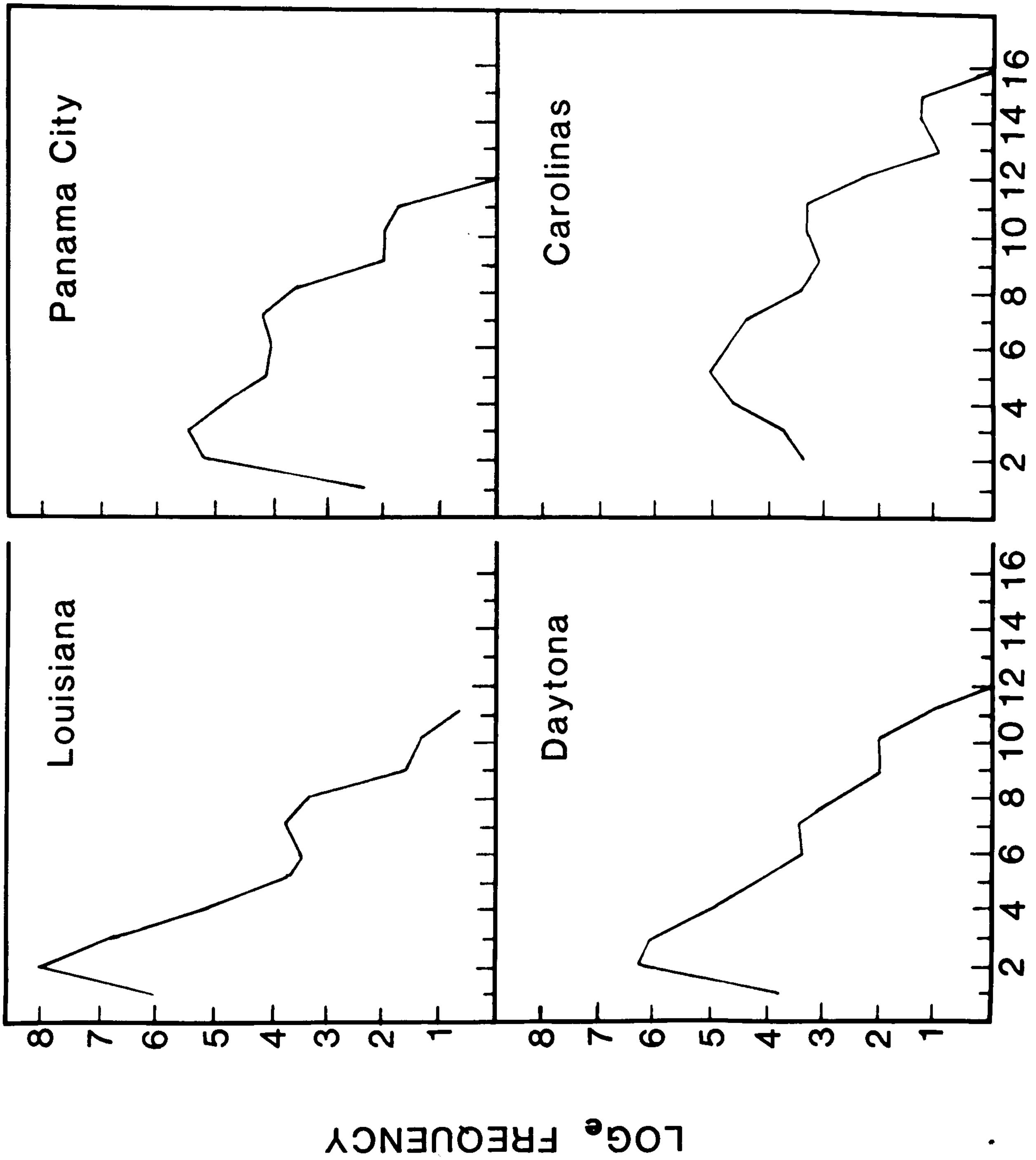

Table 2. Maximum age and growth parameters of reef fishes from different areas. Growth parameters may vary slightly when manuscripts in press or preparation are published.

SPECIES	AUTHORS	Maximum Age	Growth Parameters		
			L_∞	k	t_0
Speckled hind[1]	Matheson (in press)	15	1,105	0.088	-1.92
Snowy grouper[1]	Matheson (in press)	17	1,350	0.063	-2.32
Gag[2]	Manooch and Haimovici (1978)	>13	1,290	0.122	-1.27
Scamp[1]	Matheson (in press)	21	1,090	0.067	-3.91
Gray tile fish[1]	Ross (1978)	15	814	0.137	-1.03
Red Snapper[3]	Nelson (1980)	16	975	0.060	-0.00
Red Snapper[4]	Nelson (1980)	16	941	0.170	-0.10
Gray Snapper[5]	Manooch and Matheson (in press)	18	890	0.101	-0.32
Yellowtail Snapper[5]	Johnson (unpub. MS.)	14	--	--	--
Vermillion Snapper[1]	Grimes (1978)	10	627	0.198	+0.13
Tomtate[2]	Manooch and Barans (in prep)	9	310	0.220	-1.28
White grant[1]	Manooch (1976)	13	640	0.108	-1.01
Knobbed porgy[1]	Horvath (in prep)	17	459	0.212	-1.75
Red porgy[1]	Manooch and Huntsman (1977)	15	763	0.096	-1.88
Gray trigger fish[3]	Johnson (in prep)	--	--	--	--

1/ North Carolina and South Carolina

2/ South Atlantic Bight

3/ South Atlantic and Gulf of Mexico

4/ Gulf of Mexico

5/ South Florida, east and west coasts

young fish are essential to aging studies. The problem of size exclusion may be overcome by obtaining specimens from fisheries using a different gear, for instance trawl; by using experimental gear, for instance seining; or by investigating incidental collecting methods, such as power plant intake screens. It is essential that fish obtained from non-fishery sources be eliminated from catch curve analyses.

Samples from seasonal fisheries do not lend themselves to marginal increment analysis or other age validation techniques. Most vessels in the south Atlantic fish from about April to the end of November because of inclement weather the rest of the year. Samples from December to April were not usually available. Supplementary sampling by scientific cruises was required to provide aging structures on a year-round basis.

Another sampling-related deficiency was that sex of fish was usually unknown. This resulted when commercial landings where involved and fish were gutted at sea, or where samplers were not allowed to dissect fish which were to be sold. At other times gonads were preserved but sex was not identified on the sample sheet. Thus the sex of the fish would remain unknown until the preserved material was examined, possibly years hence. The Bioprofiles Task and Reef Fish Program should design and coordinate sampling procedures which will provide adequate sizes and sexes of fish, from the desired geographical areas and on a seasonal basis.

Several difficulties encountered were related to the preparation of hard parts for aging. Otoliths, for example, reveal much variation between species regarding focus clarity and size, and also the sectioned plane best suited for taking measurements. Structural inconsistancies necessitate close examination of otoliths representing a wide range of sizes for each species to be studied.

Large, thick scales also present problems. For some species such as red snapper and red porgy, scales of older, larger fish were too thick to read directly. Plastic impressions were occasionally required to facilitate readability.

Also, with older fish, sample sizes are small and rings are very close together. Therefore, deviations from mean annular measurements may be magnified. Care must be taken in counting and measuring rings for older fish.

Properly defining slow growth zones and rapid growth zones on otoliths, and determining the cause(s) of annulus formation were the two major problems in the interpretation of age structure markings. The literature is confusing. One writer identifies the hyaline band as the fast growth zone, while another refers to the opaque band as that of rapid growth. Both use reflected light. Occasionally authors are confused, and use both terms interchangeably in the same publication. The subject of basic chemical identity of the otolith rings does not escape this confusion. One researcher labels opaqueness as organic, yet another calls it inorganic. The point is that terminology should be standardized. Opaque represents fast or slow growth, and is either primarily protein, (organic), or calcium salt derivative (inorganic).

Factors which affect the timing of annulus formation are important. At first, our studies with the red porgy (Manooch and Huntsman 1977) and gag grouper (Manooch and Haimovici 1978) seem to indicate that even slight depressions in water temperature were sufficient to suppress somatic growth and cause the formation of annuli. Both of these species spawn in late winter or early spring. Our later research on red snapper (Nelson 1980) and gray snapper (Manooch and Matheson in prep.) suggests that markings on otoliths of these species are formed when water temperatures are elevated in late spring and summer. Both species spawn during summer. We now have an indication that what once was perceived as a temperature controlled phenomenon may actually be related to reproduction. The role of reproduction, particularly hermaphroditism, in the growth of reef fish should be studied in more detail as well as other endogenous rhythms which I believe act in tandem to form annuli on the hard parts of fishes.

RESEARCH REQUIREMENTS

Future age and growth research in the SEFC may continue successfully by methodically progressing through lists of important species. Each year two or three species could be selected, and by utilizing techniques outlined in this paper, age, growth, and mortality would be estimated. However, more emphasis should be placed on unstudied species from the Caribbean and South Florida, and also on stocks in the Gulf of Mexico. Russell Nelson's (1980) work with red snapper indicates that the accuracy of growth and yield models may be improved by analyzing data by geographical area for any given species.

Personally, I believe we need to do more than merely continue extant studies. From the standpoint of scientific challenge, as well as that of fisheries management, we must add depth to our work - investigate the processes - physiological, behavioral, and ecological - which regulate growth. Several recent papers present new concepts and methods which may be applicable in meeting our goals.

Causes of accelerated and depressed rates of growth may be studied by examining daily growth increments on fish hard parts. Brothers, Mathews and Lasker (1976) looked at daily increments on otoliths from temperate and tropical species up to six years of age and found them useful for measuring daily growth. Once determined in the laboratory, daily growth may be evaluated in terms of impact by environmental changes such as temperature, turbidity, and pollution. Studying daily rings may also prove effective in measuring the influence of reproductive cycles on fish growth. Fish held in the laboratory might have their otoliths labeled, be injected with gonadal stimulating hormones, and be allowed to complete spawning. Otoliths would then be removed from the fish and daily growth measured before, during, and after spawning. Field experimentation would follow. Perhaps one of the most applicable uses of daily growth increment studies would be to correlate spawning time with environmental factors such as moon phase, tide, weather fronts and barometric pressure, etc. Also, the early life history - the transformation from a pelagic existence to the demersal stage - could be followed.

Two other methods of measuring growth, ^{14}C labeled glycine uptake (Ottaway 1978; Ottaway and Simkiss 1979), and RNA/DNA ratios (Bulow 1970; Haines 1973; Buckley 1979; Haines 1980) show promise. Both of these new methods allow the measurement of instantaneous growth. And, although they do not give an indication of specific age, they could, by measuring instantaneous growth throughout the year, establish the effects of temperature flux, turbidity, densities of fish, structual heterogenity, etc, on the growth of fish populations. Data could then be used to generate models which would consider the factors mentioned above.

ACKNOWLEDGMENT

I wish to acknowledge the contributions of Robert Matheson and Russell Nelson, graduate students at North Carolina State University assigned to the Beaufort Laboratory, and Allyn Johnson, Panama City Laboratory for providing information pertaining to problems and future research needs in aging reef fish. Samples were obtained through the combined managerial efforts of T. R. Rice, E. L. Nakamura, and G. R. Huntsman, Southeast Fisheries Center.

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SESSION SUMMARY

Aging of Reef Fishes

by

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Two papers were presented during the session. And, although they approached the subject of aging reef fish from different levels, they agreed that validation of techniques, and reproducibility of results are critical in age and growth research. Unfortunately, validation is seldom addressed in fisheries age studies.

One of the papers dealt with a relatively new technique - examination of daily growth increments - and the implications to reef fisheries management. Not only may young fish be aged accurately, but also time of spawning, factors affecting spawning (moon phase, tide, water temperature, etc), pelagic and demersal stages of larvae, and estuarine and marine stages of juveniles may be investigated.

The other paper discussed reef fish aging studies by Southeast Fisheries Center personnel using traditional anatomical techniques - scales and otoliths. Results on aging 14 species were presented and problems and future research needs were outlined.

A discussion on aging reef fish followed. The principal objectives of this open forum were to comment on the papers presented, and then discuss current and future research on the aging of reef fish in the South Atlantic Bight, Gulf of Mexico and Caribbean. Is work already completed satisfactory? What techniques, geographical areas, species (stocks), etc. need more emphasis? How may coordination between agencies and institutions within the Region be improved?

The practicality of using daily growth increments on small fishes when length frequency data are available was questioned by Saul Saila. Brothers pointed out that while length frequencies provide a general description of early life history and growth, daily increments on otoliths provide not only accurate age and growth and time of spawning information, but also allow one to look at a variety of environmental and behavorial variables as well.

Another point discussed was that growth parameters - notably K - from different areas (south Atlantic Bight and Caribbean) are drastically different in the literature. David Olsen, Conner Davis, and Debbie Weiler mentioned that aging work in the Caribbean had used trap-caught fish aged by length frequencies while those in the South Atlantic Bight (SEFC personnel) were hook and line-captured fish aged by handparts. Differences may also be related to water temperatures, method of harvest, histories of geographically different fisheries, and major differences in fish community structure. Manooch pointed out that studies by Nelson (1980) on red snapper, and Horvath (in prep) on knobbed porgy, indicated slight difference in K related to geographical areas, and method of capture, respectively. Whether differences in growth parameters are statistically different and biologically explainable are under investigation.

Brothers was asked to give a brief description of the procedures he used to remove, prepare and examine otoliths from larval and juvenile fishes.

The comment was made that it was a shame that fish older than 200 days could not be aged by the daily increment method. Brothers indicated that this was not so. Some fish (species) may be aged to only a few days, while others may be aged for several years. In fact one may calculate a theoretical growth curve (such as the von Bertalanffy) if data extends into the adult growth stanza.

The reference to the von Bertalanffy equation stimulated a brief comment on t_0 and its value. Saul Saila mentioned that t_0 was of no real value and perhaps it should be forced through 0 when used. If the value is negative it is okay, if positive, something is wrong.

Jack Davis commented on the time of annulus formation in reef fishes. If an annulus is caused by spawning, why do young fish (immature) also develop an annulus? Manooch commented that annulus formation may be related to several endogenous physiological rhythms and that spawning is only one of many. The subject of reproduction, particularly hermaphroditism, needs to be studied in more detail and correlated to age and growth.

Manooch asked the group what they thought of reef fish aging work conducted by SEFC investigators. Is the research off base? The general opinion was no, that it is satisfactory. Brothers stated that the validation techniques look good, data appear to be reproducible, and that most of the work has involved fish which were not truly tropical in their habitats. He stated that problems may be encountered aging fish in the Caribbean.

Huntsman asked the attendees to identify species in the Caribbean which should be aged in the near future. The following were mentioned: silk snapper, blackfin snapper, coney, vermilion snapper, red hind, queen snapper, misty grouper, queen triggerfish, goat fishes, lane snapper, and wenchman. If species are identified, and the need for aging is justified, how may the SEFC work with those in the Caribbean to obtain samples? Debbie Weiler stated that her office had the manpower (in Puerto Rico) but needed financial support to purchase fish.

It was agreed that the SEFC and researchers in Puerto Rico and the Virgin Islands should establish better lines of communication relative to the common problems of aging reef fish: developing new, and standardizing old techniques, prioritizing species to be studied, and investigating sources of funding. The SEFC should continue its reef fish aging work, expanding into the Caribbean with unstudied species, and into the Gulf of Mexico with unstudied stocks, and investigate new techniques such as daily growth increments.

SESSION 2

Reproduction in Reef Fishes

Chairman
Michael L. Parrack

PATTERNS OF REPRODUCTION IN CORAL REEF FISHES

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ABSTRACT

Reproductive strategies of coral reef fishes are diverse and not well known. Most reef fishes have planktonic life history stages, although some lay demersal eggs with parental care, some are oral or body brooders, and some are viviparous.

Fertilization, hatching, initiation of feeding, assumption of demersal habits, and spawning are critical stages with increased mortality rates so that the survivorship curve is stepped.

Hermaphroditism is a reproductive strategy that has been studied extensively. Several important commercial species are protogynous hermaphrodites. Compared with gonochoristic species females of protogynous species reach maximum reproductive values earlier, then decline more rapidly. Because sex inversion leads to size differentials between the sexes, a size-selective fishery will lead to unbalanced sex ratios, and some individuals will be unable to produce their maximum number of offspring.

INTRODUCTION

Reproduction is probably the aspect of the biology over which the manager has least control. Diets can be modified and even substituted, artificial habitats can be introduced, growth can be regulated by manipulation of food and space, and population density can be maintained at specific levels. But the only way to produce more individuals is through natural biological reproduction. Our ability to control reproduction is limited to providing adequate numbers of parents and suitable conditions for courtship and spawning. In the laboratory and in the fish hatchery it is, of course, possible to administer hormones to induce spawning or to strip eggs and milt from ripe adults, but at present these techniques hold limited promise as tools for the management of coral reef fishes. (Atz 1964; May 1971).

In spite of the importance of reproduction our present knowledge of the requirements for courtship and spawning is extremely limited. For only a handful of species do we have even rudimentary descriptive data on courtship, and there is little information on requisite environmental factors such as temperature, water quality, day length, or substratum type. Most population studies begin with the recruitment of the juvenile into the adult habitat or into the harvestable sizes, although Vaughan and Saila (1976), using the Leslie Matrix, have estimated larval mortality of bluefin tuna.

This paper will review the general patterns of reef fish life history with emphasis on critical periods of high mortality. Some major aspects of reproduction are examined in the context of management and limiting factors, and effects of harvesting on population structure of some hermaphroditic groupers are projected from crude estimates of reproductive value.

LIFE HISTORY

It is characteristic of reef fishes, which are, for the most part, sedentary as adults, to have planktonic eggs or larvae or both. Coral reef environments are characteristically extremely patchy, and consist of large and small reef massifs separated by either open deep water or barren shallows that lack hermatypic environments. Were it not for the planktonic life history stages many patches of reef might remain devoid of fish life for extended periods. As it is, population of newly constructed reefs or repopulation of reefs denuded by some catastrophy usually begins within a few hours. This makes it extremely difficult to evaluate the effect of human activities on reef fish populations. For example, spawning in local areas might be inhibited by heavy visitor use, but the inhibition would be masked by recruitment from other regions.

A second consequence of this dispersal mechanism is that few reef fishes spend their lives in the same area as their parents. On a local scale there is essentially panmixis, that is, every individual has about an equal chance of mating with every other individual in the population. This may not be strictly true where persistent currents causes unidirectional drift but in general there is nearly random mating over broad geographic areas.

The normal fish life cycle consists of well-defined stanzas separated by more or less abrupt transitions. (Figure 1A). The transitional periods are generally considered to be critical times when the mortality rate jumps dramatically (Figure 1B). Especially critical times are: 1, fertilization 2, hatching 3, the time at which the yolk supply is used up and the larvae must begin to procure its own food 4, the time of transformation from a planktonic prejuvenile to a reef dwelling juvenile 5, the time of sexual maturity and 6, the time of spawning. Most of the different specializations of structures and reproductive behavior are solutions to the special problems of these critical periods.

Because there have been no quantitative studies of mortality patterns of reef fishes, the following discussion is largely conjectural and is presented in the hope that it will help to identify the data that will be needed for future management.

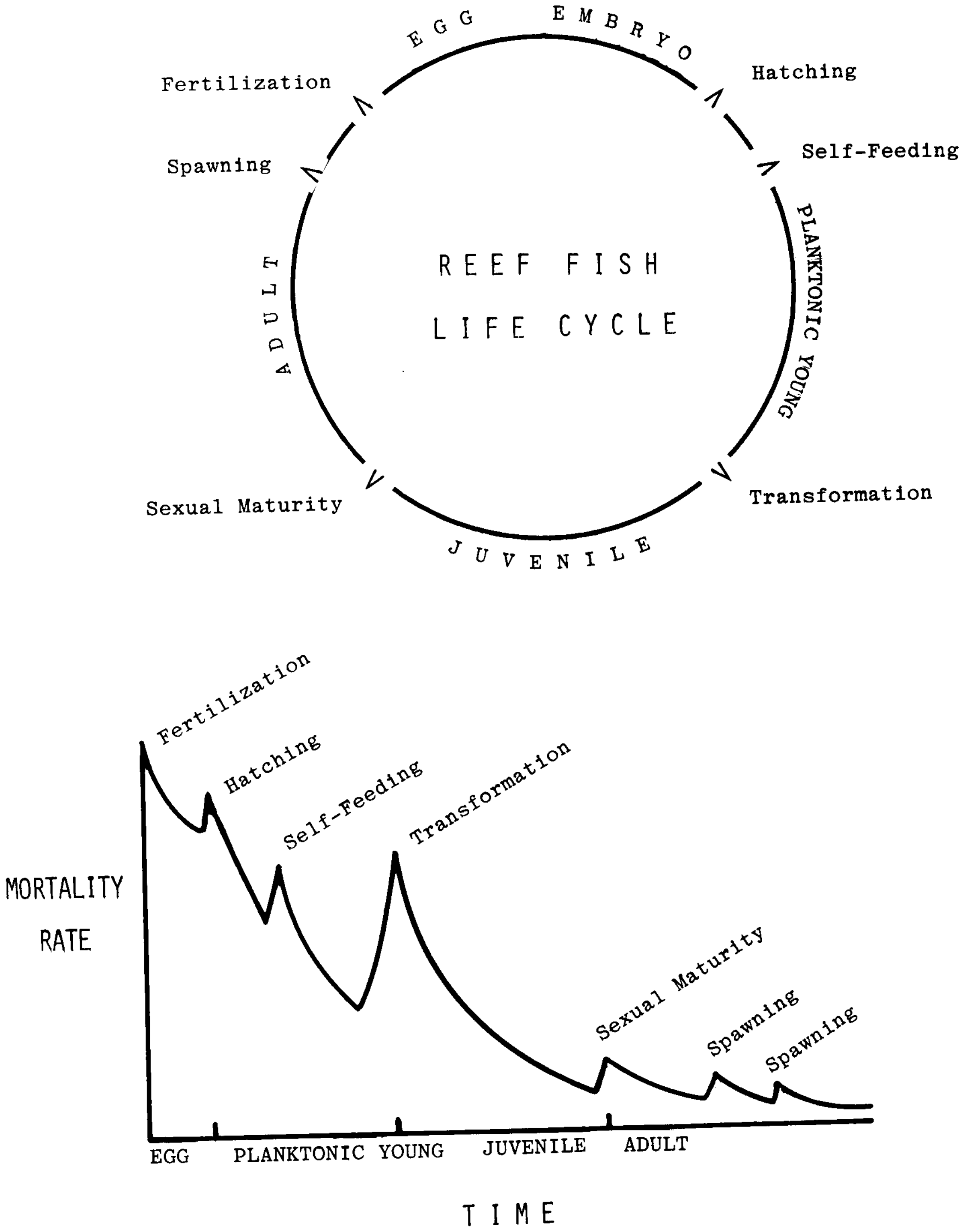


Figure 1.

A. Generalized life cycle of a species of fish having planktonic young stages. The egg embryo part of the life cycle may also be planktonic.

B. Hypothetical mortality rate curve derived from A. At the critical stages the mortality rates increase then fall off as the crisis stages are passed.

EGGS

Many reef fishes, the labrids and groupers for example, lay transparent, non-adhesive, planktonic eggs. These usually have a large oil droplet that gives them a near neutral bouyancy. Such eggs are nearly invisible in the water column and essentially disappear as soon as they are released. A few fishes, antennariids, and carapids, for example, produce gelatinous rafts of eggs. For a large antennariid this raft may be 3 feet long by 4.5 inches wide (Rasquin 1958).

There are a number of small species that follow spawning pairs and feed on eggs as they are released, causing an apparent mortality for the first few seconds. Once eggs disperse, however, mortality rates can be expected to drop to a lower level.

At the other end of the spectrum are those fishes that lay adhesive demersal eggs. These eggs are often brightly pigmented and attached to the substratum by special threads or stalks. The sergeant major Abudefduf saxatilis is a readily observed example on all West Indian reefs (Shaw 1955, Cummings 1968).

In contrast to freshwater groups I have not found any reef fishes that produce non-adhesive demersal eggs that simply fall into crevices or the interstices in gravel or rubble. Nor am I aware of any reef fishes that broadcast their eggs over sand. Apparently the abundance of demersal predators and scavengers precludes these types of eggs.

Early reports suggested that trigger fishes lay demersal eggs without guarding them, but more recently Lobel and Johannes (1980) found that at least one species cares for its eggs although the parents do not guard the nests at night. Apparently there was no predation on the eggs while the parents were absent because the egg predators were also inactive at night.

Parental care is non-existent for fishes that lay planktonic eggs but demersal spawners show many degrees of guarding the eggs. Oral brooding is common among reef fishes, such as apogonids and opisthognathids, and some groups are viviparous; brotulids and clinid blennies of the genus Starksia are examples from the Western Altantic fauna. Finally, there is parental care in pipefishes and sea horses, which transfer eggs to the male to be carried until they hatch.

One has only to watch a male sergeant major guarding eggs against wrasses and damselfish to see how necessary such care is and to appreciate the enormous physical demands guarding makes on the parents.

EMBRYOS

Although there are probably critical stages in the developing eggs these are not obvious. Hatching is a time of special stress for many fishes and we can assume that it is a period of increased mortality for both demersal and planktonic embryos.

PLANKTONIC STAGES

Pelagic young are subject to mortality from many causes. For effective dispersal they must be picked up by currents and carried for a limited time and then must be returned to the benthic habitat at the right time to transform to juveniles. While they are plankton they are vulnerable to many kinds of predators, both invertebrates and other fishes, they run the risk of drifting into hostile environments that are too deep, too shallow, or chemically unacceptable, and they are subject to mechanical damage in breaking waves and surf. Moreover, during this time most larvae must make the difficult transition from feeding on stored yolk food to feeding themselves. This transition has proved to be a stumbling block to the development of mariculture of marine fishes (Atz 1964; May 1971).

TRANSFORMATION

The end of the planktonic larval period is another critical time when young fish face a dramatic change of life style. Not only are there morphological changes in pigment, body form, and trophic structure, but the fish have to change their overall behavior pattern to a new mode of existence. Here competition assumes a new meaning, for now the transforming individual must not only find acceptable physical conditions, but it must also contend with other fish that may already occupy the sites necessary to it. Once it becomes established it must defend its site against invaders. In a sense, it is at this point that managers can begin to influence reproductive success. By providing additional juvenile habitat and by reducing competition from other species, the success rate of the juveniles could be increased. This is exactly what is done with milkfish, Chanos, and with spiny lobsters, and it holds promise for other reef fishes as well. After the juveniles are established in their definitive environment their mortality rates can be expected to drop as age and size increase, if for no other reason than that the larger they get, the fewer predators will be able to engulf them. Moreover, as they become more experienced at defense and feeding their chances of survival are increased.

SEXUAL MATURITY

For some fishes the attainment of sexual maturity means a new set of problems. Sometimes it involves establishing territories, sometimes it means a move to a new habitat, or sometimes it simply means a gradual development of adult behavior which may differ only in that it includes spawning.

COURTSHIP AND SPAWNING

Our knowledge of the reproductive mechanism of coral reef fishes is extremely limited. Although we have detailed information for some species, for most we have only fragmentary anecdotal information. (See paper by P. Colin, this volume).

In highly diverse communities unique species and sex recognition mechanisms are important to assure the union of eggs and sperm from the same species and to prevent gamete wastage. Perhaps because of the clear waters associated with coral reefs, color and shape serve as visual clues for sex recognition. Many species have elaborate courtship rituals that precede spawning (Thresher 1980).

Although seasonal climatic variations are minimal in the tropics, some species show a definite periodicity. Erdman (1976) and Munro, et al. (1973) have addressed the phenology of coral reef fishes.

From the limited information available, it appears that some species spawn almost every day of the year, others have but a short annual spawning period and still others spawn intermittently in rhythm with environmental factors such as moon and tidal phases. I do not know of any reports of semelparous reef fishes.

Some groupers may spawn at night (Guitart Manday and Fernandez 1972), but many other fishes, wrasses, parrotfishes, damselfishes, spawn in the daytime, often when the sun is near the zenith. For fishes that use visual releasers adequate light seems to be necessary.

Two mechanisms for bringing males and females together are territoriality and migration. Territoriality is well documented among smaller reef fishes. Some damselfishes defend their territories vigorously, other reef fishes merely remain in, or return to, the same spot day after day. Smith and Tyler (1972) have presented some preliminary data on the sizes of territories occupied by fishes living on a small patch of reef.

Spawning migrations are known in parrotfishes, wrasses and groupers. Generally these migrations do not involve long distances; rather they consist of assembling at the spawning areas, which are often at the edge of the drop-off. Johannes (1978) has suggested that assembling in such areas has the effect of getting eggs into currents that disperse them. Possibly another adaptation for getting the eggs into the water column is the upward spawning rushes exhibited by wrasses, parrotfishes and sea basses, among others (Thresher 1980, Colin this volume).

Courtship among reef fishes is varied. Many species spawn in individual pairs, others in groups. Sometimes a pronounced color change precedes spawning and apparently acts as a signal. But for many reef fishes the signals are behavioral, the fish approaching one another with various ritualistic movements, such as arching the body, spreading the fins and vibrating the body while swimming in short dashes in front of its partner. Often courtship culminates in a rush upward in the water column, with a brief clasping or tumbling and final separation of the pair (Thresher 1980).

Most reef fish spawn repeatedly, releasing small numbers of eggs during each episode. Mating patterns are frequently random, although some individuals spawn repeatedly with the same partner, with which they share a section of the reef when not spawning.

HERMAPHRODITISM

Two of the most important families of harvestable reef fishes, the Serranidae and the Sparidae, have members that are hermaphrodites. It is instructive to review the important aspects of this hermaphroditism and to examine the significance of this specialized mode of reproduction in the context of exploited fish populations.

For the purpose of this discussion, any species that normally has both male and female tissues in the same individual is hermaphroditic, but those in which an occasional teratological hermaphrodite has been recorded are excluded. It is generally accepted that in fishes hermaphroditism is a specialization. Smith (1975) presented evidence indicating that hermaphroditism has originated at least ten times in different phyletic lineages, and recent evidence has increased this number.

Different groups of hermaphroditic species show differences in gonad structure and in the arrangement of the sexual tissues. These differences are evidence of the independent origin of hermaphroditism in diverse phyletic lineages.

SIMULTANEOUS HERMAPHRODITISM

Simultaneous hermaphroditism is the condition in which the male and female tissues ripen at the same time. It also has been called synchronous hermaphroditism, but Reinboth (1980) has pointed out that the presence of ripe eggs and sperm at the same time does not necessarily imply that the gametogenetic processes are synchronized. Usually each sexual tissue is localized in a separate region of the gonad (named territorial hermaphroditism by D'Ancona 1952), with separate ducts for eggs and sperm. Although simultaneous hermaphrodites should be capable of self fertilization, so far only one species, the brackish water _Rivulus marmoratus_ (Cyprinodontidae), has been shown to have this capability. The few other species that have been observed spawning undergo courtship and pairing like that of gonochoristic species. Eugenie Clark (1959) studied reproduction of the belted sandfish, _Serranus subligarius_, and found that during spawning each individual assumed the behavioral role of one sex. The fish that was larger or at least more distended with eggs assumed the role of the female; the smaller fish acted as a male. It is not known if each individual released both eggs and sperms during the spawning or if the functional role matched the behavioral role. In any case, individuals could reverse their behavioral roles in successive spawning episodes if the next partner had the opposite size differential. In effect, these fish were functioning as true simultaneous hermaphrodites, with every encounter between individuals a potential mating encounter.

SEQUENTIAL HERMAPHRODITISM

Sequential hermaphroditism (transforming hermaphroditism, sex inversion, metagony) appears to be far more common among fishes, or at least it seems to have developed independently in more taxonomic groups. In this kind of hermaphroditism each individual functions first as one sex. Then its gonads transform and it functions as the opposite sex. Because the sexes are functionally (temporally) separate, the species acts as a gonochorist with a size-biased sex ratio. Only some of the encounters between individuals are potential mating encounters.

Sequential hermaphrodites fall into two categories: protandry, in which the fish function first as males, and protogyny, in which the fish function first as females. The change from one sex to the other occurs only once and is irreversible.

The factors that trigger the change from one sex to the other are not completely known. For several species there is strong evidence that social interactions with other individuals of the same species are the proximal cause of sex inversion. For some species that live in small groups, each with a single male, it has been shown that removal of the male will cause the largest female to change into a male. Recently Shapiro (1980) has shown that in Anthias squamipinnis, which occurs in large and complex aggregations, removal of several males will result in transformation of the same number of females. They do not all transform at the same time, but in sequence at intervals averaging 1.9 days. This seems to indicate that the behavior of individuals other than the dominant male also affects the sex reversal of the larger females. Reinboth (1980) has protested that this still tells us very little about the exact mechanism that leads to the inhibition of one tissue as the other flourishes. Clearly our understanding of the process is far from complete at this time.

In broad terms there are two fundamental arrangements of the germinal elements, territorial and mixed. In the territorial type the spermatogenic and ovigerous tissues are confined to the separate parts of the gonad, as is the case with simultaneous hermaphrodites. Usually these is a clearly discernible morphological boundary between the two. In the mixed type of gonad, the male and female elements are both scattered throughout the germinal epithelium. Members of the genus Rypticus (protogynous) and the genus Amphiprion (protandric) have intermediate types of gonads in which the male elements are localized, but not separated from the female elements by a definite boundry. Both have hollow, ovary-like gonads.

Because of the complete transformation of the gonad, it is sometimes difficult to determine from gross examination whether or not a species is a hermaphrodite. Histological study is essential to determine the arrangement of the tissues in the mixed type of gonad. Often it is necessary to examine material from specimens of various sizes, and collected throughout the annual cycle, to be certain that transformation occurs. The following criteria are useful:

1. Simultaneous hermaphrodites can usually be recongized from gross examination of the gonad of sexually active individuals. The whitish testicular area, with flowing milt, stands in sharp contrast to the granular yellowish ovarian region. Usually the testicular region is located on the ventral posterior part of the gonad, with a band of spermatogenic tissue encircling the common oviduct to join the sperm duct in the rear wall of the common oviduct.
2. In transforming hermaphrodites the terminal sex will have an average size larger than that of the other sex. This is, of course, not conclusive because the same effect can be due to differential growth rates or to greater longevity of one sex as in the sturgeons.
3. In many protogynous transforming hermaphrodites the overall structure of the gonad is that of an ovary, with the presence with the sperm duct in the gonad wall. Even this is not conclusive, however, for Smith and Young (1966) reported the presence of a lumen in the kelp bass <u>Paralabrax clathratus</u>, but could find no other indication that the species was hermaphroditic.
4. Final confirmation of the transformation must be based on finding a series of transforming stages showing good evidence of the progressive development of tissues of one sex and the progressive degeneration of the tissues of the other. Precocious sperm crypts in protogynous species are suggestive of transformation, but the presence of oocyte-like cells (auxocytes) must be regarded as inconclusive because such cells are frequently found in juveniles and occasionally in adults of gonochoristic species. Sometimes they appear merely to be remnants of a juvenile undifferentiated stage.

Although some cichlid fishes are reported to be ambisexual and the symbranchid "eel" <u>Monopterus albus</u> lives in freshwater, nearly all known hermaphroditic fishes are marine.

It is particularly interesting that several groups of fishes have two types of males (a condition that Reinboth has called diandry): primary males that differentiate as males, and secondary males that pass through a female phase before transforming to males. Several wrasses and parrotfishes are diandric and Reinboth (1980) cites studies by Moore that indicate that the protandric <u>Lates calcarifer</u> has a similar but opposite condition with two types of females (digyny). In the West Indian bluehead wrasse, <u>Thalassoma bifasciatum</u>, there appears to be no connection between the two kinds of males and the two color phases of the male (one like the female, the other brighter and more distinctive), or between the two spawning patterns, pair spawning and group spawning.

HERMAPHRODITISM AND POPULATION DYNAMICS

The larger serranid fishes, including the groupers, hamlets, rockfishes, coneys, graysby, and leather bass, are some of the most important food fishes harvested from coral reef environments. All of the species that have been studied so far have proved to be protogynous hermaphrodites with the mixed type of gonad. This pattern is so consistent that it is unlikely that other species will be found to differ in any important way. Relatively little work has been done on the population dynamics of any species of grouper; the most comprehensive studies so far published are probably those of Martin Moe (1969) on the red grouper of the west coast of Florida and Nagelkerken (1979) on the Graysby in Curacao. Thompson and Munro (1974) present data on the grouper fishing around Jamaica. In spite of this paucity of data it is instructive to consider the possible effects of selective cropping of certain sizes on the structure of the grouper populations.

Although it is common practice to model survivorship as a die-away curve of the form $N_t=N_0e^{-zt}$, it is apparent that this is not particularly realistic in view of the critical periods during the life cycle. Figure 2 (top) is a hypothetical survivorship curve for a reef fish cohort showing a stepped form which results from high mortality rates during the critical periods. A protogynous species has a different pattern, as indicated in Figure 2, because sexual inversion (transformation from female to male) is the same as death of a female. The female survivorship curve, therefore, has additional steps. Furthermore, males are produced only as a result of sexual inversion. If, as evidence suggests, sex inversion takes place between spawnings, the result is a saw-toothed survivorship curve for males.

In most West Indian areas groupers are harvested primarily by hook and line, fish pots, and to some extend by spearing. They are not vulnerable to trawls, seines or gill nets. Each of the three methods is selective to some extent, although not sharply so, and the result is a selectivity curve with a comparatively gentle slope. The data presented by Thompson and Munro (1974) suggest that few groupers less than 20 cm are caught. Some species show modes at 25 to 30 cm, and we can assume that all fish 20 cm and longer are vulnerable.

In general, the fishery for groupers is not selective as to species. All species are eaten, although some may be considered too small to be desirable if larger fish are available. In some areas very large fish of some species will be rejected because of the danger of their being ciguatoxic.

Groupers are long-lived fishes, the larger species probably living for twenty years of more although data are scarce. Because of their large size, older individuals have relatively few predators and survivorship of the older age classes is high, so that the stable age

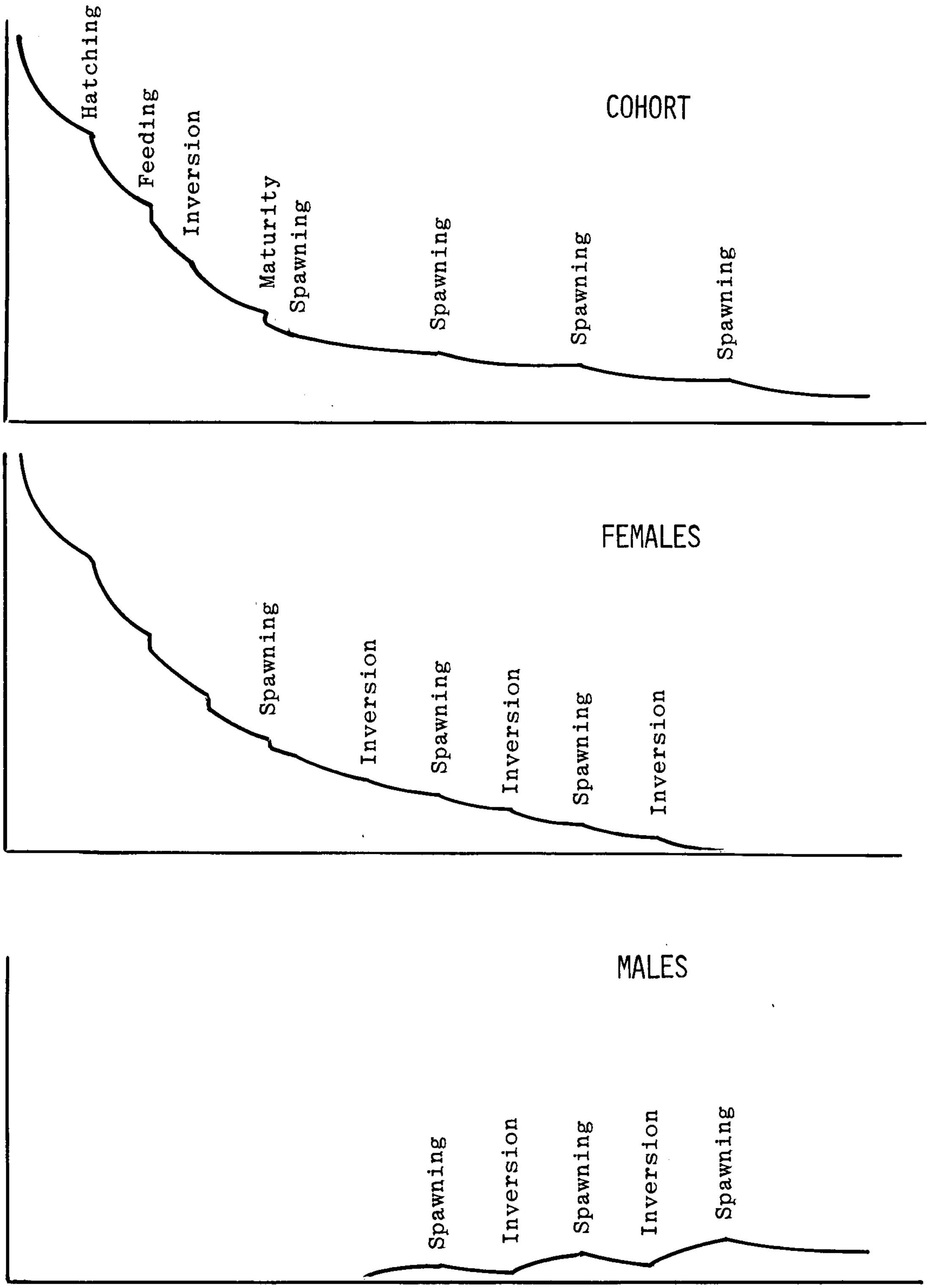


Figure 2.

Hypothetical survivorship curve for a species that is a transforming hermaphrodite. The curve for the age group (cohort) is the same as that of a gonochoristic species but the curves for the sexes are different because sexual inversion is equivalent to female death and males are produced only by sexual inversion. Vertical axis is number of individuals remaining in the population. Horizontal axis is time.

distribution includes mostly older fish. Transformation from female to male occurs over a protracted period, so that a graph of the percent of females in the population, against time, will be a sloping line between two inflection points; the lower representing the size (age) at which the first female becomes a male, the upper representing the size or age at which the last female reverses sex. (Figure 3).

The presence of exceptionally large females may indicate that some females never transform. Furthermore, the presence of exceptionally small males suggests that a small percentage of the population may bypass the female stage. These are probably not important in the present models.

Different species of groupers achieve different maximum sizes. Hence in a population of several species there will be a family of curves of percent females, each one specific for a particular species.

When we superimpose the gear selectivity curve on the percent female curves (Figure 3), we find that while all individuals of large species are vulnerable and none of the smaller ones are, there will be a bias against the males and largest females of the intermediate sized species.

REPRODUCTIVE VALUES

In order to assess the effect of differentially harvesting the sexes of several species in the same population we have to consider the cost of reproduction and the reproductive value of fish of each age class. In general, the reproductive value of a juvenile that has little probability of surviving to reproductive age is very small compared to that of an older fish that has achieved maturity and a size that assures that it will probably survive to reproduce several more times. Furthermore, older fish produce more eggs and,therefore, are more valuable.

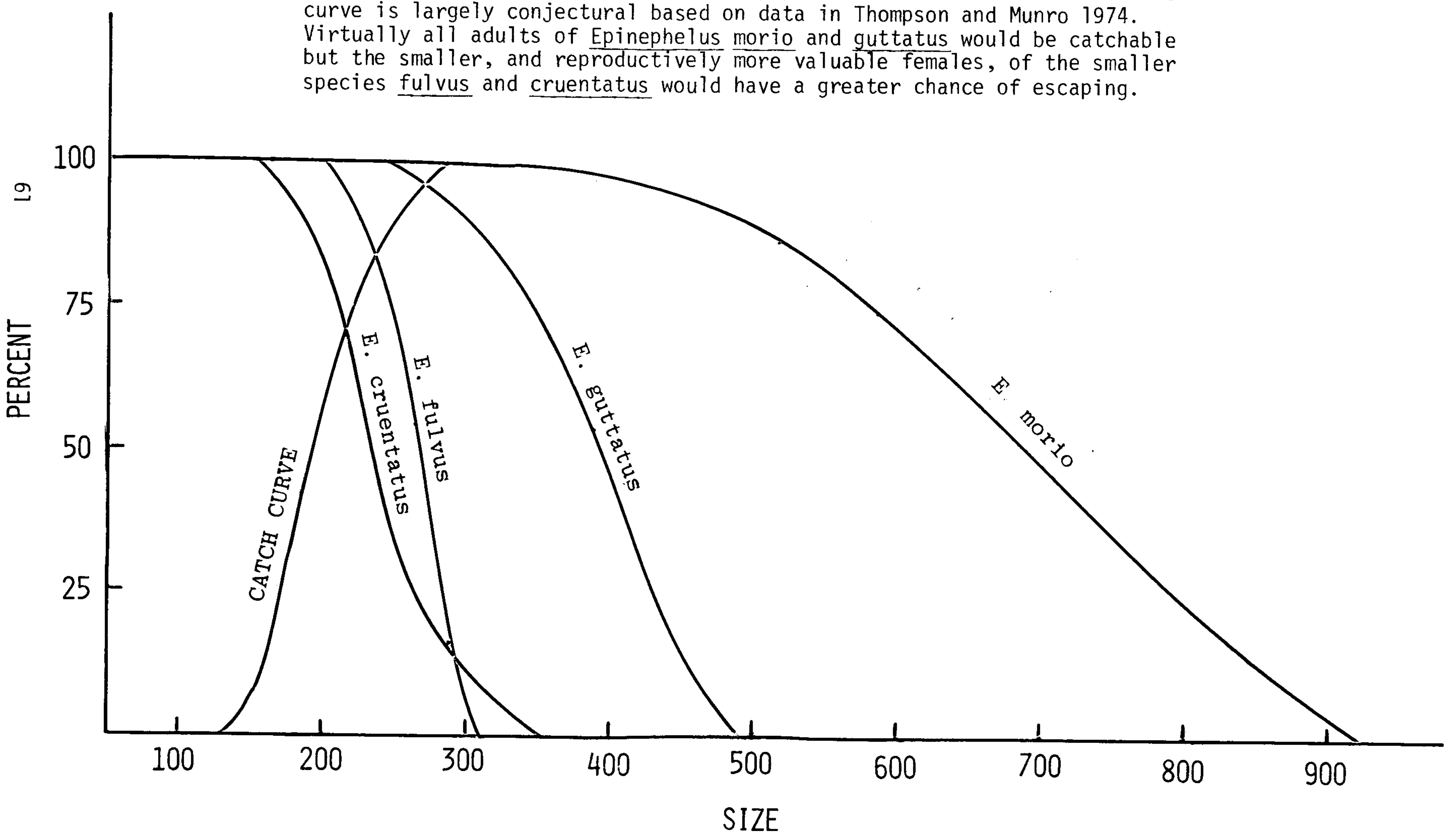
As a preliminary step toward evaluating the special effects of exploitation of protogynous species, I set up simple model populations for a gonochorist and for a protogynous hermaphrodite using the following assumptions:

1. The species spawn for the first time at age 3 and do not live beyond age 10.
2. Survivorship is 80% i.e. $Z=.22$.
3. Fecundity increases linearly according to the formula $Y=1000 + 200x$ where Y is number of recruits produced and x is age in years.
4. The species spawn once each year from age 3 to age 10.
5. Females of the protogynous species transform from age 3 to age 7 at the rate of 50% per year, i.e. $N_f=1024e^{-.69t}$
Reproductive values were calculated using the relationship

$$Vx = \sum_{y=x}^{\infty} \frac{Ly}{Lx} . My$$

Figure 3.

Effects of fishing on four species of West Indian groupers. Descending curves are percent females in the population (data for *Epinephelus morio* from Moe 1969, for *Epinephelus guttatus* and *Epinephelus fulvus* from Thompson and Munro 1974, for *Epinephelus cruentatus* from Nagelkerken 1979). Ascending curve is the percent of the population that is vulnerable. This curve is largely conjectural based on data in Thompson and Munro 1974. Virtually all adults of *Epinephelus morio* and *guttatus* would be catchable but the smaller, and reproductively more valuable females, of the smaller species *fulvus* and *cruentatus* would have a greater chance of escaping.



Where x = reproductive value of a female at age 4
Ly/Lx = probability of surviving from age x to age y
My = fecundity at age y

The relative values were then compared by dividing each Vx by Vo and plotting the results (Figure 4). It is apparent that for protogynous hermaphrodites the younger females have the highest reproductive value, and that the older females, largely because of their limited life span as females, are less important. In a gonochoristic species reproductive value of the females are sustained over a longer period of time at lower relative levels.

For species such as the graysby and coney (E. cruentatus and E. fulvus), of which the larger sizes are harvested most effectively, this is the desirable state of affairs. The smaller females are the most valuable and the least fished (Figure 3).

Obviously this model is very preliminary and before much weight can be placed on it, it would need to be augmented by age-specific mortality rates, more realistic relative fecundity data (perhaps in terms of recruits produced rather than ovarian egg counts in order to eliminate the possibility that first time spawners are more or less successful at competing for mates, or some other factor), and accurate inversion rates. Also, this model does not consider reproductive values of males. Huntsman (Personal communication Gene R. Huntsman, NMFS, Beaufort, N.C.) has constructed models exploring the concept that sex inversion rates may vary and act as a compensatory mechanism for maintaining a desirable sex ratio.

SEX RATIOS

A second effect of harvesting the larger fishes is selection against males and thus the altering of sex ratios. Thompson and Munro (1974, p. 53) noted that in exploited populations around Jamaica the sex ratio for E. guttatus was 1 male to 5.6 females but on the unploited Ocean Bank it was 1 male to 2.81 females. What effect does this have on the population?

Groupers are r-strategists, laying enormous numbers of eggs and exhibiting no parental care. Therefore, the recruitment rate of the offspring is unlikely to be directly affected by the ratio of sexes in the adult population as it might be in a species that has parental care of the eggs or young.

The question facing the fish manager is whether there is ever a shortage of mates for either sex. Unfortunately, the actual spawning of groupers has never been witnessed, but at least two species. E. striatus and E. guttatus, spawn in large aggregations (Smith 1972; Olsen and La Place 1979). Studies by Guitart Manday and Fernandez (1966) have suggested that the spawning occurs at night, although the fish apparently remain in the spawning aggregations for several days.

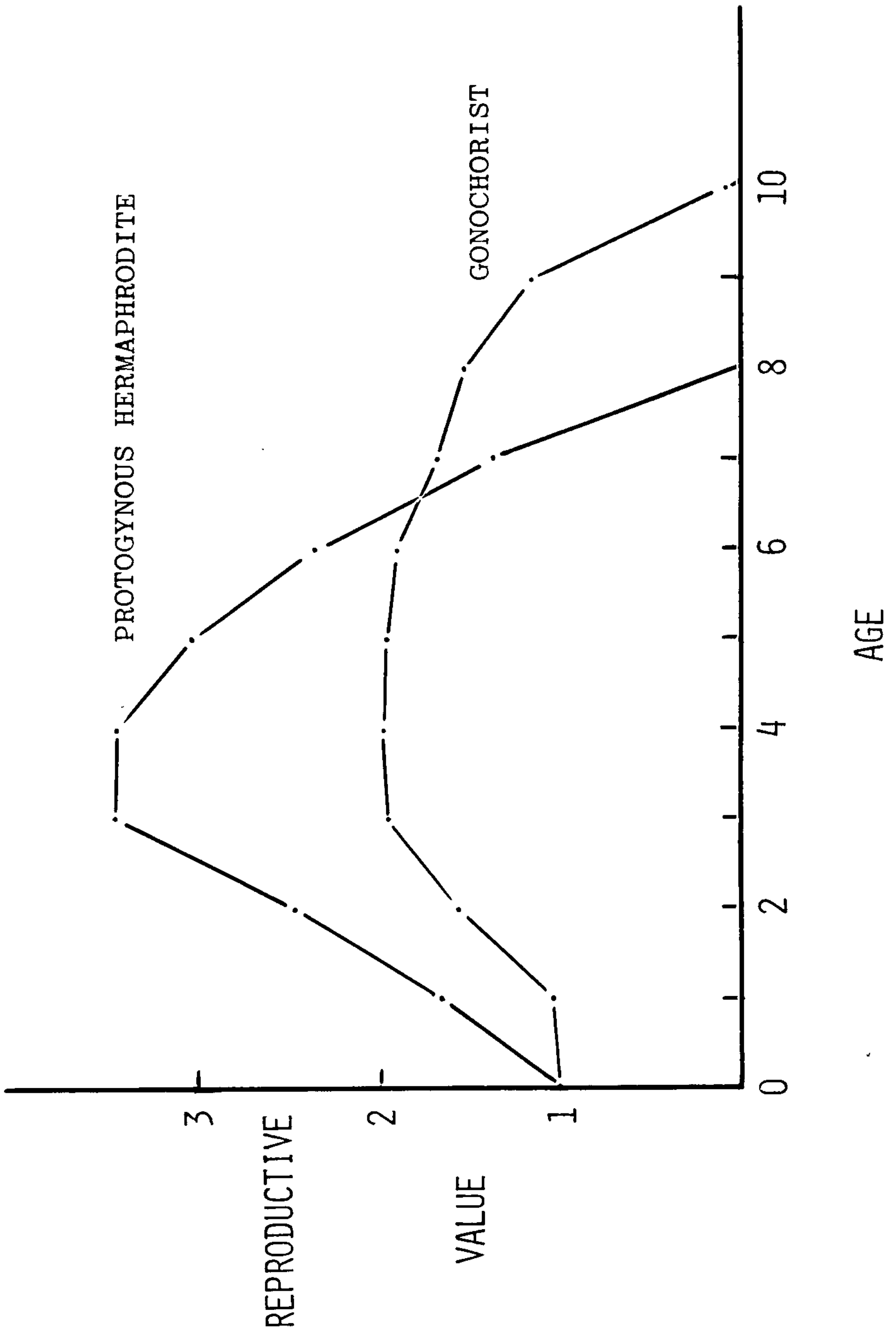


Figure 4.
Comparative reproductive values of females of species that are protogynous and gonochoristic. Protogynous females have high reproductive values when they are younger and decrease rapidly because their reproductive life ends when they transform into males.

In a series of photographs taken of a spawning aggregation off Bimini about 30 percent of the visible individuals appear in a special reversed color phase and Smith has postulated that these were functional males. If correct (and it is by no means demonstrated), then in this aggregation the spawning population consisted of 30 percent males and 70 percent females. Would it be desirable to limit the catch so as to maintain this, or some other natural spawning ratio, in the population?

Until we find out the mating patterns we will be unable to evaluate the effects of progressively unbalancing the sex ratio. Nevertheless, because the fishery is, or can be made, selective for one sex or the other, it is worthwhile considering the effects of a shortage of mates on one or the other sex. If males are in short supply, some eggs will go unfertilized. Since females appear to spawn in episodes, releasing part of their eggs in each of many matings, the likely effect is that part of the eggs of many females will go unfertilized rather than that some females will be unable to find mates. The effect would probably be the same unless the retention of eggs affects the females survival, sex inversion, or mating success in subsequent years.

If females are in short supply, so that some males are either unable to find mates or to expend all of their sperm, the population could still be affected if, for example, the unmated males were to inhibit the spawning of some females because of overly aggressive behavior. Even without assuming this, there is still the fact that surplus males are nonreproductive individuals competing with the reproducers. The most efficient population then will be one in which there are just enough males to fertilize all of the eggs that are produced. Deviation in either direction will be detrimental to any species whose population level is near carrying capacity or, in the case of harvestable species, at or near maximum sustainable yield.

There are some consequences of harvesting coral reef fishes that differ from the effects of harvesting fishes of less diverse communities. When a community consists, as many freshwater communities do, of only a few species with drastically different niches, the removal of one individual favors the growth of other individuals of the same species. There is, however, a growing body of evidence that within the community of coral reef fishes there are guilds consisting of several species that are ecologically equivalent and interchangeable. Furthermore, it has been suggested that the size of the individual fish determines its precise role in the community and this, of course, is always changing. Thus the most important or most threatening competitor is a fish of the same guild and of similar size. Combined, this means that if an individual is removed, it is most likely to be replaced by another of the same size which may or may not be of the same species. If this is true, then removal of large individuals does not necessarily confer any advantage on younger (smaller) individuals of the same species.

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REPRODUCTIVE BIOLOGY OF THE BLUELINE TILEFISH, CAULOLATILUS MICROPS (GOODE AND BEAN, 1878) OFF NORTH CAROLINA AND SOUTH CAROLINA

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Research on reproductive biology of blueline tilefish, Caulolatilus microps, reported herein is based on fish captured by hook and line fishing in depths of 70 to 235 meters off North Carolina and South Carolina from 1972 to 1977.

Monthly mean gonadsomatic index (GI) values for 138 female and 101 male blueline tilefish captured off North Carolina exhibited peaks in May and September. Initiation of gonadogenesis in March and April coincided with increasing photoperiod. In May and June, well developed and ripe ovaries were prevalent and comprised 2-4% total body weight. In July - August, developing, well developed, ripe, and spent redeveloping ovaries were all observed. In September, late developing and ripe ovaries predominated. Termination of gonadogenesis and gonad regression coincided with rapidly decreasing photoperiod in October. November through February was a period of gonad inactivity.

Size distribution of oocytes was multimodal in developing and ripe ovaries. Maturation of residual stock (previtellogenic) oocytes to the vitellogenic state was continuous and several size modes were present, but there was no sharp distinction between residual and maturing eggs in developing ovaries from March through September. Histologically, ovigerous lamellae in developing ovaries were mixtures of previtellogenic and active vitellogenic oocyte stages.

Limited data suggested that off South Carolina, blueline tilefish spawning may occur in April and again in July. Several larger females were also ripe off North Carolina in July, suggesting three spawning peaks or perhaps a more continuous spawning in that area with increased fish size.

Fecundity ranged from 210,000 ova (fish length = 412 mm TL) to 3,220,000 ova (fish length 637 mm TL) for 18 well developed and ripe females captured from April to June. Fecundity was significantly correlated with both TL and weight (g) and was best expressed by the relationship ℓn Fecundity = 0.016 + 1.832 ℓn W (r^2 = 0.78). Fecundity estimates for well developed and ripe fish captured in July were also consistent with this relationship but fecundity estimates in September fell to only 1/2 to 1/3 of the summer estimates for similarly sized individuals.

Sexual maturity (50%) in female C. microps was attained at 425-450 mm TL (age 4-5 years) and all females were mature by age 6 (> 500 mm TL). Gonadsomatic index (GI) per size class was consistently greater for females captured off South Carolina.

Males accommodate the protracted period of oogensis by maintaining essentially constant spermatogenesis during the spawning period. Two peaks (May and September) in male GI occurred but testes sampled in all months and examined histologically were found to contain spermatozoa. Large numbers of spermatozoa were present in the testicular collecting tubules from April through September. Small male C. microps (< 500 mm TL) showed little testicular development. Consistent increases in GI per size class occurred in males > 500 mm TL off North Carolina, and > 600 mm TL off South Carolina. Histological examination of testes from males 390 to 500 mm TL revealed that all contained active spermatogenic tubules and collections of spermatozoa; these fish had previously been considered immature based on the macroscopic characters of size and coloration of the testes.

Spermatogenesis in C. microps testes follows a tubular developmental pattern. Active spermatogenic tubules pervade the solid testes, are ringlike in cross-section, and generally contain crypts at all stages of development. The morphogenesis of spermatid to spermatozoa coincides with passage from the crypt to the lumen of the spermatogenic tubule. Spermatogenic tubules course medially, merge, and channel the spermatozoa into collecting tubules.

Sex ratio by size class data indicated 1) a dominance of females < 500 mm TL, 2) essentially a 1:1 ratio from 500-600 mm TL, and 3) increasing dominance of males > 600 mm TL. The abundance of small females and larger males was attributed to differential growth rates (males grow faster, females mature earlier).

Juvenile protogynous sex reversal was observed in two specimens (178 and 186 mm TL; age I). Histological examination showed in proliferating testicular mesothelium which initiated medially, progressed and extended laterally. Peripheral portions of gonads contained transitional tissue and residual oocytes, while medial portions were composed of spermatogenic tubules.

Histological examination revealed previtellogenic oocytes in the medial connective tissue of collecting tubules from eight out of 41 testes (430-700 mm TL fish) which were otherwise morphologically normal and developing actively. No transitional ovo-testes were observed, except in juvenile specimens, but we had few winter collections. The occurrence of residual oocytes in developing testes could result from recent development of residual primary female (ovarian) gonocytes from a juvenile ovarian stage.

ASPECTS OF THE SPAWNING OF WESTERN ATLANTIC REEF FISHES

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INTRODUCTION

The spawning of reef fishes has become increasingly well known during the last decade. It is an involved process and success depends on many environmental and social factors. Johannes (1978) described various spawning strategies of a wide variety of reef fishes and commented on the advantages of each. Most of his information and examples were drawn from the tropical Indo-west Pacific, particularly the Palau Islands of Micronesia, with his information on spawning in western Atlantic reef fishes having been drawn from the published literature. There is no body of local knowledge on spawning habits of reef fishes similar to that documented for Palau by Johannes (1978) for any Atlantic locale. While there is much general agreement between the concepts put forward by Johannes (1978) and what is now known regarding spawning in tropical western Atlantic fishes, some differences exist. There is an immediate need to develop fishery management plans for areas of the Caribbean and the southeastern coast of the United States and such plans should be based on available information on habits of the fishes concerned.

An intensive 20-month study of fishes producing planktonic eggs was made from November 1977 to July 1979 at an insular shelf edge station located 16 km east of La Parguera, Puerto Rico. During this period approximately 170 days were spent in the field. The station was approximately 5 km from shore at 15 to 18 m depth in an area of well-developed coral which bordered the drop-off into oceanic depths. In situ observations were made on the spawning habits of a wide variety of reef fishes in relation to various environmental parameters. Approximately 30 species were observed to spawn at some time at the study site. About one-half of these spawned on a regular basis. Observations also were made elsewhere in Puerto Rico (numerous species), Virgin Islands (scarids, mullids and others), the Cayman Islands (groupers), Jamaica (several species) and the Bahamas (several species). Some of these results have been published (Colin 1978; Colin and Clavijo 1978), but most are still unpublished. A series of publications is in preparation and the present contribution is intended as an overview of some aspects of this and other work of interest in fishery management.

Nearly all important bony food fishes of western Atlantic reefs produce planktonic eggs. The one exception is the Balistidae, the triggerfishes and filefishes. Others, such as the Siganidae, occur among Indo-west Pacific reef fishes. Planktonic eggs are fertilized externally, often with females and males swimming rapidly upward from near the substrate, turning sharply and releasing the gametes at the peak, then returning as quickly to the substrate. This movement and subsequent release of eggs and sperm have been termed the "spawning rush" and "gamete launching" respectively. Eggs, after release, are left to the fate of predators and currents.

DIFFERENCES BETWEEN WESTERN ATLANTIC AND PACIFIC LOCALES

Western Atlantic reefs characteristically have a lower tidal amplitude than those of the tropical Pacific. In most West Indian locations it is about 0.5 m but it may be 1.5 to 3.0 m on many Pacific reefs. Therefore, the currents produced by tidal highs and lows are much stronger, in general, in the Pacific than in the western Atlantic tropics, and inshore-offshore water movement is less along tropical western Atlantic coastlines. The effect of tidal variation on currents in the passes of atolls or on shorelines with barrier reefs is substantial, but such effects, even on a diminished scale, are found only along tropical western Atlantic shorelines with large shallow bays or estuaries, such as Biscayne Bay in Florida. Overall, the tidal messages available to control or influence spawning are much fainter in the western Atlantic than in the tropical Pacific. It seems logical that fishes in the western Atlantic, therefore, might be less attuned to them. If so, they probably have less importance on life history there than they do in the Indo-West Pacific. Lunar effects, such as intensity and timing of moonlight, are essentially the same in both Atlantic and Pacific and may serve as spawning cues in both areas.

Differences in current speed and direction determined with a recording current meter every 15 min seemed to have little effect on spawning behavior. Various species such as the hogfish, *Lachnolaimus maximus*, and the ocean surgeonfish, *Acanthurus bahianus*, spawned daily over periods of a month or more without regard to current direction or speed. Their spawning occurred at a certain time of day, potentially mediated by light level, irrespective of current conditions. The current speed and direction at the study site seemed controlled largely by the general westward set of the offshore current as was modified by local wind and sea conditions. On occasion the reversal of the normal alongshore current gave ample opportunity to observe that reversal did not have significant effects on the occurrence of daily spawning.

TIME AND LOCATION OF SPAWNING

As a general rule most species have been observed to spawn in the late afternoon. The actual period during which a particular species spawns can be fairly long, as much as an hour or more for the Atlantic surgeonfishes, *Acanthurus coeruleus*, and *A. bahianus*, or so short, as in some of the angelfishes, such as *Holacanthus tricolor*, that the time of spawning can be predicted within only a few minutes. In general the closer to sunset a species spawns, the narrower is the "window" of observed spawning times.

There are some striking exceptions to generalizations regarding time and location of spawning. Some western Atlantic parrotfishes, such as Scarus taeniopterus, Scarus vetula, and Sparisoma viride, spawn in the late morning, well before mid-day. Their eggs are released in normal fashion and their behavior does not appear to differ substantially from those species spawning during afternoon periods. One of this group, S. viride, spawns in the late afternoon, also.

The idea holds up well that the spawning rush of reef fishes is a method of releasing eggs and sperm largely above the range of most organisms feeding on particulate zooplankton, although the height above the bottom to which different fishes reach and the speed of the spawning rush varies considerably. Some, which release their eggs only 1 to 3 m above the substrate, have a very slow upward rush, taking as much as 5-10 sec for the upward movement. Examples are the sand tilefish, Malacanthus plumieri, and the spotted goatfish, Pseudupeneus maculatus, when it is mass spawning. Some small species, such as the harlequin bass, Serranus tigrinus, have a very quick upward rush of only about 1 m. Most larger fishes have lengthy, quick rushes as exemplified by Scarus iserti (formerly croicensis) (Colin 1978) in which the entire upward movement of 2 to 3 m and return can take less than 1 sec. In some aggregating species, such as A. coeruleus, the aggregation gradually ascends above the bottom, then subgroups rush upward rapidly from it. At the study site, the aggregation of A. coeruleus would often be found at depths of 7 to 9 m over a bottom depth of 18 m. Subgroups would rush upward to depths of only 2 to 3 m. The speed of the rush is probably in response to danger to the adults from predators. Even species that have slow upward rushes are wary and an unexpected disturbance will cause a rapid retreat to the substrate.

The height of the rush is determined, perhaps, not so much by the danger from predators, but rather by the need to release the eggs away from benthic-based zooplanktivores. On the basis of data from the Puerto Rico site, it appears that there is a period of increased danger to planktonic eggs from particulate plankton-feeding fishes immediately after release. At that time eggs are concentrated and if predators locate the cloud they can feed very effectively on the eggs in it. Various egg predators clearly can anticipate or quickly exploit spawning of other reef fishes. This was the case by Chromis cyanea and Clepticus parrae on S. iserti eggs (Colin 1978). Other immediate egg predators included the black durgeon, Melichthys niger and the yellowtail snapper, Ocyurus chrysurus. Unless the immediate egg predators arrive at the location of the gamete cloud within a few seconds, it is ignored. Potentially, it may disperse rapidly and be difficult for the predators to locate. If predators locate the egg cloud, however, they will stay with it for up to a minute or more. Whether they remain until nearly all the eggs have been consumed is not known.

A general inference that seems to have much merit is that larger reef fishes migrate to the shelf edge in order to increase the chance of the eggs being swept offshore and out of reach of reef planktivores. But one striking example in which this was not the case occurred in the Puerto Rico studies. The hogfish, *L. maximus*, spawned about 100 to 150 m inside the shelf edge along a sand-reef interface. The spawning adults were large, certainly capable of swimming the distance to the shelf edge in seconds. Some actually sheltered along the shelf edge at night. The yellowtail snapper, however, was a predator on *L. maximus* eggs immediately after their release. The snappers in their attempt to be in the best position to get the eggs sometimes interrupted the spawning rush by aggressively moving between the spawning fish. Yellowtail snappers were much less abundant in the inshore area where hogfish spawned than at the shelf break, where there were always hundreds or thousands feeding on particulate zooplankton. While yellowtail snappers did not seem to notice other species spawning on the shelf edge, they probably would have had an extremely disturbing effect on hogfish.

Spawning aggregations occur among a variety of reef fishes. Some species, such as various groupers, are believed to engage in mass spawning only once or a few times per year, while others aggregate daily over prolonged periods. Species that aggregate daily are common reef species with relatively high densities. In order that sufficient numbers be assembled, they need only migrate a few hundred meters at most. Those which aggregate for periods of a few days once or more a year, such as Nassau groupers, would need to travel an average of several km or more to achieve the numbers of individuals observed in aggregations. Aggregations of large, widely dispersed species would be impossible on a daily basis.

Spawning aggregations of reef fishes have been known to fisherman for some time. Johannes (1978) reports that native fisherman in Palau have exploited such aggregations for many years. In the West Indies aggregations of Nassau grouper have been known in some areas for many decades, and numerous reports now exist in the literature (Bardach 1958; Thompson and Munro 1974; Burnett-Herkes 1975; Olsen and LaPlace 1978). Smith (1972) was the first person to report in situ observations of such aggregations. They are known presently from several areas of the Bahamas and West Indies and it is almost certain that any island or bank with any significant populations of *Epinephelus striatus* has one or more aggregations. They aggregate shortly before the full moon in January, and potentially in February. As many as tens of thousands of individuals of several kg each are found in each aggregation. Other groupers can, but not always do, occur with or near the *E. striatus* aggregations. These aggregations are now under particularly intense fishing pressure and those that are known and accessible are in danger of being eliminated. Some, such as one which previously occurred on the eastern side of Mona Island, Puerto Rico, have disappeared, and significant percentages of fish in these aggregations are often caught in a given year. Unfortunately good fishery data over a period of years is not available for any aggregation, so it is not possible to determine if catches and sizes of individuals have been decreasing. Bermuda has closed to commercial fishing identified spawning areas during periods in which Nassau grouper and red hind are believed to be spawning, but this is the only effort I am aware of to prevent overexploitation. The importance of aggregations to reproductive success in E. striatus and other groupers is not known and needs serious consideration.

Smaller species of groupers, such as the red hind, Epinephelus guttatus, also aggregate but in a less spectacular fashion. The population off the southwestern coast of Puerto Rico seems to move to the shelf edge reefs but not laterally along the shelf edge. Rather than large groupings, there appears to be an area with concentrated red hind all along the shelf edge. Male red hind have territories, which they regularly patrol, in which several females normally occur. The males stop at each female and if she is ready to spawn the pair swim up above the bottom about 1 m and release the gametes. In one instance a second female was seen to join a spawning pair, but it is not known whether actual spawning en masse occurs. Pair spawning by the coney, Epinephelus fulvus, was also observed in a single instance, so the existence of pair spawning in these smaller groupers indicates its potential in the larger species.

Smaller species of reef fishes are known to aggregate daily for spawning for a lengthy portion of the year. The Atlantic surgeonfishes, A. bahianus and A. coeruleus aggregate daily, but have different patterns. A. bahianus aggregates in mid-afternoon during most of the winter and spring. A. coeruleus aggregates during the week just after the full moon almost certainly every month of the year. Such differences between closely related species indicates it may be risky to generalize about species for which nothing is known.

Certain areas of reefs have been identified as areas of increased spawning activity. These have often been identified as seaward projections and promontories or areas of high current flow, such as the passes of lagoons. Their is no question that such areas have concentrated spawning activity, but large areas of insular shelf edges often lack significant features and essentially present a linear surface or face. The study area off southwestern Puerto Rico lacked any large reef promontories or vertical projections. Intensive spawning activity of many species, particularly acanthurids, labrids and scarids, occurred in the absence of any distinctive features. The only potentially distinctive feature of one small portion that served as an aggregation point for A. coeruleus was the presence of a particularly broad sand channel. While structures such as promontories and areas of high vertical relief may be used as spawning focal points, they are not necessarily essential.

The use of bottom features or areas as spawning loci for extended periods is becoming evident. Colin and Clavijo (1978) examined a seaward projecting reef at St. John, U.S. Virgin Islands, and found approximately the same number of spawning Sparisoma rubripinne that Randall and Randall (1963) had found 17 years earlier. A prominent deep-reef pinnacle on the shelf edge at Discovery Bay, Jamaica was the regular spawning site of a group of S. iserti over a 4-year period (Colin 1978). This feature had the only spawning aggregation of S. iserti found along several hundred meters of shelf edge. At a reef-sand interface inside the shelf edge off southwestern Puerto Rico, which was a consistent spawning area of hogfish, individual males did not alter the boundaries of their territories over a three year period.

Many of the smaller western Atlantic reef fishes spawned daily within their home ranges. They included some parrotfishes, wrasses, tilefish, angelfishes, and butterflyfishes, many spawning only once or at most a few times per day. For most species the exact location within the home range where spawning occurred was variable.

MODES OF SPAWNING

A number of reef fishes are known to have both pair and group modes of spawning. Dual modes have been known for many years among species with initial and terminal phase males, such as many labrids and scarids, and also among some species not known to have two male phases. The spotted goatfish, Pseudupeneus maculatus, has been reported to mass spawn (Colin and Clavijo 1978) but is now known to pair spawn in the absence of large concentrations of individuals. Two surgeonfishes, A. bahianus and A. coeruleus, are known to pair spawn later in the day after mass spawning has largely ceased.

The existence of dual spawning modes in some reef fishes without two male phases indicates that potentially the commercially important aggregating species, such as E. striatus, may also successfully reproduce by pair as well as group spawning. Where overfishing has eliminated aggregations, nature may have built sufficient resiliency into the spawning strategy of fishes so that locally depleted populations can continue to reproduce and maintain the population without relying totally on outside recruitment.

The duality of spawning increases the flexibility of the spawning social system by potentially expanding the times and places spawning can occur. It might be inferred that pair spawning is easier to arrange, but that mass spawning produces additional benefits such as swamping of egg predators. Obviously either mode has advantages and together they increase the likelihood of the species producing the proper combination for reproductive success. For example, the previously mentioned surgeonfishes have pair spawning occurring later in the afternoon than mass spawning. Although the two modes overlap somewhat in timing, pair spawning continues after the cessation of mass spawning and the dissolution of the spawning groups. The cessation of mass spawning usually occurs 30 to 40 min before sunset, as light levels become relatively low and groups could easily be preyed upon by large piscivores. In pair spawning it is difficult to predict when the rush will occur. Because pairs are more difficult to prey upon, pair spawning can continue after group spawning has become too risky. The portion of the day in which eggs are produced is expanded and the late spawned eggs may have less chance of being eaten by zooplanktivores. The expansion of the period of egg production may apply to the year as a whole, with pair spawning sustaining a modest production of eggs and larvae outside of the period when group spawning occurs.

APPROACHES TO STUDYING REEF FISH SPAWNING

The investigation of reef fish spawning is greatly facilitated by the use of diving techniques. The advantages are that the occurrence of spawning can often be observed, the behavior associated with it can be documented and photographed, and collections of specific spawning individuals or eggs can be made which would be impossible using surface-operated sampling gear. Unfortunately, spawning usually occurs from late afternoon to shortly after sunset under conditions that make photography and observations difficult. Beyond the simple mechanics of diving, observers must be good fish watchers, disturbing the often shy spawning fishes as little as possible and being alert to the signals of often rapid spawning behavior at near the limits of visibility.

Some unusual, but valuable diving techniques have been developed in this work. One such technique, called tethering, is useful in observing a near stationary spawning aggregation or specific areas of bottom for prolonged periods. A permanent line is attached to the bottom with a small subsurface float on it and a loop of line on the free end. The diver tethers himself to the line, at a depth above the bottom as determined by the length of the line, by attaching the loop of line to some part of his gear with a quick release attachment. The diver then floats by inflating the buoyancy compensating vest enough to produce slight positive buoyancy. The diver floats in a stationary position without swimming above the bottom as long as currents are not sufficient to push him downward on the tether. For tethering in moderate currents, the amount of positive buoyancy of the diver can be increased. From this vantage point large areas of reef can be observed, and less disturbance is produced by exhaust bubbles since the diver is at rest and breathing is slow. At the Puerto Rico shelf edge station we tethered at depths of 10 to 12 m for 2 to 3 hrs. Diving on the bottom at 18 m would have limited time to about 60 min.

Since a diver observing reef fish spawning reduces exercise to a minimum to avoid a high breathing rate, he may quickly become chilled even in tropical waters. Hence a full wet suit is advisable under most circumstances. Breath control when using open-circuit scuba is important, since exhalation at the wrong moment can easily disturb spawning fishes enough to interrupt their behavior. Closed-circuit scuba would probably be of value in such studies, but has many disadvantages. Usually double cylinder tank rigs are used so that under normal circumstances a diver does not have to worry about running out of air. A sufficient reserve is carried so that any unusual or interesting behavior can be observed for prolonged periods.

Underwater habitats can be used to observe reef fish spawning phenomena over a period of days. In Puerto Rico diving to depths of 18 m or more limited bottom time to about one hour per day when surface based. Use of the NOAA National Undersea Laboratory (NULS-1) habitat in St. Croix, U.S. Virgin Islands, was obtained during September 1978 for 7 days. This was not an ideal month to observe spawning behavior, but we were able to determine if valuable results could be obtained.

December to February would have been a better time. Nevertheless, seven species were observed spawning, most of these every day. The underwater habitat did allow the first continuous observations over an entire afternoon of the spawning sequence at a reasonably deep shelf edge. Our mission was the only one so far at the St. Croix site to be directed towards fish spawning. For this purpose the habitat is underutilized.

Two techniques have proven valuable in obtaining eggs of reef fishes. The first consists of divers collecting the eggs from the cloud of released gametes in mid-water using small, fine-mesh dip nets. Quite a few reef fishes, particularly those that mass spawn, produce a visible sperm cloud which can persist for a minute or more. After waiting a period of 30 sec or so after gamete release for fertilization to take place, the diver swims to the sperm cloud and passes the fine mesh net, (termed brine shrimp nets in the aquarium trade), repeatedly through the cloud. The net, which has a mesh opening of 100 to 150 mm, is then everted into a plastic bag along with a quantity of water sufficient to half fill the bag. Usually I attempt to fill the bag with water from the area of the sperm cloud to further insure fertilization. The bags are then sealed, usually by tying a knot in the neck, and taken to the surface. The sealed bags are returned to the lab in buckets partially filled with seawater to eliminate total water loss from the bag due to any small leaks that develop in transit.

A second useful technique involves artificial fertilization, and holds promise in life history and rearing studies. Gametes are collected from spawning fishes specifically speared for this purpose. It is a method of obtaining quantities of fertilized eggs from species not easily approached while spawning or which do not produce a visible sperm cloud which can be strained. It was first attempted with the red hind, which has only a very limited spawning season in Puerto Rico. One or more carefully selected female and male red hinds were speared at the spawning area by a diver. They were squeezed underwater at depth to insure that they had free-flowing gametes. The fish were then hand stripped inside plastic bags and the contents mixed at depth. This method resulted in abundant fertile eggs with a 100% fertilization rate. Later it was found not to be necessary to strip the adults at depth. Rather the ripe fish were brought to the surface where the gametes were stripped and mixed. Dead groupers could be held at room temperature for up to 4 hours before stripping, although eggs produced 4 hours after death were only about 50% fertile. Subsequently this spear and strip technique was found to be effective for parrotfishes and surgeonfishes. If it is known where and when a particular species spawns, the collection of the female with eggs ready for release can probably be accomplished. This is the most difficult part since the time period when the eggs are ready for release is short. Males are no problem since they are usually running ripe for considerably longer periods. Another interesting possibility is to cross-fertilize closely related species. This was done successfully with _A. bahianus_ and _A. coeruleus_.

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SESSION SUMMARY

Reproduction in Reef Fishes

by

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The three talks, by Smith, Ross, and Colin, well illustrated the most important approaches to studying reproduction of reef fishes. The first approach, illustrated to a great extent by Smith's work, deals with reproduction patterns as evolutionary strategies and discusses how different reproductive schemes (viewed as both physiological and behavioural processes) provide solutions to various problems of maintenance of fish populations posed by the reef environment. This paper further examined the impact of an exogenous force, fishing, on the success of some reproductive schemes. The second approach, best illustrated by Colin's talk, is the detailed in situ observation and subsequent description, of reef fish reproductive behavior. Important in this approach are attempts to correlate the observed behavior with environmental factors. The results of such correlations provide the basis for the development of hypotheses about the function of the observed behavior. The third approach, described by Ross, is the detailed histological examination of gonads to provide estimates of age of maturity, time and frequency of spawning, fecundity, and in hermaphroditic species, the age and rate of change of sex. Attempts to correlate the observed phenomena with environmental factors are a critical facet of the research. The results of investigations of this third type provide the basis for hypothesis formation and are necessary to accomplishment of the first, theoretical, approach to studying reproduction in fishes.

The question posed to the Southeast Fisheries Center is what kind of research on reproduction should it be doing? Should all three approaches be followed with equal emphasis or should some assymetrical mixture be sought.

That the workshop discussions did not result in a clearcut answer to the question suggests that fairly strong arguments can be made for each of the research directions and that the best program will contain research of all three approaches. However, logic suggests that observational research on behavior and on gonadal processes must precede the more esoteric and theoretical research programs. In a nascent program, as is that of the SEFC, observational research should probably be of first priority after determining concretely how reproductive patterns can significantly affect advice required for management of fisheries for reef fish.

Several specific problems relating to reproduction were described during the discussions that deserve special mention here. Most important is our lack of understanding of grouper spawning in general and of grouper spawning aggregations in particular. We have little solid knowledge about the location, frequency, and regularity of these groupings, about their occurrence in many species, about the proportion of a stock participating in these, about their relationship to pair spawning in groupers, nor about the impact on the stock as a whole of fishing these aggregations. The research required to answer these questions ranges from simple to very complex and deserves far more attention than it has been getting. It was suggested that the most promising approach for initial investigation of the aggregation problems would be to study Nassau grouper stocks on the Puerto Rican shelf.

Another valuable discussion concerned the apparent timing of spawning in some species to coincide with certain lunar (and thus tidal) phases, presumably so that return of progeny to the parents' reef is enhanced. Similarly, some observers have hypothesized that many species spawn on the upcurrent end of islands so that progeny have the maximum probability of remaining near the parents' reef. Workshop participants pointed out important exceptions to the lunar and geographic hypotheses suggesting, as is usual in nature, that many schemes are in place and that some species are inconsistent in where, when and how they spawn.

A useful conclusion to this discussion would be to rank the importance of reproduction research against other types of reef fish research. Unfortunately that seems nearly impossible. Proper management of reef fisheries requires full understanding of the fishes and their relationship to their environment; that is management requires completing the whole puzzle. Here, as with most puzzles, all the pieces are important.

SESSION 3

Recruitment of Reef Fishes and Stock Delineation

Chariman

William J. Richards

RECRUITMENT PATTERNS IN TROPICAL REEF FISHES

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INTRODUCTION

Underpinning any fisheries program that would lead to efficient harvests of reef fish stocks must be specific knowledge of the natural processes that maintain those stocks--reproduction, dispersal and recruitment. In general, reef fishes tend to be sedentary and are dependent on substrate for protection and food. High species diversity has long been associated with tropical communities (MacArthur 1972; Connell 1978) and coral reef fishes are a leading example (Ehrlich 1975; Sale 1978). Under these circumstances it is not surprising to find that species are tightly packed on reefs and that competition for space is keen (Smith 1973, 1975, 1978; Smith and Tyler 1972, 1973; Sale 1978; see also Ogden this proceedings). Beyond such general statements about reef fishes, however, there are few hard data that can assist the fisheries biologist in recommending realistic fishing quotas, gear dimensions, and when and where open and closed fishing locations and seasons should be established. For example, we must guess about real standing crops of reef fishes (see papers on reef fish stock assessment in these proceedings) and about times and rates of reproduction and of recruitment in reef fishes. As fish biologists we might well ask therefore whether reproduction and recruitment are represented by a variety of distinct species patterns (as might be expected in a highly diverse and competitive community) or fit some overriding, common scheme that is required of most reef fishes.

Tropical fishes are subjected to less severe seasonal changes than temperate or boreal fishes. Seasonal changes are more often reflected by major shifts in current systems (see Johannes 1978 for more details) than by large oscillations in temperature and light. The higher degree of environmental constancy for tropical communities leads to a first assumption--the suggestion that processes crucial to survival, like reproduction, recruitment, and even growth, may occur over long periods of the year and, perhaps, are less tightly coupled to environmental fluctuations. Is this suggestion actually supported in fact?

In general the answer is ambivalent--both yes and no! For instance, it has been demonstrated for Caribbean fishes that reproduction, although seasonal, nevertheless occupies a long period of each year (Munro et al. 1973). But in spite of the relative constancy of their physical environment, tropical reef fishes over shorter time spans show periodic reproduction (Sale 1978; Johannes 1978).

Answers to the questions--how do reef fishes disperse their young?, how and when do reef fishes breed?, and in what manner do they recruit into the reef community?--also emphasize what studies are required to establish how reef fishes maintain their populations.

DISPERSION

Although reef fishes display reproductive behaviors from spawning in aggregations to spawning in pairs, from strict gonochorism to various forms of hermaphroditism (see Smith these proceedings), and from oviparity to viviparity, most species produce larvae that are dispersed into the plankton (Breder and Rosen 1966; Smith 1978; Sale 1978; Johannes 1978). To be sure, many families of reef fishes typically have demersal eggs (e.g. Pomacentridae, Gobiidae, Clinidae), and others are live bearers (e.g. Brotulidae, some Clinidae). But most larger tropical marine fishes produce planktonic eggs and larvae. Recruitment of each species therefore is the immediate result of events that occur offshore.

That a pelagic larval phase is central in the life history of reef fishes has not gone unnoted. Several hypotheses are championed to account for this general tactic. The most direct idea is that a pelagic larval stage assures dispersion and colonization of reef habitats, which are notoriously patchy in distribution. Also, because reef fishes are so sedentary and dependent on the reef for protection, direct colonization of reefs by adults, and especially over oceanic distances, presents each species with a very hostile, if not impossible, challenge. Thus, a larval phase becomes crucial to dispersion. Falling somewhat from recent favor, this "Dispersion Hypothesis," nevertheless, retains support (Barlow 1981).

An alternate view that finds wider support contends that reef habitats, because of the overwhelming presence of predators, are very dangerous to the eggs and larvae of reef fishes. The production of pelagic larvae, therefore, places the young temporarily out of the reach of these predators and in a relatively more benign environment (Sale 1971, 1978; Smith 1978; Johannes 1978). Although the larval phase allows for dispersion, it is not considered the primary selective force that has favored a pelagic larvae in reef fishes.

Arguments that favor either hypothesis are based mostly on anecdote and more data must by accumulated before either view can be accredited. Nevertheless, most reef fish biologists, including myself, lean more toward the latter "Diminished Predation Hypothesis" as providing a more plausible explanation for the pelagic life history phase common in reef fishes, than a "Dispersion Hypothesis." Nonetheless, the two arguments are not mutually exclusive, and dispersion for recolonization over short distance is likely as important to a species survival as is a reduction in predation pressure on its larvae.

If most fishes pass their larval lives at sea we can ask--How long do they remain at sea?, Do they colonize distant reefs? and, How do species recolonize their parental reefs? This subject is covered elsewhere in these proceedings (see Richards). It is important to emphasize that the nature of the larval life of each species will dramatically affect their recruitment. Some species have a long planktonic existence and some can even extend it (e.g. surgeonfish, Randall 1961; some pomacentrids and balistids, see Brothers this proceeding), whereas others have only a short one (e.g. haemulids, Brothers and McFarland in press; also probably lutjanids, Munro et al. 1973, and Richards 1980). Thus some species may be able to sustain life at sea until favorable conditions for settlement prevail (Sale 1970), while others must perish if favorable conditions are not soon encountered.

One can conclude that recruitment to inshore reefs is dependent on several factors--the individual species capacity to prolong larval life, the effect of currents on the dispersion and settlement of recruits onto suitable reef habitats, the constancy or periodicity in the production of eggs and larvae through reproductive drive, and the nature of the settlement site. The ability to spawn over extended periods of the year, and the ability of larvae to extend their pelagic existence should, at least in theory, lead to a greater mixing and thus greater dispersion of the young at sea. Such a strategy presumably would lead to a more constant 'rain' of recruits into reef areas. If all reef species could manage this, which they cannot, then colonization would reflect the chance openings of settlement sites on a reef. Because each species would be equally dispersed, presumably each species in proportion to its larval population density would have a more or less equal chance of settling, assuming that 'interspecific competition' is not important. Put another way, recruitment would be more or less independent of the reproductive habits of each species, and settlement more a matter of chance occurrence, a view strongly argued by Sale (1974, 1975, 1978; see also Connell 1978).

In contrast, recruitment can be viewed as ordered, the availability of specific recruits (species) being more tightly coupled to spawning activity, to the length of larval life, and to the direct effects of currents and tides on larval dispersion to favorable sites over time. That reef species become site-specific at some time in the recruitment process is axiomatic, for juvenile and adult reef fishes characteristically occupy species-specific microhabitats. The studies of Sale (1968, 1969) on the Hawaiian surgeon fish, Acanthurus triostegus, for example, clearly define a set of proximate factors that this species seeks out in settling from the plankton. The 'choice' in itself suggests an ordered set of events, but the timing of site selection may or may not occur at settlement, and at least in some species may change at various stages of the life history (McFarland 1980). This more deterministic view has been favored by Smith (1978) and Gladfelter and Gladfelter (1978), for reasons that are based largely on the community structure and diversity of adult reef fishes (but see Odgen these proceedings). Unfortunately there is very little data on recruitment processes in reef fishes (other than Sale's data) that can be applied toward this opposing view (but see section on recruitment in this paper). In recent years the observed timing of spawning in reef fishes has led to the conclusion that reproduction is often tightly coupled to astronomical events, and is not random. Why should this be so?

REPRODUCTION

The evidence available implies that two major reproductive processes occur in tropical reef fishes. First, most reef fishes spawn over long periods of each year but also show distinct spring and fall peaks (Munro et al. 1973). Thus, spawning follows a broad, often bimodal curve in seasonal activity. Of the 35 Caribbean species reported on by Munro et al. (1973) most showed a spring peak in reproduction and many a weak fall peak; more than half were reproductively active for 6 months or longer (based on the percentage of ripe fish in traps). Second, a strong tendency to both lunar related reproductive peaks and exact diel timing of spawning are common in reef fishes. Of 50 species of tropical fishes (encompassing 24 families), 23 tended to spawn near or at new moon, 35 at full moon and, 14 at the times of both new and full moon (see Table 4, Johannes 1978). A few species, such as the threadfin (Polydactylus sexfilis) and the angelfish (Centropyge potteri), spawn on or near the last or first quarter moon (Johannes 1978; May et al. 1979; Lobel 1978; see Colin these proceedings). In addition, many of these species dash toward the surface to spawn, breed at specific times of the day (usually near dusk or at night), and utilize upward projections of the reef as nearby cover when breeding or migrate in groups to breed away from the reef (for examples, see Hobson and Chess 1978; Johannes 1978; Lobel 1978; and Colin these proceedings).

Johannes (1978) and Lobel (1978) suggest that this reproductive complexity is a strategy to assure that eggs are released into ebbing currents that carry them offshore and away from reef predators. Just as significantly, they suggest that local current gyres are known in some instances to set back onto parental reef areas (Sale 1970; Johannes 1978; Lobel 1978). Larvae entrained in such recirculating current systems thus could recolonize their general sites of origin (e.g. islands). Dispersion into the plankton is considered as a specific tactic to diminish predation, and its timing as a strategy for recolonization. There is little actual data to establish these concepts as a general theory as marginally documented in Hawaii (Lobel and Reaka[1]; Lobel 1978), but mostly only anecdote (see Johannes 1978).

Current systems in the Caribbean sea, however, are capable of long distance transport, as would be expected, and local dispersion, e.g. recirculation gyres occur depending on location and time of year (Molinari et al. 1980; and see Richards these proceedings).

The recent demonstrations that spawning is actually periodic suggest that most tropical reef fishes release their eggs in pulses through a long reproductive season. Dependent on species, the pulses

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[1] Unpublished manuscript. Synchronization of reproduction with seasonal currents as a mechanism for endemism in Hawaiian marine fauna by P. S. Lobel and M. L. Reaka, Box 4157, Kailua, Kona, HI 96740.

occur at intervals of two weeks or one month. A major question arises--Does recruitment of young fish from the plankton to the reef pulse like the spawning act itself? Or is recruitment spread out over time, because of mixing and prolongation of larval life?

RECRUITMENT

In his summary on the inshore movements of young fishes Johannes (1978, Table 5, p. 75) lists only eight references and several observations by the fisherman at Palau and states, "little research has been done on the timing of inshore movements of oceanic larvae and juveniles of coastal fishes in the tropics." As limited as these data are they do indicate pulsing in recruitment, for the inshore movements of young fish often correlate with lunar cycles and tides. Of the 13 tropical species listed, 10 moved inshore on spring tides.

From a series of continuing studies concerning the life history of grunts (family Haemulidae) in the West Indies (Ogden and Ehrlich 1977; Ogden and Zieman 1977; McFarland et al. 1979; McFarland 1980; Brothers and McFarland in press; McFarland and Hillis in press) considerable data on recruitment are accumulating. One study addresses itself to the timing of reproduction and of recruitment in French grunts, Haemulon flavolineatum (Ogden, McFarland, Brothers and Shulman unpublished ms.[2] The major findings are summarized below.

1. Larval French grunts recruit from the offshore plankton onto inshore reef structures from March through October. Recruitment was still in progress as of November, 1980. There are seasonal peaks in late spring and early summer.
2. Specific recruitment pulses have a mean period of 14.6 ± 0.6 days (95% CI).
3. The recruitment pulses peak at the first and last quarter moons.
4. Larval life is short, 15 days or less (Brothers and McFarland in press) and presumably spawning activity peaks just before or at each new and full moon (based on otolith aging of individual recruits). Thus, spawning which has never been observed in haemulids, like recruitment seems to follow a bilunar cycle (Munro et al. 1973).
5. Grunt larvae repeatedly occupy the same sites, but seem to be influenced by the presence of other fish, i.e., they display some sort of site-preferences.

We conclude from this study that reproduction, the length of larval life, and the recruitment of young grunts onto reef structure are tightly coupled to lunar events and, presumably, to some tidal scheme. In general, spawning on spring tides, which occurs in several reef species (see Colin these proceedings), could improve the chance that fertilized eggs are transported offshore (Lobel 1978). We have observed adult French grunt schools during periods of full moon, at dusk, and at several different locations near St. Croix, but unfortunately we

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[2] Ogden, John--West Indies Lab, P.O. Box 4010, Christiansted, St. Croix, U.S.V.I. 00820.

have not witnessed the spawning act. We cannot verify as fact, therefore, our prediction that grunts breed on a lunar basis. The actual timing of reproduction in grunts temporarily remains in doubt.

There is no doubt, however, that larval recruitment in grunts is periodic and highly ordered (we actually have predicted the timing of future recruitment pulses and verified by direct observation the 'rain' of young grunts onto reef sites).

It has been suggested by Sale (1978, p. 97) that recruitment represents a lottery or a gamble of sorts for the limited living space on the reef. The offshore 'larval pool' of potential recruits represents a reservoir of reef species from which individual species only "...manage very occasionally to colonize vacant patches of habitat." Although this may well be true of some reef species, as we have observed in French grunts there seems to be very little gambling for limited space. Young French grunts colonize the same reef sites throughout the breeding season. The sites are repeatedly opened to new recruits through growth and migration of the older recruits from the settlement sites. In this process there seems to be a lack of randomness in the occupation of space because the same species (presumbly the 'correct-species') arrives, settles and occupies the same sites over and over again. In addition, competition for a settlement site certainly exists in some reef fishes (Sale 1976), and in grunts the presence of older fish seems to inhibit the further use of an established settlement site (Ogden, McFarland, Brothers and Shulman unpublished ms.).

CONCLUSIONS

A singular tentative conclusion issues from our limited knowledge of reproductive and recruitment processes in reef fishes. The generation and ultimate recruitment of pelagic larvae back to the reef by virtually all reef fishes appears to be a highly ordered process and, thereby, provides a predictable sequence of events. Although random occurrences can momentarily perturb this sequence, over time and space it has been a successful strategy for perpetuating each reef species. Fisheries biologists can assume, as a first approximation, that the timing of reproduction and recruitment in a reef fish is highly predictable. The impact, for example, of excess fishing, or the establishment of seasonal quotas and size limits on recruitment should be amenable to analysis. But a word of caution; reef fishes are components of a highly diverse and interactive community. As Ogden has indicated in these proceedings, we have little idea of how the removal of one species will affect other components of the community. The resilience therefore of any single reef species to fishing may depend as much on what happens to other community cohorts as it does on size of the standing crop.

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PLANKTONIC PROCESSES AFFECTING ESTABLISHMENT AND MAINTENANCE OF REEF FISH STOCKS

by

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INTRODUCTION

One of the most intriguing unanswered questions we face is how does an island, situated in the midst of a strong oceanic current, sustain itself of populations of animals which have pelagic early life stages? One obvious answer is from upstream sources, but when the upstream sources do not exist or when the length of larval life does not coincide with current speeds the problem is complicated further. Since these questions impinge on arriving at suitable strategies for the management of reef resources, it is necessary to gain an understanding of the factors and mechanisms which control the recruitment of animals.

The purpose of this paper is to provide background material and to outline types of experiments needed to solve the problem. Two major components are involved - the biological factors of the species and the physical factors of the environment. These two aspects insure successful recruitment.

BIOLOGICAL FACTORS

In considering biological factors we need to know the species involved and their basic life histories - by basic I mean the mode of spawning these species utilize, their fecundity, and the amount of parental care. If offspring are pelagic and uncared for, what are their major characteristics - length of larval life stages, swimming ability of these stages, depth distribution by age, food levels necessary for survival, and predation factors? As one investigates specific cases, this list of questions can be easily expanded.

An interesting aspect of this problem is that one would expect fishes of shore waters to exhibit a great deal of parental care. The opposite is true for 66 families of bony fishes inhabiting coral reefs in the Caribbean (Randall 1968): 74% have pelagic eggs and 92% have pelagic larvae. These percentages are probably higher because there are several families where types of eggs and larvae are not known (Breder and Rosen 1966). I have found pelagic larvae of many reef families to be major components of the pelagic ichthyoplankton in the Caribbean and Gulf of Mexico (Houde et al. 1979; Richards [1]; Richards in press). Members of Scaridae and Labridae were major components of the pelagic realm. Scarid larvae were in the top ten in both occurrence and number in both winter and summer collections made in the Caribbean. Goby larvae were also very abundant, especially offshore in the Gulf of Mexico, although they may not be larvae of reef gobies since the larvae have yet to be identified to specific taxa. In my Caribbean studies I found larval representatives of 50 of the 66 reef fish families listed by Randall (1968).

Many of these larvae remain in the plankton for a considerable length of time. From rearing studies, Houde and Potthoff (1976) showed that a sparid, *Archosargus rhomboidalis*, was planktonic for at least 16 days; Saksena and Richards (1975) showed that a pomadasyid, *Haemulon plumieri*, was planktonic for about 20 days; and Richards and Saksena (1980) showed that a lutjanid, *Lutjanus griseus*, was planktonic for at least 26 days. The time durations found in laboratory rearing studies (and there are many more) have been confirmed by field observations by McFarland (1980). His observations combine direct observations of field behaviors coupled with otolith ageing methods, which provide information on daily growth. The daily growth increments on otoliths provide an accurate method for ageing tropical fishes throughout all their life stages and also denote major changes in ecobehavior (Brothers 1979). Lobel (1978) has hypothesized that reef fish spawning is associated with time of day and month to occur at peak ebb flows of tidal currents.

PHYSICAL FACTORS

Circulation patterns around islands are extremely complex, according to R. A. Berkley (personal communication, Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, Hawaii). Not only islands, but island groups, seamounts, and banks modify the environment in a number of ways: they perturb the flow, enhance mixing, cause upwelling which can enrich the photosynthetic layer, reflect or refract surface and internal waves, generate planetary waves, and add materials such as fresh water, sediments and detritus. In addition, recent observations indicate that islands and other mid-ocean structures have wakes which may be vital factors in the distribution mechanisms of plankton. Physical factors control movements of plankton and some recent studies of the Gulf Stream reveal interesting insights to the relation between planktonic communities and currents (Wiebe et al. 1976).

The current patterns in the Caribbean Sea are quite complex, due in part to the antillean arc which intersects the westward flowing current. Molinari et al. (1980) studied the movements of surface currents

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[1] Richards, W. J. "Kinds and abundance of fish larvae in the Western Central Atlantic" Miami Laboratory, Southeast Fisheries Center, Miami, FL 33149.

using Lagrangian drifters tracked by satellite, and they detected a complex system of meanders and eddies of various scales. The remaining of some of their buoys for over 5 months indicates that long residence times are available for some plankton. The meanders and eddies were produced by advection in the surface wind drift layer and by geostrophic flow. Using pilot charts of surface drift velocity, Richards and Goulet (1977) developed an operational surface drift model which also depicted meanders and eddies. These did not remain as long, however, as those indicated by the buoys of Molinari et al. (1980). Both sources reveal very complex current systems. Local currents near shore must also be extremely complicated, considering local wind effects, uneven bottom topography and deflections of tidal waves. Dynamic effects have also been noted recently in the water column. Proni et al. (1978) detected unusual particulate spires and walls in regions of current systems. The forces causing these events must also contribute to the distribution of larvae.

PROPOSED SOLUTION TO THE PROBLEM

Factors which affect the distribution of spawning products are many and varied. The complexity of the problem was recognized in 1977 by a planning group which met at the direction of UNESCO. I was a member of that group, and a skeleton of a research plan was developed (International Oceanographic Commission 1978). This plan emphasized that closely integrated oceanographic-ichthyoplankton research was necessary. The purpose was to investigate how nearshore fish populations are controlled and the mechanisms of recruitment to the fish stock. In addition plans were included to investigate the existing situation in the trap fishery of the Lesser Antilles to determine how scientific data may be used to assist rehabilitation and management. The plan described areas which would be ideal for study plus aspects of the research needed. Subsequent to the meeting, several of us inquired as to the best approach to carry out the plan. Basically this research is expensive and would require the dedication of a lot of ship time and personnel. To reduce the scope of the research would jeopardize the experiment. As of this date, it is still unclear if the project could be carried out. IOCARIBE has hired a project manager for this, and a planning meeting is scheduled for later this year.

This IOCARIBE plan is presented here because its original distribution was quite limited. The plan is as follows: Any efforts to rehabilitate and properly manage small island fisheries require in-depth knowledge of oceanographic factors that regulate reproduction, growth and recruitment of fish stocks. Such knowledge, when complete, should allow development of predictive ecosystem models necessary for long-term fishery management, including changes caused by the fishery itself. Necessary information included:

a) Circulation patterns affecting movement of fish eggs and larvae;
b) The availability of nutrients and the mechanism of their supply;
c) The amount of primary productivity providing energy to the ecosystem.

Such information can only be gained through an intensive interdisciplinary program co-ordinated with ongoing fishery programs which will collect appropriate data.

It was agreed that the basic study of the trap fishery and its management must be conducted in an overfished area, and that WECAF would need to make a major input in relation to fishery problems.

It was agreed that two main areas should be designated for the study:

a) St. Kitts-Nevis. The trap fishery is well developed and over-exploited, but interpretation of fishery and oceanographic data will be complex.
b) St. Lucia. The trap fishery is less well developed and there are immediate plans for the collection of fishery statistics. Recruitment data will be relatively easy to obtain because the oceanographic regime is apparently less complex.

An important question to be answered in both areas is whether recruitment depends on local stock or originates from some other source. In both areas it is considered necessary to collect data on fisheries, ichthyoplankton distribution and abundance, water transport, nutrient chemistry and productivity.

A simple outline of the proposal and divisions of responsibility is given below.

<u>Program description</u>

A) St. Lucia Project
  1) Oceanographic (IOCARIBE)
    a) St. Lucia Passage
      (1) Circulation
      (2) Ichthyoplankton
      (3) Chemistry, primary production, zooplankton.
    b) St. Vincent Passage
      (1) Circulation
      (2) Ichthyoplankton
      (3) Chemistry, primary production, zooplankton.
    c) Up-stream
      (1) Circulation
      (2) Ichthyoplankton
      (3) Chemistry, primary production, zooplankton.
    d) Down-stream
      (1) Island Wake
      (2) West of island wake
      (3) Circulation
      (4) Ichthyoplankton
      (5) Chemistry, primary production.

2) Fisheries (WECAF Project and St. Lucia Fisheries Department)
    a) Catch/effort (C/E) and assessment
    b) Spawning season and fecundity
    c) Nursery and recruitment information
    d) Maximum sustainable yield (MSY) and optimum yield (OY)

B) St. Kitts/Nevis Project
  1) Oceanographic (IOCARIBE)
    a) Circulation
    b) Ichthyoplankton
    c) Chemistry, primary production, zooplankton
  2) Fisheries (WECAF Project and local Fisheries Departments)
    a) St. Kitts
      1 - C/E and assessment
      2 - Modify gear and methods
      3 - Monitor C/E
    b) Nevis
      1 - C/E and assessment
      2 - Monitor C/E and report assessment

The nature and type of data to be collected in each area is similar and is as set out in the following paragraphs.

C) Ichthyoplankton

Samples will be collected to determine horizontal and vertical distribution patterns and diurnal changes. Sampling will be undertaken upstream from the island, in the island shadow and to the west of the shadow. These will be related to water transport, nutrient chemistry, plankton and productivity.

Sampling must extend over at least one year at minimum intervals of three months. It may be necessary to increase the sampling effort during known seasons of fish reproduction.

Samples will also be used for total analysis of zooplankton and the potential food sources for fish larvae.

D) Water Circulation

A water-mass circulation study around the shelf of an island should consider the following environmental parameters
1. Currents and net transport at different levels of the water column
2. Tidal variations
3. Meteorological parameters (wind regime, precipitation and evaporation rates, etc.)
4. Wave regime
5. Land drainage
6. Bathymetric survey

The investigation of the inter-relationship among these variables entails monitoring for at least fourteen continuous days during each season of the year. Measurements of the physical variables should be undertaken jointly with biological and chemical studies for the area. Sophisticated measuring methods should be employed to prevent data loss and waste of effort. The methods suggested are as follows:

1. Use of current meter systems (monitoring, release units, etc.) (Eulerian measures)
2. Lagrangian tracking by means of radio, or theodolite-tracked drogues, dye patches, and surface drifting objects
3. In situ meteorological and wave regime parameters monitoring buoys
4. In situ tidal gauges
5. Bathymetric surveys from small and large boats depending on closeness to the shoreline (portable recorders close to shore)
6. Wherever possible, data acquired by satellite remote sensing equipment should be obtained as a part of the program. This will include wave spectra, surface winds and currents.

The methods of analysis will be as follows:

1. Spectral analyses of waves, currents and wind regime (computer programs)
2. Correlation analyses of wind, currents, tidal variations by means of statistical and diagrammatic methods (for example: progressive vectorial diagrams)

This investigation is specifically designed to support biological data necessary to elucidate the fisheries problems or solutions being sought (net transport to determine distribution patterns of larvae).

E) Chemistry, productivity

In situ C^{14} uptake primary production measurements in Atlantic and Caribbean sides in and out of island shadow and on island shelf. Coincident measurement of nutrient and biochemical parameters including

NO_3^-, NO_2^-, NH_4^+, PO_4 = SIO_4 = ATP

ATP (for total microbial biomass)

Chlorophyll (plant biomass)

Dissolved and particulate organic carbon
Dissolved and particulate organic nitrogen
Temperature
Salinity
Dissolved oxygen
Alkalinity
Nitrogen fixation

An oceanic platform that will allow performance of these analyses at sea will be essential.

Data on chlorophyll and sea surface temperature will also be acquired through satellite remote sensing systems.

F) Fisheries

The fisheries study will concentrate on an evaluation of the trap fisheries in the Lesser Antilles. Such evaluation can be based on estimates of catch, effort and area fished in the various islands as well as recruitment to the stock. Improved estimates would be obtained if it were possible to manipulate these fisheries. It is agreed that the WECAF Project should be requested to be the responsible agent for implementation of the program.

The objective is to estimate the state of exploitation of the fish resources, in particular those caught in the trap fishery, and to estimate if there are any simple indices which can be used to estimate the state of exploitation for those for which little information is available, for islands in the Lesser Antilles with special emphasis in Santa Lucia, St. Kitts, Montserrat and Antigua.

The basis for this study will be a statistical sampling program, designed by an expert in the field who also should ensure uniformity and standardization in the countries participating in the program. The sampling program should be designed to give sufficiently reliable results for a moderate cost and limited use of personnel. The UNDP/FAO/WECAF project could be requested to assist in the program by providing a statistician.

The statistics should include catches by species or species groups, by fishing ground, some information on size composition, maturity, etc. The data should be analyzed at regular intervals in order to follow and eventually modify the program if necessary.

G) Training, Education and Mutual Assistance in the marine sciences (TEMA)

Every effort will be made to include scientists and students from the region in the conduct of the program including field work, data collection and data reduction.

H) Time Schedule

It is estimated that two years will be required for planning and that the program should aim to commence on 1 January 1980. The group noted that it was not necessary for St. Kitts and St. Lucia parts of the program to be conducted simultaneously and it would be possible to operate the program on a phased basis.

I) Finance

The principal financial requirement is support for ship time and for personnel. ISTPM (France), NOAA (USA) NSF-IDOE (USA), Sevastopol Hydrobiological Institute (USSR), NERC (UK), Royal Navy (UK), National Marine Fisheries Service (USA), Canadian Committee on Oceanography (Canada) might be approached for donation of ship-time.

In conclusion I present this plan again to make two points. First, the problem is very complex, and second, the solution will not come simply. The IOCARIBE plan will solve the problem, but it needs interest from the scientific community and support from funding agencies.

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SESSION SUMMARY

Recruitment of Reef Fishes/Stock Delineation

by
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The two papers presented in this session (Mechanisms and timing of recruitment in reef fishes by W. McFarland and Planktonic processes affecting establishment and maintenance of reef fish stocks by W. Richards) elicited enthusiastic discussion which resulted in 40 typed pages of transcript. This transcript is in the chairman's files but it is too long to reproduce here. Rather this summary is a brief synopsis of that discussion.

The question of what actually happens to the eggs and larvae during their planktonic life stage was discussed at some length. Our understanding of this is not very good, but recent research advances including the study of otolith growth rings, behavior of adults, discrete depth sampling, oceanic circulation, distribution of organisms in the water column, and behavior of eggs and larvae should lead to a solution to many of the problems. Not only must the shallow water reef fish be studied but the deep reef fish as well. This latter group presents greater problems because of the difficulty of performing direct observations in deep water.

The affects of oceanic currents on distribution yielded the observation that currents and counter currents coupled with vertical movements of young stages of fish might be the mechanism for maintenance of larval stocks in the vicinity of their parents. This led into the possibility that electrophoretic and morphometric studies of stocks indicate that islands may constitute distinct genetic stocks and that offspring are not swept away despite long pelagic lives. If this is the case, then small areas can be managed independently although much contrary information is also available.

The practicality of ichthyoplankton surveys for reef fish was questioned because so few larvae of reef fish are encountered. The reply to this is that this is an indication of the relatively few numbers of some snappers and groupers in comparison with other reef fish such as labrids and gobies. Larval surveys have provided reliable indices of spawning stock sizes for reef fishes. Ichthyoplankton surveys are cost effective if all the fish are of interest, and they become of decreasing cost effectiveness as the number of species of interest declines. For specific reef fishes of low abundance, sampling intensity may have to be increased to obtain sufficient numbers for analysis. Larval identifications are of little problem because of recent advances and the simplicity of rearing them from eggs for identification purposes. However, identification of preserved eggs in the plankton is very difficult although living eggs have many distinct characters which are lost using current preservation techniques.

The general question of management was raised and it was pointed out that management of these resources should not be for protein alone. In areas of clear warm water the fish have a great value from a fish watcher's view. Also, in areas like the Caribbean where numerous sovereign states exist, the necessity of international management must be addressed especially if populations from different states are interdependent.

In conclusion, given adequate support, research can answer many of the questions concerning recruitment mechanisms. The research techniques are available and if carried out many fundamental questions could be answered in five years and probabilities are high to quickly advance our depth of knowledge so that management questions could be adequately addressed.

SESSION 4

Assessment of Reef Stocks

Chairman

Richard O. Parker, Jr.

METHODS FOR ASSESSING REEF FISH STOCKS

by

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INTRODUCTION

In the strict sense, an assessment is the evaluation of property, usually for the purpose of taxation. In fisheries research, the term assessment has a number of meanings ranging from the enumeration of a fish population to the complete description of the status of the stock in its ecological setting. Assessment, in this paper, will be used synonymously with determination of the abundance of individuals of a given population (enumeration). Important management information that can be obtained by monitoring the abundance of fish populations includes defining the stock or stocks in a management unit, and estimating stock replacement (growth and recruitment) and stock mortality (losses) from natural and/or fishing causes, emigration or immigration.

Trends in population abundance can be estimated from information dependent on, or independent of, the commercial and recreational catch of a given species. The least expensive method of estimating population size, and other temporally associated parameters (recruitment, mortality, etc.), is through analysis of fishing effort and samples of the catch. Often estimates of population parameters based on catch and effort data appear reasonable because of time and financial constraints and are used as gospel without any validation of their reliability. Estimates of abundance independent of catch information are complementary to estimates from analysis of catch statistics. Values obtained by both methods may be compared in order to test their validity. Independent estimates also are often necessary if adequate catch statistics do not exist or if catch per unit of fishing effort does not reflect stock size, such as a fishery lightly fished. Only stock assessment independent of catch will be discussed further.

Even the seemingly simple task of determining population abundance, the objective of resource surveys, may appear impossible due to the great diversity of reef fish species, habitats, behavior and interactions. The fisheries assessment challenge is compounded by a seeming lack of interest, reflected in funding levels, to promote the necessary technological development for obtaining accurate estimates of population size. At present, we must arbitrate between a mandate to obtain assessment information to manage the reef fish fishery and the lack of research funds with which to tackle a complex ecological/behavioral situation.

The objectives of this paper are 1) to discuss several factors which should be considered prior to selection of an assessment technique, and 2) to point out advantages and disadvantages of several methods of obtaining estimates of reef fish abundance.

PRELIMINARY CONSIDERATIONS

The demand for assessment estimates now has caused some fishery biologists to jump into research without necessary preparation, while others, seeing the complexity of the problem, avoid it. To elevate any of the present reef fish assessment techniques to a science will require much more planning to obtain a quantifiable end product and to achieve greater understanding of the biology of the species groups. Premature assessment research with poorly defined goals will result in more money spent to obtain estimates that have little or no validity. Reef fish assessment will require a multidisciplinary approach involving a detailed consideration of each variable.

Several topics should be addressed before selecting a method or technique for assessing a particular reef fish stock. The group requesting the information must define the management objective and identify the stock segment. The importance of early communication between managers and biologists in the development of research/assessment goals cannot be overstressed (Hennemuth et al. 1980; Suomala and Yudanov 1980). If a yield estimate is desired, assessment might be directed at only the exploitable fraction of the stock or those adults available to a given gear type. The approach would be different if interest were in the adjustment of a quota, which case an estimate of the number of annual recruits would be needed. If interest were in year-class success or strength, enumeration of pre-recruits would be required.

Both the accuracy and the validity of abundance estimates should be considered before selecting assessment techniques. The need for accuracy in estimates of abundance increases directly as exploitation of the stock and the need for proper regulation increases (Gulland 1969). If snapper and grouper stocks were thought to be fully exploited in most areas, then an accurate abundance estimate would be desirable. The validity of an abundance estimate is based upon the degree to which specific assumptions are met during sampling (Lackey and Hubert 1978). Assumptions for various enumeration techniques might include: factors affecting population abundance remain constant throughout the sampling period; all members of the stock are equally available to the sampling method; mortality occurs only during part of the year.

After the segment of the population to be assessed is identified, the accuracy necessary is determined, and assumptions are evaluated an assessment gear can be selected. Selection should be based on the ability of the gear to obtain quantitative and representative samples of the population segment of interest. Gear selectivity should be known or quantitatively estimated. Both avoidance of net configurations by large fish and movement through netting by small individuals are qualitative examples of the gear selectivity possible from behavioral response of fish to a trawl sampling device.

The statistical sampling characteristics of a technique or gear should be considered. The distribution of catches from a chosen gear type may represent a normal distribution (large trawls) or a negative binomial distribution (diver counts).

Information on fish distribution within a specific reef habitat should be incorporated into a statistically valid sampling design. If segments of the stock are stratified by depth, habitat or microhabitat, the following items should be known or accounted for: 1) the distribution and area of strata; 2) the stock density distribution (relative abundance) within and among strata (with estimates of variance): and 3) the stock density distribution within substrata, if they exist. Although many reef fish may be uniformly or normally distributed throughout a habitat, many of the commercially or recreationally important species appear to be contagiously distributed within a habitat, which itself is contagiously distributed within the region.

Estimates of density distributions could be an independent research objective prior to assessment. It is often easier to determine the distribution and relative density of a stock than to estimate numbers of individuals. A combination of less expensive non-assessment gears or techniques may provide the necessary distributional and behavioral information. All the above fish density values (distribution of population, variance, and area of strata) may be responsive to innumerable environmental factors that are difficult to evaluate.

SELECTED TECHNIQUES

The possible combinations of techniques used to enumerate mixed species populations are infinite, yet a funding priority must be placed upon one or several methods having the greatest potential. Several brief examples of the trade-off between quantitative assessment (Table 1) techniques and estimated implementation costs might stimulate discussion.

SWEPT AREA COUNTS

One of the least expensive techniques is trawling (not necessarily bottom trawling). Standardized trawling provides an index of relative abundance adequate for many population comparisons. Much valuable information can be obtained from long-term trawl surveys in areas where fish distributions and behavior allow effective sampling by bottom trawl gear (Clark 1979). These conditions are not generally true for reef species, but trawls may be applicable under specific conditions. Bottom trawling indices of abundance would be limited to the adults

Table 1. Methods for estimating abundance of reef fish populations independent of catch information.

Method	Advantages	Disadvantages	Survey[1] Speed	Estimated[2] Expense
Direct enumerations (expansion of partial counts)				
Active (spatial sequence)				
Divers	flexible, positive identification, behavioral information	depth limitations, avoidance, attraction	S	H
Submersibles			S	H
TV and photos	not depth limited	interpretation of size and distribution	M	M
Hydroacoustics	not depth limited	interpretation of size, subjective	R	M
Lasers	accuracy	depth limitations, development phase	R	H
Local depletion fishing	life history information	gear selectivity, avoidance, disruptive	M	M
Passive (temporal sequence)				
Fixed TV and photos	repeated sampling	gear maintenance	M	M

(Table 1 cont.)

Method	Advantages	Disadvantages	Survey Speed[1]	Estimated Expense[2]
Indirect enumeration				
Abundance indices (standarized efforts)	life history information	gear selectivity; avoidance		
Trawls	positive identification, lengths	effectiveness range; disruptive	M	L
Traps and nets			M	L
Hooks and lines	positive identification, lengths	effectiveness range; disruptive	M	L
Local counts	positive identification	extrapolation	M	M
Correlated Counts		quantitative relationships		
Ichthyoplankton surveys	year class strength	predictive information	R	M
Pre-recruit indices	year class strength	predictive information	M	M
Passive acoustics	simple gear	development phase	M	L
Predator relationships	unknown	development phase	M	M
Mark/Recapture	growth & movement information	recovery effort in open systems	S	M-H

[1] R = rapid; M = moderate; S = slow

[2] H = high; M = medium; L = low

or juveniles of those species groups which; 1) routinely move away from high relief habitats nightly (grunts) or seasonally (possibly snappers, Cummins, Rivers and Struhsaker 1962) or 2) live in grass beds or low relief habitats (some porgies, juveniles of vermilion snapper and several groupers). Vertical stratification of some grouper species over habitats unavailable to bottom trawls (Jones 1980 personal communication[1]) indicates that discrete depth midwater trawling may increase the number of species which could be adequately collected by trawling without habitat destruction and gear loss.

Most fisheries biologists would agree that trawls should be upgraded to semi-quantitative gear by incorporating routine monitoring of net size and configuration during each collection, possible with a sonic device (Fig. 1) like that described by Wathne (1977). Installation of the moderately expensive equipment to measure trawl net size and additional gear to maintain desired sampling depths should be followed by quantitative sampling to estimate species availability and vulnerability to the specific gear, if an estimate of absolute abundance (standing stock, Edwards 1968) is required. The great variability in trawl catches due to time of day, season, habitat, weather, etc. (Gulland 1969), necessitates strict standardization or knowledge of the relationship between environmental factors and catch. Also, trawl calibrations can be conducted by comparing catch to in situ fish densities estimated from headrope mounted cameras and/or submersible counts (Zaferman 1980). After the above equipment, research, and development expenses, trawling would still be limited in assessment of reef fish species. The potential of trawl sampling should be evaluated to define the species groups which could be assessed adequately and the information complementary to stock assessment which could be gained.

VISUAL COUNTS

Visual abundance estimates and visually directed sampling from the sea floor by divers or submersibles produce superior quality results within a relatively narrow area for those species which are not attracted to or avoid the observers. Local population density estimates for black sea bass in low relief habitats from diver counts (Powles and Barans 1980) compare favorably with historical catch estimates from cohort analysis (Low 1980). Abundance estimates from biologist/diver counts of larger/dominant reef fish species have been very similar to those obtained by rotenone collections (Stone et al. 1979). Although valuable community comparisons can be made by development of "importance values" (Jones and Chase 1975) or ranked index of abundance (Jones and Thompson 1978), serious consideration must be given to statistical analysis of counts from transect sampling (Burnham, Anderson, and Laake 1980, Quinn and Gallucci 1980). Problems of avoidance of, or attraction

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[1] Dr. R. S. Jones, Director, Johnson Science Laboratory, Harbor Branch Foundation, Inc., Ft. Pierce, Florida.

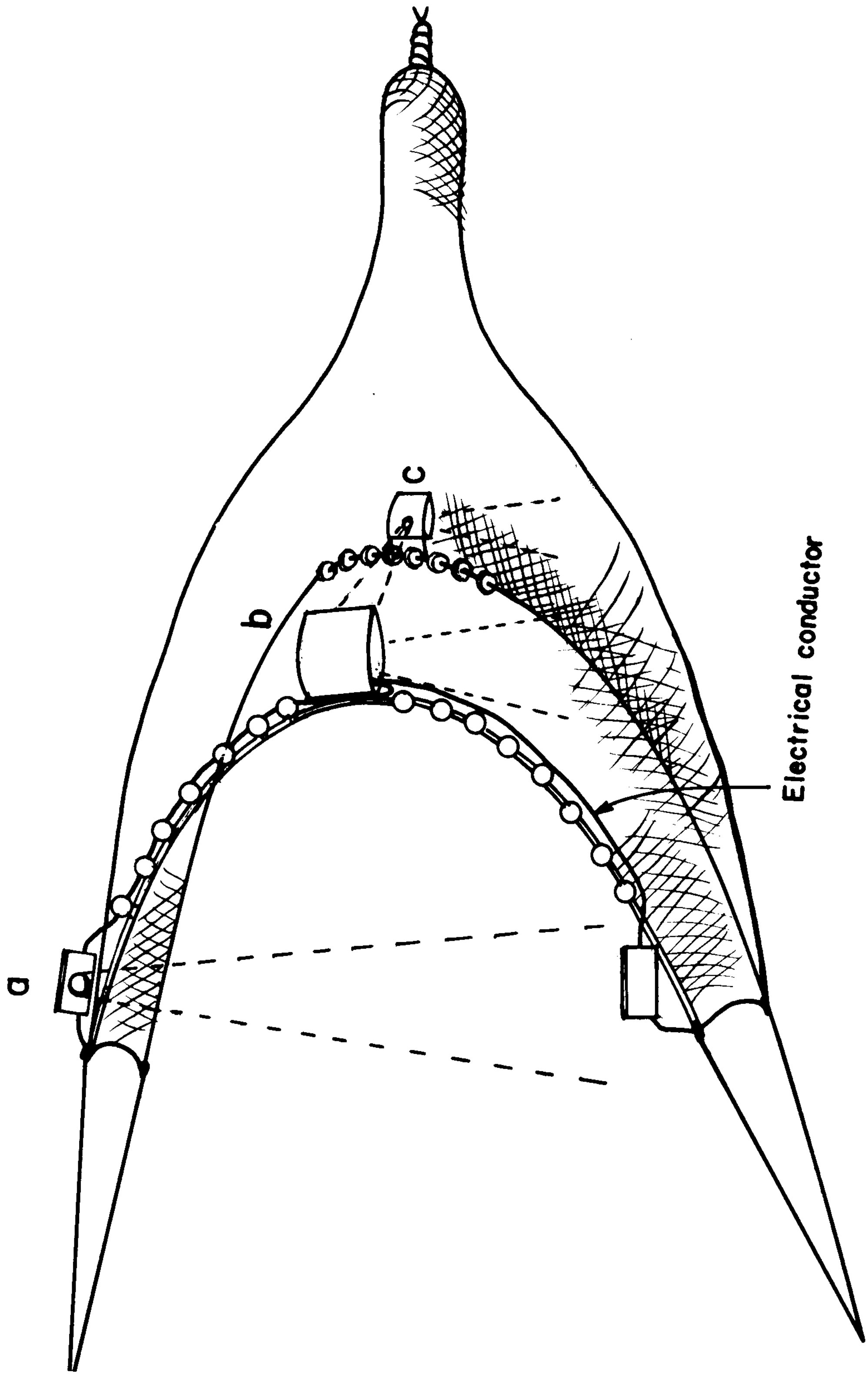

Figure 1. Schematic drawing showing relative locations of sonic system components: a) is wing unit, b) is headrope unit and c) is footrope unit (Photo from Northwest Fishery Center, NMFS).

to, the visual sampling source by given reef species groups may be evaluated by calibration/verification between visual techniques. The effects of several limitations, such as narrow field of view, slow coverage speed, water clarity and variability between counts, could be reduced by increasing observation frequency temporally or spatially, but this increases the assessment cost. The cost of a visual assessment technique at a single location usually precludes replication throughout the region or along a cline of habitats. Extrapolation of a locally determined abundance estimate to a regional estimate, however, may be highly inaccurate due to varying fish density over space.

Observations from submersibles (Fig. 2) and/or by divers (Fig. 3), which provide information on microhabitat distributions, behavior, community structure and trophic exchange, are complemetary to quantitative enumeration by other techniques. Also, the quality of information from direct observations makes visual techniques valuable for confirmation/calibration of other remote assessment techniques (Zaferman 1980). Although visual techniques appear limited in their application to regional assessment of reef fish populations, there is a great need for the information from these techniques to develop and verify other enumeration methods.

ACOUSTIC COUNTS

The cost of an acoustic abundance estimation technique, after the necessary research and development, would be considerably more than is presently spent on reef fish "assessment," but much less than the cost of routine submersible assessment. Hydroacoustic techniques, if used alone, presently have many limitations, but recent developments and the possibility of rapid enumeration of regional stocks may justify careful evaluation of the potential of acoustics.

Acoustic methods can determine regional density distributions of reef fish in general (Fig. 4) or by species groups, if species identifications are confirmed until acoustically recognizable behavioral characteristics are defined and verified (Fig. 5). Hydroacoustics and supplementary sources can relate fish distributions to types of relief (habitats) and/or oceanographic variables (Hewitt, Smith, and Brown 1976) and can enumerate relatively large species (adult snapper, grouper or jacks) individually separated and at a distance above the bottom determined by the hardware. Achieving the potential of an acoustic technique requires retaining the present advantages (wide area coverage, reduced fish avoidance, and operation over high or low relief without gear damage) while overcoming some of the present limitations.

Three important hydroacoustic limitations which require research are 1) analyst bias in echogram interpretation, 2) need for species identifications and 3) acoustic resolution of fish close together or near the bottom. Even experts disagree about interpretation and dependability of "quantitative" fish counts by acoustics under all at-sea conditions (Suomala and Yudanov 1980). The eventual commercial development of a high resolution side scan sonar with the ability to

Figure 2. Research submersible "Johnson-Sea-Link II" used in reef fish behaviroal and ecological studies (Photo from Harbor Branch Foundation, Inc.).

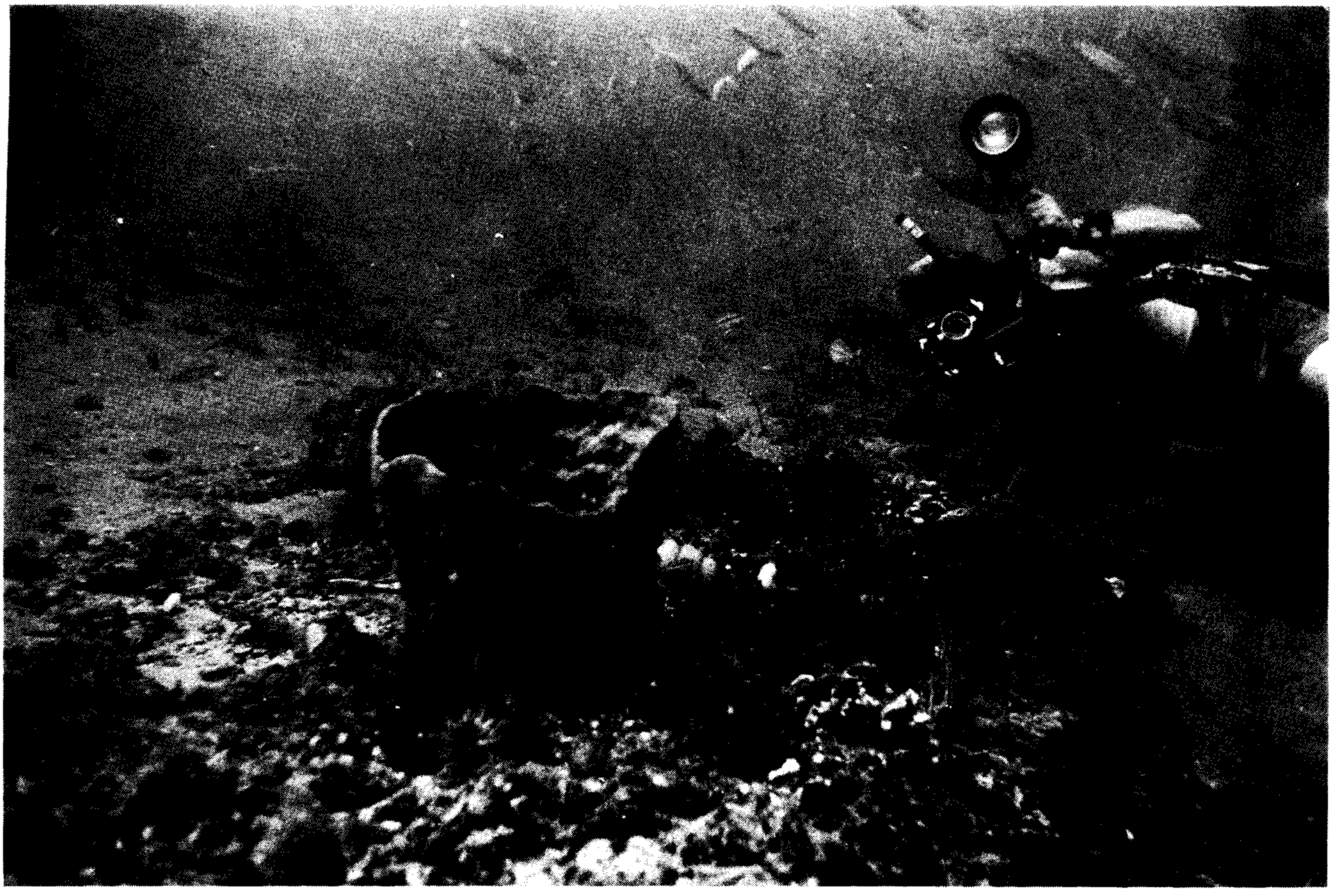

Figure 3. Fish photographed for species confirmation of diver conducted enumeration transects (Photo from Georgia Department of Natural Resources).

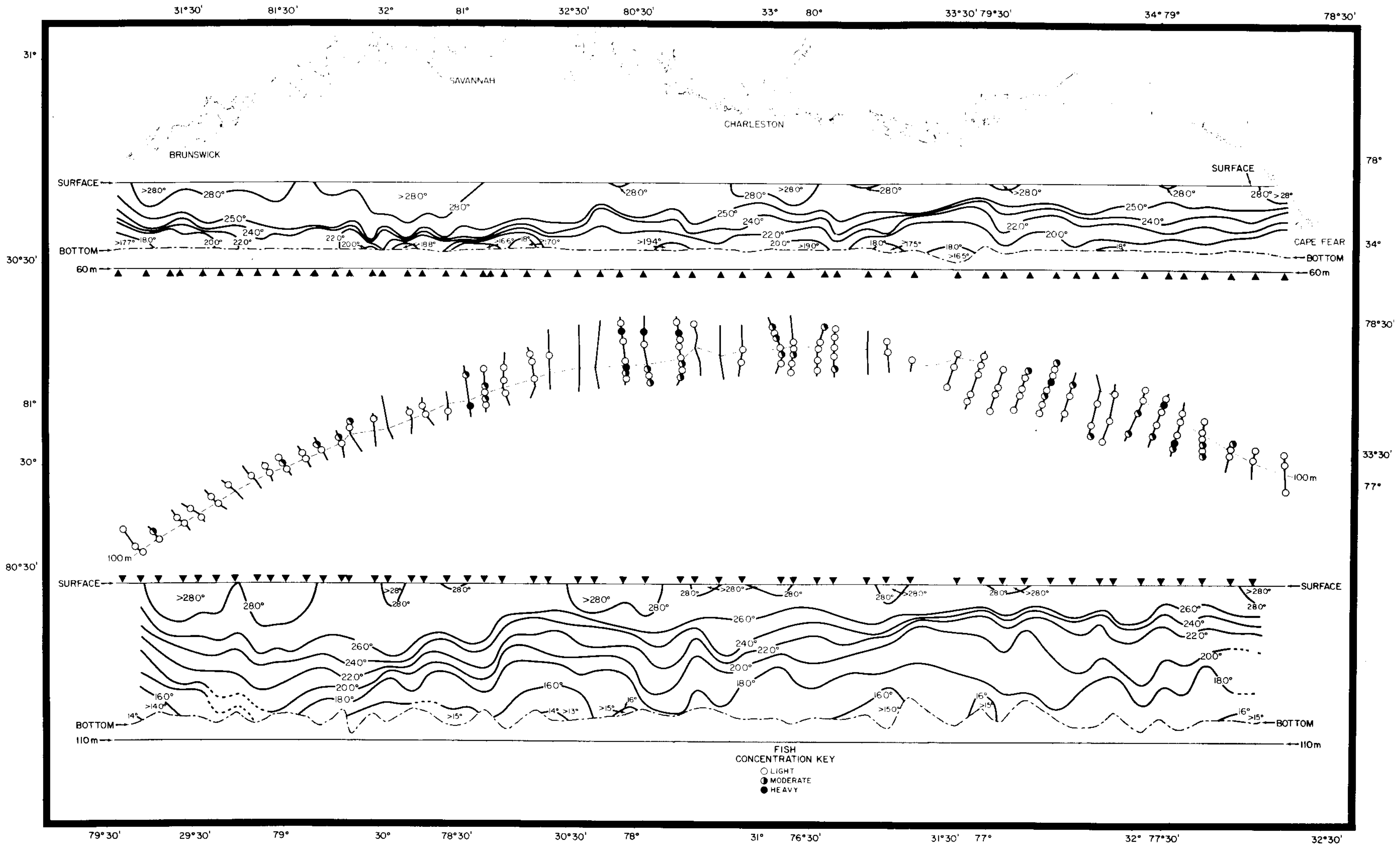

Figure 4. Distribution and relative abundance of general fish concentrations determined by hydroacoustics and cross shelf thermal fronts in the South Atlantic Bight during Summer, 1979.

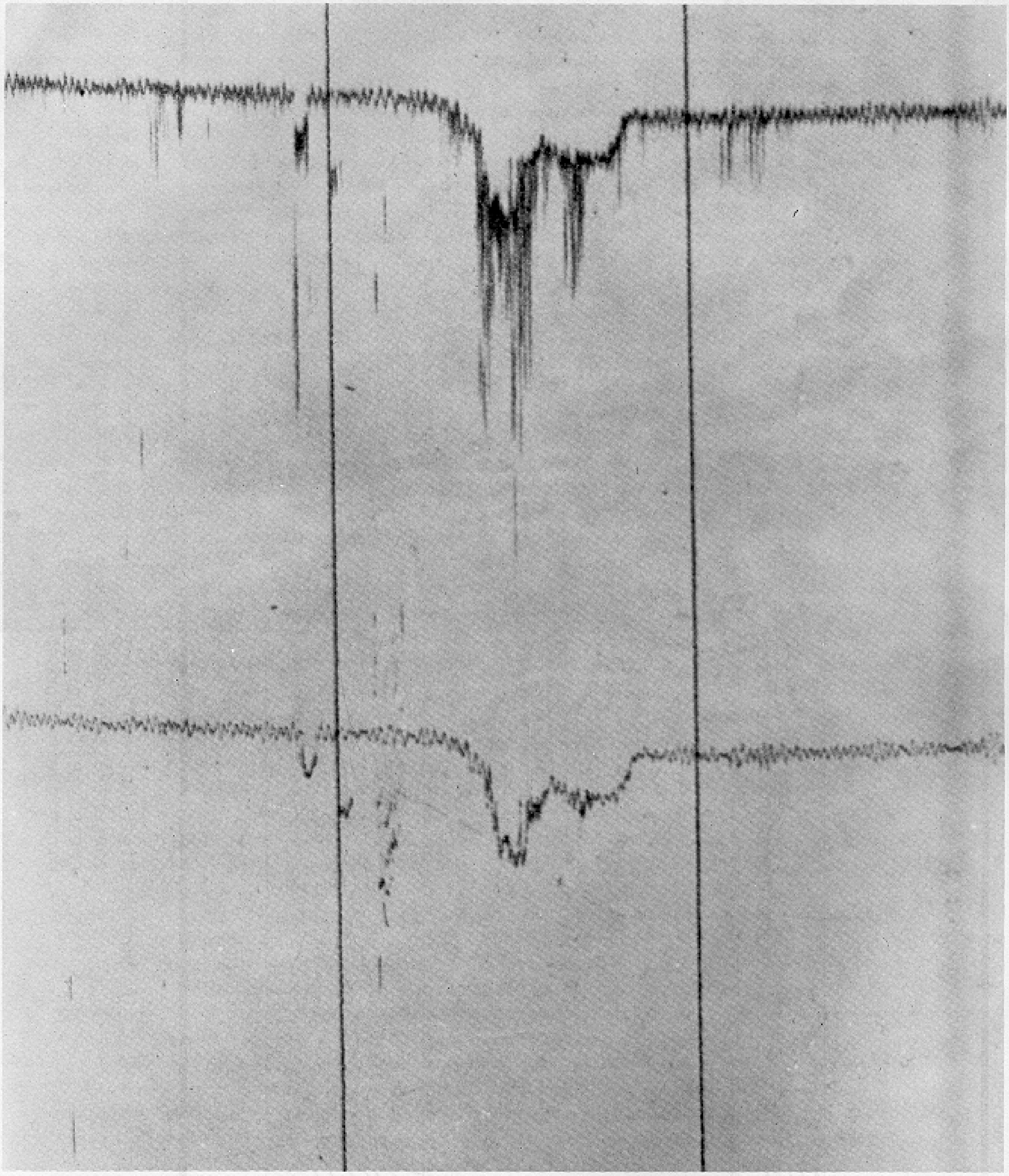

Figure 5. Echogram from hydroacoustic survey with species groups confirmed by underwater television.

estimate individual fish size and swimming configuration may eliminate much of the observer/analyst biases. A new side scan sonar system has the ability to distinguish individual fish of 20 cm or less swimming over high relief or sand bottoms (V. Holliday, personal communication[2]), but the towfish (Fig. 6) is too large and fragile for routine deployment. With high resolution capabilities developed in a solid state towfish of about 50 lbs., the increased resolution should allow enumeration and length determination of most reef fish of commercial interest. Lack of positive species identifications can be compensated for by routine TV or still camera species confirmation. Hydroacoustic assessment, in itself like the remote underwater fisheries assessment system "RUFAS", is not the answer; a combination of gears will be necessary to provide species confirmation and provide specimens for closely related life history and populations age estimates.

Further limitations to the development of an acoustic assessment technique are the present attitudes and opinions regarding hydroacoustic assessment. These can be lumped into two classes: 1) acoustic assessment is costly and doesn't work so we should continue low funding of traditional methods (to obtain little or no quantitative information) and 2) acoustic assessment has limited application presently, but with calibration, standardization and situation-specific research and development, it has the potential of becoming a cost-effective quantitative tool in the near future. Most biologists and administrators justify poor assessment techniques by citing low levels of support funding, but the problem may be deeper. Already, biologists have been browbeaten into communications with statisticians, and many would like to avoid similar interactions with electricians and engineers, who are probably getting paid more than most fisheries biologists. The second class of attitudes includes two groups of scientists, those who realize the deficiencies of the present acoustic approach, but feel the immediate need for abundance information justifies conducting biomass surveys without the necessary calibration and standardization, and those who are working toward establishment of necessary standards and conducting stock specific ground truth prior to or concurrent with acoustic surveys. The latter is the only group responsible for developing application of the acoustic tool. It is past time for fisheries administrators and biologists to reevaluate the hydroacoustic techniques in light of the slowly accumulating progress and shift to the more optimistic class 2 attitude.

Although the acoustic technology is available to incorporate into a total assessment package, application would require hardware modification and system calibration for the specific task. Acoustic assessment still has problems associated with hardware development and interpretation of the data, but little progress will be made until questions are answered along the way. As with all enumeration methods, if the disputed verification and calibration were possible with another technique, then acoustics methods would be necessary only if they were more cost effective. The ultimate advantage of a rapid method of

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[2] D. V. Holliday, Director, San Diego Laboratory of Tracor Sciences and Systems, San Diego, California.

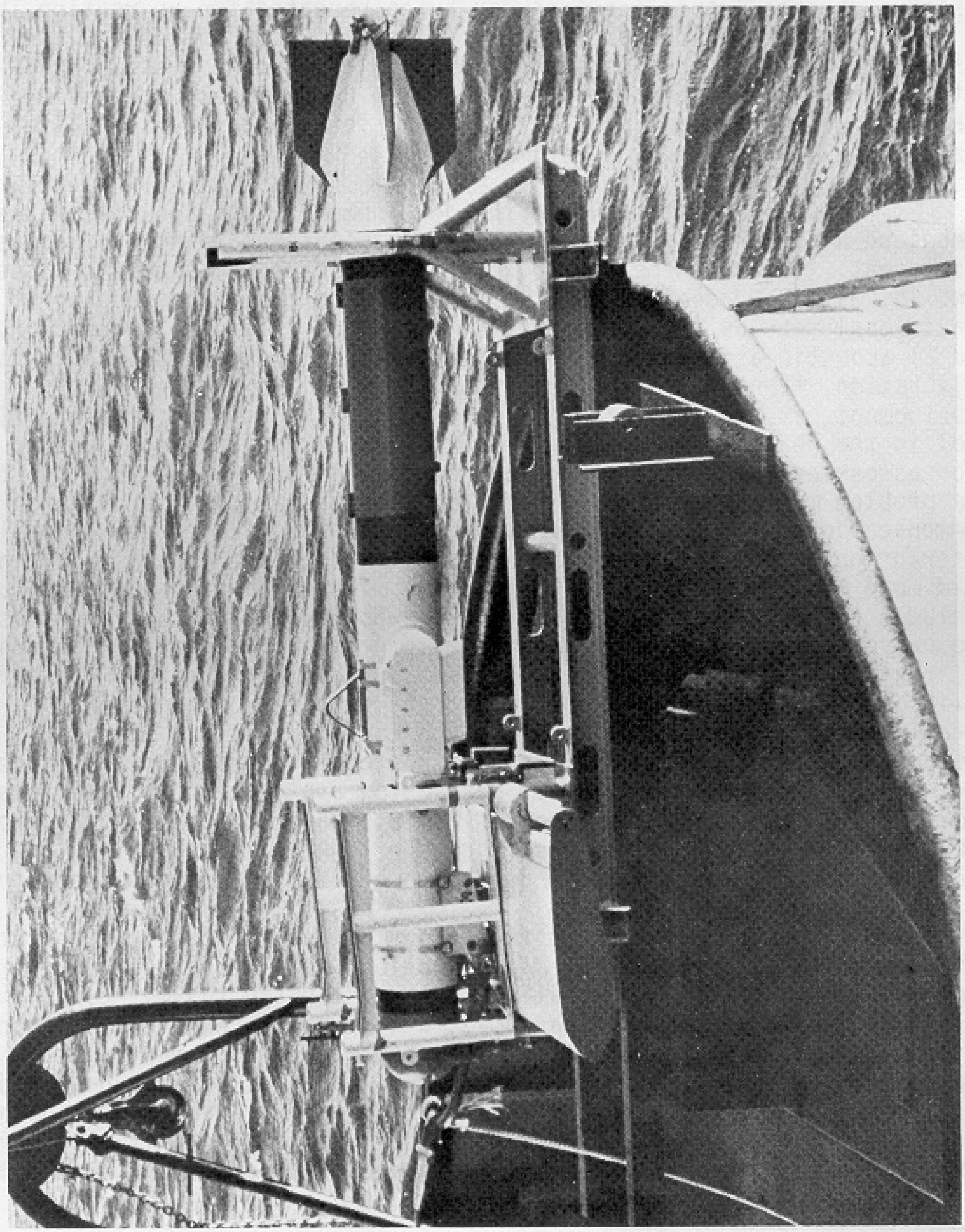

Figure 6. High resolution side scan sonar in predeployment position onboard the R/V <u>Dolphin</u> (S.C. MARMAP Program).

locating fish concentrations via satellite directed acoustic transecting and the associated allocation of greatest assessment effort to priority areas might outweigh the presently discouraging need for continued development of the technique. In a monitoring mode, habitat variability and low personnel requirements are additional advantages of hydroacoustic assessment. The speed of the survey would allow pre- and post-"season" or "quota" regional sampling to assist management.

COMPLEMENTARY TECHNIQUES

A combination of complementary methods (for concurrent in situ positioning, calibration, species verification, density confirmation, etc.) will be necessary to provide an abundance estimate of a single reef fish group with similar distributional and behavioral patterns. Comparisons of techniques for estimating fish abundance have shown that the most satisfactory estimates resulted from interpolation between two or more near-simultaneous measurement with different methods/gears (Uzmann et al. 1977).

A species group with different characteristics may require a completely different combination of techniques or only a slight modification of the first technique (i.e., fish counts with echo ranging vs echo sounding sonar). A more flexible original system design would allow assessment of fish groups with more divergent characteristics with less modification to the original combination of techniques. The integration of data from several complementary techniques for abundance estimates by species/group will depend on interfacing and analysis methods more sophisticated than the present level (i.e., rough verification of sonar or trawl records with TV or still cameras (Fig. 7) and comparison of diver/submersible fish counts). The distributional/behavioral research basis for development of the assessment system should proceed first on those species groups of greatest economic importance. The combination of assessment techniques for a given species group will ultimately include species selective removal gear to catch specimens for monitoring population size and age structure, growth rate and sex reversal. This would provide management information supplementary to stock abundance.

The rationale for investing scarce research dollars into development of an assessment technique must be dictated by ultimate values of the resultant data and cost effectiveness of obtaining the information. An assessment technique and associated hardware system for the relatively small and diverse reef fish stocks must maximize flexibility of design to allow application in several fisheries of both benthic and pelagic stocks. After development of a system, interagency gear sharing, like cooperative farming, must be continued to increase cost effectiveness and offset the expense of sophisticated electronic hardware.

The diversity of reef fish and fisheries result in no one fishery generating enough catch/dollar value to justify the costly development of a group specific or non-flexible assessment technique. The justification for spending a large percent of the present total

Figure 7. Camera, television and still, and light systems used in fish and invertebrate confirmations (Photo from S.C. Marine Resources Dept.).

catch value of a given reef fishery on management directed abundance research is the ultimate development of a cost effective combination of techniques which will routinely produce abundance estimates with confidence limits acceptable for management of the fishery. Although management objectives are being set by the Fishery Management Councils, none have defined the justifiable cost limit of development of a stock assessment technique to monitor the effectiveness of their management actions. None have initiated an economic analysis to estimate the long-term management benefits of stock abundance information. Managers and administrators responsible for the allocation of research funding will have to decide between progress toward the development of a long-term assessment plan through a logical series of research objectives or continued research on hit and miss life history information generated to satisfy an immediate need.

In summary, I feel strongly that reef fish stocks can and should be assessed independent of catch, but the complexity of this task will require an integrated plan of cooperative research on species distributions, species behavior, gear efficiency and cost effectiveness. Efficient research efforts would be directed toward a predefined management goal. A progression of research tasks prior to population assessment and after definition of the management objective might include:

1) surveys, possibly acoustic, to define major fish distributions to assist development of the ultimate sampling strategy,
2) group specific behavioral studies, possibly by submersible, to define microhabitat distributions and provide information necessary for a rational choice of assessment techniques for that group,
3) tests, evaluations and calibrations of the chosen combination of gears/techniques for standardized long-term stock assessment monitoring, and
4) confirmation/verification of the assessment estimates by statistical comparison with catch dependent or other independent assessment methods. Each step should be critiqued by qualified scientists and managers for evaluation of the success of the previous step and the ultimate cost effectiveness of stock assessment prior to initiation of the next research step.

ACKNOWLEDGMENTS

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REEF FISH ASSESSMENT-SNAPPER/GROUPER STOCKS IN THE WESTERN NORTH ATLANTIC SOUTH OF CAPE HATTERAS, NC

BY

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INTRODUCTION

Snapper-grouper stocks represent one of the Southeast region's valuable resources. They have been exploited by commercial fishermen since the late 1800's (Carpenter, 1965), and increasingly by sport fishermen in the past several years along the south Atlantic (Huntsman, 1976) and Gulf (Nakamura, 1976). Consequently a high priority has been placed on assessment of snapper-grouper stocks by fishery management councils, but data to provide realistic estimates have not been available. Historical survey cruises were designed to provide information only on relative abundance and potential exploitation. Stock assessment has been frequently used to describe relative abundance within specific geographical areas. Published estimates on the size of snapper-group stocks (Klima 1975, 1976a, 1976b) have been based primarily on fishery dependent landing data, although density values calculated by Bullis and Struhsaker (1970) were based on fishery independent exploratory trawling information. In this paper I address only assessment techniques based on fishery independent surveys and will make only one comment pertaining to fishery dependent estimates. Frequently, landing data are suspect because of combining species into single categories for statistical reporting purposes. When this occurs only estimates within large groups, i.e. snapper-grouper can be provided.

Comments herein will concentrate primarily on snapper-grouper resources and the efforts expended in the name of assessment. Although many reef fish are caught with traps, trawls, and hand lines, only a few species have significant commercial value. Fishes for aquarium sales will not be considered as they represent a unique utilization and are too small for human consumption. Major emphasis will be on fishing gear (traps, trawls, and lines) rather than on remote sensors and visual systems.

SNAPPER-GROUPER SURVEYS

Finfish surveys have been conducted by the National Marine Fisheries Service (NMFS) and its predecessor Bureau of Commercial Fisheries (BCF) throughout the western North Atlantic south of Cape Hatteras (Fig. 1) on shallow and deep shelf areas as well on as the upper slope. Primary and secondary target species and families of reef fish are listed in Table 1. Fishing gear included trawls, traps of several varieties, and lines (bottom longline, handline, vertical longline, electric and mechanical fishing reels). In addition, remote sensors such as the remote underwater fishery assessment system (RUFAS, Fig. 2), video pan and tilt system (Fig. 3), submersibles, and divers have been used to define habitat and stocks.

Since 1950 more than 30 cruises to assess reef fish stocks and faunal assemblages have been made by vessels from the NMFS Pascagoula Laboratory, primarily in the Gulf of Mexico and the Caribbean. In addition, the United Nations Food and Agricultural Organization (FAO) sponsored a series of cruises within the Caribbean Fisheries Development Project. FAO activities were centered in the Caribbean and off the northeast coast of South America.

Considerable detail is available on distribution and relative abundance but only limited information on life history and habitat. Data needed to estimate standing stocks include: density estimates, expressed in weight or number of individuals; amount of habitat, defined in terms of ecologically relevant divisions; and areal estimates within each division. Biomass can be calculated from estimates of density and habitat. Total stock or stock segments can be computed using Gulland's (1975) estimate of potential yield.

FISHING TRAWLS

Trawl estimates of standing stock density (kg/ha) use the area swept method. Measures of horizontal trawl opening (but not vertical opening), vessel speed, and length of tow are necessary. Estimates represent only stocks present on the trawlable portion of the habitat. The estimates are better descriptors of snapper than grouper populations since snappers move off the reef habitat more freely than the more sedentary groupers. Since snappers, however, are often found above the vertical trawl opening the snapper population may be underestimated. Surveys using roller rigged trawls have been made along the east coast of the U.S. and off Yucatan (Cummins, Rivers, and Struhsaker 1962, and Captiva and Rivers 1960). Most surveys provided little or no insight into population size, since stations were based on "good" fish signs and not randomly selected. Trawl surveys also may be destructive to "live" bottom areas. No recovery time data is available for trawled areas.

DISTRIBUTION OF NMFS AND FAO REEF FISH ASSESSMENT ACTIVITIES

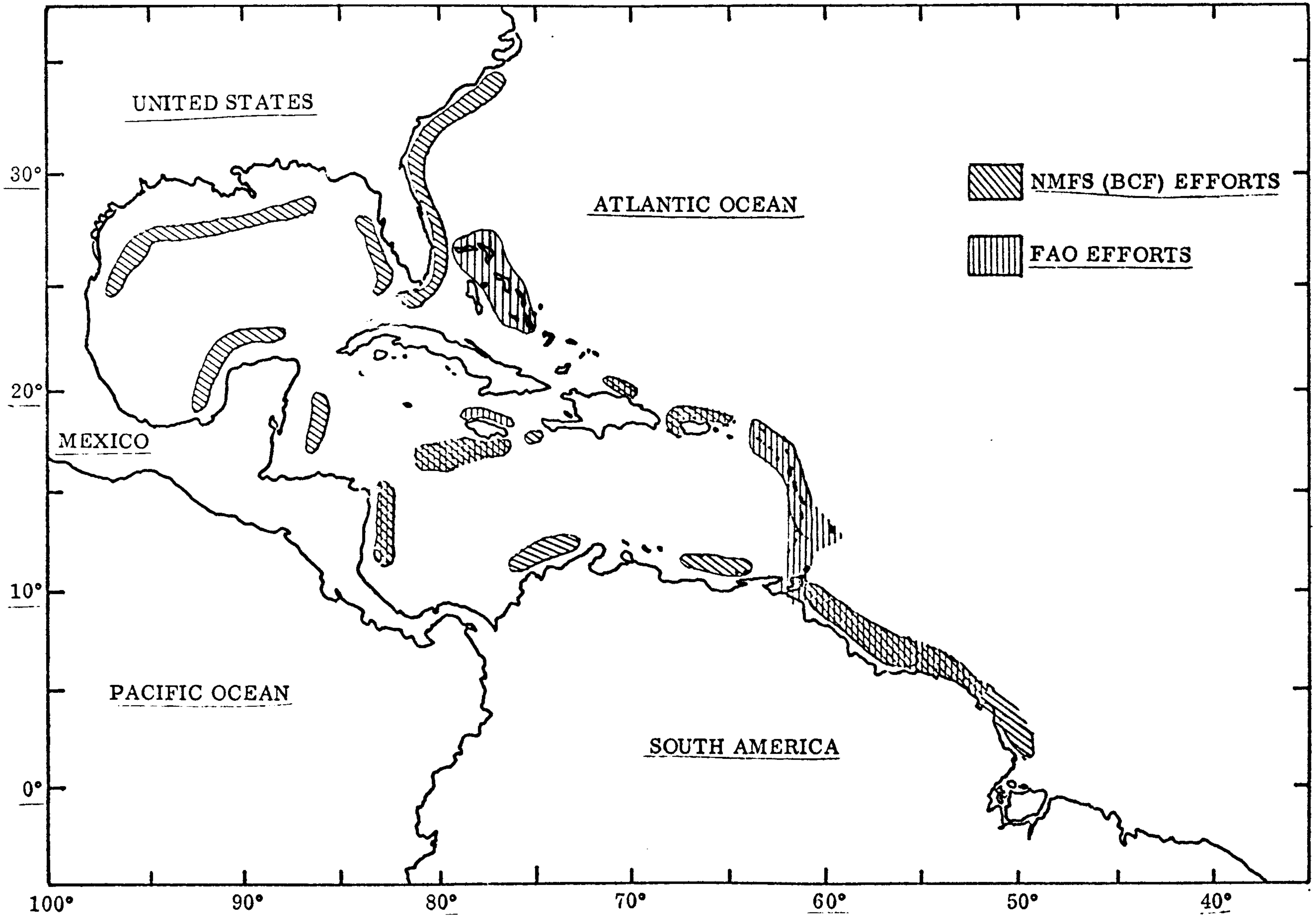


Figure 1. Distribution of reef fish "assessment" throughout the western North Atlantic, south of Cape Hatteras, N. C. by National Marine Fisheries Service (NMFS) and the Food and Agricultural Organization of the United Nations (FAO).

Table 1. - Target species and secondary reef fish familes caught during NMFS reef fish activities

Target species by families	Secondary families
Lutjanidae	Acanthuridae
Lutjanus campechanus	Balistidae
Lutjanus purpureus	Carangidae
Lutjanus synagris	Chaetodontidae
Lutjanus vivanus	Ephippidae
Lutjanus analis	Holocentridae
Pristipomoides aquilonaris	Kyphosidae
Pristipomoides macropthalmus	Labridae
Rhomboplites aurorubens	Lutjanidae
Etelis oculatus	Pomadasyidae
Ocyurus chrysurus	Priacanthidae
Serranidae	Scaridae
Epinephelus flavolimbatus	Scorpaenidae
Epinephelus guttatus	Serranidae
Epinephelus morio	Sparidae
Epinephelus niveatus	Sphyraenidae
Epinephelus mystacinus	
Mycteroperca phenax	Species from many other teleost and elasmobranch families are also taken off the reefs
Mycteroperca microlepis	
Mycteroperca interstitialis	
Branchiostegidae	
Lopholatilus chamaeleonticeps	
Caulolatilus spp.	

RUFAS - UNDERWATER VEHICLE OF THE SYSTEM

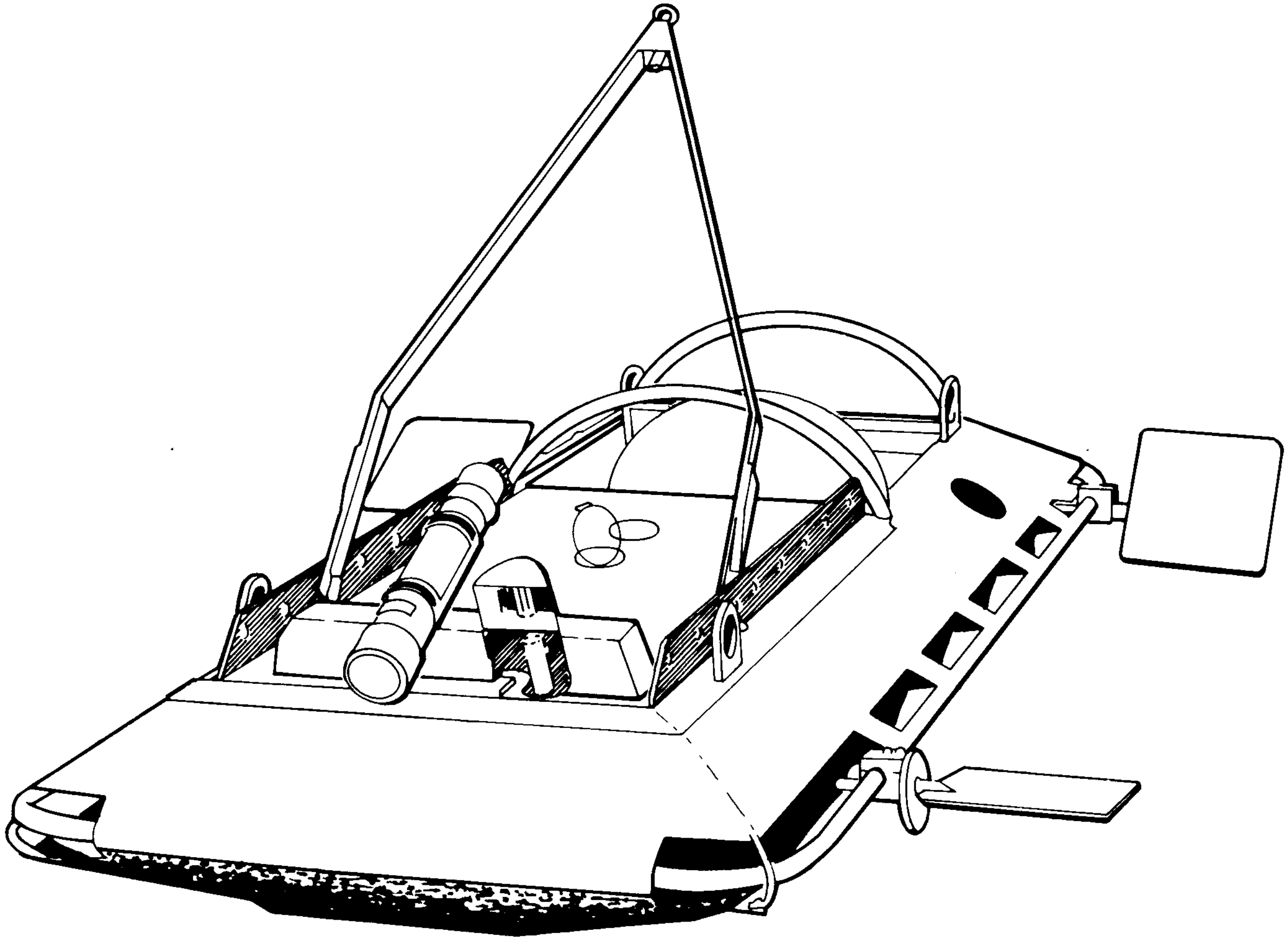
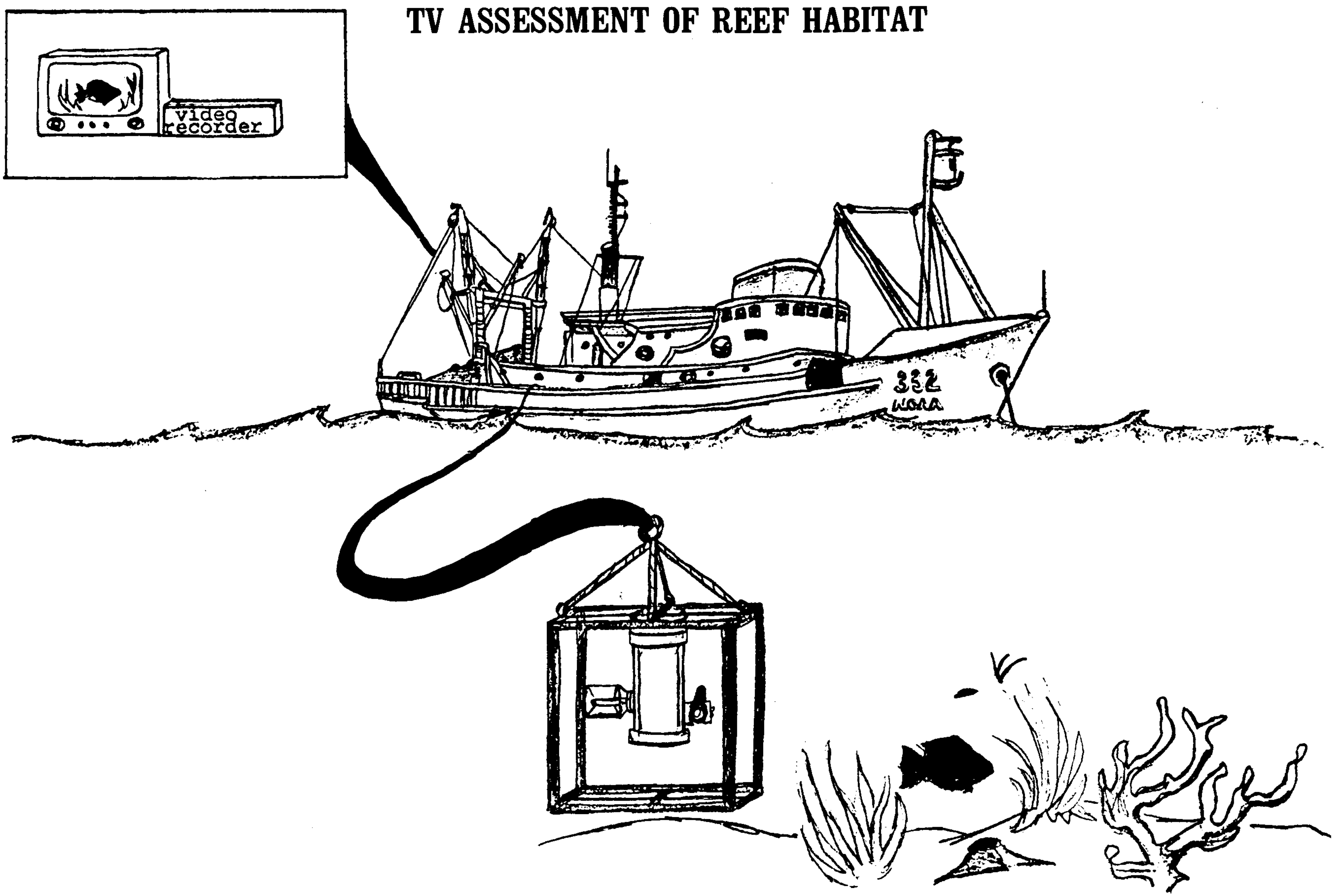


Figure 2. Diagrammatic illustration of the Remote Underwater Fishery Assessment System (RUFAS).

Figure 3. Diagrammatic illustration of a pan and tilt television reef habitat assessment system.



Extensive areas on the continental shelf throughout the South Atlantic and off the northeast coast of South America are available for trawl surveys. Assessment based on trawling would require cooperative endeavors, including the use of acoustic or visual systems (side scan sonar, submersibles, towed remote sensors, TV, photographic, or in some cases divers). Offbottom trawls could be used over non-live areas. By providing information on faunal composition and density of target species, trawl surveys allow a more realistic examination of remote sensing images made in the proximity of trawl stations.

Trawling for shrimp and ground fish may kill large numbers of young snapper and grouper, and thereby reduce population sizes. The Gulf Reef Fish Management Plan (1980) estimates that 78 million red snapper of all sizes (predominantly less than 0.23 kg) are caught by shrimp and groundfish fleets in the northern Gulf of Mexico. Shrimp fleets could cause snapper-group mortality in the South Atlantic, Caribbean, and northeast coast of South America, although no reports of snapper catches by South Atlantic shrimp boats exist.

TRAPS

Rough bottom cannot be trawled without causing extensive damage to the habitat. Assessment techniques, therefore, require the use of passive gear, such as traps, rather than active fishing gear. Non-trawlable habitats generally are found in insular or offshore continental regions. Relief can be in the form of pinnacles (Flower Garden Reefs of Texas), precipitous drops (shelf edge in most insular regions), or slab rock (Florida Middle Grounds and South Atlantic). Trap design, method of fishing, and bait used are subjective, and fishermen use their personal design and fishing technique. The only item of general agreement is that the funnel should be directed downward where it empties into the trap. Trap designs includes arrowhead, West Indian Z, Australian D and O, S traps, rectangular, modified Z, Cuban rectangular, and others. Traps are constructed of several sizes of chicken wire or nylon mesh, with reinforcing steel bars or bamboo and wood for support. Traps may be modified to increase longevity, but otherwise are quite similar. Types of bait and its placement in the traps vary considerably. Some fishermen claim that after soaking for a few days, traps become self baiting with small fish.

Traps must be placed on level or gently sloping bottom. On steep slopes they tumble down and are lost or battered out of shape. Traps on strings are generally placed about 15 to 30 meters apart. String sets of single pots are placed 100 to 105 meters apart (Wolf and Chislett 1974). Species composition of catches varies with depth. Shallow water sets catch more secondary species (grunts, triggerfish, and angelfish) and deep sets catch more snapper-grouper.

Trapping by NMFS (BCF) has been limited. In one series of experiments with a photo recorder on the trap, red snapper were observed entering and leaving the trap with ease. Some species have a propensity to enter traps and certain tagged fish have been recaptured many times (Randall 1962).

Because the attractiveness of traps or bait is not known, and because some species enter and leave traps with ease, it is difficult to estimate densities from trap catches. Efficiency coefficients must first be determined, but this task is difficult. Population assessments based on tagging are possible, but tagging a sufficient number of fish to assure a reasonable number of returns may require a lot of time and money. Tagged/untagged ratios can provide population estimates for shallow and intermediate depth reefs, but not for deep reefs because tag returns are usually too few. Shallow water estimates can be verified by using visual assessment techniques (divers, submersibles, TV, or photographic systems).

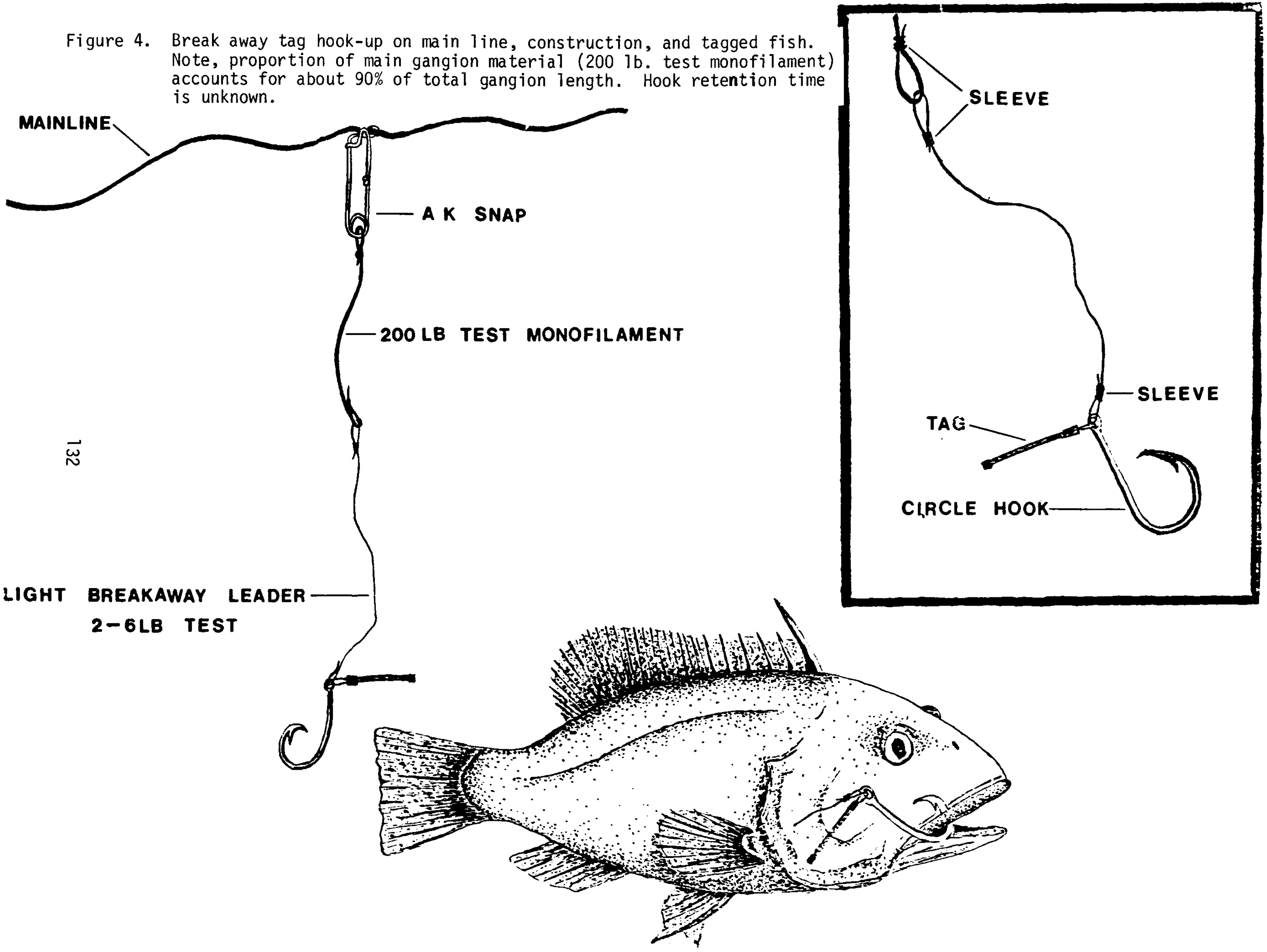
LINE GEAR

Bottom longlines, handlines, vertical lines, and electric or mechanical fishing reels can be used anywhere, but are most applicable on rough, steep-sloped areas where other gear cannot be used. Handlines and electric reels on large vessels are inefficient gear in depths exceeding about 200 m, because the vessels drift and lift hooks off the bottom. Small sail or motor vessels can maintain position and keep hooks on the bottom at depths exceeding 300 m by jogging into the wind or current. Bottom longline gear is frequently fished in deep water at the shelf edge or on the slope, but species composition of catches may be biased because site selection is not random. Hook size tends to make catches selective, since small-mouthed fish cannot be hooked properly with large hooks and large fish may escape easily from small hooks. Bottom longline gear cannot provide population estimates unless relatively large numbers of fish are tagged. Tagging fish from these depths, however, is nearly impossible, since the fish do not have sufficient time to decompress, and nearly all die at the surface. Fish that are alive may be punctured to release trapped gas and then tagged but survival rates, while unknown, would appear to be low. Break-away tags (Figure 4), may be more successful, but hook retention rates and mortality rates of tagged fish are unknown. This technique has been used along the east coast (Churchill Grimes[1/], personal communication) and holds some promise.

There have been handline and bottom longline explorations at depths of 30 to 400 meters throughout the Caribbean sponsored by the Caribbean Fisheries Development Project. Effort was directed toward demonstrating the feasibility of establishing a viable snapper-grouper fishery. Because research was oriented toward commercial exploitation and only good "fish sign" stations were selected, the data are biased on the high side. Results in terms of species selection and distribution are similar to ours (Kawaguchi 1974), but population enumeration is impossible.

[1/] Churchill B. Grimes, Dept. of Horticulture and Forestry, Cook College, Rutgers University, P.O. Box 321, New Brunswick, New Jersey 12409.

Figure 4. Break away tag hook-up on main line, construction, and tagged fish. Note, proportion of main gangion material (200 lb. test monofilament) accounts for about 90% of total gangion length. Hook retention time is unknown.



STOCK ASSESSMENT

At this time, we should be aware that computed density estimates have serious shortcomings. The non-random selection of fishing areas introduces a significant bias into the data regardless of fishing methods. Each gear type has its own built-in deficiency. Data sets have been haphazard, biased, and often not applicable for quantification. Despite these difficulties information can be deduced on faunal assemblages, relative abundance of species groups, distribution, broad habitat definition, and identification of potential stock exploitation areas.

Enumeration of snapper-grouper stocks within the South Atlantic, Caribbean, Gulf of Mexico and along the northeast coast of South America is difficult. Over the years effort by various governmental agencies has been implicitly directed toward the demonstration of commercial feasibility. Fishing stations, therefore, were selected for high fish density to demonstrate high catch rates. In spite of biases the data are useful in determining location of high fish density areas and in defining their carrying capacity.

HABITAT EVALUATION

Because of patchy species distribution, evaluation of habitat and carrying capacity is of prime importance in establishing realistic assessment techniques. Evaluation may be with electronic gear such as side scan sonar or up-to-date, over-the-side photo/video systems, which have the capability of rapidly delineating bottom topography in measurable units. Survey techniques should initially employ rapid assessment gear throughout given geographical regions. Once completed, a mosaic of habitat types can be constructed and additional effect devoted to delineation of important microhabitats within broad ecological areas.

The importance of habitat evaluation is seen in several FAO cruise reports. During M/V FREGATA cruises off Surinam and Guyana from August to December 1969, fishing occurred over the following bottom types: rock, rock and sand, rock and mud, sand, sand and mud, and mud. From listed data (Table 2) it is obvious that bottom habitats of some mud had reduced catches, whereas the rock sites (except rock-mud) had high catches. Further evaluation is needed to define critical habitat based on catch rates. Catch rates on coral, rock and coral, and coral and sand (Table 2) are divergent, the lowest being on coral sand habitat of Pedro Bank. Removal of yellow tail snapper from the Honduran catch, however, reduces the weight of snapper caught per hook to .03 kg. This low catch suggests that sand coral habitat is less productive for demersal snapper-grouper species than either coral or coral and rock habitats. Deepwater habitat in the Gulf of Mexico displays considerable mud, mud and rock, and rock. Each type is variously productive but mud shows both high and low production. Relief rather than composition may be the key factor in snapper/grouper/tilefish distribution (Nelson and Carpenter 1968).

Table 2. Catch composition of snapper-grouper and total weight listed by area and bottom type based on FAO cruise data (M/V FREGATA 69-6, 7, 8 and 9, Aug-Dec 1969: and M/V ALCYON 69-4, 5, 6, 7, and 8, Apr-Aug 1969). Reported as total kilograms caught per electric or mechanical reel hook per hour.

	Surinam and Guyana		
	Bottom Type		
	Rock	Rock and Sand	Rock and Mud, Mud, Sand and Mud
Total Weight Kg	1328.0	509.0	72.0
Total Snapper Weight Kg	1241.0	509.0	66.0
Total Grouper Weight Kg	69.0	-	6.0
Sets Made	22.0	3.0	10.0
Average Hooks/Set	24.1	30.0	25.9
Average Hours/Set	10.2	6.7	9.8
Kg/Hook/Hour	.25	.84	.03

	Honduras	Antigua & Barbuda	Pedro Bank	
	Coral and Sand	Rock and Coral	Coral	Coral and Sand
Total Weight Kg	4187.0	758.0	681.0	58.0
Total Snapper Weight Kg	1278.0*	681.0	587.0	3.0
Total Grouper Weight Kg	0	26.0	12.0	.5
Sets Made	26.0	14.0	19.0	7.0
Average Hooks/Set	16.6	15.0	16.9	9.3
Average Hours/Set	10.6	12.9	5.9	7.9
Kg/Hook/Hour	.92	.28	.36	.11

*Yellow tail snapper accounts for 90% of the snapper weight. This is a semi-pelagic snapper species rather than the typical demersal snapper species.

Habitat is an important factor in reef fish distribution. Patchy distribution of snapper-grouper species occurs temporally and spatially, as demonstrated by spawning aggregations of grouper in the Virgin Islands (Olsen and La Place 1979), the concentrations of red snapper off the Guyana coast (cruise report M/V CALAMAR #33) and the high concentrations of snowy grouper caught with an off bottom squid trawl (cruise report F/V PESCAPUERTA SEGUNDO Cruise 78-01, NMFS Pascagoula, MS). Red snapper catches as reported by the M/V CALAMAR off Guyana ranged from 0 to 3,483 kg. During 3 M/V CALAMAR cruises, 8,228 kg were caught, with 43% being taken from one station that exhibited a low rock outcrop about 6 feet above the surrounding bottom. This spot is located approximately 30 miles from a similar area at which the M/V FREGATA caught a similar number of red snapper in two days. Both areas showed low relief profiles and appeared to be ecologically similar.

Snapper schools, are more compact, dense, and mobile than grouper schools except for spawning aggregations. Grouper are generally more territorial and display greater dispersion within a reef system, and show only limited movement within the reef (Randall 1962) habitat. Seasonal breeding aggregations of grouper, numbering up to 150,000 fish, may represent a significant portion of the grouper population within defined geographical areas (Olsen and La Place 1979). During a cruise of the PESCAPUERTO SEGUNDO (Spanish squid trawler) 1,070 snowy grouper weighing 7,331 kg were taken at two trawling stations off South Carolina in 204 and 236 meters. Trawls were off-bottom squid trawls with bobbins, and were fished about 1 meter above the sea floor. Ecological factors, such as temperature, may be as important as bottom composition in determining the distribution of deepwater snapper-grouper species.

Increased soak time of bottom longlines may result in decreased catch rates (Kawaguchi 1974), suggesting that fishing lines either immediately encounter fish on the bottom or do little to attract new fish. Escapement and possibly predation could also be high on fishes left on the line for 4 to 6 hours. The patchy, rather than random, distribution of hooked fish over the entire fishing line suggests that once the line is set those fish which encounter the line and its bait quickly react and are hooked.

Deepwater snapper-grouper appear to be distributed in a nonrandom manner on the upper slope. Heavier concentrations of fish are seen at the shelf break regardless of depth (Fig. 5) and highest catches generally are made along the shelf edge or the immediate down slope. Bottom composition, gradient, and temperature are important in the distribution of slope animals. Insular reef fish species are generally associated with bottoms of sand, rock, coral, and sponge. Continental reef and non-reef species are generally associated with bottoms of mud, sand, rock, coral and sponge. The Yucatan Slope furnishes a good example of faunal components changing with bottom composition. Along the northeastern slope, which has a gentle gradient and mud bottom, few snapper-grouper but many tilefish are taken,

Figure 5. Shelf break near 100 fathoms off the Yucatan. Note fish markings along upper edge. Ledge depth is about 120 fathoms and deep break is about 200 fathoms with no fish sign along the intermediate or lower shelf breaks.

ECHO TRACE OF SHELF BREAK, SHELF EDGE AND SLOPE BREAK WITH DISTRIBUTION OF FISH TRACES

all in intermediate zones. In areas where slope gradient is steep and the bottom is rock and coral, few if any tilefish are caught. Habitat evaluation in terms of faunal components, gradient, bottom composition and temperature is important in determining distribution and relative abundance of reef and nonreef fish species. It represents an initial perception pertaining to distribution of reef fish species. Some effort has been expended in an attempt to delineate reef fish habitat out to 50 fathoms along the contiguous U.S., but results have been less than anticipated.

Historical data sets which include catch rates and bottom type should be evaluated to delineate density and associated habitat type. Density plots of snapper-grouper species could indirectly provide preliminary information on carrying capacity. Habitat evaluation in high catch density areas coupled with estimates of carrying capacity may provide a first estimate of population levels and potential exploitation.

SNAPPER-GROUPER DISTRIBUTION

When considering biomass or standing stock, attention must be directed toward the distribution and behavioral patterns of the species involved. Snapper-grouper species are demersal throughout their postlarval lives. Younger fish generally are found in shallower depths. Considerable overlap is noted between snappers and groupers, although a species progression is evident inshore to offshore.

Major species of snapper taken throughout the western North Atlantic south of Cape Hatteras include the red *Lutjanus campechanus* and *L. purpureus*, mutton, *L. analis*, lane, *L. buccanella*, wenchmen, *Pristipomoides*, and vermilion, *Rhomboplites aurorubens*. In addition, the queen snapper, *Etelis oculatus*, though not numerous, also has been found. Snapper distribution is as follows: red, lane, mutton and vermilion snapper are generally taken in shallower depths (less than 100 m), blackfin and silk snapper at intermediately depths (100 to 200 m), and wenchmen and queen snapper at depths greater than 200 m. Fish in the more southerly latitudes should prefer increased depths if temperature exerts an overriding effect on bathymetric distribution.

Grouper display this same general pattern. Groupers in the genus *Mycteroperca* i.e. (*phenax*, *microlepis*, *interstitialis*, *venenosa*, and *bonaci*) are generally taken in the inshore areas along with red and gag grouper, *Ephinephelus morio* and *E. microlepis*. Snowy and warsaw grouper *E. niveatus* and *E. nigritis* are most frequently caught in intermediate depths, and yellowedge and misty, *E. flavolimbatus* and *E. mystacinus*, are caught in the greatest depths. Grouper are generally caught in deeper water than snapper, i.e. intermediate depth for snapper is almost 150 meters, but for grouper is about 250 meters; offshore distribution for snapper is about 200 meters, but for grouper is about 300 meters.

HOW BEST TO ASSESS REEF FISH STOCKS

This question is easy to ask, but difficult to answer. Neither trawls, traps, lines, or visual assessment can provide reliable estimates of population size or species composition. Expenditure for research has been inadequate in terms of money, manpower, or survey shiptime. The inability to realistically assess reef fish stocks should not imply that previous efforts have gone for naught, but that we must begin looking to other scientific disciplines for assistance. Future assessment cannot rely exclusively on trawls, traps, or lines but must begin to use various electronic gears, such as side scan sonar, to provide a rapid assessment of habitats. Because of diversity of fauna and habitats within the ecosystem, it is necessary to define species or faunal assemblages to be assessed. Distributional differences of snapper-grouper species are noted in terms of depth, season, and size of individual fish (Roe 1976, Kawaguchi 1974, and Thompson 1978). Considerable effort has been expended by FAO throughout the Caribbean and adjacent areas and by NMFS throughout the western North Atlantic south of Cape Hatteras. This extensive data base should be appraised in terms of snapper-grouper concentrations for habitat delineation. If there are strong habitat preferences, consistently high densities of snapper-grouper species should occur at certain localities, and sampling, therefore, should be stratified. Habitat evaluation may best be accomplished by using both visual and electronic techniques. In some cases initial assessment with electronic survey gear could provide a rough approximation of numbers, but little or no information on species or size composition. For example, where bottoms are gentle with few or no disruptions, fish counts may be quite accurate. In areas where the bottom is rough or rocky, some form of systematic sampling would be required. Fishing gear also could be used to determine species composition, faunal components, and stock density for specific habitats. Trawls should be measured throughout each haul and standardized. Presently, density estimates based on trawling are minimal. Estimates of density and species composition based on trawl samples, in conjunction with visual and electronic assessment of habitat, can provide data on carrying capacity. In areas where trawls cannot be used, passive sampling gear, such as traps and lines, can be employed. Shallow water fish may be marked with tags or clipped in some form to provide future identification. Deep water species may be tagged using break away tags on bottom longline gear.

SUMMARY

Considerable expenditure of time and money has been allocated to survey snapper-grouper stocks, define species composition, and provide data for further exploitation of these stocks. A variety of fishing gear, including trawls, traps, and lines such as handlines, electric and mechanical reels, bottom longlines, and vertical lines, have been used. Stock and habitat assessment also has been made by using towed remote sensors, such as RUFAS for video and photographic coverage, drift video and photographic systems, submersibles, and divers.

Data from fishing and remote sensors are limited for estimate of population size. Limits are quantitative rather than qualitative. Trawls sample only selected areas, which may not include areas of maximum density. Trawl efficiency is presently unknown and estimates of biomass from trawl samples do not consider the portion of the stock in the water column above the trawl. Traps and line gear are passive and fish are either attracted to the gear or encounter it by chance. Bait and gear attraction rate and distance are unknown, but some data suggest that the gear has little or no attractive value. Where embolism is no problem, trap-caught fish can be tagged and returned. Longlines create hooking stress that may cause a higher overall mortality than traps. Break-away tags provide an opportunity to tag *in situ* and reduce tagging-induced stress. Tag returns within the proximity of the tagging area may provide a preliminary estimate of deep water snapper-grouper stocks as well as information concerning species movement.

Remote sensor systems have severe depth limitations. RUFAS is unable to operate at greater than 50 fathoms and does not have automatic flight control to maintain desired depth. It may be useful for shallow water habitat assessment, but not for stock assessment, since few fish are seen. Fixed video and photo cameras do not lend themselves to stock assessment because water clarity and slow towing speed are problems. Habitat and assessment evaluation using both RUFAS and pan and tilt drift video systems present enumeration problems. Fish are often seen on the drifting pan and tilt unit, but seldom by the towed RUFAS. Fish appear to be frightened by RUFAS and attracted to the pan and tilt system. Submersibles are excellent vehicles for habitat evaluation, but are useless for estimating stock size or density. They may be the best visual system available for counting large species. Submersibles present considerable survey and logistic problems, because of their slow survey speed, limited coverage, and high cost.

Habitat can be evaluated rapidly by side scan sonar or other sophisticated electronic gear. Once habitat has been defined, assessment of carrying capacity by habitat types throughout the survey area may be possible. After definition of carrying capacity and delineation of habitats, a first cut estimate of snapper-grouper populations may be computed. Additional effort will result in continual upgrading and refinement in population estimates.

Proper evaluation of snapper-grouper stocks and their habitat will require a considerable outlay of funds to increase efforts concerning environmental and habitat appraisal and realignment of manpower in terms of research activity and ship survey time. This effort will require coordination between fishery scientists and scientists from other disciplines. Resource assessment is a complex undertaking and requires more input than merely dropping some fishing gear where signs are good. A solid, well designed survey using random sampling methods in conjunction with habitat evaluation is required if realistic values are to be provided on the size and availability of snapper-grouper stocks throughout the southeast. This effort should have a high priority for future NMFS research.

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SESSION SUMMARY
ASSESSMENT OF REEF STOCKS

by

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Introduction

This session was devoted to methods of assessing reef stocks by means other than analysis of recreational and commercial catch-effort data.

Barans presented the overview paper in which he stressed the importance of planning to obtain a quantifiable end product and a greater understanding of the biology of the species. Particular consideration should be given to gear selectivity and sampling design. Complementary sampling gear should be used to obtain the best estimates of abundance. The paper by Gutherz discussed the assessment efforts of the Southeast Fisheries Center. He pointed out that reef fishing has increased considerably in the past several years, and that this has caused fishery management councils to place high priority on assessment of snapper-grouper stocks. The importance of sampling design and multigear surveys was again emphasized. The advantages and disadvantages of the various sampling techniques were discussed in both papers as well as the importance of gear mensuration.

In my paper I showed that still photography cannot be used for reef fish abundance counts because many fish fade into the background and cannot be counted. By comparing mark-recapture data to diver counts I also showed that too few fish are tagged and recaptured during large area (1/2 mile x 3 miles) reef fish studies for meaningful estimates by mark-recapture techniques. I further presented data showing that counts made from submersibles are as good as those made by divers. Thus, submersibles can be a useful tool when attempting to measure reef fish stocks over large areas and in deep water inaccessible to divers.

Discussion

Jack Damman said that Caribbean shallow water reef fish are being fished near maximum sustainable yield. There is an urgent need to explore and develop, if possible, deep water (100-300 fms) fisheries. Submersibles and side scan sonar may be the best methods of exploring these areas.

Churchill Grimes and Charles Barans emphasized the importance of visual techniques for stock assessment and a need to use a variety of complementary sampling gears.

John Ogden emphasized the large species diversity and complex systems on reefs and that all species are important in these systems and should be studied. Jack Damman suggested that applying methods for measuring terrestrial populations be looked at more closely. Gene Huntsman asked if extrapolation from quadrat counts would be better than line transects. Joe Powers and Saul Saila favored line transects and multiple gear sampling.

Gene Huntsman proposed the ultimate stock abundance sampling gear, REEFFAS, REEF Fish Assessment System. This system would consist of several color television cameras mounted in a frame that could be lowered from a vessel to the bottom and would photograph the entire hemisphere of visibility in which it sat. Multiple images could then be projected in a hemispherical viewing chamber aboard the vessel such that an observer inside the chamber would have essentially the same view as a diver sitting on the bottom. Such a device seems achievable with todays technology. Development of this instrument would combine the advantages of placing man in the sea with the low cost, deployability, and safety of remote techniques.

Suggested order of research

1. Explore deep water (100-300 fms) reef fisheries in the Caribbean. Shallow water reef fisheries are near maximum sustainable yield.

2. Develop new stock assessment sampling gear. Current gear is inadequate or too costly to do the job appropriately.

    A. 360° viewing system
    B. shadow graphing side scan sonar

3. Calibrate stock assessment sampling gear so that complementary sampling results can be compared.

4. Determine the amount of reef fish per-unit-area of habitat, and measure the amount of habitat. Then determine reef fish biomass by multiplying the two. Potential yield, independent from that obtained from catch-effort data, can then be calculated from the biomass estimate.

SESSION 5

Reef Fish Communities

Chairman

Edmund S. Hobson, Jr.

FISHERIES MANAGEMENT AND THE STRUCTURE OF CORAL REEF FISH COMMUNITIES

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INTRODUCTION

In recent years the concept of the biological community has been applied with great frequency by investigators of coral reef fishes. The simplest definition of a community is an assemblage of populations of fishes. It is essential, however, to stress the number and complexity of interactions between fish fauna and invertebrate and algal components of the reef as well as interactions between fish species themselves.

Reef fish communities are amenable to study on a small scale because of the relatively sedentary nature of many species and the extraordinary regularity of movement in others. Thus, minimal or predictable interchange of fauna can be assumed between nearby habitats. There will be relatively few connections between a section of a large reef and contiguous sections on the other side. Most biological research on coral reef fish communities has been on small natural and artificial structures, but management must occur on a much larger scale. Therefore, the legitimacy of generalizing from research on small structures to application on a large scale is not yet known.

From the point of view of management, knowledge of certain aspects of fish community structure is critical. 1) What relationship is there between island characteristics, primary productivity and fisheries potential? 2) What effect do reef structure and resources have on the fish fauna? 3) What is the trophic structure of reef fish assemblages and how is it altered by fishing pressure? What long term effects does this have on the coral reef community? 4) Under what conditions will the fish community bounce back from the disturbance of fishing? When will it be permanently altered along with other elements of the coral reef community? 5) How is recruitment of juvenile fishes affected by local and regional depletion of fish populations? 6) What biological and physical factors determine successful recruitment into the coral reef system? The state of our knowledge on these questions and their relevance to fisheries management problems will be discussed below.

METHODS OF STUDY OF REEF FISH COMMUNITIES

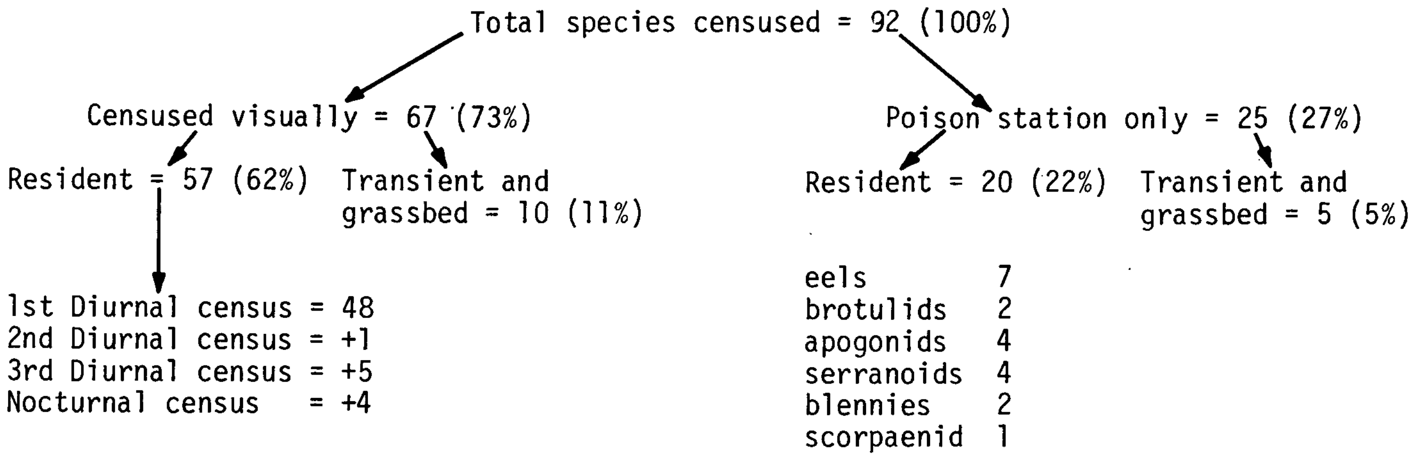
Traditional fisheries methods such as hook and line fishing, traps, nets, and trawls have generally not been useful in assessing reef fish stock, primarily because of sampling difficulties and the complex three-dimensional nature of the reef substrate. Visual techniques of various kinds have been used in nearly every piece of scientific research on coral reef fishes, and we predict that visual techniques will eventually prove to be of great usefulness in reef fisheries management (see for example Great Barrier Reef Marine Park Authority, 1978). Figure 1 shows a census made on a patch reef approximately 10 meters in diameter in St. Croix. The reef was censused visually on several occasions both day and night and then was poisoned with rotenone to capture the highly cryptic or hole-dwelling species that would be expected to be missed in any visual census. Sixty-seven species were censused visually. Note the rate at which species were added following the first diurnal census and the number of species added during the one nocturnal census. Twenty-five additional species, all either small, transient, or cryptic species that could be accurately censused visually, were collected after treatment by rotenone. The investigator using visual techniques must accept the fact that certain components of the fish fauna will be missed, and make certain that the level of census accuracy is compatible with the goals of the study. An extension of the visual technique involves the use of both still and movie cameras. These have been used to film transects or sample smaller areas repeatedly and may be later viewed at leisure, often on a frame-by-frame basis. Although television has been rarely used because of its expense, it will doubtless prove to be a useful tool in the future.

Experimental and manipulative techniques have been used to great advantage by researchers on coral reef fishes. These techniques have been quite varied but often employ artificial structures, particularly those made of concrete blocks or common materials. Other variations on these techniques involve the removal of selected components of the reef fish community, such as large predators, or the defaunation of whole structures with subsequent study of the re-colonization events. Often these experimental techniques provide the only means whereby relatively complex questions about reef fish communities may be approached.

REEF FISH COMMUNITY STRUCTURE

Coral reef fish communities consist of a large number of species. In an assessment of a 10m section of a 150m wide reef in St. Croix by both visual techniques and fish toxicants a total of 125 species was recorded (Ogden, unpubl). On an even smaller patch reef 92 species were recorded (Table 1). The total fauna of St. Croix is estimated to be approximately 400 species. Thus in these structures and small areas of larger structures approximately 1/4 of the total species for the region can be found. A great many species found on coral reefs are relatively rare, represented at most by one or two individuals. Only a very few are represented by large numbers. It is often tempting to consider these as the "important" members of the community and to ignore the large numbers of rare species. Alteration of the numbers of certain rare species, however, such as large predators may have extensive effects in the community.

Table 1


Total species censused = 92 (100%)
Censused visually = 67 (73%)
Resident = 57 (62%)
Transient and grassbed = 10 (11%)
1st Diurnal census = 48
2nd Diurnal census = +1
3rd Diurnal census = +5
Nocturnal census = +4
Poison station only = 25 (27%)
Resident = 20 (22%)
Transient and grassbed = 5 (5%)
eels 7
brotulids 2
apogonids 4
serranoids 4
blennies 2
scorpaenid 1

The populations composing a community have a characteristic age structure which is often easy to observe because of the striking color differences between juveniles and adults. In the highly territorial damselfishes such as the three-spot damselfish, Eupomacentrus planifrons, juveniles occupy marginal habitats and constitute a pool of recruits ready to move in to adult habitat as space becomes available. The rate at which this process occurs is not known.

Closely related to age structure is size structure. Smith (1978) shows the distribution of the mean sizes of the largest specimens collected from a community of coral reef fishes in the Bahamas. The means form a monotonically increasing smooth curve. Each species appears to be larger than the next smaller species by a constant fraction. The cause of this peculiar size distribution is not known but it may be assumed to be a result of the interaction of the species constituting the community. Age and size structure are very responsive to fishing pressure. As fishing pressure increases size and age tend to shift towards smaller individuals and eventually smaller species.

Reef fish communities have a trophic structure. It has become convenient to divide the complex trophic structure of the community into a set of guilds - all the members of a guild having the same method of feeding. Depending on the way in which guilds are defined there may be a large number or a relatively small number of guilds in any reef fish community. Table 2 shows a comparison of a small number of guilds in St. Croix and in Enewetak in the Marshall Islands (Gladfelter, Ogden and Gladfelter, in press). One may be impressed by either the similarities or the differences between the two locations. For instance, note the striking diversity of planktivores in Enewetak and the greater number of crustacean feeders in St. Croix. The other guilds appear to be about equally represented in the two sites. From the standpoint of individuals, perhaps the differences are a bit more obvious. Division of the community into guilds shows a clear separation between the many species in the community. However, within a given guild, there may be fine partitioning of food and space resources or extensive overlaps. The extent to which members of a guild partition or overlap has important implications in community responses to disturbance.

ARE REEF FISH COMMUNITIES PREDICTABLE FOR SIMILAR HABITAT STRUCTURES?

In recent work on the structure of coral reef fish communities, two general points of view have emerged. Sale (1975, 1977) and others (Talbot, Russell and Anderson 1978) suggest that high diversity in coral reef fish communities is maintained by chance arrival of larval colonists to unpredictably available habitat space. This view is countered by work on reef structures in the Caribbean and in the Gulf of California where communities were relatively predictable for particular types of habitat. This finding leads to the conclusion that adaptive responses to habitat, competition, and predation cause the orderly structuring of reef fish communities (Smith 1973; Smith and Tyler 1975; Molles 1978). One problem in trying to reconcile this controversy is that work in both locations has been on relatively small

Table 2

Principal food category	Principal activity period	ST. CROIX			ENEWETAK		
		Mean No. individuals per reef	Percent (individuals)	Approximate No. species	Mean No. individuals per reef	Percent (individuals)	Approximate No. species
Plants	Diurnal	329	38.8%	22	156	25.5%	37
Plankton	Diurnal	10	1.2%	4	151	24.7%	20
	Nocturnal	30	3.5%	8	48	7.9%	8
Crustacea	Diurnal	11	1.3%	8	100	16.4%	34
	Nocturnal	69	8.1%	21	24	4.0%	11
Invertebrates	Diurnal	180	21.5%	28	108	17.7%	49
	Nocturnal	200	23.3%	8	-	-	-
Fish	Diurnal & Nocturnal	18	2.1%	17	31	5.0%	19

structures. Gladfelter et al. (in 1980) tried to resolve the problem by doing comparative studies, one in the Caribbean and another in the Central Pacific. They used the same observers and applied the same visual censusing techniques to large reef structures of similar size, ranging from several hundred square meters to several thousand square meters. Using a similarity index that compared all possible pairs of reefs and the abundances of all species on the reefs, the observers constructed a dendrogram showing similarities of the patch reef fish faunas. The reefs of particular structural characteristics in both locations are in clusters. The average similarity levels of clusters in both locations were approximately 0.6. The general conclusion is that with a relatively small amount of reef structural information (depth, height, location with respect to major reef fronts and the open ocean) the fish community of a reef can be predicted with a reasonable degree of accuracy. Because of the habitat and food specializations characteristic of many reef fishes, structures that are sufficiently large to contain a broad range of available habitats eventually will be colonized and inhabited by particular species whose requirements are met. The predictable nature of fish assemblages becomes then very important in our understanding of the potential range of response of the reef fish community to disturbance.

RESPONSES OF REEF FISH COMMUNITIES TO DISTURBANCE

The responses of biological communities to disturbance is a very active area of research in modern ecology. Here we broadly define disturbance as adjustments to the structure of the community brought about by predation, fishing, storms and any other factors that would tend to eliminate segments of the fish community. From the standpoint of a fishery, perhaps the most elementary question we may ask is: what is the effect of the removal of a single individual from a reef fish community? If we remove a single territorial damselfish, we might expect several possible outcomes. The territory might remain unoccupied, the contiguous territories of neighboring damselfish might expand to include the vacated territory, or a juvenile might move in to occupy the vacated space. All three of these outcomes have been observed. If we remove a large predator from a reef such as a grouper, for example, what might we expect the outcome to be? Spear fishermen will claim that removal of a large grouper will lead to the relatively rapid substitution of a similar individual often located in the same exact section of the reef. In other examples, this obviouly would not occur. It is important to distinguish what happens over the short term with what happens over a longer term. Because of the relatively stochastic nature of short term recruitment it may not be possible to predict the actual species which will take over when an individual is removed. Over a longer term, however, this prediction might become possible.

The more complex question is what is the effect of the removal of larger numbers of individuals from the reef fish community? Depending on the trophic level of the individuals removed, we might expect dramatic effects in the individuals occupying the trophic level directly below the fishes removed. Working in benthic communities, Paine (1966) and Lubchenco (1978) have shown that removal of the top carnivore or herbivore in a sub-food web of a community can lead to striking adjustments in the diversity of the prey species. The prey species differ in competitive abilities and in the absence of predation the superior competitor will dominate the community. This has been called the keystone species concept, and may have application to management decisions with reef fishes although very little is presently known. Ogden (unpublished) showed that the removal from a small patch reef of large numbers of the herbivorous sea urchin, Diadema antillarum, led to very long-lasting and broad-scale changes in the structure of the algal-coral association on the reef. There was a dramatic increase in the biomass of algae on the reef and a subsequent decrease in the number of stony coral colonies present. Algae are superior competitors for space compared to stony corals. One might expect that following a disturbance a reef would eventually recover to the previous state. However, the small reef denuded of Diadema has not returned to its original condition after seven years (Ogden, unpubl.). Whether or not we might expect similar changes to occur in the algal community if, for example, we were to remove large numbers of grazing fishes such as parrotfishes, is not known. Diadema itself may be an example of an organism which has apparently responded dramatically to the overfishing of its predators. West Indian reefs in some locations support very high densities of Diadema; up to 20 per m^2. Randall (1967) lists over 15 species of reef fishes which he found to have Diadema in their gut contents. Many of these fishes are also major species in the fish trap fishery. It is at least conceivable that removal of the larger individuals of these predatory species has led to broad-scale adjustments in the density of Diadema populations.

Ogden and Ebersole (in press) studied the events following the construction of a large artificial reef on the south coast of St. John in 1960 (Randall 1963). Approximately two years following its construction the reef had been colonized by approximately 55 species of reef fishes (Fig. 1, data from Randall (1963)). At this time Randall (1963) surrounded the reef with a net, poisoned all of the fishes and listed them by species and abundance. Ogden and Ebersole (in press) returned in 1975 and did detailed visual censuses each year for 4 years. Their results indicate that recolonization of the reef following defaunation resulted in a fish fauna virtually identical to the original one. Brock, Lewis and Wass (1979) found the same result following the fish defaunation of a patch reef in Hawaii.

Disturbance, depending on what portion the reef community it acts upon, can produce opposing results. Alteration of the resources of the reef, either physical structure or the food supply, can lead to major alteration in the composition and abundance of the fish fauna. In contrast, removal of whole fish assemblages appears to result in no long-term changes in fish community structure given an adequate period for recolonization. The effects of continuous removal of certain parts of the fish community as occurs with fishing are not yet understood.

RECRUITMENT OF REEF FISHES

Critical to our understanding of responses to disturbance is a much more detailed knowledge of the reproductive periodicity, planktonic

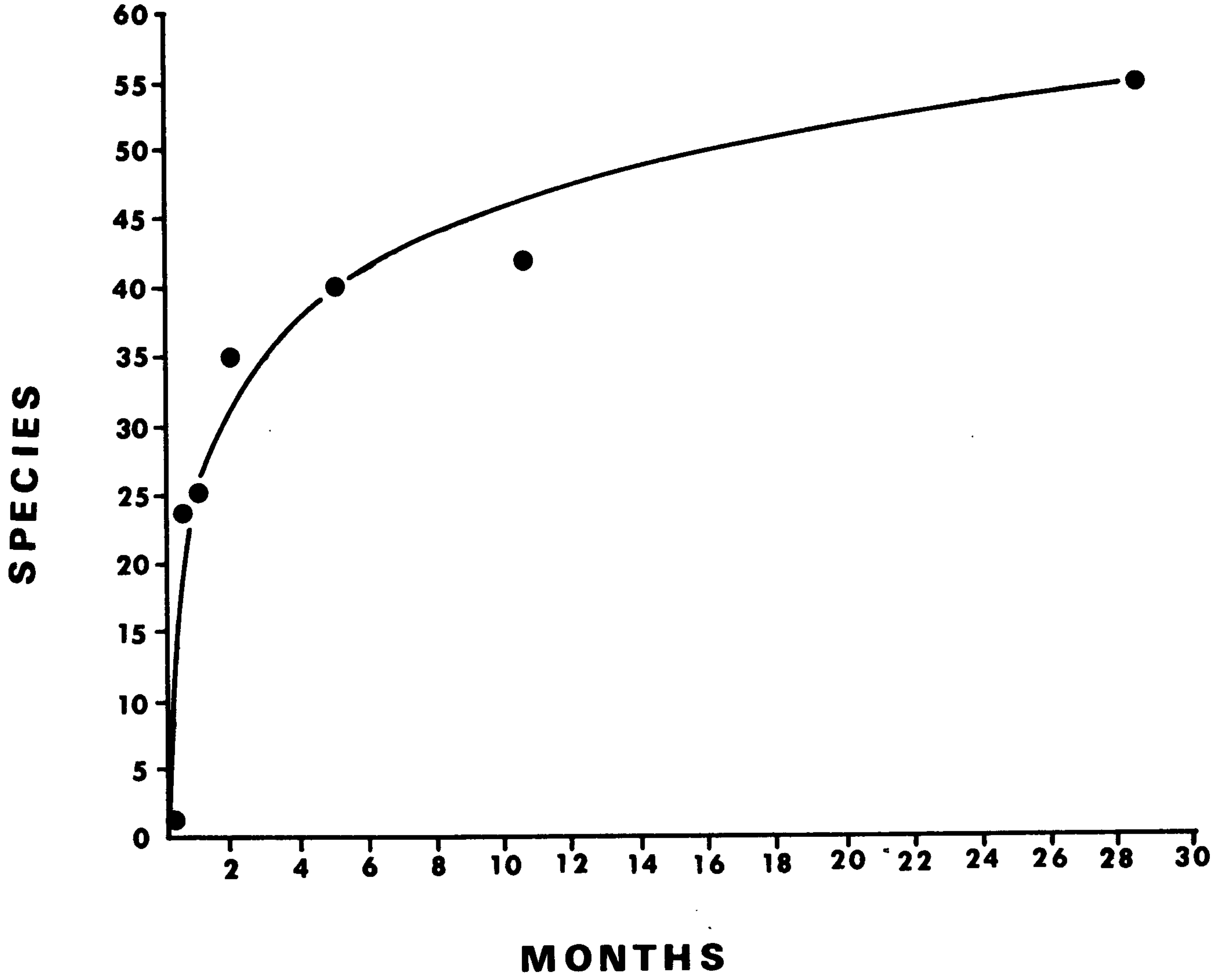


Figure 1. Colonization curve for Randall Reef, St. John, U.S. Virgin Islands.

larval life, and events surrounding recruitment from the plankton. What are the events that occur between recruits as they settle and what interactions occur between recruits and established residents? Shulman et al. (in prep.) studied the early events of recruitment, examining a series of artificial reefs intensively for a short period of time from an underwater habitat. Thirty reefs were constructed of which half were experimentally colonized with a single territorial damselfish (Eupomacentrus leucostictus), the beaugregory. The most dramatic result is that their presence inhibits colonization by reef butterflyfish and surgeonfish. The timing of recruitment of particular larvae also influences the eventual structure. Shulman et al. (in prep.) show that when snappers and grunts settle simultaneously on the same structure they may coexist. But if snappers arrive first and grow large enough to become picivorous, the settlement of grunts is precluded.

Recruitment may be either by plankton or by migration of juveniles from nearby habitats. For example, Ogden and Ebersole (in press) surmise that much of the recruitment to Randall Reef occurred via migration. The patterns of this process may be quite interesting. Shulman (personal communication) has shown that recruitment of fishes to small structures has a particular pattern in relationship to the distance these structures are placed from a major reef. Recruitment to identical structures is lowest near a major reef and increases to a point about 30m distant from the reef beyond which it appears to decrease. The reasons for this pattern are presently under investigation, but may have great relevance to the placement of artificial reef structures designed to increase reef fisheries.

PRODUCTIVITY POTENTIAL OF REEF FISH COMMUNITIES

Although the standing crop of reef fishes is high, available estimates (Brock 1954; Bardach 1959; Randall 1963; Goldman and Talbot 1976) ranging up to nearly 2 metric tons/hectare are undoubtedly too high. These high estimates are the result of assessments in overly restricted areas or assessments which include species that are resident in or dependent upon communities, such as seagrass beds, that are closely associated with coral reefs. A critical question approached in this workshop is how reef fish stocks may be assessed. In spite of a high standing stock, productivity of reef fishes may be low. Productivity may be especially low for classes which form the basis of most reef fisheries. The coral reef is one of the most productive biological communities on earth, but because of the close connections in symbiosis between many reef organisms, it can be thought to be a "closed" system. Thus we find that many reef dwelling fishes such as grunts (Pomadasyidae) either feed elsewhere in seagrass beds, for example or are found during their juvenile stages in seagrass beds or mangrove swamps. These interdependencies upon different habitats make it extremely important that communities such as mangroves and seagrass beds be assessed along with coral reefs when the fishery potential of an areas is considered.

The islands of the Caribbean are essentially bathed in water which has been considered a "biological desert". Levels of nutrients are extremely low. An island has the potential of increasing or enriching its nearshore waters by various means. Table 3 shows a hypothetical island productivity gradient involving island size, island height (directly related to amount of rainfall and terrestrial runoff), area of bank, and complexity of coastline, such as embayments that would support growth of mangroves. We would speculate that the primary productivity potential of an island and also the productivity of potential fisheries would move along such a gradient. The relationships between the physical characteristics of islands, primary productivity, and fisheries productivity merit further investigation.

CONCLUSIONS

The coral reef fish community is a diverse assemblage of species populations with complex interactions. The fishery based on this community is locally very intense and equally diverse. This complexity will force managers to make decisions based on greatly increased effort in research at the community level. The techniques used will be new or greatly modified from the traditional fisheries assessments, monitoring and management methods which have been used in less complex fisheries. This does not mean however that the biology of individual species can be ignored in favor of community level structures. Implicit in our future understanding of reef fish community function and response is a greatly increased level of knowledge of reef fish biology: reproduction, recruitment, growth, feeding and energetics. Although we are lacking in most cases even an elementary knowledge of these factors, it is possible to proceed with tentative management steps while we also initiate the multidisciplinary studies that will verify or modify those steps in the future.

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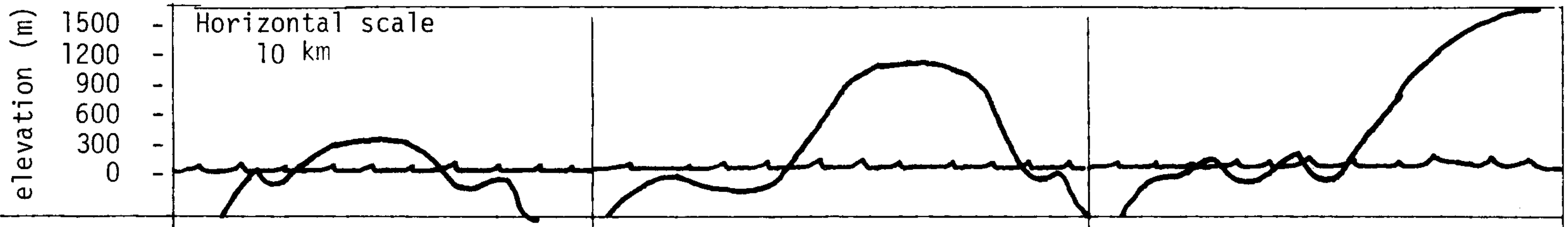
Table 3

Hypothetical island productivity gradient for the Caribbean.



Feature/Parameter	Small, low, dry island	Larger, higher, wet island	Very large, high, wet island
Physiographic detail			
shelf	small	medium	large
coastline	relatively smooth	convoluted	complex, many bays, offshore cays
Climate/Oceanographic			
rainfall/runoff	sparse	seasonally heavy	permanent rivers
current/wave action	strong to severe	medium	coast protected
Sediments/nutrients			
detritus accumulation	low, much export	medium	high
sediment organics	low	medium	high
terrigenous influence	negligible	moderate	high
General Biological Features			
coral reefs	well-developed	shelf edge	offshore
seagrasses	sparse or absent	patchy	abundant
mangrove	sparse or absent	patchy	abundant

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THE STRUCTURE OF FISH COMMUNITIES ON WARM-TEMPERATE AND TROPICAL REEFS

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INTRODUCTION

Nearshore fish communities are structured in response to local conditions, and so are best characterized by comparing communities from differing ecosystems. Particularly insightful are comparisons between communities at different latitudes because community structure is known to vary with latitude in many groups of animals and plants (Wallace 1878; Fisher 1960). In general, communities at lower latitudes include a greater variety of organisms, and Pianka (1966) contended that knowledge of this relationship between latitude and diversity aids understanding natural selection on community organization. These concerns should be of particular interest to the Southeast Fisheries Center because the Reef Fish Program of that organization spans a variety of communities on both warm-temperate and tropical Atlantic reefs.

This presentation compares the structure of fish communities on warm-temperate and tropical Pacific reefs. The comparison is between reefs at Santa Catalina Island, California (lat. 33°28'N, long. 118°29'W) and at the Island of Hawaii (lat. 19°30'N, long. 155°35'W). Although the data represent just two locations, the concepts developed are based on widespread experience in tropical and temperate seas. Only the major points of the study are outlined here, details are in a manuscript now being prepared for publication. I consider trophic relationships the primary forces in determining community organization. The comparisons involve counts of the fishes seen while using SCUBA along established 25 x 4 m transect lines in four representative habitats between shore and depths of 20 to 35 m at each location. Details of the methods used, with discussion of its strengths and weaknesses, are given elsewhere (MS, in prep.).

THE REPRESENTATIVE HABITATS

A major difference between the two locations is in their predominant biological features. The warm-temperate Californian habitats are dominated by benthic macroalgae, whereas the tropical Hawaiian habitats are dominated by scleractinian corals. Thus, the four Californian habitats were characterized as: 1) a kelp-forest habitat, which was dominated by a dense stand of giant kelp, Macrocystis pyrifera; 2) an algal-field habitat, where the major feature was an expanse of low algae, mostly Dictyopteris zonaroides; 3) a coralline habitat, dominated by a rich covering of coralline algae, mostly Calliarthron tuberculosum; and 4) an algal mat habitat, which featured a dense turf composed chiefly of *Plocamium pacificum*, and other red algae. In comparison, the four Hawaiian habitats were characterized as: 1) a protected reef habitat, which was dominated by a variety of massive and branching stony corals, mostly *Porites* spp.; 2) a boulder habitat, where the major biological features were encrusting corals, especially *Porites lobata*, and isolated heads of *Pocillopora meandrina*; and 4) an outer drop-off habitat that was dominated by fields of branching corals, mostly *Porites compressa*. These predominating biological features, both warm-temperate and tropical, were strongly influenced by three variables: nature of the underlying substrate, water depth, and relative exposure to wave surge.

Another major difference between the two locations was the extent to which the character of their habitats changed over time. The Californian habitats changed continuously and profoundly during more than eight years of monitoring (1972 to 1980), but during an even longer span (1969 to 1980) I failed to detect comparable transformations in the Hawaiian habitats. Significantly, this major difference between the two environments seems related to normal life-history characteristics of the predominating biological features--the profound changes associated with the rapidly progressing life stages of the large brown and red algae in California, in contrast to the relative absence of change in the comparatively slow-growing corals in Hawaii. In addition, during the course of the observations cited here, grazing organisms--primarily mollusks and echinoderms--often substantially affected the condition of the algae-dominated Californian habitats, but fishes and other organisms that preyed continuously on the Hawaiian corals failed to have a comparable impact. There were exceptions: for example, a severe storm during January 1980 generated wave surge that reached to exceptional depths and devastated the fragile branching growth of *Porites compressa* in some parts of the study area. But it is, in fact, the infrequence of such events that makes them especially noteworthy. Equally devastating episodes of storm damage to the dominant stands of algae are commonplace in California, and so pass without special notice.

THE FISH COMMUNITIES

There are far fewer species of fishes in the warm-temperate Californian habitats than in the tropical habitats. For example, I counted only 38 species on 33 transect lines over three years (1972 to 1975) in the four Californian habitats, compared to 133 species on 22 transects over one year (1969 to 1970) in the four Hawaiian habitats[1].

This difference in numbers of species between the two locations can be linked to their trophic relationships. Despite their great variety, forms can be grouped on the basis of how much the feeding morphology of each has diverged from that of its more generalized ancestor. The pro-

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[1] Additional data from two of the four Californian sites (1975-1980), and from three of the four Hawaiian sites (1974, 1977-1980) are not included but are entirely consistent with these figures.

liferation of actinopterygian teleosts from a relatively few ancestral forms early during the Cenozoic, which led to most of the species in present day reef communities, was a radiation from these generalized types (Gosline 1959; Shaeffer and Rosen 1961; Hobson 1974).

GENERALIZED FEEDERS

The generalized feeder, in simplified form, is a large-mouthed predator adapted to directly approach and seize prey that are fully exposed to the attack. These prey are small enough to be manipulated, yet large enough to be grasped; and they lack armored encasements, as well as strong spines, spicules, or other noxious components that would make them unpalatable to fishes without appropriate specialized feeding equipment. Although even the most primitive fishes on modern reefs have some trophic specializations, many can be loosely grouped as generalized feeders. They include most of the piscivores, as well as many predators on motile crustaceans that have a dimension greater than about 2% of the predator's standard length. Generally these prey are moving when captured. The predators that feed on fishes are most active by day or during twilight, but those that feed on crustaceans are active primarily after dark, when the crustaceans are most exposed to straightforward attacks. Fishes with these characteristics on Californian or Hawaiian reefs represent the families Muraenidae, Holocentridae, Scorpaenidae, Hexagrammidae, Serranidae, Priacanthidae, Apogonidae, Carangidae, Haemulidae, Sciaenidae, Cirrhitidae, Cottidae, Clinidae, Gobiidae, and Bothidae. Significantly, fishes with these characteristics were represented by similar numbers on both warm-temperate and tropical transect lines: 21 (of 38:55%) on the Californian reefs, 27 (of 133:20%) on the Hawaiian reefs.

SPECIALIZED FEEDERS

As noted earlier (Hobson 1974): "Most fishes inhabiting tropical reefs today . . . represent specialized offshoots from the main teleostean line." The specializations referred to are linked to trophic relationships and are the basis for much of the variation in form that occurs among the fishes in coral-reef communities. These specializations involve an array of feeding structures and behaviors adapted to cope with specific defensive characteristics of their prey (Hobson 1974). Three major categories are evident: 1) predators on sedentary prey on substrate, 2) herbivores, and 3) diurnal planktivores.

Predators on sedentary prey on a substrate, the most diverse group, reflect in their feeding structures and behaviors the myriad defenses used among the vast array of sedentary organisms that populate reefs. Typically, these prey are fortified with toxic or noxious components, like spines, spicules, nematocysts, or tough, fibrous tissues; or they are encased in heavy armor. Predators that would feed on them require specialized feeding structures--generalized feeding equipment will not do the job. Thus, the strong oral or pharyngeal teeth in many of the Embiotocidae, Labridae, Balistidae, and Tetraodontidae (to mention species on the Californian or Hawaiian reefs) are capable of crushing the armor of stony corals, echinoids, or mollusks. And the digestive system in many of the Chaetodontidae, Monacanthidae, and Canthigasteridae can tolerate the spicules, nematocysts, and fibrous tissues of sponges, hydroids, and tunicates. Some can even digest such materials as coral mucus. Other prey are safe from the generalized predators because they rest in crevices or beneath sediments, but many in crevices are taken by specialized fishes with protruding snouts, like certain of the Chaetodontidae, and many buried in sediments are detected and captured by fishes with sensory barbels, like species of the Mullidae. To capture forms like tiny amphipods, which here are considered sedentary when at rest on a substrate, the predator must perform delicate manipulations and movements that are beyond the capabilities of most larger generalized predators. Well suited for this task, however, are the small mouths and agile bodies in many species of the Labridae, and other families. Species with feeding specializations of this sort were far less numerous in the warm-temperate habitats than in the tropical habitats: 11(of 38:29%) on the Californian reefs, 57 (of 133:43%) on the Hawaiian reefs.

The Herbivores share certain characteristics with species in the previous category. Most notably, they tend to have relatively small mouths that are part of highly evolved feeding systems. In fact, five of the families with representatives in the previous category--the Pomacentridae, Chaetodontidae, Blenniidae, Balistidae, and Monacanthidae--also include herbivores. And some species feed regularly on both plants and sedentary animals. Clearly the distinction between these two categories is indistinct. In both there has been strong selection for plasticity in feeding structures and behaviors, and features adaptive for plucking invertebrate animals from the seafloor need little modification to graze on benthic plants (Hobson 1974). The major evolutionary challenge for the herbivores has been the acquisition of means to digest plant tissue, and among marine fishes this feature is widespread only among the more advanced groups (Hiatt and Strasburg 1960). A few families seem to be primarily, or entirely, herbivorous. On Californian or Hawaiian reefs these include the Kyphosidae, Scaridae, and Acanthuridae. Although most of the herbivores take their food from the seafloor, some feed on plant fragments drifting in the water column. Consistent with the specialized feeders in the previous category, herbivores were far less numerous in the warm-temperate habitats than in the tropical habitats: only 3 (of 38:8%) of the species on Californian reefs were considered herbivorous (and with some question), compared to 36 (of 133:27%) on the Hawaiian reefs.

Diurnal Planktivores, too, have highly specialized feeding morphologies that have diverged markedly from those of their more generalized ancestors. Most are characterized by modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively consume tiny organisms in the water column (Davis and Birdsong 1973). These specializations are adaptive because zooplankters that populate the nearshore water column by day, including cladocerans, copepods, and various larval forms, tend to be very small--less than 2 mm in their greatest dimension (Hobson and Chess 1976). Prey of this size are too small for all but juveniles of most generalized predators. Representatives on Californian or Hawaiian reefs include species of the Atherinidae, Chaetodontidae, Pomacentridae, Acanthuridae, and Balistidae--all of them strictly diurnal feeders. Obviously the planktivorous habit is shaped by very different selection pressures at night, because an entirely different array of fishes are involved at that time. A generalized feeding morphology becomes adaptive after dark, and except for enhanced sensory development that permits hunting in dim light (e.g., large eyes in the Holocentridae), and an upturned mouth in some (e.g., holocentrids of the genus Myripristis), the noctural planktivores have feeding equipment like that of other generalized predators, and are included with them in this analysis (first category, above). This agrees with the fact that most zooplankters taken by fishes above reefs after dark are among the larger crustaceans and other organisms that enter the water column only at night (Hobson and Chess 1976; 1978, discuss this point).

DISCUSSION

The points made in this report need support beyond the brief outline presented above. This support exists in the greatly expanded coverage of this material now being prepared for publication, which takes the comparisons to the species level. Here my intent has been simply to show basic differences in community structure under differing environmental circumstances, and to suggest there is much predictability once environmental circumstances are defined.

Probably there are multiple and complex reasons why so many kinds of organisms are more diverse at lower latitudes (for reviews of some hypotheses, see Pianka 1966, and MacArthur 1969). There is widespread opinion, nevertheless, that tropical species tend to be more specialized (e.g., Cowell 1973). Although some investigators doubt that increased specialization is at heart of tropical diversity (e.g., Sale 1976), the larger number of species in the more tropical of the two environments studied here clearly stems from a much greater proportion of specialized feeding types. The number of generalized feeding types is about the same in both regions. This would appear to be a fundamental difference in the structures of nearshore teleostean fish communities between tropical and temperate seas. I suggest, however, that the greater diversity of teleosteans on Hawaiian reefs relates to characteristics of the coral reef habitat, rather than to more general features of tropical latitudes. So in this comparison of teleostean communities, I am, in fact, comparing communities in specific habitats--the Hawaiian coral reefs and the Californian kelp beds--rather then communities at specific latitudes. And as I pointed out earlier (Hobson 1974), much of the diversity among higher teleosts expresses adaptations to coral reefs.

The present study indicates that the more diverse array of fish species in a coral-reef community reflects the more complex system of trophic relationships in that environment. This, in turn, stems from the high proportion of specialized feeding types that can exist there only because the coral-reef environment remains relatively unchanged during the lives of most inhabitants. A contrasting condition exists in the temperate kelp forests, where the habitat experiences frequent and profound transformations related to the changing life stages of the predominating macroalgae. Such variable surroundings discourage narrowly defined specialized feeding modes. Favored instead are more generalized feeders than can accommodate the existing diverse and unpredictable food supply.

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TROPICAL MARINE SANCTUARIES AND THEIR SIGNIFICANCE IN REEF FISHERIES RESEARCH

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The concept of preserving marine areas of beauty or of special importance has been very slow to develop. This is understandable, for it has been only in the last few decades that man has entered the sea with face masks, swim fins and SCUBA on a large scale. Also, there has long been a general belief that the resources of the sea are inexhaustible so there should be no need to preserve marine life. The same sort of thinking has led to the pollution of our oceans with all sorts of wastes of terrestrial origin ranging from sewage to atomic residue.

It was not until 1935 that an area of the sea was included within the jurisdiction of the U.S. National Park Service. This was Fort Jefferson National Monument at Dry Tortugas off southern Florida. The monument, however, was created for the fort, not the marine gardens.

Even today in the United States, only 17 areas administered by the National Park Service incorporate marine sectors within their boundaries. Six are national parks: Biscayne Bay, Channel Islands, Glacier Bay, Olympic, Redwood (boundary extends 1/4 mile beyond high-tide mark but the State of California maintains jurisdiction over the waters), and Virgin Islands; two are national monuments: Buck Island Reef and Fort Jefferson; eight national seashores: Assateague Island, Canaveral, Cape Cod, Cape Hatteras, Fire Island, Gulf Islands, Padre Island, and Point Reyes; and one, Gateway, is a National Recreation area. Some, such as Acadia National Park in Maine, have boundaries extending to the low-tide mark, and hence may control tide pools, but jurisdiction is lacking for the adjacent sea.

The maritime states have established state parks on their coasts, but as in the National Park System, relatively few contain areas of the sea under full control by the states. In Florida, for example, the only marine environment the state has jurisdiction of is in John Pennekamp Coral Reef State Park (which includes Key Largo Coral Reef Reserve). This marine park is a large one, 21 miles long and 4 miles wide (Voss 1960). Florida also has 31 other aquatic preserves but it does not own the aquatic areas of these sites (Audrey Dunham, personal communication, Department of Natural Resources, State of Florida).

The first marine reserve established in the Hawaiian Islands was the Hawaii Marine Life Refuge at Little Mokuoloe Island (Coconut Island) in Kaneohe Bay, Oahu, the site of the Hawaii Institute of Marine Biology of the University of Hawaii. There are now six major marine parks in the islands which are termed marine life conservation districts. The best known in heavily visited Hanauma Bay on Oahu. The island of Hawaii has two such districts, both on its long Kona coast: Kealakekua Bay (where Captain James Cook was killed by Hawaiians in 1779), and newly created Lapakahi in the north just south of Mahukona. Lanai has one, Manele-Hulopoe (consists of two bays and a point), and Maui, two: the adjoining bays of Honolua-Mokuleia and the islet of Molokini in the channel half way to Kahoolawe. In addition, Maui has the Ahihi-Kinau Natural Area Reserve.

The atoll of Rose Island, including the lagoon and outer reef, in American Samoa is a Wildlife Refuge. The Office of Marine Resources of the Government of American Samoa has recommended that Fagatele Bay on Tutuila and the reef off the Rainmaker Hotel in Pago Pago Bay be set aside as preserves. These are also listed in the Coastal Zone Management Plan.

Guam has no marine preserves, though there has been agitation to create them.

The Trust Territory of the Pacific, long administered by the United States, is without any significant marine parks. The Seventy Islands Marine Sanctuary in the Palau Islands has no effective enforcement today. A small area of Enewetak, Marshall Islands, was unofficially declared a reserve, but with the recent return of Enewetakese to their atoll, no attempt has been made to continue this sanctuary.

The Philippine Islands seem to have a good start on a marine parks program. The Hundred Islands National Park on Luzon was established in 1940, Manila Bay Beach Resort National Park in 1954, and Agoo-Damortis Shore and Territorial Waters on Luzon in 1962. Eight other sanctuaries were proclaimed by President Marcos in 1970 (Randall 1971). Since then reserves have been set aside at the Southern Luzon Marine Biological Station, Macajalar Bay Marine Biological Station, Puerto Galera Marine Biological Station and Reserve on Mindoro, and Matabungkay Bay, Luzon. Of these Philippine reserves White[1/] has written, "The idea that these 'national parks' and 'marine sanctuaries' actually exist because of their existence on paper is mistaken. There is not in actuality any mechanism functioning within the national government to manage the above-listed areas."

Philippine reefs and marine life, in general, have suffered greatly from dynamite fishing, destructive methods of fishing with nets, use of poisons, collection of sea turtles and eggs, and the taking of coral for export in spite of laws banning these activities.

Although there has been little success in enforcement to protect marine life and establish real reserves in the Philippines at

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[1/] Unpublished manuscript, Phillipine marine parks past and future status, by Allan White, Environment and Policy Institute, East-West Center, Honolulu, Hawaii.

the national level, mention should be made of two small marine sanctuaries which have developed and are enforced locally. One is the sector of fringing reef in front of the diving resort, Dive 7000, in Batangas, Luzon. The other consists of the reefs off 500 m of shoreline of the western part of Sumilon, a 23-hectare island which lies just east of the southern tip of Cebu (White, 1979). This was established by Dr. Angel C. Alcala, Vice President for Research, Extension and Development of Siliman University, Dumaguete City, Negros. He directs the marine laboratory of this university, which has a small field station on Sumilon Island.

Indonesia has the most diverse marine flora and fauna in the world. It is also the most heavily populated archipelago (140 million); its people are concentrated in coastal areas and dependent to a considerable degree on the sea for protein. As might be expected, a program of marine conservation has been slow to develop. There are three protected marine areas in Indonesia, all in the Moluccas: Pulau Pombo and Banda (both marine parks) and Margasatwa (wildlife reserve). Management of these areas, however, is virtually nonexistent (Rodney V. Salm, personal communication, c/o Directorate of Nature Conservation, Bogor, Indonesia).

In a manuscript entitled "Progress in Creating a Marine Reserve System in Indonesia," Alan Robinson, Nicholas Polunin, Knut Kvalvagnaes and Matheus Halim have discussed the many practices that are deleterious to the marine biota and environment in Indonesia: overfishing, pollution, fishing with explosives and poisons, mining of coral, removal of sand from beaches, lack of proper management of the marine aquarium fish trade, unrestricted exploitation of sea turtles, land clearing resulting in siltation in aquatic areas, development of coastal marsh land for human settlement, conversion of mangrove areas into fish ponds, and the harvesting of mangrove for export as pulpwood.

These authors are encouraged, however, by the increased activity of the Directorate of Nature Conservation within Indonesia's Forestry Department, the country's subscription in 1979 to the Convention on International Trade in Endangered Species (CITES), and the creation of a Minister for Development Supervision and Environment. They outlined the need for large conservation areas zoned for a marine national park which would be open to visitors for the purpose of nature study and appreciation, a strict marine reserve intended as an undisturbed research site, a marine recreation zone planned for high-density recreational uses, and a buffer zone. The Pulau Seribu, an archipelago lying immediately north of Jakarta, is an area well suited to the establishment of such a marine conservation area.

The expansion of existing terrestrial preserves in Indonesia to include adjacent marine areas is also proposed. An example is the Komodo National Park, a 60,000 hectare area of the Komodo-Rinca island group in the Lesser Sunda Islands where the world's largest living lizard (Varanus komodoensis) is found. It is suggested that 70,000 hectares of the sea up to 1 km offshore be added to the national park boundaries. Also, a management plan has been drawn up to extend the boundaries of the Bali Barat reserve into the sea to include coral reefs. These extensions not only provide protection to the marine life but are important in terms of ecosystem integrity and more effective management. The authors ended their paper stating "Substantial progress has been made in planning for various marine parks and reserves, but much work remains before such plans are effectively implemented."

The Kingdom of Tonga has established four marine reserves (Wilkinson 1977), the most significant of which is the Fanga'uta lagoon of the main island of Tongatapu. This lagoon, actually an estuarine region, has an area of 2,830 hectares. It is an important nursery ground for many fishes; several species of penaeid shrimps also are found there. The other reserves are Nui Aunfo Point at the northwest end of Tongatapu and the two small islands of Malinoa and Monuafe to the north.

In French Polynesia the only marine sanctuary is the atoll of Taiaro which lies in the Tuamotu Archipelago 300 nautical miles ENE of Tahiti. It was designated as a permanent reserve for science on August 1, 1972, and given the name Reserve Integrale W. A. Robinson. Protection of all forms of life was extended in February, 1973, to the lagoon and a zone of the sea 1 kilometer around the atoll. Visitors must have special permission to land. William A. Robinson is the owner of the atoll and President of the Administrative Committee. The address for the Secretary of the Committee is P.O. Box 866, Papeete, Tahiti.

Australia had its first marine park at Green Island on the Great Barrier Reef in 1938. Later Heron Island and nearby Wistari Reef of the Capricorn Group were added as reserves. Progress since then in marine conservation has been slow. On June 20, 1975, the Great Barrier Reef Marine Park Act became law. This established the Great Barrier Reef Marine Park Authority which is responsible for recommending areas as part of the Marine Park system and preparing zoning and management plans for these areas. Early this year the first section of the Great Barrier Reef Marine Park was proclaimed. It covers 1,180,000 hectares at the southern end of the reef (encompassing Heron Island).

Concern has been expressed about the possible adverse effects of coastal land development in Queensland on adjacent sectors of the Great Barrier Reef (Bennell 1980). Foremost are the many forms of water-borne pollution such as sewage, oil spills, siltation from soil erosion, and run-off of agricultural chemicals. The same concern applies, of course, to many other protected areas in the sea. There should be some control over the land use adjacent to marine parks.

Lord Howe Island, a speck of land between Australia and New Zealand at 31°31'S that is said to have the southernmost coral reefs in the world, has set aside sections of reef and Ned's Beach (where visitors can wade into the water and feed fishes by hand) as reserves (Randall 1980). These conservation areas have no formal status under New South Wales law. It has been recommended that full national park status be extended to a major portion of the island, including its coral reefs (McMichael and Talbot 1969).

Ballantine and Gordon (1979) reported on New Zealand's first marine reserve, an area of 500 hectares from Cape Rodney to Okakari Point on the North Island. This was opened in 1977, 12 years after it was first proposed. Although outside the tropics (at nearly 35°S), the annual range of sea temperature is 14-21°C and some subtropical forms of marine life are found there.

In 1975 Japan had 23 marine parks, but only one, Okinawa-Kaigan, is in a warm-water area (Tamura 1975). By 1977, however, nine more marine parks were added in the Ryukyu Islands: Kasari-Isanto, Surikozaki, Setouchi, Kametoku, Yoronto, Taketomijima-Takidonguchi, Taketomijima-Shimobishi, Kurashima-Kyanguchi, and Aragusukujima-Maibishi (Marine Parks Center of Japan 1977).

The Republic of South Africa's first park to incorporate part of the sea was Tsitsikama Forest and Coastal National Park which lies midway in the Cape south coast, hence in the Temperate Zone. Recently St. Lucia Marine Park (which includes Sodwana Bay) in KwaZulu at 27-28°S was added; this preserve includes reef areas. There is also Trafalgar Marine Park, a small reserve in Natal near Durban.

To the north in Mozambique, Bazaruto National Park and Paradise Island Maritime National Park should be noted. In the Mozambique Channel the French Island of Europa is a marine national park. The atoll of Aldabra north west of Madagascar is also a marine and terrestrial reserve.

Ray (1968) outlined plans for marine parks in Tanzania, but only in 1975 was legislation passed to establish some of these areas as parks. Because enforcement has not yet taken effect, there is as yet no protection for the marine life.

There are three national marine parks in Kenya: Malindi, Watamu, and Kisiti. I visited the Malindi and Watamu parks in 1979 and was impressed with the organization and enforcement of these reserves. In addition there is an extensive new park area in the north of Kenya, the Kiunga National Marine Reserve.

In the Red Sea, Israel's management of the east coast of the Sinai Penisula has been outstanding (Clark 1977; Fishelson 1980). The first marine park was established at Eilat at the northern end of the Gulf of 'Aqaba. Ten large coastal reserves now exist along the eastern shore of the Sinai. These sanctuaries, particularly the ones at Eilat and Ras Muhammad at the southern tip of the peninsula, have attracted thousands of fish watchers and undersea photographers. It is hoped that Egypt will continue the reef conservation policies when it recovers the Sinai. Israel also has two marine reserves on its Mediterranean coast.

In Sudan the use of spearguns and the collecting of shells, coral, and marine fishes for aquaria have been prohibited since 1975. Two areas are closed to commercial fishing: Sanganeb Atoll (15 miles NE of Port Sudan) and Dongonab Bay. A new marine fisheries act which will provide the legal basis for establishing parks, reserves, and closed areas is expected to become law soon.

The governments of the Republic of the Maldives and the Republic of the Seychelles are to be commended for the ban of spearfishing in their waters. These two island groups have enjoyed an increasing number of tourists in recent years, particularly from Europe. Many of the tourists are skin divers or SCUBA divers, and no small number are underwater photographers. They have been attracted to these islands by the well-developed reefs, colorful marine life and clarity of the water. With spearfishing eliminated, photographers are able to approach fishes more readily. The Seychelles has Sainte Anne Maritime National Park, and the various diving resorts in the Maldives provide local protection for marine life.

India has no marine parks. A recommendation was made to the government in 1976 to declare the uninhabited atoll of Sukheli Pav in the Lakshadweep Islands (= Laccadive Islands) a national marine park (Menon 1979), but no action has been taken. More recently another park has been proposed for a chain of 20 small islands in the Gulf of Mannar-Palk Strait area off SE India (Menon MS).

Sri Lanka has one marine park at Hikkaduwa on the southwest coast of the island which was established in 1956. There has been no effective enforcement, however. If publicity is given to a site as a marine park without providing the means to protect the marine life therein, it may be to the detriment of the area. Such is the case with Hikkaduwa. A well-known resident diver in Sri Lanka, Rodney Jonklass, has written the author of this marine park, "It swarms with divers and is utterly devastated; there are hardly any corals left and the few fishes are so terrified you need 10,000 ASA film and an underwater infra-red tele lens to get a photo of one. Jokes apart - the fishermen never did respect this place, and although there is no spearfishing permitted (by the hoteliers), netting and line fishing go on apace." The author visited Hikkaduwa in 1979 and though it did not seem "utterly devastated," it certainly was less attractive underwater than many other places around the island. There is no doubt that it has suffered as a result of its marine park status without protection of the marine gardens.

Turning to the western Atlantic, the U.S. Virgin Islands has the lead from the standpoint of percentage of coastline devoted to marine sanctuaries, largely because of the Virgin Islands National Park on St. John. Fabulous Buck Island Reef National Monument is St. Croix's only marine reserve (Randall and Schroeder 1962). The most populous of the three American Virgin Islands, St. Thomas, has no marine preserves, but there are serious plans for them.

Puerto Rico also has no marine parks, in spite of a long-term effort on the part of a dedicated few to establish a sanctuary for the island's famous Phosphorescent Bay (Anonymous 1968). Six major sites of the island, however, have been recommended to the Secretary of Commerce for designation as marine sanctuaries by the Department of

Natural Resources of the Commonwealth of Puerto Rico. The Marine Protection, Research and Sanctuaries Act of 1972 authorizes the Secretary, with the approval of the President, to designate ocean areas as marine sanctuaries. The six recommended sites include marine habitats of La Cordillera, Culebra and Vieques; Salinas-Jobos; Caja de Muertos (largest island on Puerto Rico's south coast); a large area of southwest Puerto Rico which includes Phosphorescent Bay, one other luminescent bay, and La Parguera; the islands of Mona and Monito; and the island of Desecheo.

Elsewhere in the Caribbean, marine parks or national parks or sanctuaries containing marine areas have been established for the following countries:

Antigua: Diamond Reef Marine Park.
Barbados: Barbados Marine Reserve (2.5 km of west coast from Colony Club Hotel to Sandy Lane Hotel).
Barbuda: Pilaster Reef Marine Park.
Colombia: Parque Nacional Natural Isla de Salamanca, Parque Nacional Tayrona, Parque Nacional Natural Corales del Rosario, Sanctuario de Flora y Fauna Cienaga Grande Sta. Marta, and Santuario de Floro y Fauna Los Flamencos.
Costa Rica: Tortuguero National Park and Cahuita National Park (on the Pacific side, Santa Rosa National Park and Cocos Island National Park).
Dominican Pepublic: Los Haitises National Park and Del Este National Park.
Guadeloupe: Parc National de la Guadeloupe (proposed).
Honduras: Gulf of Fonseca Mangrove Reserve and Bay Islands National Park.
Jamaica: Ocho Rios and reef outside Cornwall Bathing Club, Montego Bay.
Martinique: Reserve Naturelle de la Caravelle.
Mexico: Underwater Sanctuary of Cozumel (15 mile section of reef on SW side of the island).
Netherlands Antilles: Underwater Park Bonaire and National Park Washington-Slagbaai, Bonaire.
Panama: Portobelo National Park (proposed).
Trinidad and Tobago: Buccoo Reef Marine Preserve, Tobago.
Venezuela: Morrocoy National Park, Archipelago de los Roques National Park, Mochima National Park, Medanos de Coro National Park, Laguna de Tacarigua National Park, and Laguna de Resinga.

Legislation has been passed in the Cayman Islands to create underwater parklands and preserves, but no areas have yet been designated.

The Bahamas have long prohibited the spearing of fishes by persons using SCUBA; the law provides for confiscation of the gear of a violator, including his vessel. In addition, there are the following marine preserves: Peterson Cay near Freeport, Grand Bahama; Pelican Cay Park near Hope Town, Abaco; the sea gardens off Athol Island, New Providence; Inagua National Park (contains a small marine area), and the

Exuma Cays National Park. The last-mentioned consists of a 22-mile section of the Exumas between Wax Cay Cut and Conch Cut (Randall and Ray, 1958; Ray, 1961).

A marine preserve is in effect a closed area, long recognized as a tool in the regulation of some fisheries. The preserve differs, of course, in its permanence. It also differs in extending protection to an entire community such as the coral reef, or more than one community, whereas a closed area generally applies to a single species of commercial importance.

The most important resident food fishes of the reef community are usually the groupers and snappers. Also of value are some semi-pelagic fishes such as jacks and barracudas which often prey heavily on the smaller reef fishes; thus from the trophic standpoint they are members of the coral reef community. The larger carnivorous fishes are invariably the first that are fished out from the reef habitat, whether by hook and line, traps, gill nets or spearfishing. By eliminating these top predators we put nature out of balance. As would be expected, the herbivores and omnivores become more numerous which may result in overgrazing of benthic algae and impeding the normal settling of the larvae of benthic animals. The abundance of the noxious long-spined sea urchin, Diadema antillarum, in the Virgin Islands is probably related to the overfishing of the queen triggerfish (Balistes vetula) and the larger grunts (especially Anisotremus surinamesis and Haemulon macrostomum) and porgies (Calamus spp.) which feed heavily on this echinoid.

The problem of the impact on the community due to elimination of the largest predaceous fishes is accentuated in the case of groupers (Epinephelus spp., Cephalopholis spp., etc.) because they are protogynous hermaphrodites, beginning mature life as females and changing over to the male sex when older (Smith 1965). When fishing effort is directed, as it so often is, to the larger individuals of the species, the result for groupers is a diminution of males in the population with an obvious disastrous effect on reproduction. The wrasses (Labridae) and parrotfishes (Scaridae) are also protogynous hermaphrodites.

It is clear that setting aside sectors of reefs as preserves to maintain the populations of groupers and other large food fishes is a wise procedure. Even if only 5% or less of the reef environment is protected, the larvae from the successful reproduction in the preserves can seed the adjacent unprotected areas.

Although the above discussion has emphasized the importance of protecting the larger food fishes, it is well to point out that the increasing take of small colorful coral reef fishes for the aquarium trade may result in depleted stocks of certain species on restricted available reefs. Marine sanctuaries serve to maintain these stocks as well. Furthermore, by placing the favorite snorkeling reefs off limits to collectors of fishes and other marine life, the antagonism and confrontation of fish watchers and undersea photographers and the collectors can be significantly reduced.

Having sectors of reef as inviolate preserves is of great importance to the scientist who wants to study the community in its natural state with the populations of the various animals and plants unaffected by man. Once spearfishing and certain netting techniques are abolished, the fishes lose their fear of man and can be observed closely. This confers distinct advantages to many different aspects of biology. The systematist can link juvenile stages which may differ markedly from adults by underwater observation of intermediate individuals. Or he may pair the very differently colored males and females of sexually dichromatic fishes such as most of the wrasses and parrotfishes. Not surprisingly, males and females of these fishes have often been given different scientific names.

The value of preserves for the behaviorist is obvious. Direct observation of feeding will often solve problems of the identification of the food from the stomach contents of fishes which may be rapidly altered by trituration or digestion. Predator-prey relationships and diurnal vs. noctural activity are best studied on unaltered reefs. This is even more true for such things as the observation of spawning and **cleaning symbiosis.** Fishes are not apt to enter into these more intimate behaviors with predators nearby. Fishes recognize man with a spear or net as a predator far more readily than one would expect. The recruitment of juveniles to a reef is another phenomenon best studied on a natural reef. Also, the marking or tagging of fishes for the study of movements and growth is greatly facilitated when fishes can be closely approached.

Marine parks are of exceptional value to underwater photography of fishes, whether by the marine biologist or layman. Many species of fishes on unprotected reefs where spearfishing and netting have been in effect cannot be approached close enough to be photographed. The author has from experience chosen marine parks in various parts of the world as listed above for undersea photography.

The term park denotes both recreation and conservation. Not infrequently these two aspects are incompatible. Heavy visitation to a marine park can result in damage to reefs by such things as the breaking of coral by anchors. Visitors often feed reef fishes which causes some species to follow divers and snorkelers closely, thus altering the normal behavior of these fishes. This problem is best solved in the same way that it has on terrestrial parks. Within the larger parks certain sectors are designated wilderness areas, and every effort is made to keep these as pristine as possible.

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SESSION SUMMARY
REEF-FISH COMMUNITY STRUCTURE

by

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The concept of a reef-fish community is inseparable from the broader concept of a reef community. Both are abstractions based on groups of interrelated organisms that have in common a dependence on definable reef systems. Typically a reef community is structured with three major elements:

1) The various species involved are distributed in relation to the specific physical features of the reef.

2) The various species are represented by individuals of specific sizes and ages.

3) The various species include an array of feeding types (e.g., planktivores, herbivores, piscivores, etc.) that reflect the physical features of the reef.

Despite their dependence on a particular reef, members of a reef community may depend as well on certain neighboring habitats. Some grunts (Haemulidae), for example, use reefs as daytime resting places but at nightfall migrate to surrounding regions where they forage throughout the night.

A reef is characterized by a particular set of physical features that determine the mix of fishes that live there. The fauna, therefore, is predictable. So regarding the current controversy over whether community structure is a product of orderly or chaotic processes, the position here is that order prevails. This view implies a predictable partitioning of food and habitat that permits a variety of management tactics. It should be possible, for example, to estimate how many individuals there are of a given species by mapping its favored habitat. Beyond this, it should be possible to predict the pattern a species will follow in repopulating reefs from which many of its members have been removed. These possibilities address certain major problems facing the National Marine Fisheries Service and so should be recognized. Suggested here are ways to assess existing stocks, and also to anticipate the effects of natural and unnatural disturbances on these stocks--both major responsibilities of the Service. Disturbances referred to here include not only removal of faunal elements by fishermen and other exploiters, but also transformations of a reef's physical features by storms and other processes.

Following the obvious and important descriptive studies needed to define reef communities and their dynamic systems, specific questions can be addressed experimentally. For example, what is the impact on the community to recover, or can it ever return to its previous state? When components of the fauna are removed, certainly chance is a major force in determining their immediate replacements. Conditions at any given time favor recruitment of one species over another. Perhaps the major determinant is the relative numbers of planktonic larvae of the various species that happen to be settling on the reef when the vacancy develops. This likely has been determined by a complex mix of factors unrelated to circumstances on the reef, which nevertheless become under these circumstances important to the reef system. The sequence in which the recruits arrive is important, too, because some will exclude others. On West Indian reefs, for example, snappers (Lutjanidae) will block subsequent establishment of grunts. So to predict the long-term effects of disturbances on a reef community, knowledge of recruitment patterns is essential.

To measure the impact of natural or human-induced disturbances on reef communities we need points of comparison and controls for the experimental work--that is, communities unaffected by the disturbance. Such communities are becoming scarce, which points to a developing need for preserves.

There are of course other good reasons to establish preserves, which leads to controversy--how should a preserve be used? To some, preserves are needed so that people can observe, photograph, and generally mingle with, the reef community. But such activities are incompatible with most scientific investigations. On other hand, the activities of scientists are themselves disturbances that upset those other people who are convinced that preserves should be places where the animals are left completely to themselves. Then there are those perhaps more pragmatic individuals that see preserves as sources of recruits to repopulate surrounding areas with marketable forms that have been depleted by exploiters.

The solution to reconciling these conflicting views probably lies in defining areas within preserves to serve each function. That is, an area where the inhabitants can be viewed and photographed, an area where they can be studied by scientists, and a third area where they are left to themselves.

Attempts to establish preserves worldwide have had little success. In some places, like Israel, they have done well, but in most places, including most of the western Pacific, preserves have been effectively resisted by people that have traditionally fished the reefs. A solution to this particular problem may be to issue lifetime permits for those who have used the reef, but no new permits, so that in time the users will be phased out.

To most effectively select locations for preserves, or to gain the information needed for effective management of reef communities, we must be familiar with the basic patterns in community structure. This familiarity, however, can come only by integrating information from differing ecosystems. Community structure can be expected to reflect local conditions. These considerations are of special concern to the Southeast Fisheries Center because its reef fish program throughout the tropical and subtropical western Atlantic includes so many different habitats.

An example of how knowledge from differing ecosystems defines basic patterns of community structure exists in the comparison between a central Pacific coral reef and a warm-temperate Pacific kelp forest being made by the Tiburon Laboratory, Southwest Fisheries Center. Major difference in the structure of reef communities in these two locations have been related to trophic relationships, which are considered primary forces in determining community structure.

There are many more species on the coral reef than in the kelp forest, although there does not appear to be many more indiviuals. This greater number of species in the more tropical region is centered among species with highly specialized feeding equipment--the number of species with generalized feeding equipment is about the same in both regions.

Although it is one of the oldest generalizations of biogeography that the numbers of animals and plants tend to increase with decreasing latitude, this relationship has not previously been related to community trophic-structure. The great number of species in the more tropical of these two reef communities, however, relates to characteristics of the coral reef habitat, rather than to move general features of lower latitudes. The more diverse array of species in the coral-reef community is an expression of a more complex system of trophic relationships. This, in turn, stems from the high proportion of specialized feeding types that can exist there only because the coral-reef environment remains relatively unchanged during the lives of most inhabitants. A contrasting condition exists in the temperate kelp forests, where the habitat experiences frequent and profound transformations related to the changing life stages of the predominating macroalgae. Such variable surroundings discourage narrowly-defined, specialized feeding modes. Favored instead are more generalized feeders that can accommodate the existing diverse and unpredictable food supply.

Areas of Study Needed to Better Manage Reef-Fish Communities

Items 1 to 3 are in rough order of recommended sequence, but ideally there would be much overlap and interaction.

1. Basic patterns of community structure must be understood. These can be identified by integrating information from descriptive studies of reef fish community structure in different environments. Each study of a local reef system would define such characteristics of component species as population size, habitat preferences (based on distribution of individuals among the habitats on that reef), and temporal variations in distribution (including diel and seasonal migrations).

2. Trophic relationships, which are major determinants of community structure, can be identified by descriptive studies that center on gut contents relative to foods available, and which are heavily supplemented with direct observations of the interspecific activities involved.

3. <u>Patterns of reproduction and recruitment</u> must be identified to understand the dynamics of community structure. Descriptive studies are needed to profile natural reproduction and recruitment patterns, and once these are defined, experimental studies are needed to identify the impact of disturbances (in particular the impact of humans) on these natural systems.

4. <u>Identifying and establishing preserves</u> is an important activity. Careful selection of preserve sites that will serve the multiple functions outlined above requires intimate familiarity with a wide range of potential locations. The sociological aspects of gaining popular support for preserves in general, as well as specific sites, also needs study.

SESSION 6

Modeling of Reef Fisheries

Chairman

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TOWARDS MODELS OF REEF FISH EXPLOITATION

by

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INTRODUCTION

Fish populations associated with tropical reefs have been of considerable ecological interest in the study of community structure, stability and dynamics (Sale 1974; Low 1971). As nations in the tropical zones have developed, reef fish communities have been increasingly recognized and utilized as valuable economic and recreational resources (Marr 1976; Pauly 1979). Although little is known of the impact of exploitation, pollution and other human activities on reef systems, reef fisheries continue to be an important resource in the Caribbean, Gulf of Mexico, and western tropical Atlantic Ocean (Miller and Richards 1980; Boardman and Weiler 1980). There are some fundamental constraints on our knowledge of reef ecosystems and, thus, on management. In particular we know less about the dynamics and structure of communities on reefs fish than of fish communities from more temperate latitudes. Yet we are forced to use theory and technical tools which were largely developed for analyzing and managing temperate fisheries. In this paper we will examine problems encountered when standard fisheries assessment models are used with reef fish systems. We will first outline characteristics of reef fish ecosystems, reef fish populations/stocks, and fisheries associated with them and contrast these to temperate systems. Then we will present a simple illustrative model based on the characteristics of reef systems and examine the ramifications of exploitation on the dynamics of populations. Finally, we will make recommendations based upon our results as to directions in which research on fisheries models should proceed.

REEF FISH SYSTEMS

The tropical reef ecosystem has been variously described as being stable in its dynamics and exceedingly complex in structure

(Emery 1978). In order to characterize these notions from a model development standpoint, we must, however, be a bit more descriptive. Therefore, we hypothesize the following relationships to exist in the reef fish community. Most of these points have been published elsewhere. Also, Pauly (1979) presented a list of characteristics of tropical multispecies fisheries which encompasses most of this discussion.

The tropical reef ecosystem will typically exist with many species and/or stocks of fish in the community. As a system, the ratio of biomass to productivity will be large, indicating the relatively greater use of energy for maintenance of the population.

Natural mortality at the population level is higher in tropical systems than in comparable temperate systems. This natural mortality is predominated by predation by piscivorous fish. Thus the community itself is characterized by being composed of a large number of predators and the dynamics of each population is more related to biotic rather than abiotic factors.

Each population exhibits relatively little surplus production. But since a common successful reproductive strategy is to produce a large number of gametes to combat the predation problem (Johannes 1978), the potential maximum reproductive rate may be large.

The dispersal of larval fish and juveniles is very important in a patch environment. Colonization by new individuals and the migration into and out of habitats by these fish are common. The patchiness and irregular spatial structure of the environment in tropical reef systems lead to well organized spatial heterogeneity. Hastings (1977) has shown that passive dispersal and spatial heterogeneity can be powerful stabilizers in predator-prey systems. The relationship of reef fish to available habitat (space) and competition for that space is strong (Sale 1978). Habitat specialization of reef fishes is common with much specificity of territories - or home ranges. Yet there is considerable overlap of suitable habitat between species. The effect of competition for habitat is confounded with predation. If a fish is expelled from, or cannot find a suitable site, its chances of mortality by predation are extremely high. The actual cause of mortality may be competition or predation, depending on your point of view.

Fisheries associated with tropical reef systems tend to center on stocks which are the top predators in the system. Much of the gear used in these fisheries, however, is more size-specific than species-specific, i.e., all fish of a given size are susceptible to the fishery. Also, the habitat itself becomes the target of fishing effort, for a reef is concentrated and its location is predictable. Fishing effort takes place directly at a target area (reef) and catches whatever is there. This situation, however, is not necessarily unique to reef fisheries.

Because fisheries are multispecies, individual species may be depleted during economic development of the fishery. Clark (1976) points out that rational economic behavior will lead to extinction of a species when: (1) the price obtained is greater than the cost of extracting the last individual; and (2) the harvester's discount rate is greater than two times the maximum recruitment rate. The multistock harvesting gears and the relatively short time horizons which fishermen associate with reef systems tell of the risk which reef fish communities face. Modeling these systems to provide management advice will require incorporation of these unique features.

A REEF FISH COMPETITION MODEL

Exploitation of fish stocks with the characteristics outlined in the previous section may induce some static and dynamic behaviors which are contrary to standard single-species fisheries theory. So that these unique features might be explored, we hypothesized a simple two-species model which captures most of the salient features of reef-fish systems. Using this model we will show the impact of exploitation upon the populations. We are not proposing that this model be the approach that we take in developing management models. Instead we use it to illustrate the behavior that reef fish populations are likely to exhibit and the problems which will arise when standard fisheries models are utilized.

Assume that we are concerned with a system consisting of only two populations whose numbers (or biomass) are denoted by P_1 and P_2. Let us also assume a simple variation of the logistic equation to describe the dynamics of these populations. The variation incorporates a term denoting the amount (area or volume) of effective habitat available to the populations:

$$\frac{dP_1}{dt} = \frac{a_1P_1}{(A-d_2P_2)} - \frac{b_1P_1^2}{(A-d_2P_2)^2} \qquad (1)$$

$$\frac{dP_2}{dt} = \frac{a_2P_2}{(A-d_1P_1)} - \frac{b_2P_2^2}{(A-d_1P_1)}$$

where a_i, b_i and d_i are parameters and A is the amount of total habitat. Equations (1) describe the dynamics of the population as a simple Schaefer production function of the population density. However, the amount of habitat available to P_1 depends upon the amount being used by P_2, and vice versa. Thus, the parameters d_1 and d_2 denote the quantity of total habitat utilized by a unit of P_1 and P_2, respectively. The above model assumes that all biological characteristics of natural mortality, growth and reproduction are incorporated into the parameters a_i and b_i. Then any interaction between populations is through the competition for available habitat. Thus, the model focuses on the dependence of the populations on habitat, which has been suggested as being extremely important to reef fish communities (Sale 1978; Dale 1978).

We will refer to this dependence as spatial competition throughout this paper. After discussing the results of this version of the model, we will expand it to include the effects of dispersal and migration.

Using (1), the following conditional equilibrium solutions are obtained

$$P_1^*|P_2 = (A-d_2P_2)(a_1/b_1)$$

$$P_2^*|P_1 = (A-d_1P_1)(a_2/b_2),$$

where P_i^* P_j is the equilibrium level of P_i given that P_j is fixed. The unconditional equilibrium solution (P_i^*) is also found:

$$P_1^* = A\left[\frac{a_1b_2 - a_1a_2d_2}{b_1b_2 - a_1a_2d_1d_2}\right] \qquad (3)$$

$$P_2^* = A\left[\frac{a_2b_1 - a_1a_2d_1}{b_1b_2 - a_1a_2d_1d_2}\right]$$

Note that (3) reduces to the standard Schaefer formular for carrying capacity when there is no spatial competition ($P^*_i = A(a_i/b_i)$, when $d_1=d_2=0$). Inclusion of the spatial competition terms has caused a reduction in equilibrium population levels (carrying capacity).

Let us expand upon (1) to include a yield term (Y_i), assuming that the yield is directly proportional to the population size and to the effective effort, i.e.

$$Y_i = q_if_iP_i \qquad (i=1,2), \qquad (4)$$

where q_i is the catchability coefficient and f_i is the effective effort) giving

$$\frac{dP_1}{dt} = \frac{a_1P_1}{(A-d_2P_2)} - \frac{b_1P_1^2}{(A-d_2P_2)^2} - q_1f_1P_1$$

$$\frac{dP_2}{dt} = \frac{a_2P_2}{(A-d_1P_1)} - \frac{b_2P_2^2}{(A-d_1P_1)^2} - q_2f_2P_2 \qquad (5)$$

Throughout this analysis we will assume a multistock fishery exists, as is common in most reef fish fisheries. Thus, effort is directed at the assemblage of fishes and not directly at a particular stock ($f_1=f_2=f$).

Using (5), the following conditional relationships may be found

$$P_1^*|P_2 = \frac{a_1}{b_1}(A-d_2P_2) - \frac{q_1 f (A-d_2P_2)^2}{b_1} \tag{6}$$

$$Y_1^*|P_2 = \frac{a_1P_1}{(A-d_2P_2)} - \frac{b_1P_1^2}{(A-d_2P_2)^2} \tag{7}$$

$$\max(Y_1^* | P_2) = MSY_1 \quad P_2 = a_1^2/4b_1 \tag{8}$$

$$P_1^{opt} | P_2 = (A-d_2P_2)a_1/2b_1 \tag{9}$$

where Y_1^*/P_2, $MSY_1 | P_2$, and $P_1^{opt}|P_2$ are the equilibrium yield, maximum sustainable yield and population size of P_1 which produces MSY_1, respectively, given that P_2 is fixed at a particular level.

Equations (6)-(9) may be related to the fishing effort using (4) to produce the equilibrium solutions of population size and yield as a function of effort. However, the analytic solution cannot be obtained. Thus, it is difficult to explore the ramifications of the model from the analytical form. Instead we will examine some numerical results of the model presented graphically.

Let us assume that our two populations are governed by the logistic parameters in Table 1. We assume that the available area is unity (A=1). Also, the populations have been scaled such that the carrying capacity of each (with no competition) is unity. The maximum recruitment rate (when the population is small) is 0.15 and 0.20 for population 1 and 2, respectively; and the maximum production is 3.75% and 5% of carrying capacity, respectively. We will vary the values of the competitive parameters (d_1 and d_2 and the catchability coefficients (q_1 and q_2) to examine the ramifications of the model.

SINGLE SPECIES EXPLOITATION

When species one is being exploited alone ($q_1 = 0.0001$, $q_2 = 0$) and there is competition for space, several results occur in the equilibrium production curve (Fig. 1). Competition for space results in (1) the carrying capacity being reduced; thus the range of population sizes at which species one can exist is constrained; (2) the maximum productivity (MSY_1) is rather severely reduced as d_2 increases (Fig 1B-1C); and (3) the peak of the productivity curve is shifted backward, i.e., the population size which produces MSY_1 is less than one-half of the carrying capacity. The shift is more extreme as d_2 increases. As is expected with a backward peaked yield-population curve, the resulting yield-effect curve is also skewed to the right. The population size of species two (P_2) reacts to the shifts in P_1 by increasing as P_1 decreases

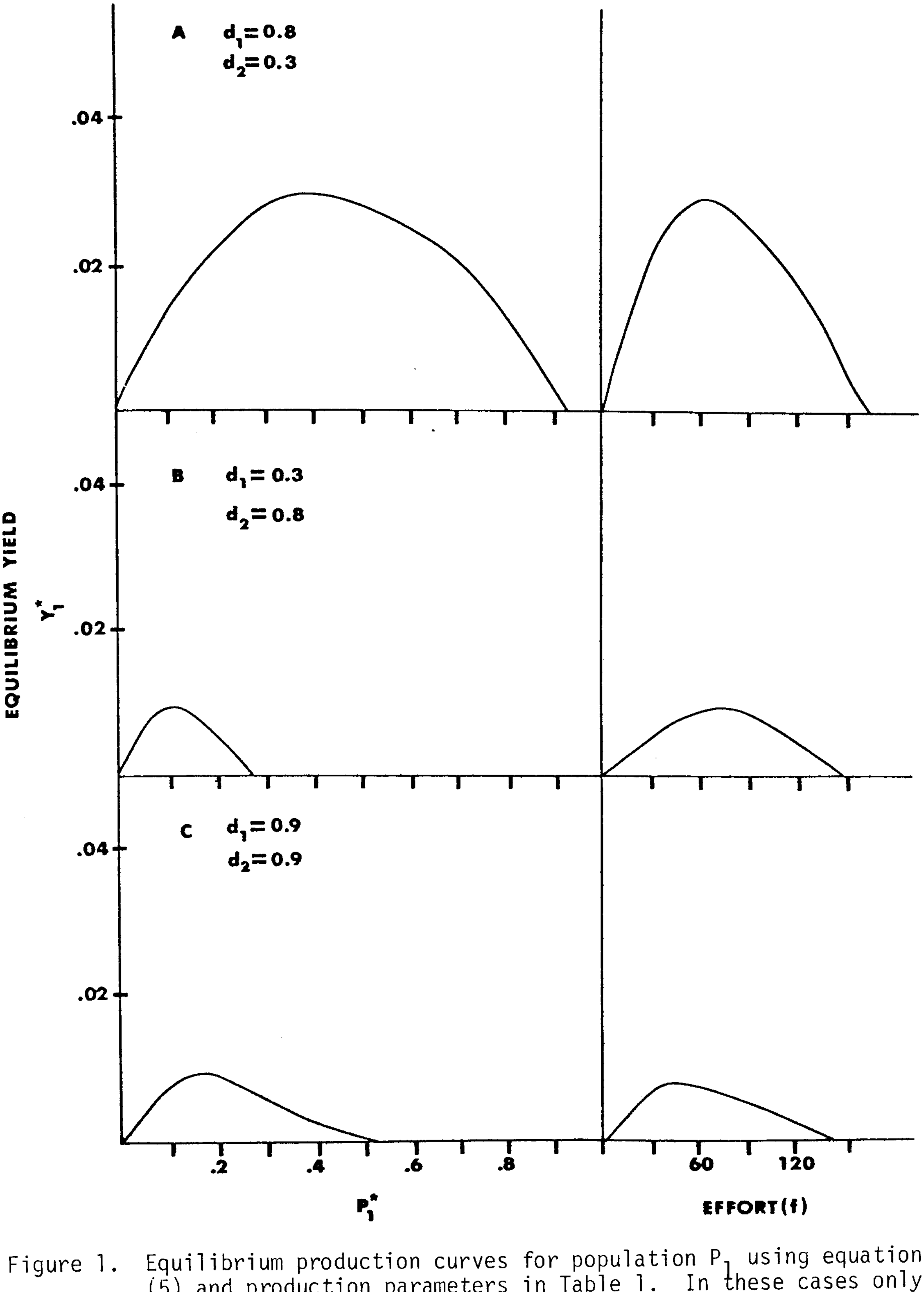

Figure 1. Equilibrium production curves for population P_1 using equation (5) and production parameters in Table 1. In these cases only P_1 is exploited ($q_1=0.001$, $q_2=0$). In 1A $d_1=0.8$, $d_2=0.3$; in 1B $d_1=0.3$, $d_2=0.8$; in 1C $d_1=d_2=0.9$.

and vice versa. The magnitude of the change in P_2 is defined by the competition parameters (d_1 and d_2).

MULTISPECIES EXPLOITATION

When both species one and species two are being exploited, both the static and dynamic analyses become more interesting. If both species are equally catchable ($q_1 = q_2 = 0.0001$) and there is considerable mutual competition for space ($d_1=d_2-0.9$), then the less productive population, species one, exhibits a slightly backward peaked yield-population curve (Fig. 2). But species two has an equilibrium curve in which there is an increase in the population size with an increase in fishing effort. This phenomenon becomes more pronounced when the catchability is reduced ($q_2=0.0005$; Fig. 3) and when the competition affects species two more than species one ($d_1=0.8, d_2=0.3$; Fig. 4). It also shows that in a multi-species fishery, yield may stay fairly constant with effort. As the most susceptible stock becomes depleted, the yield of other stocks increases with no change in stock size. Thus, the fishery may sequentially deplete each of the stocks without a concurrent reduction in yield.

The above is essentially a static analysis in which the equilibrium curves are shifted by exploitation and competition. Next we will look at the dynamic change in the populations as they move toward equilibrium. Figure 5 shows the movement of P_1 and P_2 when they are perturbed away from equilibrium, or equilibrium itself is shifted due to fishing effort. One of the more important points to note from Fig. 5 is the large decrease in population levels when the initial level is high. Levels P_1 and P_2 are reduced considerably with P_1 being close to equilibrium levels. Then P_2, the less catchable species, increases but on a much slower time scale. Meanwhile, when the populations in non-equilibrium are at low levels, they are faced with increased risks due to random environmental factors.

MIGRATION AND DISPERSAL

Let us expand upon our previous approach (equations (1) and (5)) to include the impact of emigration and immigration. We will make no distinction whether this migration is in the form of larvae, juveniles, or adults and will only be concerned with the movement of fish biomass (or numbers). Assume that the immigration rate (dI/dt) is a decreasing function of population density, whereas the emigration rate (dE/dt) is an increasing function of population density. For illustration we will assume these functions to be linear

$$\frac{dI_1}{dt} = g_1 - \frac{h_1 P_1}{(A-d_2P_2)}$$

$$\frac{dE_1}{dt} = k_1 + \frac{l_1 P_1}{(a-d_2P_2)}$$

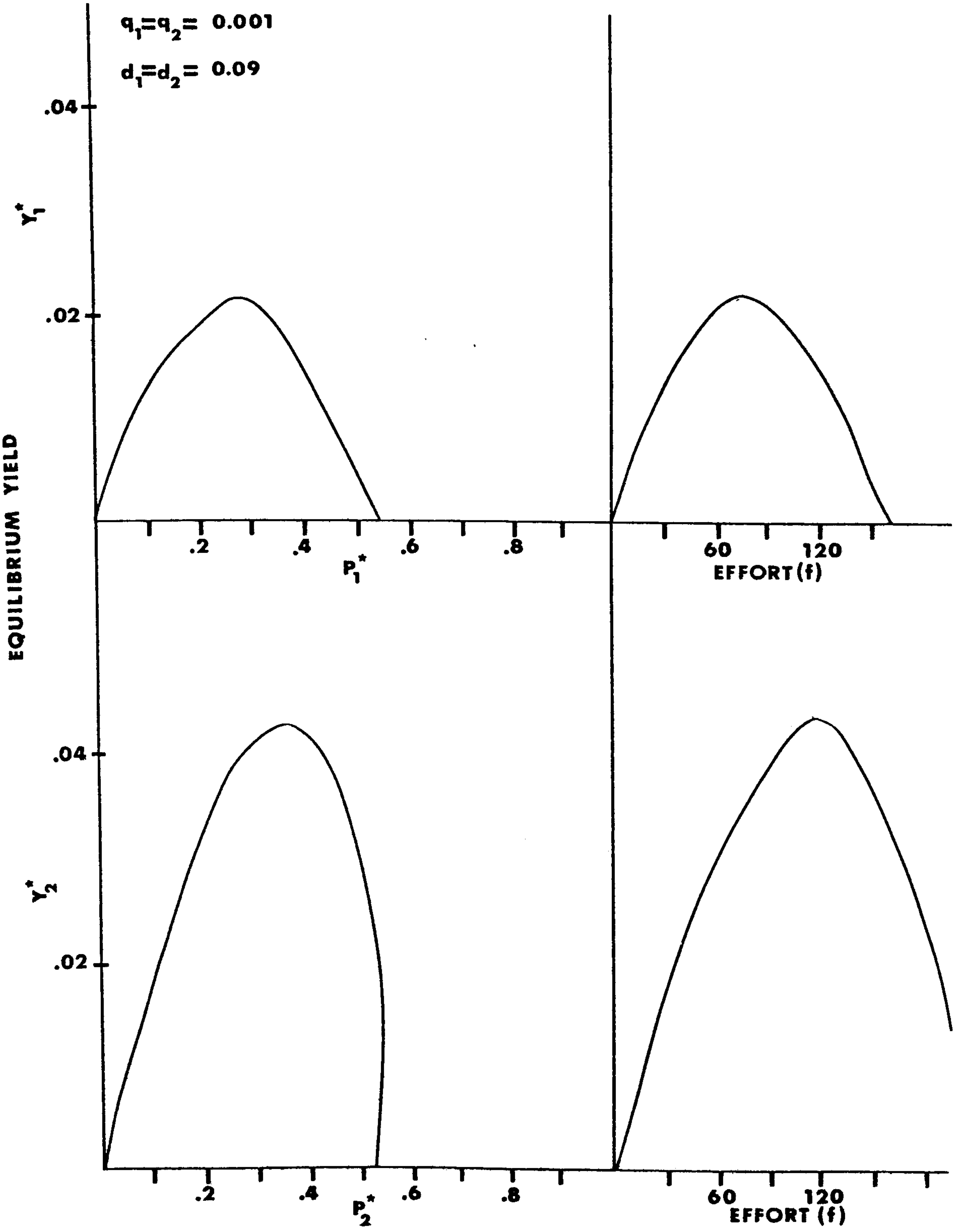

Figure 2. Equilibrium production curves for P_1 and P_2 using equation (5) and production parameters in Table 1. In this figure $q_1=q_2=0.001$ $d_1=d_2=0.9$.

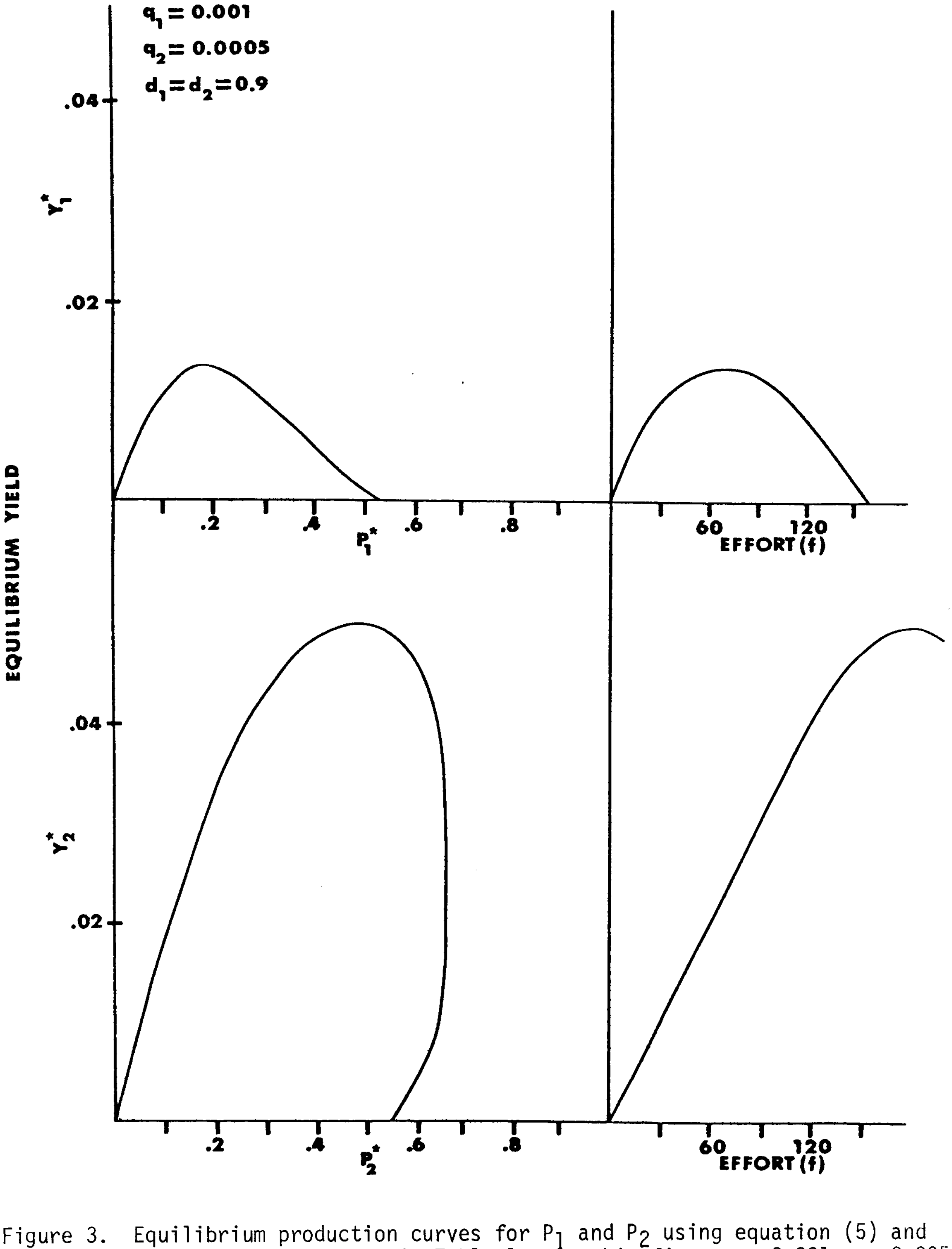

Figure 3. Equilibrium production curves for P_1 and P_2 using equation (5) and production parameters in Table 1. In this figure q_1=0.001, q_2=0.005 and d_1-d_2=0.9.

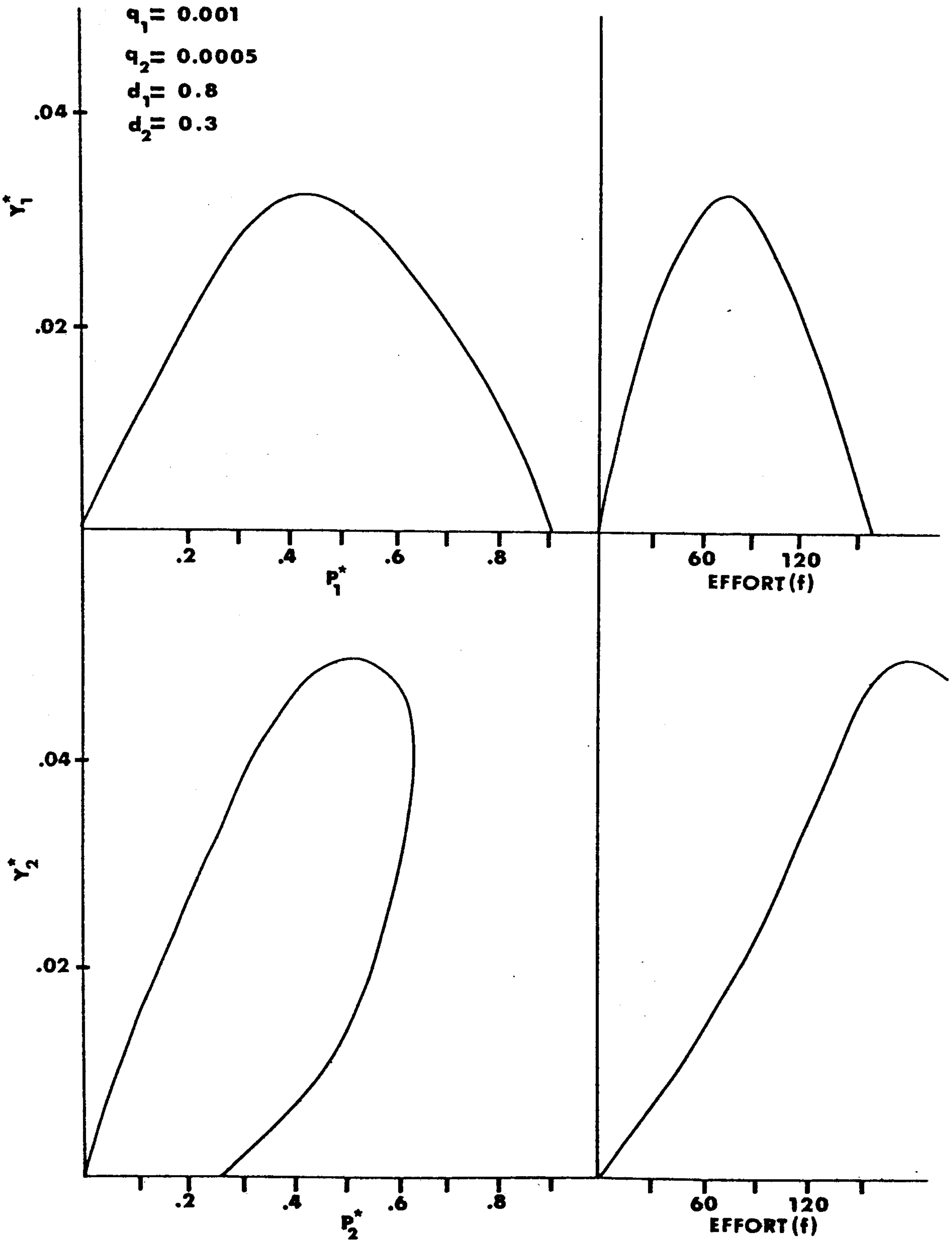

Figure 4. Equilibrium production curves for P_1 and P_1 using equation (5) and production parameters in Table 1. In this figure q_1=0.001, q_2=0.0005, d_1=0.8, and d_2=0.3.

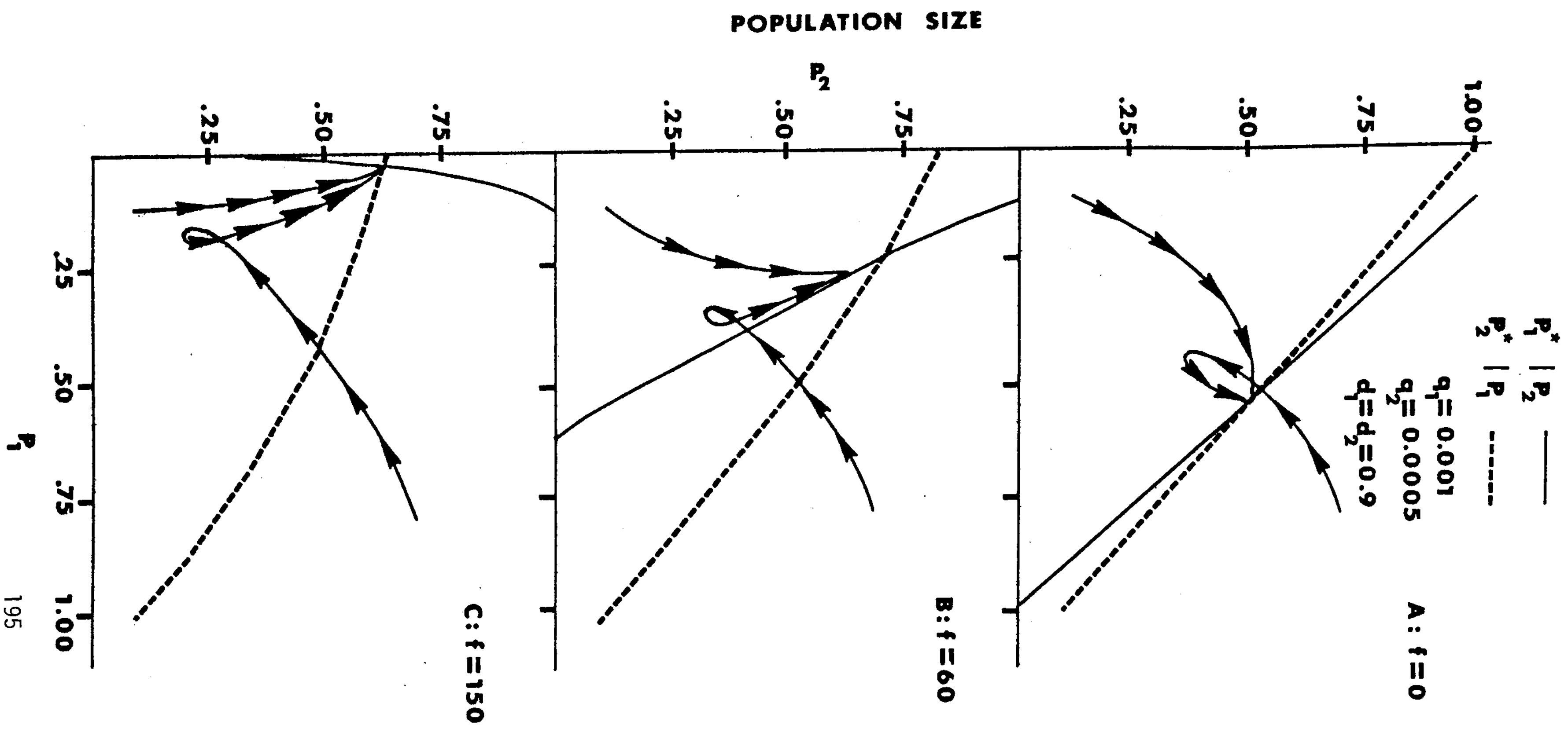

Figure 5. Dynamic trajectories of P_1 and P_2 toward equilibrium (arrowed curves). Solid curve is equilibrium value of P_1 given P_2 is fixed, dashed curve is equilibrium value of P_2 given P_1 is fixed. Model is equation (5) with Table 1 production parameters and q_1=0.001, q_2=0.0005, and d_1=d_2=0.9. In 5A effort is zero: f=0; 5B:f= 60; and 5C:f = 150.

Combining and reparameterizing to get the net migration rate dM/dt (where $\frac{dM}{dt} = \frac{dI}{dt} - \frac{dE}{dt}$) we obtain

$$\frac{dM_1}{dT} = r_1 + \frac{s_1P_1}{(A-d_2P_2)} \quad ; \text{where } r_1 = (q_1 - k_1) \qquad (10)$$
$$s_1 = (h_1 - l_1)$$

The parameter r_1 is the migration rate when P_1 is zero and s_1 is the slope of the curve. The population density (given P_2 is fixed) at which net migration is zero is $r_1/(-s_1)$. Normally, the slope would be negative. However, if our reef system is a dispersal source of production rather than a sink, then the slope may actually be positive. Equation (10) may be incorporated into (5) to get the dynamic equations:

$$\frac{dP_1}{dt} = r_1 + \frac{P_1(a_1+s_1)}{(A-d_2P_2)} - \frac{b_1P_1^2}{(A-d_2P_2)^2} - q_1fP_1$$
$$\frac{dP_2}{dt} = r_2 + \frac{P_2(a_2+s_2)}{(a-d_1P_1)} - \frac{b_2P_2^2}{(A-d_1P_1)^2} - q_2fP_2 \qquad (11)$$

The equilibrium solutions to (11), when there is no fishing effort (f=0) are

$$P_1^* = \frac{A(Q_1-Q_1Q_2d_2)}{1-Q_1Q_2d_1d_2}$$
$$P_2^* = \frac{A(Q_2-Q_1Q_2d_1)}{1-Q_1Q_2d_1d_2} \qquad (12)$$

where

$$Q_1 = \frac{1}{2b_1}\left[a_1+s_1 \pm \quad ((a_1+s_1)^2 + 4b_1r_1)\right]$$
$$Q_2 = \frac{1}{2b_2}\left[a_2+s_2 \pm \quad ((a_2+a_2)^2 + 4b_2r_2)\right]$$

The parameter Q_1 is the equilibrium density of P_i when there is no spatial competition. Once again, the analytic solution for Y_i and P_i as a function of f cannot be obtained. Therefore, we will look at the simplified case in which there is no spatial competition ($d_1=d_2=0$) and use the results of the previous section to deduce the effects of migration and competition acting together.

Assume that the net movement of fish of species one is into the system when P_1 is small and decreases as P_1 increases ($r_1>0$; $s_1<0$) and net migration is zero at a population level less than the carrying capacity with no migration. The resulting equilibrium production curve (Fig. 6A) shows a population size producing MSY, which is lower than the equivalent level when there is no migration. Also the maximum population size is reduced. The MSY level, itself, may increase or decrease, depending upon the magnitudes of r_1 and s_1.

If the population relies a great deal on outside sources for its production, i.e., if the reef is a sink from which there is little emigration ($r_1>>0$; $s_1<<0$), then maximum productivity levels may occur at population sizes very close to zero (Fig. 6B). Thus a fishery may exist off the production from outside the system. In this case, there would be a time series of equilibrium yields which would increase with an increase in effort until P_1 was dangerously close to zero. Then any random environmental buffeting which might occur could result in extreme risks to the population.

When the system is a source of production for other reefs, then the resulting production curve is more interesting. In this instance the emigration rate is positive even from small population sizes. Thus, $r_1 <0$ and $s_1 >0$. In this case yield exhibits two distinct equilibria for a given of effort (Fig. 6C). The point P' is a stable equilibrium, while P" is unstable. If the population level falls below P", then it will have the tendency to be reduced further toward zero. The standard usage of catch-per-unit-effort and Schaefer production models would mean that the unstable behavior in Fig. 6C would be ignored.

DISCUSSION

The spatial competition and migration-dispersal models have illustrated several features of reef fish systems which make management and the development of management models difficult. Competition for space tends to constrain both the range of population sizes at which a fish stock can exist and the productivity levels which it can achieve. Additionally, this competition will cause maximum productivity of the populations which are most susceptible to the fishery to occur at population sizes closer to zero than without competition. If a reef fish population relies a great deal on the immigration of production from outside sources, then maximum productivity may occur at even smaller population sizes. Conversely, if the reef fish system is a major contributor of production to other reefs, then populations within the system may also be drawn toward small population sizes if the population level drops below the unstable equilibrium level for a given amount of effort. Additionally, the dynamic movement of the population levels when there is competition for space may cause a given stock to drop to very low levels before it recovers toward equilibrium.

In general, many of the migration and competition factors which we have discussed may bring about reductions in population size,

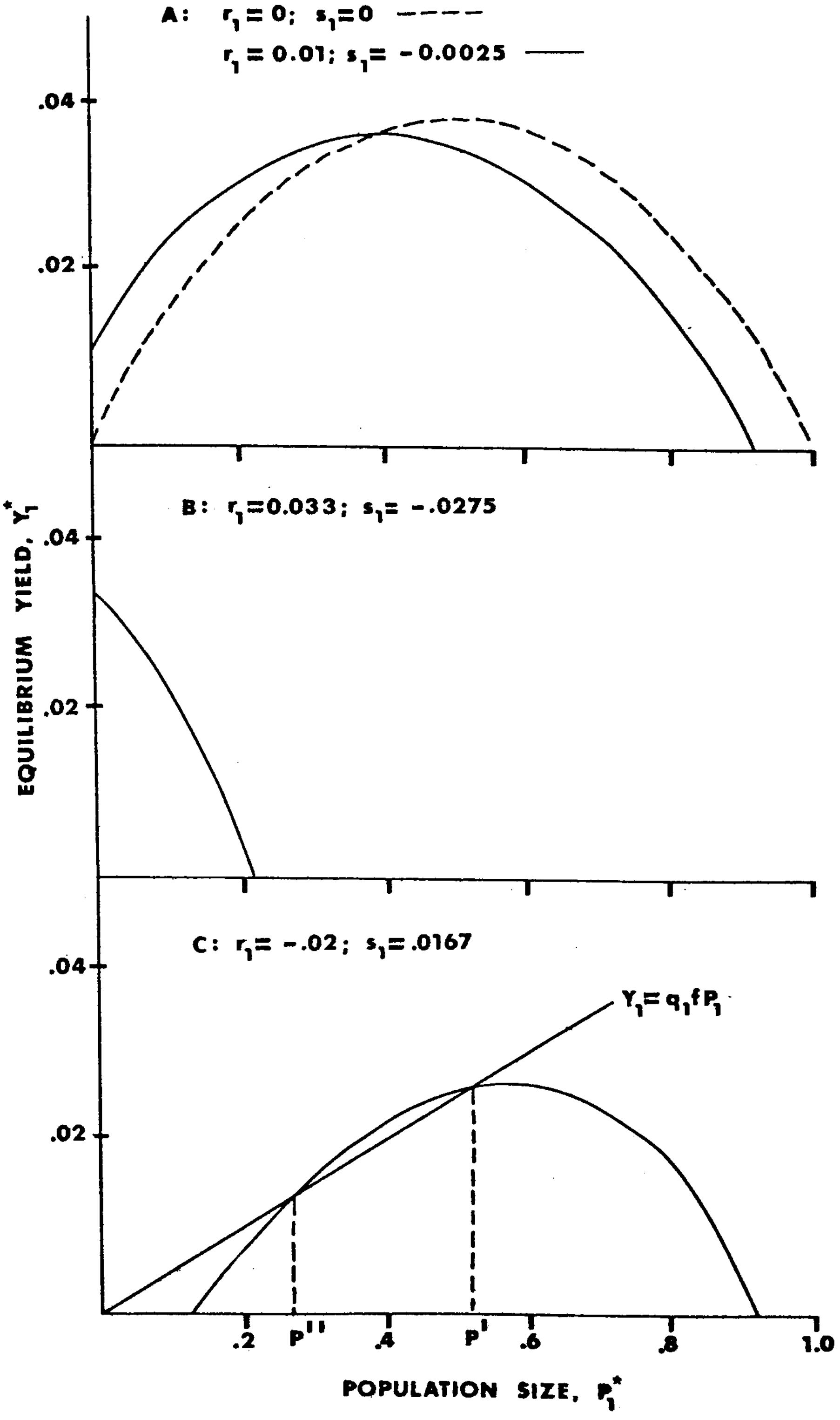

Figure 6. Equilibrium production curves when there is no spatial competition ($d_1 = d_2 = 0$). In 6A the dashed curve is when there is no migration ($r_1 = s_1 = 0$), and the solid curve is when there is moderate migration ($r_1 > 0; s_1 < 0$). In 6B, the population is a large sink of immigration ($r_1 >> 0; s_1 << 0$). In 6C, the population is a source of emmigration ($r_1 < 0; s_1 > 0$). The points P' and P" in 6C are stable and unstable equilibrium population levels for a given amount of effort, respectively.

either in dynamic or static solutions. Reef fish systems have evolved in such a fashion that these sorts of production curves have been very successful in the face of the small magnitude of random perturbations with which they are faced. However, the scale of man-induced perturbations (through exploitation, degradation of the habitat and interruption of dispersal of production) are much greater. Therefore, management policies should account for and guard against the unique behavior of the system in which population levels are low and there is an increased risk of depletion due to random and directed effects.

One factor which has not been discussed, herein, is a suitable criterion for management. As was shown by the competition model, a policy of maximizing total sustainable yield may systematically deplete some species. If this is carried to an extreme, the total fishery may collapse. Therefore, maximum total sustainable yield or maximum sustainable yield for several individual species may not truly protect the reef fish system. Since we are not presently at a state of knowledge in which every interspecific interaction can be studied and quantified, statement of management criteria becomes more of an art. For some time, it seems we will be attempting to maximize a weighted mean of the sustainable yields of important species subject to constraints on the minimum levels of other species in the system (both exploited and unexploited) which are important to the dynamics of the system. This implies a course of study and assessment of fish stocks which may not be exploited by fishing effort.

What, then, is the course which we should be taking in developing models to address these features of reef fish systems? The modeling approach should be two-pronged. First, we have to develop models of the migration and dispersal processes. In particular, the source and sink of reproductive products must be defined as functions of oceanographic conditions (Leis and Miller 1976). These must be quantified in terms of rates in complex versions of models such as equation (10).

Secondly and concurrently, we must develop models based upon assessment data of the important species in the system, both exploited and unexploited in which the dynamics are related to each other and to the available habitat. Competition for space in a stochastic environment (Sale 1978) may be modeled as a Markov chain in which the probability of a unit of habitat is occupied by a given species depends upon the numbers of each competing species and the species individual occupying that space in the previous time period. Through this approach we can develop long-term (equilibrium) solutions and still have the mathematical mechanism to investigate the transitional dynamics. Spatial competition models must then be melded with dispersal models before management policy can be developed.

Finally, in developing management advice from these models, we should take a stochastic, adaptive strategy. Our models will not faithfully mimic the system in all instances, especially in circumstances for which we have little theory and data, such as when population levels are low. Therefore, we must acknowledge the risk that the model outputs are random variables and the uncertainty in that the model structure itself may be wrong. When stochastic variations of equation (11) are developed for the reef fish system, then decision analysis using Markovian models (Mendelssohn 1980) and other stochastic procedures (Walters and Hilborn 1976; Hilborn 1979) may be used to formulate management stragegy which may be quickly adapted to the acquisition of new data and the stochastic interactions within the complex reef fish system.

Table 1. Parameter values for the non-competitive case of the two species system (equation (5)). See text.

Parameter	Value	Parameter	Value
Species 1		Species 2	
a_1	0.15	a_2	0.20
b_1	0.15	b_2	0.20
d_2	0.0	d_1	0.0
$\underline{a}/P_1^* \mid f=0$	1.0	$P_2^* \mid f=0$	1.0
MSY_1	0.0375	MSY_2	0.0500
A	1.0	A	1.0

$\underline{a}/P_1^* \mid f=0$ is the equilibrium carrying capacity

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MARKOV MODELS IN FISH COMMUNITY STUDIES - SOME BASIC CONCEPTS AND SUGGESTED APPLICATIONS

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ABSTRACT

The Markov method is suggested as a means for summarizing some types of fisheries data and for predicting the time path of certain variables of interest. The basic concepts of Markov chains are introduced and an example using hypothetical data for the Lake Victoria mixed species fishery is provided. The example illustrates some of the information it would be possible to obtain and utilize from this type of analysis. The results of the worked example suggest that the method may have utility in some types of fisheries investigations including mixed species coral reef fisheries.

INTRODUCTION

Fishery scientists have been interested for some time in characterizing or summarizing how tropical reef fish communities (or other multispecies fish communities) respond to various levels and types of exploitation or other perturbations over time and what the likely composition and yields from these communities will be in future time periods. Given this interest or objective, one is then interested in methods that will accomplish these purposes and that are reasonably straightforward to apply. Within this context the objective of this work is to briefly consider the concept of a Markov chain process and to suggest its potential utility in analyzing some reef and other multispecies fishery problems where time-ordered data exist over some reasonable time span.

It is generally recognized that the fish diversity of tropical coral reefs is probably higher than that of any other marine ecosystem. Emery (1978) has suggested that there may be over 2,000 species present on large Pacific continental barrier reefs. Connell (1979) has indicated that in addition to the high fish diversity on coral reefs, the reef building corals themselves consist of a large number of species which appear to exist in open nonequilibrium systems. The response of the corals to intermediate level disturbances is thought to account for much of this diversity. It is evident from the above that both the reef fish community and the coral reef environment are diverse and complex. In addition, tropical lake fisheries (exemplified by Lake Victoria) are also complex, consisting of diverse gear types and up to 200 species, with adults ranging in length from 6 cm to 2 meters (Marten 1979b).

Conventional approaches to fishery management in such systems may not be applicable or even possible in some instances.

A recent symposium on stock assessment in tropical small-scale fisheries (Saila and Roedel 1980) has resulted in some alternative approaches to fishery management which includes modified stock production models and applications of graph theory. However, no detailed consideration of Markov models was provided. Saila and Parrish (1972) first suggested a stochastic matrix model for studying exploitation effects on fish communities. This work is an attempt to expand and formalize some of these initial concepts and to indicate possible applications.

MARKOV PROCESS CONCEPTS

A very brief sketch of some of the concepts of a Markov chain process will be given and the assumptions, definitions and theorems necessary for a simple example will be stated. An excellent discussion of finite Markov processes is provided by Kemeny and Snell (1960) for those interested in details which are well beyond this introduction.

If in any given sequence of experiments or observations the outcome of each particular experiment depends on some chance event, then any such sequence is called a stochastic process. The process is finite if the set of possible outcomes is finite. There are many types including Markov chain processes.

A definition given by Kemeny et al. (1959) is as follows: "A Markov chain process is determined by specifying the following information: There is a given set of states ($s_1, s_2, \ldots s_n$). The process can be in one and only one of these states at a given time and it moves successively from one state to another. Each move is called a step. The probability that the process moves from s_i to s_j depends only on the state s_i that it occupied before the step. The transition probability P_{ij} which gives the probability that the process will move from s_i to s_j is given for every pair of states. Also an initial starting state is specified at which the process is assumed to begin."

The transition probabilities P_{ij} can be represented in the form of a transition matrix P:

$$P = \begin{array}{c|cccc|} & s_1 & s_2 & \cdots & s_n \\ \hline s_1 & P_{11} & P_{12} & \cdots & P_{1n} \\ s_2 & P_{21} & P_{22} & \cdots & P_{2n} \\ \cdot & \cdot & \cdot & \cdots & \cdot \\ s_n & P_{n1} & P_{n2} & \cdots & P_{nn} \end{array} \qquad (1)$$

where $\sum_j P_{ij} = 1$ for $i = 1,2,\ldots n$ rows and $j = 1,2,\ldots n$ columns (2) and $P_{ij} > C$ for all i and j (3)

The elements of Eq. (1), the P_{ij}'s denote the probability of moving from state s_i to s_j in the next step. Since the elements of this matrix are nonnegative and the sum of the elements in any row is 1, each row of the matrix is called a probability vector and the matrix P is a stochastic matrix. This matrix, together with an initial starting state, completely defines a Markov chain process. Given this information, we could determine the outcome of, say, the nth step.

It is also required that all states be accessible, that is, there is a non-zero probability of moving from state i to state j in a finite number of time steps. If this condition is met the chain is called irreducible (Feller, 1950). For the transition matrix [P] to be irreducible, a sufficient condition is that some power of this matrix has only positive components. If this is met, the transition matrix [P] defines a Markov chain process that is regular.

This study deals with regular Markov chains. The following are two theorems relating to the existence and uniqueness of an equilibrium solution.

Theorem 1. If P is a transition matrix for a regular chain then:

1. The powers P^n approach a matrix T as n increases.
2. Each row of T is the same probability row vector w.
3. The components of w are all positive.

Theorem 2. If P is a transition matrix for a regular chain and T and W are in Theorem 1, then the unique row vector w is the unique probability vector such that

$$wP = w \tag{4}$$

These theorems are from Kemeney et al. (1959) and from basic linear algebra. They state that if P is a transition matrix for a regular chain there exists a unique vextor w that is both a fixed vector for P and a probability vector. The distribution at time n tends toward this vector irrespective of the initial distribution or starting state.

These theorems can be used in deriving an equilibrium solution for a stochastic matrix.

From Theorem 1

$$P^n \rightarrow T \text{ as } n \rightarrow \infty \tag{5}$$

and

$$T = e'w \tag{6}$$

where $e' = (1, 1, \ldots 1)$ and w is the equilibrium row vector. Therefore, an easy way to derive the equilibrium vector is to multiply P by itself a large number of times. This is called powering the matrix.

Another basic type of Markov chain is an absorbing Markov chain. A state in a Markov chain is an absorbing state if it is impossible to leave it. That is, $P_{ij} = 1$ when $i = j$. A Markov chain is absorbing if, a) it has at least one absorbing state and b) from every state it is possible to go to an absorbing state, but not necessarily in one step. This results in the following Theorem 3: In an absorbing Markov chain, the probability that the process will be absorbed is 1.

Given the above definitions, assumptions, and concepts, an attempt will be made to apply some of these to the development of a method for the analysis of exploitation effects on fisheries.

MODEL AND HYPOTHETICAL EXAMPLE

Marten (1979a,b) has presented an interesting management strategy based on an analysis of Lake Victoria's artisanal fishery. The possible solution to the overfishing problem suggested by analysis of catch statistics from a large number of apparently isolated fishing locations along the periphery of the lake is that catches can be improved by increasing the fishing effort directed toward the large predatory species and essentially reducing them to near extinction. It seems clear that this concept should be examined further in view of its important implications, possibly for artisanal reef fisheries as well. The raw data which Marten (1979c) used were unavailable for this report and apparently have not yet appeared in formal publication. However, it is believed that the Markov model approach suggested herein could be used effectively for further analysis of these raw data and to analyze the response of this type of fishery to the proposed management regime.

The Markov process model makes no postulates about underlying mechanisms, but it is believed its properties may aid in the analysis of some types of catch records and other fisheries data, such as those described by Marten (1979a), and those resulting from mixed species reef fisheries. This model type has been applied with some success to geological studies (Krumbein and Dacey 1969), to plant studies (Anderson 1966; Horn 1975) and to animal population studies (Bartlett 1960). It should be pointed out that some applications of the model, such as the one illustrated, require sampling of fish catches in both time as well as in space. This implies a high degree of sampling effort, which is a difficult process in developing areas.

For the purposes at hand it is assumed that the management strategy proposed by Marten (1979a,b) has been put into effect and some data are available after this imposed management strategy. Since Marten indicated that _Tilapia_ yields are expected to consist of more than 40 percent of the total yield under optimum fishing, the weight yield of _Tilapia_ expressed in kg km^{-2} quarter-$year^{-1}$ is the variable whose responses over time are to be analyzed. In this example the yields of _Tilapia_ are arbitrarily grouped into class intervals which define admissible states for the model. These are: s_0 = 0-50, s_1 = 51-100, s_2 = 101-150, s_3 = >151, expressed as hundreds of kilograms per square kilometer per quarter year interval. A larger number of stages may be desirable for some purposes, but this grouping is considered adequate for illustrative purposes.

Assume that data from a sample of 49 landing sites listed by Marten were tabulated for two years (8 quarterly intervals) providing a total of 392 yield observations from which the following transition matrix is developed:

$$P = \begin{array}{c} \\ s_0 \\ s_1 \\ s_2 \\ s_3 \end{array} \begin{array}{c} \begin{array}{cccc} s_0 & s_1 & s_2 & s_3 \end{array} \\ \begin{bmatrix} 0.69 & 0.21 & 0.08 & 0.02 \\ 0.24 & 0.58 & 0.11 & 0.07 \\ 0.05 & 0.26 & 0.36 & 0.33 \\ 0.03 & 0.28 & 0.27 & 0.42 \end{bmatrix} \end{array} \qquad (7)$$

This transition matrix is easily generated from a tally matrix of yield class frequencies by forcing the probabilities in each row to add up to 1.00.

One of the problems in fishery applications of Markov models is to determine if, or when, it is acceptable to treat the succession of yields (or any response variable) in a time sequence as a Markov process. The first-order Markov property requires that each observation depends only upon the observation at the preceding point. This seems reasonable if the observation points are not spaced too closely or too widely. Formal statistical tests (Anderson and Goodman 1957; Billingsley 1961) for this Markov property are available and should be applied. The observed data, structured as a transition probability matrix, are tested under the hypothesis of an independent-events model against a first order Markov chain alternative. These tests have not been applied to the hypothetical data presented in the transition matrix.

The transition matrix (eq. 7) provides, in itself, some insight into the dynamics of the process, in this case the dynamics of Tilapia yields. For example, the entries on the main diagonal indicate that there is a fairly high tendency for yields to remain in a given yield class interval from one quarter to the next. The probabilities on the main diagonal tend to be larger than the other elements in each row. This stability may be due to the arbitrary definition of the class intervals. It is also noted that there is some tendency for improved yields in the 101-150 kg X 10^2 yield range (i.e. state s_2). That is, the probability of increasing to the >151 yield class is 0.33 compared to a probability 0.36 of remaining in that class. These are clearly almost the same. Comparisons of the likelihood of an increase or a decrease of any yields from a given state may simply be made by summing the elements to the right of the diagonal in that row for increases and summing to the left in that row for decreases. For example, with a beginning state of s_1, the probability for an increase is 0.18 and for a decrease is 0.24. It is also evident from an examination of the transition matrix that the most probable outcome excluding remaining in the same class is that the yield goes up or down one class interval in one observation period.

Given the transition matrix described above or the transition matrix and a starting vector (i.e. the starting distribution of yields), it is possible to analyze the structure that the fishery would eventually reach if the above conditions persisted through time. This has some interesting management implications in fisheries as suggested previously. It was indicated in the section on concepts that for regular Markov chains the equilibrium yield distribution does not depend on the initial starting vector, nor does the time that it takes to reach equilibrium. However, the rate at which the starting distribution approaches equilibrium obviously depends on the starting distribution. When the transition matrix (eq. 7) is powered, the equilibrium yield distribution which results is:

$$w = [.322\ .363\ .166\ .149] \tag{8}$$

This equilibrium distribution vector (eq. 8) is accurate to two decimal places after raising the transition matrix to the 15th power.

The meaning of the equilibrium in this context is defined as that distribution for which the average number of yields changing to a given yield class per quarter-year equals the average number of yields changing to another yield class. This must be considered statistical in nature for the entire fishery, but dynamic for an individual sample area. In other words equilibrium does not imply that there is no change in yields over the yield classes. Instead the concept of equilibrium explicitly assures that changes in yield classes occur, but on the average factors acting to increase the yields from a given class value are exactly counterbalanced by factors acting to decrease yields from this class value.

There is also the possibility of premultiplying the transition matrix by a row vector of an initial distribution of yields in each state to derive the structure for the next period. Repeating this process will trace the path of the yield distribution en route to equilbrium.

ABSORBING CHAINS

A brief exploration is made of absorbing Markov chains using the same data as illustrated previously. The definition of absorbing states and indeed the example provided is artificial. However, it will illustrate another possible use of Markov models for complex fisheries problems. A state has been defined as an absorbing state in a Markov chain if it is impossible to leave it. Furthermore, a Markov chain is absorbing if it has at least one absorbing state and from every state it is possible to go to an absorbing state.

For the purposes of this example assume that states s_0 and s_3 are absorbing. In this case we assume that whenever the yield goes to the 0-50 interval or to the >151 value, it stays in these classes. In canonical form the transition matrix for this example is:

$$\begin{array}{cc} & \begin{array}{cccc} s_0 & s_3 & s_1 & s_2 \end{array} \\ \begin{array}{c} s_0 \\ s_3 \\ s_1 \\ s_2 \end{array} & \left[\begin{array}{cc|cc} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ \hline 0.24 & 0.07 & 0.58 & 0.11 \\ 0.05 & 0.33 & 0.26 & 0.36 \end{array}\right] \end{array} \qquad (9)$$

In the above matrix (9) there are two absorbing states s_0 and s_3 and two nonabsorbing states s_1 and s_2. Let the lower right sub-matrix of (9) be Q. Then the elements of $(I-Q)^{-1}$ give the mean number of periods in each transient state for each possible non-absorbing starting state. The I indicated above is an identity matrix consisting of all zeros except for one's in the main diagonal. The subtraction of matrices and inversion results in

$$(I-Q)^{-1} = \begin{array}{cc} & \begin{array}{cc} s_1 & s_2 \end{array} \\ \begin{array}{c} s_1 \\ s_2 \end{array} & \left[\begin{array}{cc} 2.664 & 0.458 \\ 1.082 & 0.749 \end{array}\right] \end{array} \qquad (10)$$

From this it is found that starting in state 1 the mean number of periods in state 1 before absorption is 2.664 and 0.458 in state 2. If the elements in each row are summed the mean number of periods required for a given starting state before being absorbed is obtained. This results in the following vector:

$$\begin{array}{cc} s_1 & \multirow{2}{*}{} \\ s_2 & \end{array} \left[\begin{array}{c} 3.122 \\ 2.831 \end{array}\right] \qquad (11)$$

In this example the mean number of periods before absorption starting in state 1 is 3.122 and 2.831 for state 2.

Next consider the probability that an absorbing chain will finish in a particular absorbing state. Let the lower left submatrix of (9) be designated as R. Then if $(I-Q)^{-1}$ in Eq. 10, is postmultiplied by R the following probabilities result:

$$\begin{array}{cc} & \begin{array}{cc} s_0 & s_4 \end{array} \\ \begin{array}{c} s_1 \\ s_2 \end{array} & \left[\begin{array}{cc} 0.662 & 0.338 \\ 0.347 & 0.655 \end{array}\right] \end{array} \qquad (12)$$

The interpretation is as follows. For example starting in state s_1 there is a 0.662 probability of absorption by s_0 (low yield) and an 0.338 probability of absorption by s_4 (namely high yields). For state s_2 there is a lower probability of ending with low yields and a relatively high 0.653 probability of achieving the desired goal of sustained high yields.

A few ways in which Markov chains can be used in fishery studies have been suggested. It is believed that these will suggest many further applications. In general, a characteristic that can be quantified can be analyzed in this fashion as long as the conditions stated previously hold reasonably well.

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SESSION SUMMARY

MODELING OF REEF FISHERIES

by

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The objective of this session was to present and discuss models of reef fish populations and reef fish fisheries which might contribute to management of these resources. In particular, emphasis was to be given to modeling techniques which could describe those unique aspects of reef fish ecosystems and fisheries which are so integral to their function.

The session began with a paper given by myself in which a standard fisheries production model was modified to incorporate competetion between two species for a limited amount of available space. The assumption is that reef fish competition may not be on the level of species interaction, but rather at the level of the individual competing for living room. Competition of this sort tends to cause maximum sustainable yield to occur at population levels less than that without competition. Also, two species competing for space may be sequentially affected by increasing fishing effort. The impact of alternative sources of recruitment to a reef population was also discussed.

Saul Saila presented the next paper, the subject of which was the use of Markov chain models in studying fish community and population dynamics. He reviewed the theory of such models and presented an example for which the stochastic models might prove useful for reef fish management. The need for models of reef fish populations which incorporate stochastic events explicity and which allow multispecies interaction to be handled efficiently make Markov models likely candidates for further investigation.

In the session's final paper (not printed in these proceedings) Gene Huntsman discussed the interaction of fishing with protogyny, a common mode of reproduction in reef fishes. Recognizing that the interaction of the natural mortality rate with a fixed sexual-transition rate results in a constant population sex ratio, Huntsman and Bill Schaaf hypothesized that departures from that sex ratio would decrease the reproductive fitness of the population. To examine the effect of fishing (which can alter the sex ratio) on reproductive fitness Huntsman and Schaaf constructed six protogyny-fishing models based on life history parameters of the graysby, Epinephelus cruentatus. One of the models, a control, simulated the effect of fishing on reproduction of an animal like the graysby in all ways except that it was gonochoristic, (normally bisexual), and thus had a sex ratio that was constant over all levels of fishing. A second model represented a protogynous population with a fixed sexual-transition rate, while the remaining four models allow examination of the effects of fishing on protogynous populations which compensate for fishery-induced changes. Three of those models are of populations that compensate by adjusting the transition rate in different ways, the fourth model simulates compensation through increased growth.

All of the modeled protogynous populations lost reproductive fitness far more rapidly than the gonochoristic population did. The suggestion is that protogynous populations may need more careful management than do normal ones. Examination of a common management strategy, size limits, suggested that fixing the minimum size captured equal to the size of a seven year old fish would maintain maximal yield/recruit (and probably yield) no matter how large F became. And equally important the seven year equivalent size limit completely negated any impact of fishing on reproductive fitness regardless of whether the population was gonochoristic or protogynous.

Much of the discussion during this session centered upon biological aspects of this last paper. Interest was generated by this model as a means of investigating scientific hypotheses, whereas, the first two papers were dealing with reef fish populations at the level of fisheries interaction. The conclusion to be drawn from this discussion is that there are different levels of modeling reef fish populations each of which can contribute to research and management. Models may be developed to depict individual fish at a reef to study behavior and community structure. Other models may describe population interaction and exploitation such that management advice may be generated. Yet future efforts in reef fish research should encompass both of these levels of models.

Additionally, it was acknowledged that a fundamental problem in reef fishery studies was a lack of adequate time series for fisheries data. It would seem that this obstacle can be overcome only by transferring data between tropical reef systems such as those in the South Pacific with those in the Caribbean. Also smaller scale experimental studies should be designed to shed light on those factors of competition and community structure which are critical to fisheries management. Modeling exercises provide a focus for directing field activities. They tend to illuminate those variables which contribute the most to uncertainty about scientific management. It is to that purpose that the results of this session served, i.e., the identification of areas of considerable uncertainty in reef fish management.

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