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WHOI-NEFC Fisheries Ecology Seminar Series A Summary

by

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June 1985

Technical Report

*Partial funding provided through the National Marine Fisheries Service
as part of a cooperative agreement with the Woods Hole Oceanographic Institution
and through a grant to the Center for Analysis of Marine Systems
of the Woods Hole Oceanographic Institution.*

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A Summary

The Steering Committee

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ABSTRACT

This report summarizes the findings of the joint WHOI-NEFC seminar series on recruitment processes in marine fish populations. The seminar series reviewed the status of knowledge of the recruitment process together with on-going research in this field. From the seminars presented it was evident that potentially important biological and physical processes which may control recruitment occur throughout the entire first year of life. It is important to understand the causes of recruitment variability in order to know the degree to which density dependence controls marine fish population dynamics. Future research, therefore, should not focus on a single process or life stage but instead should evaluate all potentially important processes throughout the first year of life.

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INTRODUCTION

Management of commercial fish populations requires accurate assessment and reliable forecasting of stock size and composition. Knowledge of underlying ecological processes is required in this regard. Such an understanding can best be obtained through collaborative research, both across scientific disciplines as well as between academic and governmental institutions. Toward this end, the Woods Hole Oceanographic Institution and the Northeast Fisheries Center (NMFS, NOAA), in 1981, established a cooperative agreement promoting joint research, including data analysis and synthesis. As part of this cooperative agreement, a series of bi-weekly seminars in fisheries ecology took place between April and October, 1984. This seminar series, summarized herein, addressed the central problem in fisheries ecology today, that of recruitment variability in fish populations.

Recruitment is the single most important natural event controlling year class strength and fishable biomass. Thus, there is a major thrust in fisheries ecology to understand the processes controlling recruitment variability. A recent series of fisheries ecology workshops has dealt with this subject (Fish Ecology I, II, III) culminating in an outline of research objectives labeled REX for recruitment experiment (see Rothschild, 1982). Since the last workshop, various aspects of REX are being carried out while new hypotheses are emerging. The WHOI-NEFC fisheries ecology seminar series was formed in order to summarize the status of knowledge of the recruitment process, to review on-going research, and to develop potential collaborative research objectives between the two institutions. A list of seminars together with abstracts

and synopses of talks, as provided by the speakers, is attached.

Seminars were also recorded on audio-visual tapes and are available from the institution archivist (WHOI).

Since information presented in the seminars is overlapping, this summary presents a general overview of our understanding of the recruitment process based on all seminars and ensuing discussions. Individual seminars are referenced (by number, see list) according to the specific information they provide. Similar as well as contrasting views are presented. Testable hypotheses and an outline of proposed research are offered for subsequent discussion sessions.

RECRUITMENT VARIABILITY

I. Statement of the Problem

Interannual variability in biomass of exploited fish populations is due to variations in growth, recruitment, and mortality (both natural and fishing; 2; Sissenwine, 1984). The bulk of natural variability (i.e., excluding fishing effects) is caused by fluctuations in recruitment. Passage of good and bad year classes through a fish population is the dominant natural event controlling population size. Furthermore, fish populations often rely heavily on one or two very large but infrequent year classes to maintain themselves, these cohorts constituting the bulk of total population biomass, growth, and fecundity (2,9; Grosslein and Hennemuth, 1973). It is of paramount importance, therefore, to understand the causes of variable recruitment and in particular the combination of events leading to extraordinarily large year classes (2,9). Thus recruitment variability and how it relates to the environment is the central problem in fishery ecology (2; Sissenwine, 1984).

This problem is unlikely to be fully resolved in the near future but perhaps within the next two or three decades. It should be understood that even when this problem is resolved and accurate forecasting of fish population abundance becomes possible, within the broader context of fishery management, this information must be considered together with socio-economic and political constraints which may carry equal or greater weight (1; A. Peterson, introductory remarks).

II. Stock-Recruitment Relations and Density Dependence

The lack of correlation between spawning stock size and subsequent recruitment to the fishery is well-known in fishery biology (2,3; Clark et al., 1982). Traditional theoretical models, however, are based on the assumption that recruitment is a density dependent compensatory function of spawning stock size (e.g., models of Ricker, 1954 and Beverton-Holt, 1957; 3). Thus, recruitment variability is considered by fishery biologists as density independent random deviations (noise) about the true underlying density dependent relationship (2,3; Sissenwine, 1984). From the theoretical standpoint, a number of compensatory mechanisms can be envisioned, but, from the empirical view, stock recruitment models are not borne out by the data. Only in rare instances is there a suggestion in the data of compensation at high stock size (2; Clark et al., 1982). For most species, recruitment appears to be density independent except at very low stock sizes when recruitment is also low. Several more recent stock recruitment models have modified the Ricker and Beverton-Holt models and examined the relative importance of density dependent and independent terms (3; Sella and Lorda, in

press; Deriso, 1980; Shephard, 1982). Such models have been combined with yield per recruit models to predict stock sizes and, although there is considerable uncertainty in the recruitment equations, these yield models at least account for recruitment overfishing (3; Shephard, 1982; Sissenwine et al., 1984a).

There are two main problems with the interpretation of stock-recruitment data. First, it is necessary to know the measurement error associated with each individual estimate of stock and recruitment so that the actual degree of natural variability can be determined. Estimates of both stock and recruitment are usually based on virtual population analysis (VPA) but the error associated with this method is unknown at present (3). Work is in progress at the University of Washington addressing this problem (3). The results of several recent papers on stock and recruitment suggest that measurement error alone can obscure any underlying relationship (3; Ludwig and Walters, 1981). Lack of correlation between VPA and survey estimates of age one fish for some species (e.g., Georges Bank silver hake) is indicative of the potential severity of this problem although other species show good correlations (5; E. B. Cohen, unpub. data). It is very important therefore to be able to determine confidence intervals for VPA estimates. A recent paper by Collie and Sissenwine (1983) presents a method of stock assessment based on research vessel survey and commercial catch data in which measurement error in survey estimates is taken into account. The errors associated with commercial catch statistics and the assumption of constant natural mortality were not evaluated. Until such errors in stock assessment methods are resolved, the true natural variability in stock recruitment data cannot be known.

The second problem with interpreting stock recruitment data deals with the underlying theoretical relations. This problem actually goes beyond stock recruitment relations and deals with the concept of density dependence vs independence in fish populations. The theory of fishing is based on the concept of compensation leading to stable equilibria; as stated above, recruitment variability is considered as noise imposed on the underlying relations by the environment (2,3; Sissenwine, 1984). Over the past thirty years or so, population biologists have been arguing for or against either density dependence or independence in determining population dynamics (see Cold Springs Harbor Symposium, 1958). Recent papers have suggested that density independent factors may be more important in controlling population size, i.e., that populations are in a continuous state of non-equilibrium and local extinctions do in fact occur (3; H. Caswell comment; Strong, 1984; Sousa, 1984). If this view is correct, certain fundamental concepts in fishery biology need to be revised, e.g., there would be little meaning to such concepts as surplus yield and density dependent multispecies interactions. High variability in stock-recruitment data for most exploited species of temperate marine fish which have pelagic eggs and larvae indicates that density independent processes are overwhelmingly dominant. On the other hand, compensatory growth and fecundity have been demonstrated for some species, e.g. Georges Bank haddock (2; Clark et al., 1982) and, for this latter species, lower recruitment may occur at highest stock densities (3; Clark et al., 1982). With respect to recruitment, some investigators feel that knowledge of the causes of recruitment variability will allow better understanding of the underlying density dependent relations (2,3) whereas

others believe that the density independent variability in recruitment actually may drive the system (H. Caswell comment). In light of the available data, consideration must be given to both views.

Density dependence operates through intra- and interspecific competition and predation. Competition for food among larval and adult fish is unlikely. Larval fish are too sparse in the water column to effectively control their prey populations (4,7,10,12; Cushing, 1983; Davis, 1984); other zooplankton predators such as chaetognaths, mysids, euphausiids, and gelatinous forms are generally much more abundant and thus regulate the prey concentrations available to the fish larvae (c.f., Davis, 1984). Growth rates and length-weight data of adult fish show little variation, implying that on the whole food is not a limiting factor (2,5,16; Sissenwine, 1984). The total demand for food appears highest among juvenile fish so that competition may be relatively more important at this life stage (5,11; J. Steele comment; Anderson and Ursin, 1977; Sissenwine et al., 1984b). Density dependent predation within and between species, if it occurs at all, appears to have the greatest impact on survival of pre-recruit fish (2,5). Since all multispecies fisheries models are based on the assumption of intra and inter-specific density dependence, it is critical to determine the degree to which adult fish prey on juveniles and larvae and whether juvenile fish regulate their own food supply.

If one accepts the notion of density dependent growth and predation, simple predator-prey models can be derived which exhibit multiple stable equilibrium points (8; e.g., May, 1977). Stochasticizing the predatory component of such a system at the lower frequencies of variability

characteristic of the ocean environment leads to appearance and disappearance of model populations at time scales similar to those observed historically for several marine fish stocks (8; Steele and Henderson, 1984). Thus, even if the concept of compensation is accepted, major shifts in stock size may occur in the absence of any fishing mortality, although fishing pressure increases the frequency of such "flips" in the system (8; Steele and Henderson, 1984). It remains uncertain whether the same effect can be obtained when prey and predator populations are represented in age structured models with predation operating chiefly on pre-recruits. Introduction of differential mortality and a time lag between pre-recruit and reproductive stages may act to buffer the system against sudden shifts in abundance. This requires further study.

III. Causes of Recruitment Variability

The search for understanding variable recruitment has involved both empirical (correlative) and process oriented studies (2; Sissenwine, 1984). Empirical studies have attempted to correlate recruitment with environmental variables while process oriented research has searched for causal mechanisms determining recruitment. Empirical studies have generated many statistically significant correlations between recruitment and the environment (Carruthers, 1951; Sissenwine, 1974; Hayman, 1977) but provide little insight into cause and effect (2). There are many other problems with this approach leading to the inability to predict post-publication events (2). On the whole, however, empirical studies do indicate that there is a relationship between the physical environment and recruitment variability (2; Sissenwine, 1984). They also suggest what processes should be studied in the future. Process oriented

studies, on the other hand, have examined the causes of pre-recruit mortality in more detail.

A. Pre-recruit Mortality

Survival rate during the pre-recruit stage largely determines recruitment variability; spawning biomass is much less variable (2,3). Pre-recruit mortality operates on eggs, larvae, and juveniles, the former two usually being planktonic and the latter nektonic or demersal. Mortality occurs from starvation, predation, disease, parasitism, and toxic pollution. Starvation and predation are believed to be the dominant sources of natural mortality for most commercial marine fish species which have offshore populations (2; cf. Pitcher and Hart, 1982; Sissenwine, 1984). In addition, physical transport of pre-recruits out of a given spawning/nursery area is also considered a major source of mortality since surrounding waters are typically unfavorable for survival, although actual mortality may be due to predation or starvation. Most process-oriented research has focused on the egg/larval stages so that very little information is available on juveniles (2,4,5,11,12). The relative importance of the three dominant sources of mortality (predation, starvation, and physical loss) to egg/larval survival will be discussed first. A discussion of the relative importance of egg/larval vs. juvenile survival in determining recruitment success will follow.

1. Egg/Larval Mortality

a) Starvation vs. Predation

The current conflict over whether starvation or predation is more important in determining larval fish survival may be largely semantic.

Implicit in the starvation hypotheses (e.g. Hjort, 1914; Lasker, 1975; Cushing, 1975) is that starvation may not be the actual cause of death but simply that reduced food levels cause increased mortality. This can happen in three obvious ways: 1) actual starvation, 2) reduced predator avoidance capability, and 3) reduced growth rate which prolongs the larval stage thus increasing the period exposed to predation. The starvation hypothesis, stated in this way, is not inconsistent with a predation hypothesis which allows food limited growth rate. It is inconsistent, however, with the idea that fish larvae always grow at maximal temperature dependent rates so that food has no effect on length of larval life, or predator avoidance ability. The latter predation hypothesis says that all mortality is due to predation and that food is never limiting. Both the former predation hypothesis and the starvation hypothesis, on the other hand, imply that most or all of the mortality is due to predation but that food limitation can act to increase the degree of this predation. Thus a lack of actual starvation does not imply food has no effect on mortality.

The effect of food concentration on growth and survival of fish larvae has been examined in a number of field and laboratory experiments (4,7,10; e.g., Houde, 1975, 1977, 1978; Laurence, 1974; Werner and Blaxter, 1980; Lasker et al., 1970; Lasker, 1978; Cohen and Lough, 1983). Significant variation among species and between individuals within a species has been found. Generally, laboratory experiments have shown that both survival and growth increase asymptotically with prey density. Earlier laboratory experiments found that maximum growth and survival occur at food concentrations much higher than those typically encountered in the sea (4; for

review see Hunter, 1981; Houde, 1982). It has been subsequently found that food requirements and mortalities observed in laboratory experiments sometimes can be abnormally high and the researcher often may be working with "dying" larvae (4; Houde, 1982). Laboratory mortality rates decrease with the rearing skills of the investigator, however, and in more recent studies low mortalities have been achieved at food concentrations equivalent to those found in the sea (4,11; Houde, 1982).

In addition to density of prey, biochemistry of larvae and their prey has been examined (10; e.g., Scott and Middleton, 1979). Lipid levels and composition are most variable and are relatively more important to larval growth (10; Roman, 1982). Since zooplankton prey typically feed on a wide variety of phytoplankton species and fish larvae feed on a variety of zooplankton species, from the nutritional standpoint, the diet of larval fish is likely to be well balanced. Thus absolute concentration of prey may be more important than chemical or species composition in determining growth rate.

High larval survival in mesocosms at food concentrations equal to average concentrations found in the field suggest that starvation per se is not the dominant source of mortality (6; Oiestad, 1983). The bio-energetic models of Laurence (1983) have shown that starvation is relatively more important for haddock than cod on Georges Bank (7). Predation mortality has been estimated from laboratory and field experiments to be roughly twice starvation mortality for Bay anchovy larvae in Biscayne Bay (4). Thus actual starvation can be an important, but not dominant, source of mortality depending on the species. Starvation mortality is thought to be relatively more important during the first 1-2 weeks of feeding (4,11; Houde, 1982; Hunter, 1984). If laboratory

estimates of required prey densities are abnormally high, then starvation in field populations may be less important. There does appear to be an effect of container size on larval survival and food requirements for some species; further quantification of this effect is needed (4).

Although prey concentrations in the sea may be generally high enough to prevent death by starvation, they are not high enough to allow for maximal growth and development (4,7; eg., Houde, 1982; Laurence, 1982). In fact, fish larvae are capable of consuming 100-300% of their body weight per day at high food concentrations and although their assimilation efficiencies are low (20-60%), their net growth efficiencies can be quite high (40%; 4; Houde and Schekter, 1980; Eldridge et al., 1977; Stepien, 1976; Hunter and Kimbrell, 1980; Laurence, 1983). Thus, fish larvae appear to have evolved to maximize consumption and growth (4). Unless food concentrations are unusually high, larval growth will be food limited in the sea (4). RNA/DNA studies show that field caught larvae grow at high rates when prey densities are also high (5,11; Buckley, 1984). Captured larvae, however, may represent only survivors whereas suboptimally growing larvae may have already succumbed to predation (Buckley, 1984).

If fish larvae do grow submaximally in the sea, as the preponderance of evidence suggests, length of larval life must be a function of prey density. Seemingly minor extensions of the larval phase can dramatically increase total mortality even if the mortality rate remains constant (4; Houde, 1982). Food limited growth may also reduce predator avoidance capability thus increasing the mortality rate itself (4). Conversely, fish larvae growing maximally can sustain high predation rates because the larval stage duration is compressed (4).

Actual coupling between zooplankton density and recruitment success varies with species and may depend on the degree of localization of the spawning stock (12; Sherman et al., 1984). Peak spawning of some species is localized in time and space and is in synchrony with peak prey abundance in the area. Other species spawn over much larger areas for longer periods of time (12; Sherman et al., 1984).

The micro-distribution of larval fish and their prey has not been well studied but is important in determining food availability and thus growth and survival of the larvae (4). Unknown aggregating mechanisms at fine and micro-scales can lead to patches of prey several orders of magnitude more concentrated than background. Patches are often associated with physical density gradients (fronts, thermoclines, etc.) but can also occur in the absence of any detectable physical structure, implying biological aggregating mechanisms (4; Houde, 1982). The micro and fine scale environment (MFE) of fish larvae was pointed out as an area of critical importance in Fish Ecology III (Rothschild and Rooth, 1982) and is an important subject for future research (4,7). Such small scale processes should be examined in conjunction with meso-scale processes so that population survival can be estimated (16).

Predation as modified by food availability is clearly the usual dominant source of egg/larval mortality (aside from physical advection discussed below). Very high survival rates (50-90%) have been reported for herring, winter flounder, and cod reared in predator free enclosures and large bags even at prey concentrations approximating field levels (6,7,12; e.g., Oiestad, 1983). This of course does not imply that food is not limiting in the sea. Experiments at elevated prey concentrations where predators are not excluded

would also be expected to show high survival. Because of logistical constraints, such experiments have not been done. High field mortality rates of yolk sac larvae relative to eggs and older larvae have been reported, but in some cases this was due to the relatively high retention of eggs and older larvae but extrusion of newly hatched larvae through the meshes of the nets used (4). Mortality rates of fish eggs can be very high and variable indicating high and variable rates of predation (11; Hunter, 1984).

Numerous predators of larval fish have been identified including macrozooplankton, squid, and planktivorous fishes (11; Hunter, 1984). Little information is available concerning the rates of feeding by these predators on fish larvae owing to the sparsity of larval fish in their diets relative to other prey, rapid decomposition rates of larvae in their guts, and inability to quantitatively sample certain of the predators including juvenile fish and gelatinous zooplankton (2,5,11; Sissenwine, 1984; Hunter, 1984). The recent work of Moller (1984) suggests that medusan predation can be important. Immunological techniques may be helpful in qualitative identification of species of fish in predator stomachs (11,12; Hunter, 1984). Egg cannibalism has been estimated to be 30-40% of the natural egg mortality for some species of anchovy (11). The degree of inter and intra-specific predation by fish on larvae and juveniles has not yet been quantified (11).

b. Physical Transport

Empirical and theoretical modeling studies have shown that passive drift of eggs and larvae out of the spawning area is a potentially important source of pre-recruit mortality (2,13,14; e.g., Walford, 1938; Sissenwine, 1984;

Flierl and Wroblewski, in press). There are several physical mechanisms by which eggs and larvae can be lost from a spawning area. These include diffusion, flow-through type advection, time dependent motions such as tidal flow, and intermittent events such as warm-core ring entrainments and storm induced flows (13). Frequency of warm-core rings impinging on Georges Bank during the spring and summer appears loosely correlated with good and bad year classes of haddock and cod (13; Flierl and Wroblewski, in press). Simple one dimensional biological/physical models show that entrainment of shelf water by rings can cause significant mortality of eggs and larvae (13). Such models are depth and cross-shelf averaged, however, so that the vertical and horizontal extent of the off shelf transport could not be evaluated. Empirical evidence suggests that rings may enhance or reduce advective loss of larval fish from Georges Bank depending on the spatial relationship between the ring and the larvae (14). Rings may improve the degree of recirculation on Georges Bank thus reducing advective losses to the southwest while at the same time cause off-shelf transport on the eastern half of the bank (14). The location and size of larvae would be critical in such a case (14).

In addition to rings, atmospheric events may also affect recruitment (13,14). Nelson et al. (1977) found good correlation between off shelf Eckman transport and subsequent recruitment in atlantic menhaden, and Chase (1955) obtained similar results for Georges Bank haddock, although both relationships have failed in recent years. Davis (in press) has suggested that strong winds during winter and early spring (Dec-Feb), prior to spawning, can reduce the size of the subsequent (May-June) peak in larval fish prey populations on Georges Bank. Only in rare years are winds low enough and rings infrequent

enough between December and June to allow for stability of the water column. Such a year was observed in 1975, and haddock recruitment was extraordinarily high that year. R. Lasker has shown that stability in the water column may be required for successful recruitment of the northern anchovy (11; Hunter, 1984). He has hypothesized that if upwelling is too strong or weak, prey aggregations at densities required for larval survival are not found (11; Hunter, 1984). In order to determine the relative importance of physical losses (or any other potential causes of mortality for that matter) to total egg/larval mortality, it is necessary to examine the variability of such losses as well as their absolute magnitudes (14).

2. Larval vs. Juvenile Mortality

Very little information is available on juvenile stages of fish populations (2,4,5). This is due largely to sampling problems which include avoidance of plankton nets, lack of midwater trawl surveys, and avoidance/escapement of and limited availability to bottom trawls. In spite of this, there has been some controversy as to whether survivorship of egg/larval or juvenile stages is more important in determining recruitment (2,4,5,6,11,12). Several arguments have been made to stress the relative importance of the juvenile stage in determining strength of recruitment (2,5).

First, good correlations have been seldom found between recruitment and abundance of older larvae from ichthyoplankton surveys (2,5). Significant relationships have been found, however, between spawning and abundance of eggs/newly-hatched larvae collected in surveys (2,5). Significant relationships have also been observed between survey collected age one fish and recruitment estimated from VPA (2,5). This evidence implies that

recruitment is set somewhere between late larval and late juvenile stages (2). The potentially large measurement errors associated with estimating late larval abundance (larvae at this stage are scarce, more patchy, and better able to avoid plankton nets) as well as with VPA estimates of recruitment have not been adequately quantified and could in themselves cause spurious results (3). For example, as mentioned above, for Georges Bank silver hake, lack of correlation between VPA and survey estimates of age ones has been shown (5). In addition, no correlations have been reported between late larval abundance and number of eggs spawned, whereas good correlations have been found between eggs-young larvae and spawning (2,5). Whether this de-coupling between abundance of young and old larvae is due to the environment or to sampling bias is not known. Evidence that recruitment can be set during the larval stage is found in the study of Bannister et al. (1974) which showed that high larval survival in North Sea plaice is preserved through the juvenile stages.

Another argument that the juvenile stage is important in determining recruitment is that total mortality of juveniles is as great or greater than that of eggs and larvae (2,5). Although the instantaneous mortality rate is higher for eggs and larvae the duration of this stage is shorter than the juvenile stage (2,5). H. Caswell (WHOI) has pointed out, however, that, since it is the variability in recruitment we are interested in, the variability in mortality (total or instantaneous) rather than its absolute magnitude is the important parameter. From preliminary calculations, it appears that there is no consistent trend for recruitment variability to increase with the absolute magnitude of mortality (see attached Caswell note). This requires further investigation. It is clear nonetheless that if the magnitude and variability

of total mortality are approximately equal for juvenile and larval stages, the relative importance of each stage to recruitment will be about the same.

Other evidence of the importance of juveniles comes from modeling studies. Sissenwine et al. (1984b) have examined the role of pre-recruits (larvae and juveniles combined) in an energy budget of Georges Bank (2,5). From knowledge of recruitment and initial size of the cohort spawned together with assumptions of exponential growth and mortality, they estimated production and consumption by pre-recruits to be over twice that of the exploited population (5). Their model also showed that predation was the dominant source of pre-recruit mortality (5). Since within the pre-recruit phase, total biomass, production and consumption is highest for the juvenile stage rather than the egg/larval stage (11), the juvenile stage is a key component. J.H. Steele has pointed out that multispecies models of the Ursin type require food limited growth of juveniles in order to maintain a multiple species system (5). Thus the juvenile stage is a critical one and juvenile mortality may depend on food supply as well as predation. From the above, it is obvious that juvenile mortality is potentially very important in determining recruitment and that further study of this life stage is required (cf. Cohen et al., 1984).

An important aspect of the current quest for information on juvenile fish ecology is the motivation behind it. Fishery biologists once focused almost entirely on the exploited population and found unexplainable high variability in recruitment. This led to studies of egg/larval ecology because of the high mortality rate during this period of life. Apparent lack of correlation between larval abundance and recruitment together with other arguments stated

above have now promoted emphasis on the juvenile stage. Fishery ecologists, then, appear to seek answers to the recruitment problem in areas where little or no research has been done. In light of the potentially large but as yet unquantified errors associated with VPA estimates of recruitment and exploited stock size as well as errors in estimating larval abundance, it is very important to more critically evaluate existing data on recruitment variability, exploited stock size, and larval abundance. This can be done concurrently with on-going research into larval, juvenile, and adult fish ecology.

Another motivation for studying the juvenile stage is that fundamental theories in fishery biology hinge on the assumption of density dependence (2,3). There appears to be a continuing search for density dependent mechanisms (2, H. Caswell comment).

Density dependence can occur through competition or predation. It was originally thought that competition among larval fish for food was an important density dependent process (4). Now it is generally accepted that larval fish are too sparse relative to other zooplankton predators of similar size to have any significant effect on abundance of their prey; thus, competition between larval fish is not likely to occur (2,4,11). The sparseness of larval fish relative to similar sized plankton, together with the generalized feeding habits of predators on this size range of zooplankton, suggests that large fluctuations in larval abundance is not likely to trigger functional or numerical predatory responses. Given the high density and potential consumption rates of invertebrate predators and large losses due to physics, together with the large variability in both processes, these two sources of mortality may be relatively more important than fish predation to

larval mortality and recruitment. If this is the case, density independent processes must dominate during the larval stage.

In the juvenile stage, density dependent processes are thought to dominate (2; Sissenwine, 1984). As mentioned above, modeling studies have found the energy requirements and production are highest in this stage. Mortality of juveniles is due to some combination of food limitation and predation/cannibalism by older fish and squid (2,5,11). Thus, predation mortality and competition for food may be most intense during this stage.

If recruitment is determined during the juvenile stage, recruitment is more likely to be a density dependent process, and the basic concepts in fishery biology are correct. On the other hand, density independent processes operating during the larval phase may in fact determine recruitment, and the researcher must be open minded to this possibility.

Furthermore, it may well be that the relative importance of larval vs. juvenile survival to recruitment varies both interannually and interspecifically. In this case, recruitment processes are less general and perhaps more difficult to resolve.

In sum, recruitment is the result of a multiplicative of biological and physical processes occurring throughout the first year of life with density independent factors appearing generally more important during the planktonic phase and density dependence most pronounced for juveniles. Subtle between year differences in mean instantaneous mortality rate of pre-recruits can greatly influence the level of recruitment. Pre-recruit mortality varies in time and space due to episodic biological and physical events. It is only in occasional years that the combination of factors is such that recruitment is very high. In most years, one or more factors operate to reduce recruitment.

IV. Management Context

Recruitment research will, hopefully, lead to a better understanding of fish population dynamics and consequently more accurate stock assessments and forecasts of production; these are two important types of information for management (15). Socio-economic and political considerations, however, are often more important aspects of fishery management although little is known of these components (15). With accurate stock assessments and production forecasts, a fishery resource can usually be managed with an acceptable degree of risk, but the risk is rarely taken in favor of the resource (15).

The fishery manager is concerned only with the product of recruitment (i.e., stock size and composition) not with the actual process itself (15). In order for a research scientist to provide the manager with accurate forecasts, an understanding of the recruitment process is necessary (15,16). Although it has been argued that a fishery can be adequately managed in the absence of any information about the resource, the historical record proves this is not so. Ignorance of recruitment overfishing is a well known cause of collapse in commercial fish stocks, and such collapses have had significant socio-economic impact. Thus W.E. Ricker (1977) has stated that intelligent fishery management requires accurate assessment of fish population dynamics. This in turn requires an understanding of the recruitment process.

FUTURE RESEARCH

I. General Statements

From the total of information presented during the WHOI-NEFC seminar series two general statements can be made:

1) Potentially important biological and physical processes which may control recruitment occur throughout the entire first year of life. It is clear that the juvenile stage may be quite important in determining recruitment and that very little is known about this life stage. It is equally clear that the larval stage also may contribute significantly to recruitment variability. The only evidence to the contrary is the lack of correlation between survey estimates of late larval abundance and VPA estimates of recruitment, and this could well be due totally to measurement error as discussed above. Available evidence suggests that total mortality is equally high and variable in both the larval and juvenile stages.

2) It is important to understand the causes of recruitment variability in order to know whether density dependent population dynamics in fishes is a viable concept. Density independent processes probably dominate larval mortality whereas density dependent mortality may be relatively more important for juveniles. If this is in fact true, then it is critical to know the degree to which recruitment is established in the larval vs juvenile stage because this will provide insight into the importance of density dependent population growth.

Hypotheses

Based on this summary information, a number of hypotheses can be generated:

- 1) Factors controlling recruitment variability are not restricted to a single developmental stage but in fact occur throughout the first year of life.
- 2) Predator abundance/consumption is variable between years and a major cause of variability in larvae and perhaps juveniles as well.
- 3) Food availability significantly affects larval and/or juvenile growth, and length of life stage, thus increasing exposure time to predation; this food availability is variable between years and a major cause of recruitment variability.
- 3a) Micro and fine-scale (centimeter to meters) concentrations of prey are more important than larger coarse and meso-scale (kilometers to hundreds of kilometers) distributions of prey in determining food availability to larvae and perhaps juveniles as well.
- 3b) Water column stability affects pre-recruit survival, i.e., recruitment (Lasker hypothesis).
- 4) Physical losses are an important source of pre-recruit mortality and recruitment variability.

Suggested Research Plan

The interrelationships between these hypotheses reflect the multiplicative nature of the recruitment process. Future research, therefore, should not focus on a single process or life stage but instead should evaluate all potentially important processes throughout the first year of life. Only in this way can the relative contribution of each process to total recruitment be found. Furthermore, such research should be continued for at least 2-3 years to obtain measures of the interannual variability in each process.

To reduce the complexity of such a research program, a single representative fish species should be chosen as the target species. It is suggested that Georges Bank haddock be chosen as the target because: 1)

Georges Bank haddock has already been identified as one of three target species for recruitment research on-going at NEFC, 2) Stock-recruitment data for Georges Bank haddock is typical of many marine species (i.e., highly variable with a few unusually large year classes), 3) a long historical record of population cycles in this species has been established.

Research on this species should include: 1) critical analysis of existing data sets, 2) continuation of present modeling studies, and 3) implementation of new field and laboratory experiments and development of numerical/analytical recruitment models.

1) Top priority in analyzing existing data should be quantification of measurement error in the stock-recruitment relationship and in survey estimates of late larval abundance. Analysis of measurement error in VPA can perhaps be done in conjunction with work on-going at other institutions (eg. University of Washington). Standard errors of larval abundance should be determined. As has been done in many previous larval studies in other areas, avoidance of towed net samplers by late larvae can be estimated by comparing day/night hauls and catches by nets of various diameters. Mathematical modeling of the avoidance reaction can also be done.

2) Present modeling studies involving larval energetics and food requirements should be combined with models of spatial relation of larvae and prey to determine critical scales of prey patchiness for pelagic pre-recruit growth (hypothesis 3a). The range of larval life span as influenced by food should be combined with hypothetical predation rates to estimate the impact of food-limited growth on recruitment (hypothesis 3). Models can also be developed a priori to investigate, from theoretical grounds and published

information, the avoidance/escapement reaction of juvenile fish to mid-water and bottom trawls.

3a) New field research should be developed within the context of hypotheses 1-4. For larval fish, on-going modeling studies should be used to guide field sampling strategies for larvae, predators, and prey. Micro-scale patchiness of larvae and prey at density interfaces should be sampled using novel devices such as that developed by Owen (1981). Fine to meso-scale distributions of larvae, predators, and prey can be found using vertically stratified hauls with plankton nets and trawls. Sampling strategies should be developed to estimate abundance of gelatinous zooplankton-potentially dominant predators of pelagic pre-recruits. Current meters (moored and acoustic profiling), drogues, neutral bouyancy floats, and remote sensing should be used to determine the flow field and monitor physical loss mechanisms. Dye studies may be helpful in estimating vertical mixing rates. Physical measurements must obviously be done concomittantly with biological studies.

3b) Methods must be developed to quantitatively sample juvenile fish. A priori models of avoidance reactions may be helpful. Ultimately information of the sensory cues used by the juveniles and late larvae to detect the samplers may be required; this may involve laboratory behavioral studies. Day/night catch ratios and differential catch by different sized trawls (i.e., MOC10 and MOC20) may provide indexes of avoidance. Sampling with hydroacoustics and submersibles may also provide quantitative and qualitative measurements of juvenile fish abundance and distribution.

3c) Knowledge of the vertical and horizontal distributions of juveniles in relation to prey and predators is required. Stomach content analyses of

both juveniles and their potential predators is necessary. Immunofluorescence may prove helpful in identifying prey species in the stomachs. Predators of juveniles can be sampled with conventional bottom trawls and other standard fishing gear. Such surveys should be conducted at the same time and locations as the pre-recruit surveys.

A basic outline for a field program (cruise chronology and activities list) is presented (pp. 31-32) for subsequent discussion sessions. Perhaps joint research could be conducted using Canadian, UNOLS, and NOAA vessels.

In addition to field sampling, laboratory and enclosure experiments may be useful in hypothesis testing and model parameter estimation. Laboratory experiments should involve the quantification of feeding energetics for juveniles and behavioral interactions for both larvae and juveniles. Experiments should be designed to determine patterns of activity, feeding, aggregation mechanisms, search patterns, prey selectivity, digestion, assimilation, and food conversion rates. Given that predators on the pre-recruits can be identified during the field phase of the study, laboratory and enclosure experiments can be designed to estimate the effect of pre-recruit size and condition and predator search patterns and feeding behavior on the degree of predation. Further laboratory work can be done on pre-recruit avoidance mechanisms, recovery from predatory attack, and residence times of identifiable eggs and larvae in guts of predators. Such information together with field estimates of predator and pre-recruit distributions can be used to develop an encounter model of predation.

The above outlined research project is obviously a large one, and perhaps, because of funding constraints, only portions of such a project can

be achieved. It should be stressed again, however, that all potential mechanisms affecting pre-recruit mortality should be investigated together throughout the first year of life. If only one life stage (eg. juveniles) or one process (eg. predation) is studied, the relative contribution of this process or life stage to total recruitment variability will remain unknown, and, as in past studies, only correlations with recruitment can be made. Current knowledge of the recruitment process as reviewed by the NEFC-WHOI seminar series does not warrant such an approach. The Northeast Recruitment Experiment (NEREX) of NEFC presently involves laboratory, field, and modeling studies to document growth and mortality over the first year of life of cod, haddock, and yellowtail flounder. This program could perhaps serve as a core for a larger multi-institutional program which would increase available shiptime as well as the intensity and extent of biological, physical, and chemical sampling.

If Georges Bank is chosen as the study site, it is possible that the recruitment research could be carried out as part of a larger multi-institutional study of the whole ecosystem. The Georges Bank Project of the Coastal Research Center at WHOI is nearing completion of the Georges Bank book. Several investigators whose research does not directly relate to the recruitment problem (this includes contributors to the Georges Bank book as well as other investigators at WHOI and elsewhere) have expressed a definite interest in involvement in a joint research project on Georges Bank. The Northeast Recruitment Experiment (NEREX) of NEFC presently involves laboratory, field, and modeling studies to document growth and mortality over the first year of life of cod, haddock, and yellowtail flounder. This program could perhaps serve as a core for a larger multi-institutional program which would increase available shiptime as well as the intensity and extent of biological, physical, and chemical sampling.

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HYPOTHETICAL SCHEDULE OF CRUISES

JAN	1		
FEB			
MAR	2	3	
APR	4	5	
MAY			
JUN	6	7	8
JUL	9		
AUG			
SEP	10		
OCT	11	12	
NOV			
DEC	13	14	

CRUISE ACTIVITIES

Cruise	Activity
1,14	Deployment/retrieval of moored current meters.
2,4,6	Egg/larvae and prey surveys, initial rapid mapping with bongos (1 m and 1/4 m MOCNESS and hydrocasts at selected stations), subsequent micro- and fine-scale sampling in larval patch.
3,5,7	Larval predator survey (bottom and midwater trawls, 10 and 20 m (MOCNESS), gelatinous zooplankton sampling (SCUBA diving?), current mapping with acoustic doppler and neutral buoyancy floats.
8,12	Large predator survey (ground fish bottom trawls).
9,10,11,13	Juvenile fish survey, midwater/bottom trawls (10 and 20 m MOCNESS).

LIST OF WHOI-NEFC SEMINARS

NUMBER	SPEAKER/AFFILIATION	TOPIC
(1)	Allen Peterson, Jr./NEFC (Director)	INTRODUCTION TO SERIES
(2)	Michael Sissenwine/NEFC-Woods Hole	WHY DO FISH POPULATIONS VARY?
(3)	Michael Fogarty/NEFC-Woods Hole	STOCK RECRUITMENT RELATIONS
(4)	Edward Houde/Univ. Maryland	LARVAL ECOLOGY AND RECRUITMENT
(5)	Edward Cohen/NEFC-Woods Hole	POSTLARVAL/JUVENILE MORTALITY VS. RECRUITMENT SUCCESS IN GEORGES BANK STOCKS
(6)	Victor Oiestad/Inst. Mar. Res., Bergen, Norway	PREDATION ON FISH LARVAE AS A REGULATORY FORCE ILLUSTRATED IN ENCLOSURE EXPERIMENTS WITH LARGE GROUPS OF LARVAE
(7)	Geoffrey Laurence/NEFC-Narragansett	MODELLING EFFECTS OF FOOD LIMITA- TION ON COD AND HADDOCK LARVAE
(8)	John Steele/WHOI (Director)	LONG-TERM FLUCTUATIONS IN FISH STOCKS
(9)	Richard Hennemuth/NEFC-Woods Hole	STATISITCAL VARIABILITY IN RECRUITMENT AND SIGNIFICANCE TO FISHERIES
(10)	Michael Roman/Univ. Maryland	PRODUCTION AND NUTRITIONAL VALUE OF ZOOPLANKTON FOR FISH LARVAE
(11)	John Hunter/SWFC-La Jolla, CA	PREDATION AND THE RECRUITMENT PROCESS
(12)	Kenneth Sherman/NEFC-Narragansett	IS THERE A COUPLING BETWEEN ZOOPLANKTON AND RECRUITMENT?
(13)	Glenn Flierl/M.I.T	IMPACT OF WARM CORE GULF STREAM RINGS ON SURVIVAL OF SHELF FISH LARVAE
(14)	David Mountain/NEFC-Woods Hole	IMPACT OF GEORGES BANK CIRCULA- TION ON EARLY LIFE STAGES AND RECRUITMENT
(15)	Allen Peterson/NEFC (Director)	PERSPECTIVE OF A MANAGER
(16)	Michael Sissenwine/NEFC-Woods Hole	PERSPECTIVE OF A RESEARCHER

NAME: MICHAEL P. SISSENWINE
AFFILIATION: NEFC-WOODS HOLE
TITLE: WHY DO FISH POPULATIONS VARY?

ABSTRACT:

Fish populations vary because of density dependent and independent processes that determine recruitment, growth and natural mortality, and in response to fishing. Most of the natural (non-fishing) variability is associated with recruitment, presumably the density independent effect of fluctuating environmental factors.

Numerous empirical models have been used to explain recruitment variability. While "statistically significant" correlations are plentiful, most empirical studies are flawed because they (1) use an inappropriate proxy for recruitment, (2) are data exploration exercises that are not based on a plausible hypothesis, (3) do not consider, simultaneously, physical variables and spawning biomass, and/or (4) fail to test predictions on independent data (i.e., not used to establish correlation). As a result, many empirical models fail to predict post-publication events. Furthermore, fundamentally different empirical models may be indistinguishable because they account for virtually the same proportion of variability in recruitment.

Process oriented studies of recruitment variability have focused on starvation, particularly of first feeding larvae. Starvation may be related to the amount of suitable food, the contagious nature of its distribution, currents which transport eggs and larvae, the match or mismatch of the annual reproductive cycles with the annual production cycle of prey, and the stability of the environment.

Only recently has a new hypothesis emerged. It is that predation is the major cause of prerecruit mortality. It is supported by (a) evidence of prey concentrations which are adequate for a high survival of larvae as indicated by laboratory and modeling studies, (2) lack of evidence of starvation for field collected larvae, (3) a high survival rate of larvae in large, predation free, enclosures, (4) the high mortality rate of eggs and yolk-sac larvae which are not subject to starvation, and (5) the identification of fish and invertebrates as predators of egg, larval and post-larval stages.

At least for some systems, fish consume most of their own production. Two important implications are that fish populations are probably able to compensate for fishing, and post-larval mortality must be high, thus affecting recruitment. The lack of correlation between larval abundance and recruitment also implies that year-class strength is not established until the post-larval stage.

Physical factors are presumed to be responsible for recruitment variability. There are numerous possible mechanisms if recruitment is determined by starvation of larvae. It is less apparent how physical factors are related to variability in predation mortality of post-larvae.

NAME: M. J. FOGARTY
AFFILIATION: NEFC-WOODS HOLE
TITLE: STOCK RECRUITMENT RELATIONSHIPS

ABSTRACT:

The relationship between spawning stock size and recruitment is of fundamental importance in the development of management strategies for exploited fish populations. It is axiomatic that harvested populations should not be reduced to levels below which recruitment is endangered. Despite the critical importance of the recruitment overfishing question, little progress has been made in empirically demonstrating stock recruitment relationships. To a large degree, this reflects both high levels of natural variability (presumably due to environmental effects) and observational error. With few exceptions it is not possible to directly measure population size and estimation error can be considerable. It has been demonstrated that measurement error alone can effectively obscure an underlying stock recruitment relationship. These factors indicate the need for an inductive approach to evaluating stock recruitment relationships.

Classical developments in stock-recruitment theory embody the concept of compensatory population regulation. The Ricker and Beverton-Holt stock-recruitment models differ in degree of compensation with the former quite strongly compensatory. The derivation of both models will be described to demonstrate differences in underlying assumptions. Possible compensatory mechanisms which have been identified include cannibalism, competition for breeding sites, competition for shelter or living space, and competition for food, resulting in reduced growth (and hence greater vulnerability to predators). The Ricker model is strongly dependent on cannibalism as a mechanism.

Generalizations of the Ricker and Beverton-Holt models have been proposed which are more flexible and which also allow depensation at low spawning stock size. Considerations for multistage life history strategies will also be described and the possibility of multiple equilibrium points will be discussed.

Finally, progress toward the development of stochastic models of stock-recruitment relationships will be described. Applications of stochastic differential equations, stochastic difference equations and Markov processes will be discussed.

NAME: EDWARD D. HOUDE
AFFILIATION: UNIVERSITY OF MARYLAND
TITLE: LARVAL ECOLOGY AND RECRUITMENT

ABSTRACT:

Fluctuations in year-class abundances result from variable survival during the early life stages. Survival of larvae depends on availability of food, growth rates, stage duration, transport to favorable nursery areas and predation rates. Characteristics of teleost larvae, the ability to feed and grow, survival relative to prey abundance, and larval energetics are discussed. Larvae from several taxa are compared as are those from high and low latitude regions. Starvation and predation are considered as sources of larval mortality, and the temporal-spatial scales of fish larvae and prey distributions are discussed in the context of the recruitment problem. Hypotheses that consider how the ocean environment influences larval survival and recruitment are presented and some possibilities for future research are proposed.

NAME: EDWARD B. COHEN

AFFILIATION: NEFC-WOODS HOLE

TITLE: POSTLARVAL/JUVENILE MORTALITY VS. RECRUITMENT SUCCESS IN
GEORGES BANK STOCKS

ABSTRACT:

Traditionally the study of processes regulating recruitment variability has focused on the earliest life stages of fish, i.e., eggs and larvae. Recent work at the Northeast Fisheries Center has shown that mortality during the postlarval/juvenile period is at least as high as during the earlier phases of life. Although the actual mortality rate is lower for the juvenile fish because of the long duration of the postlarval/juvenile period the cumulative mortality is at least as high as during the egg and larval stages, and is about 98-99%. It is not surprising that recruitment is set in the postlarval/juvenile period as there is no correlation of egg or larval number of mortality and subsequent year-class strength. There is, however, a good correlation of number at the juvenile stage and subsequent recruitment for several commercial species on Georges Bank.

While year-class strength is undoubtedly determined by several factors that vary in their influence from year to year, it appears that predation on pre-recruit fish by other fish is an important mechanism in most years. Starvation, while an important source of mortality especially in the younger larvae, does not appear to be the limiting process on Georges Bank. Physical loss of eggs and/or larvae may be an important process in certain years.

NAME: HAL CASWELL

AFFILIATION: WHOI

TITLE: MORTALITY AND VARIABILITY: IS THERE A NECESSARY RELATION?

ABSTRACT:

In the discussion following Ed Cohen's seminar this morning, the question was raised of the extent to which variability in post-larval mortality (e.g., due to predation) could explain variability in recruitment success. The claim was made that, because the mortality rates measured for these stages was so high, even small variation in those rates could generate enormous variation in recruitment. The following rough calculations are presented for discussion; they suggest that there is more here than meets the eye.

The basic phenomenon involved is mortality experienced by a cohort of animals in stage 1 at time 0, $N_1(0)$, which require T time units to reach stage 2, $N_2(T)$. If the instantaneous mortality rate is μ , then

$$N_2(T) = N_1(0)\exp(-\mu T). \quad (1)$$

The problem here is to investigate the way in which variation in μ gets translated into variation in $N_2(T)$, as a function of the values of μ and T. There are several possibly relevant approaches; I will consider them in order.

1. Variation in $N_2(T)/N_1(0)$.

This quantity, which I will denote by $R(T)$, is the ratio of individuals produced per individual input. It could correspond, for example, to a ratio of recruits to spawned eggs, or recruits to larvae, etc. From (1) it follows that

$$R(T) = \exp(-\mu T) \quad (2)$$

If we consider variability around some mean value of $R(T)$, we can write

$$\sigma^2(R) = (\partial R / \partial \mu)^2 \sigma^2(\mu) \quad (3)$$

where R/μ is evaluated at the mean. Differentiating (2) gives

$$\partial R / \partial \mu = -T \exp(-\mu T) \quad (4)$$

from which

$$\sigma^2(R) = (T e^{-\mu T})^2 \sigma^2(\mu) \quad (5)$$

From (5) we can evaluate the relative variability in R caused by variability in μ : it DECREASES with μ and is maximized when $T = 1/\mu$.

The accompanying figure shows some examples for $\mu = 1, .1, \text{ and } .01$ (note the different scales on the graphs).

On the basis of these results, it appears that the variance in R is actually most sensitive to variance in instantaneous mortality when that mortality is low, not when it is high.

2. The Coefficient of Variation of R .

An alternative is to examine the coefficient of variation of R :

$$CV(R) = (R)/R$$

as a function of the CV of u . From (5) we obtain

$$CV(R) = \mu T * CV(\mu) \quad (6)$$

That is, when the variances in R and μ are both scaled relative to their mean values, $CV(R)$ does increase with μ . Unfortunately, this does not seem to be the measure of variation of interest to fisheries ecologists.

3. Variance in $N_2(T)$ Directly.

Finally, it is possible to evaluate the variance in $N_2(T)$ directly. In a sense, this seems to be the most relevant measure of variance to fisheries management.

From (1), we obtain

$$\log N_2(T) = \log N_1(0) - \mu T \quad (7)$$

and thus

$$\sigma^2(\log N_2) = \sigma^2(\log N_1 + T^2 \sigma^2(\mu) - 2TCov(\log N_1, \mu) \quad (8)$$

This expression is independent of the value of μ unless $\sigma^2(u)$ or $Cov(\log N_1, \mu)$ vary with μ . Such variation might well occur, but its existence would seem to be something to investigate, not assume.

CONCLUSION

It appears that there is no consistent trend for variability in recruitment caused by variance in mortality to increase with absolute magnitude of that mortality.

20

RELATIVE VARIANCE, $U=0.1$

1

RELATIVE VARIANCE, $U=1$

1500

RELATIVE VARIANCE, $U=0.01$

NAME: VICTOR ØIESTAD

AFFILIATION: INSTITUTE FOR MARINE RESEARCH, BERGEN NORWAY

TITLE: PREDATION ON FISH LARVAE AS A REGULATORY FORCE, AS
ILLUSTRATED IN MESOCOSM STUDIES WITH LARGE GROUPS OF
LARVAE

ABSTRACT:

Mesocosm studies were carried out during 1976-83 with a number of commercially important marine fishes (Atlantic cod, Atlantic herring, capelin, and European plaice) to examine their population dynamics in relation to food supply and to predators. The studies involved the release of populations of yolk-sac fish larvae in a 4,400 m³ basin during 1976-79 and in a 60,000 m³ pond during 1980-83. Larval populations ranged from 3,000 to 1.2 million.

The conclusions that can be drawn from the basin and pond experiments in 1976-83 may be summarized as follows:

- (a) marine fish larvae have a very high potential survival rate, even at marginal feeding conditions;
- (b) fast-growing and healthy larvae may be very susceptible to predation;
- (c) from metamorphosis onward, larvae of some fish species are voracious predators of other fish larvae; and
- (d) predation involves not only the prey that are ingested but also those that succumb to injuries inflicted by predators.

The relevance of these results to field studies is obvious. Less attention should be devoted to feeding conditions and more should be given to studies of predation and competition. In nature, if starvation accounted for a daily mortality rate of 5-10%, about 30-50% of the fish larvae should be in a state of starvation, but very seldom have starving larvae been found in sea samples. Selective predation (i.e., predators searching for starving larvae) is not very likely, because this implies that the water column is surveyed daily by predators looking for weak larvae. Most of the predators either are fast-swimming (fish fry and euphausiids) or encounter fish larvae accidentally by co-occurrence (hydro-medusae).

Future research should emphasize *in situ* studies in the open sea. Relevant equipment and hypotheses should enable researchers to determine why a potential 50-90% survival of fish larvae to metamorphosis, as demonstrated for cod and herring, becomes much less than 1% in the open sea.

NAME: GEOFFREY LAURENCE
AFFILIATION: NEFC-NARRAGANSETT
TITLE: MODELLING EFFECTS OF FOOD LIMITATION ON COD AND HADDOCK
LARVAE

ABSTRACT:

The results of modelling food limitation of Georges Bank larval cod and haddock are presented. The model used is a stochastic model based on probabilistic food encounter with a bioenergetic framework. The predicted output is a food consumption estimate resulting in individual and population growth and/or survival. Inputs to the model consist of empirical results from numerous laboratory experiments and process-oriented sea cruises conducted by Northeast Fisheries Center personnel and relevant research from the literature. The predicted food requirements of the model are used in conjunction with estimates of abundance and distribution of larvae and zooplankton prey from Northeast Fisheries Center MARMAP cruises to assess the question of food limitation. Comparison made between the two species indicate that haddock are more food limited than cod, but that food limitation per se is most likely not the single dominating factor controlling early life success for either species in most years.

NAME: JOHN H. STEELE

AFFILIATION: WHOI (DIRECTOR)

TITLE: LONG-TERM FLUCTUATIONS IN FISH STOCKS

ABSTRACT:

Many pelagic fish stocks change rapidly in abundance, with intervening periods of about 50 years. The physical environment does not display such abrupt changes but has a variance that increases with time. A simple population model with multiple equilibrium states exhibited the observed behavior when subjected to this type of stochastic variability. The periodicity exhibited by the model is of the same order as the observations. Thus the assumption by fisheries management of a natural persistence in stocks is questionable.

NAME: RICHARD C. HENNEMUTH

AFFILIATION: UNIVERSITY OF MARYLAND

TITLE: STATISTICAL VARIABILITY OF RECRUITMENT AND SIGNIFICANCE TO
FISHERIES

ABSTRACT:

The increase in collection and analysis of fisheries data since the postwar expansion and the development of more comprehensive routine surveys permit reasonable retrospective studies of recruitment. The longer-term perspective provides definition of variation, its effects on fisheries, implications for management, and further studies of what causes it. Most information is from species of the temperate oceans subject to fishing, and the one observation per year provides a limited data series. Most recruitment studies are based on knowledge gained from hindsight. Statistical analyses need to be considered which will permit appropriate inferences, most importantly the limits to them. The speaker will present past data, results of studies from them relating to defining variability, some aspects related to management applications, and thoughts about current and further study.

NAME: MICHAEL R. ROMAN

AFFILIATION: UNIVERSITY OF MARYLAND

TITLE: PRODUCTION AND NUTRITIONAL VALUE OF ZOOPLANKTON FOR FISH
LARVAE

ABSTRACT:

Laboratory research has demonstrated that larval fish survival is directly related to their available food. Thus factors which control the distribution, production and nutritional value of zooplankton to a large degree, determine the successful recruitment of fish species. Our understanding of the distribution of larval fish prey has evolved as a consequence of changes in sampling strategy. Micro- and fine-scale variability in the abundance of zooplankton may strongly influence the recruitment of larval fish. In contrast, research on the production or "turnover time" of zooplankton in the ocean has not evolved as rapidly. Measurements of zooplankton production have been limited by the technology of sample collection and knowledge of the processes that control zooplankton recruitment, mortality and growth. Both zooplankton production as well as biochemical composition are influenced by the quantity and quality of their available food. Copepods vary in their biochemical composition among species and developmental stages of the same species on diurnal, several day and seasonal time scales, with depth as well as geographically. Both laboratory and field research has demonstrated that the survival of larval fish is affected by biochemical composition of their prey. Larval fish feeding behavior may have evolved to maximize the food quality of their ingested prey.

NAME: MICHAEL R. ROMAN

AFFILIATION: UNIVERSITY OF MARYLAND

TITLE: PRODUCTION AND NUTRITIONAL VALUE OF ZOOPLANKTON FOR FISH
LARVAE

SUMMARY:

Three aspects of zooplankton ecology which influence larval fish survival and growth are zooplankton abundance, zooplankton production, and the nutritional value of zooplankton for larval fish. Early laboratory experiments on the rearing of larval fish found that the zooplankton densities required for minimum survival (10%) were usually far in excess of those found in the marine environment. This paradox was later found to be a result of poor culture techniques, inadequate nutritional composition of the zooplankton for the larval fish, and biased measurements of zooplankton densities in the sea. Zooplankton are not randomly distributed, therefore integrated tows result in biased estimates of the densities of zooplankton that are available for larval fish. Both in vertical and horizontal planes, zooplankton abundances are usually highest at density interfaces (e.g. at the base of mixed layers and at fronts). There are also maxima in zooplankton densities which are not coincident with any apparent physical discontinuity. Such biological interfaces can be the result of phytoplankton production maxima, previous sites of zooplankton recruitment, social aggregations or a past physical event such as a breaking internal wave. As the technology of zooplankton sampling continues to advance and we resolve zooplankton distributions on finer scales, it is often found that "critical concentrations" of zooplankton for larval fish survival do exist in the ocean. Important research topics which should be addressed by fisheries biologists are the time and space scales which control the formation and maintenance of zooplankton aggregations. For example, storms may disrupt aggregations of prey to below "critical concentrations" for larval fish survival. However, the mixing of storms is necessary to input nutrients into the euphotic zone in order to balance sinking losses, thereby maintaining both primary production and zooplankton stocks. An important factor affecting fish recruitment may thus be the interval between storms, allowing a sufficient "set-up time" for zooplankton aggregations and their utilization by larval fish.

Another important time factor for larval fish recruitment is the production or "turnover time" of their zooplankton prey. One cannot predict zooplankton production from biomass estimates. Production/biomass ratios of zooplankton vary by over 2 orders of magnitude. The same degree of variance has been found for the ratio of zooplankton production/phytoplankton. Thus marine systems vary in their efficiency in the conversion of primary production to zooplankton production.

Techniques for estimating zooplankton production have not changed appreciably in the last 50 years. Cohort analysis of zooplankton is

tedious, labor-intensive and requires frequent sampling of the same population, a criteria that is rarely met in marine systems. Laboratory studies have shown that zooplankton survival, growth and egg production increases with the amount of available food. However, as these relationships are more critically examined, it is becoming increasingly evident that food quality can be the key factor which regulates zooplankton production. One cannot predict zooplankton growth or reproduction from biomass estimates of phytoplankton because of the differences in the nutritional value of phytoplankton as well as the utilization of non-phytoplankton food such as detritus and protozoa by zooplankton.

As an estimate of in situ zooplankton production, investigators have measured various biochemical "indices" of growth such as RNA, RNA/DNA, DNA, and DNA polymerase. The growth estimates obtained with these biochemical measurements have been inconclusive because: they usually apply only during exponential growth, their induction and degradation time often makes them "uncoupled" from protein synthesis, and because of different cell differentiation, life stages and species in the zooplankton samples used. A promising technique for the estimation of in situ zooplankton growth and recruitment is based on the incorporation rate of carbon (^{14}C) into various biochemical fractions (protein, lipid, polysaccharide) of zooplankton. The incorporation rate of carbon into protein can be a good estimate of protein synthesis, which determines zooplankton growth rate. The rate of lipid synthesis in adult zooplankton is often closely coupled to the rate of egg production and hence production of nauplii for larval fish.

The nutritional value of zooplankton for larval fish has usually been inferred indirectly from data on the food requirements of fish species used in aquaculture. Zooplankton are low in carbohydrates, however, fish can be reared on carbohydrate-free diets. The protein content and amino acid composition of zooplankton is usually sufficient to meet the nutritional requirements of larval fish species. Most research on the variation in biochemical composition of zooplankton has focused on lipids. The quality and quantity of lipids in zooplankton can vary with species, developmental stage, seasonally, geographically with depth in the water column. Lipids are used by zooplankton in the production of eggs (50% lipid) and as energy reserves. Because lipids have twice the caloric value per unit biomass than either proteins or carbohydrates, lipid content usually determines the caloric value of zooplankton for larval fish. Seasonal differences in both the quantity and quality of zooplankton lipids are usually related to their diet. Zooplankton have limited ability for the de novo synthesis of polyunsaturated fatty acids. Thus the fatty acid composition of zooplankton is influenced by the lipid composition of their prey and if the prey lack their essential fatty acids, the growth and survival of larval fish will be reduced.

Phytoplankton influence larval fish survival indirectly by controlling zooplankton production and directly by supplying essential fatty acids, vitamins and protein. Laboratory studies have shown that the sur-

vival of larval fish is enhanced if phytoplankton are included in tanks with larval fish and zooplankton. This "green tank" effect is likely a consequence of larval fish feeding on zooplankton with full guts. Zooplankton with full guts can contain 10-20% more protein and carbohydrate per unit weight than zooplankton with empty guts. In addition the essential vitamins A and C, which zooplankton cannot store, are available to the larval fish in phytoplankton. Particular species of phytoplankton can enhance larval fish survival and growth because they contain more essential fatty acids. Field research has shown that zooplankton have higher incidences of full guts during certain periods of the day as well as at certain depths of the water column (i.e., chlorophyll and photosynthesis maxima). Larval fish behavior may have evolved so that they concentrate their feeding effort in both space and time to optimize their ingestion of nutritionally superior prey.

NAME: JOHN R. HUNTER

AFFILIATION: SWFC-LA JOLLA, CA

TITLE: PREDATION AND THE RECRUITMENT PROCESS

ABSTRACT:

The literature on the early life stages of marine fish is reviewed and the predatory processes that may be significant in the early mortality of egg and larval stages discussed. The mortality of eggs and yolk-sac stage larvae typically range from 10% to 50% per day indicating a high and variable rate of predation, and predation may continue to be the dominant source of mortality in later larval and juvenile life stages. Significant starvation mortality has been documented for some marine fishes, but it seems to be restricted to 1-2 weeks after yolk absorption whereas the recruitment process continues through the first year of life. The recruitment process is an ontogenetic ecological problem involving all life stages from egg through juvenile. Thus the life stage specific vulnerability to predation and changes in predator fields are critical to the understanding of the recruitment process. These issues are discussed in relation to the ontogenetic ecology of the northern anchovy and other fishes.

NAME: JOHN R. HUNTER
AFFILIATION: SWFC-LA JOLLA, CA
TITLE: PREDATION AND RECRUITMENT¹
SUMMARY:

Variation in rates of starvation, growth and predation during the first year of life are the factors causing year class variation in marine fish stocks. The evidence for starvation and predation mortality in the sea is discussed below. Early studies on the effect of food density on larval survival indicated that the average densities in the sea were far below those required for survival (D 300 nauplii/L). More recent work in large enclosures and in bags indicate that such high densities are not required for survival and that the food densities required for growth are relatively common in the sea. The best evidence for larval starvation is histological identification of starving larvae in the sea. These studies indicate that rates of starvation may be high in some localities (at the first feeding stage) but insignificant in other localities. These studies also indicate that high rates of starvation (42% dying per day) are restricted to the initial 1-2 weeks of feeding. The mortality rates of embryonic marine fishes are often very high and variable indicating high and variable rates of predation. Survivorship is high (4-10% survival at metamorphosis). In enclosures, where predators are excluded indicating that predation is probably the largest source of larval mortality in the sea. In short, the best evidence to date indicates that starvation mortality is restricted to the initial 1-2 weeks of feeding whereas predation is a dominant source of mortality throughout the first year of life.

Animals identified as predators of pelagic larvae and juveniles range from small zooplankton (copepods, amphipods, euphausiids, shrimp and crab larvae, Chaetognaths, and ctenophores) to large jellyfish, squid and planktivorous fishes. Studies in small containers indicate that predation by small crustacea seems to be limited to the yolk-sac stage as rates of consumption of larvae decrease by 50% or more at the onset of feeding. Consumption of yolk-sac larvae by copepods decreases by 50% when an alternate food source is of equal density to the larvae. A laboratory study indicates that chaetognaths are unimportant predators but field evidence (possibly biased by "cod end feeding") contradicts this view. The large jellyfish, such as Aurelia, are known consumers of larvae and in Kiel Fjord they consume 2-5% of the standing stock of herring larvae per day. These mortalities were not correlated with

¹Much information discussed in this lecture is presented in the review: J. R. Hunter 1984. Inferences regarding predators on the early life stages of cod and other fishes. In: E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal (eds.), The propagation of Cod Gadus morhua L. Flodevigen rapportser., 1, 1984: 533-562. Additional material was from unpublished work of G. Theilacker (Starvation histology); R. Owen (Fraction of biomass = larval anchovy) and P. Smith (model indicating changes in fundamental rates necessary to produce 5 X changes in abundance by life stage. All of these people are at the SWFC, La Jolla, Calif.

recruitment. The abundance of jellyfish appears to be sporadic and dense concentrations seem to be most common in partially enclosed areas.

Larval fish have been observed in the stomachs of many invertebrate predators taken at sea including calanoid copepods, amphipods, chaetognaths, jellyfish and ctenophores. At times fish larvae constituted 50% of the stomach contents. These are usually casual observations, the species of larvae were not identified with certainty and the daily loss rates not estimated.

Most plantivorous fishes consume eggs and larvae of marine fishes but again rates of consumption are seldom estimated. An exception is consumption of pelagic eggs by planktivorous fishes. Egg cannibalism by Northern, Peruvian, and Argentinian anchovies ranged from 28-39% of the natural mortality rate of the eggs. Fishes are probably major predators of the later life stages as well. Owing to rapid digestion of larvae in the stomachs of their predator's and difficulties in the identification of digested larvae, these rates have yet to be measured.

In general, fish larvae are an incidental item in the diets of their predators. In the California Current where anchovy is by far the most abundant larva, anchovy larvae (at the station of maximum abundance for a survey) comprise only 0.2-0.3% of the biomass of the plankton assemblage. Thus other zooplankton usually dominate stomach contents of larval predators. On the other hand, the density of pelagic eggs and occasionally yolk-sac larvae (herring) are sufficiently concentrated for predators to feed selectively on egg or yolk-sac larval patches. Diffusion rapidly reduces the patchiness of egg and larvae so that by the end of the yolk sac stage the larvae may be so dispersed that selective feeding on patches by predators becomes rare. Subsequently, as the larvae mature and begin to school and thereby become more aggregated, they become sufficiently concentrated to attract predators. The cohort of a marine stock usually reaches maximum biomass in the juvenile stage. Thus at some time in late larval or in juvenile life, the cohort may have sufficient biomass to exhibit density dependent growth.

Predator avoidance is a function of many intrinsic maturation events, such as the onset of schooling, changes in visibility or detectability of larvae by predators, and changes in the latency and speed of the avoidance response. Extrinsic factors that affect predation include low forage and temperature which depress growth and cause fish to remain longer at more vulnerable life stages. Starvation causes deterioration of larval escape response but this seems less significant than the increase in the duration of the life stage induced by starvation. Maturation of sensory systems which enable more rapid initiation of an avoidance response may be the most important factor responsible for the decline in vulnerability with larval size.

The late larval stage (10-35 mm) of the northern anchovy is potentially the most variable in survivorship, as 5X decline or 5X increase in

survival are possible within the normal range of growth and mortality rates. On the other hand, a 5X decline in abundance seems possible at all life stages. Thus all life stages must be included in the search for recruitment mechanisms. The rare large year class may be one that grows rapidly and experiences no unusual increases in mortality over the first year of life. Although starvation may directly affect larval survival during only the initial 1-2 weeks of feeding, variation in growth can affect survivorship at all life stages because of size specific predation. Growth of anchovy larvae and juveniles varies seasonally, inter-annually, and thus, annual variation in growth may be an important factor in survival.

Future work on recruitment and predation should focus on the development of quantitative (intercalibrated) sea samplers and sampling designs for all life stages of fish and their predators. The incidence of predation must be expressed as a fraction of the observed mortality of larvae and juveniles. This requires estimation of the rate of gastric evacuation of fish of all life stages by their key predators and the development of methods to identify the species of ingested larvae. Immunological techniques might be helpful in this regard. Predator models will be useful in interpreting results, but substantial progress depends upon measurement of the annual variation of mortality, growth and consumption by key predators of all life stages in the sea.

NAME: KENNETH SHERMAN

AFFILIATION: NEFC-NARRAGANSETT

TITLE: IS THERE A COUPLING BETWEEN ZOOPLANKTON AND RECRUITMENT?

ABSTRACT:

This seminar is divided into two sections addressing: (1) the spawning strategies of continental shelf fishes in relation to hydrographic conditions and plankton production, and (2) ichthyoplankton and fish recruitment studies in large marine ecosystems (LME's).

The first part of the seminar concentrates on studies conducted in continental shelf waters between Cape Hatteras and Cape Sable. Spawning strategies of various fish species appear related to topographic features and circulation patterns which, in turn, play a key role in the maintenance of the stocks. Peak spawning of several important species is shown to be in synchrony with increasing abundance of their copepod prey. Other species have developed a ubiquitous spawning strategy, allowing these populations to increase rapidly in response to favorable conditions.

The second part of the seminar focuses on larval and fish recruitment studies conducted by NMFS in several LME's under federal fisheries jurisdiction. To improve abundance forecasts of recruitment success of incoming year classes, two assessment strategies are used: (1) fisheries independent surveys of fish eggs and larvae employing grid surveying techniques to back-cast spawning stock sizes, and (2) other process-oriented studies to elucidate mechanisms controlling the annual recruitment success of new year classes. Processes under investigation include growth and mortality of eggs in relation to density dependent and independent conditions, and in relation to predator fields. Field sampling provides measures of the spatial and temporal variability adequate to measure changes in spawning stock sizes off the northeast coast, and in the California Current areas.

NAME: DAVID G. MOUNTAIN

AFFILIATION: NEFC-WOODS HOLE

TITLE: IMPACT OF GEORGES BANK CIRCULATION ON EARLY LIFE STAGES
AND RECRUITMENT

ABSTRACT:

The circulation of water on Georges Bank is characterized by an around-bank movement and also by a high exchange rate that results in a relatively short residence time for water on the bank. These characteristics have the potential to promote both the survival and mortality of planktonic fish larvae on the bank. The importance of circulation to recruitment does not require that advective loss to be a dominant source of mortality in pre-recruit fish. Instead the interannual variability in advective loss must be sufficiently large to cause large variability in pre-recruit survivorship, at least in some years.

The primary mechanisms for advective loss are the entrainment of water from the bank by Warm Core Rings, the wind driven transport of surface water off of the bank, and the transport of water westward from the bank past Nantucket Shoals. Observations indicate that considerable variability exists in all mechanisms. Relating the observations to recruitment is complicated by the short time and space scales of the physical processes and the characteristic patch distribution of the larval population. The same physical process acting at a different time or place could have very different effects on larval mortality. For this reason retrospective analysis of seasonally averaged physical parameters may never reveal actual physical-biological relationships in recruitment. In general, existing physical and biological data are insufficient to support or deny an advective loss hypothesis of recruitment variability.

Future work on the circulation of water on Georges Bank should focus on the recirculation of water around the western end of the bank. This aspect of the circulation is little known and represents a process in which the retention or loss of a major portion of the water circulating the bank is determined.

NAME: ALLEN E. PETERSON, Jr.
AFFILIATION: NEFC-WOODS HOLE (DIRECTOR)
TITLE: NEFC-WHOI FISHERY ECOLOGY PROJECT
ABSTRACT:

Introduction

In my introductory comments at the first seminar in this series, I asked you to remember that fishery management and resource management were not synonymous; in fact, they are very different, and an understanding of the differences is fundamental if a viable dialogue is to be achieved between the fishery manager and the resource scientist.

A fishery manager must be concerned with everything that affects a fishery. The resource is only one of many considerations and may be the least consideration at times. Social, economic, and especially political concerns frequently are more important to the manager in day-to-day decisions.

Resource management is much narrower than fishery management. As implied, it relates to doing something directly designed to affect the resource, usually achieving some prescribed level of production.

The problem comes when we mix the two. Fishery managers are schizophrenic. Usually they try to deal with the resource component of the fishery management equation, but are then driven by other factors in their decision-making and are thwarted in achieving their intended results.

The Management Equation

This is the way we generally depict the management equation:

$$M = R + (H + D + C)$$

where

M = Fishery management
R = Resource
H = Harvesting
D = Dealer
C = Consumer
P = Politics

But in reality, management is closer to:

$$M = \frac{R}{(H+D+C)} \times P + 1$$

The divisor + 1 reflects the need to have a majority of support to take any action.

It's only when we make the clear distinction between the two that we can effectively manage a fishery or a resource.

What Do Managers Need?

To do an effective job, managers need lots of information, but they rarely have enough. The greatest deficiency is in understanding the social aspects of fishing, and secondly, economics. It's impossible to understand the politics other than to know it is highly variable, unpredictable and cannot be planned for, only reacted to. Currently the only good information managers have is on the resource and even the quality of that information is highly suspect, particularly if it is not consistent with the managers' desired outcome.

For the purpose of this seminar, let's focus on the managers' resource data needs.

Managers need two types of resource information; accurate indexes of abundance and forecasts of surplus production. THE MANAGER DOESN'T CARE ABOUT THE RECRUITMENT PROCESS -- ONLY THE PRODUCT OF THAT PROCESS.

With good forecasts and an understanding of which way the stocks are heading, good managers should be able to reasonably manage fisheries at acceptable risks. BUT KEEP IN MIND THOSE RISKS WILL RARELY BE TAKEN TO THE BENEFIT OF THE RESOURCE. As a rule, a fishery manager will be driven by the other parts of the equation.

WHAT IF'S

Now what if the fishery manager:

1. Had more information,
2. Could better predict the outcome of his actions,
3. Could control the other components of the equation, or
4. Could control the resource component?

I could speculate on each of these "what ifs", but for the purpose of time, let's examine the last.

Let's assume that as a result of our joint NEFC/WHOI Fishery Ecology Project we achieve a full understanding of the dynamics of the recruitment process. For example, we know that if the population of silver hake is reduced there will be compensating increase in haddock stocks. This should be helpful to the managers. Simply by fishing down silver hake we

could increase production of haddock, getting the best from both, high production of hake and greater yield of haddock.

I suspect that even if such a relationship exists, it probably would not be possible for us to effect the appropriate fishing patterns to accomplish the objective. Unless we have a totally authoritarian management system, it simply would not be possible to put enough pressure on silver hake to fish them down unless the fishermen want to do so. I don't know all the reasons why fishermen fish, but one is to make money. Unless they can make money catching silver hake, they won't fish for them. And if they can make money, they won't be inclined to want them fished down to low levels of abundance.

I also suspect that such relationships will not be so direct. Instead of producing more haddock, we'll probably find that we get more dogfish or something else we don't really want. THE ECOSYSTEM IS COMPLICATED AND IT IS NAIVE TO BELIEVE THAT SIMPLE RELATIONSHIPS WILL HOLD WITH ANY REASONABLE LEVEL OF PREDICTABILITY. If the relationships are complex, they will only complicate the management equation and make it even less workable.

Conclusion

I reiterate my views that the resource is only one component of the fishery management equation. Fishery management is going to be driven by many factors that will, in the short run, tend to override attempts at resource manipulation.

The fishery manager is not going to be concerned about the recruitment process, only in its product. To the extent that we, as scientists, need to understand the process to make the forecasts of production, we can ride on the coat-tails of the managers. Beyond that need, we'll need different justifications.

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c/o Coast Guard R & D Center
Avery Point
Groton, CT 06340

Library
Physical Oceanographic Laboratory
Nova University
8000 N. Ocean Drive
Dania, FL 33304

NOAA/EDIS Miami Library Center
4301 Rickenbacker Causeway
Miami, FL 33149

Library
Skidaway Institute of Oceanography
P.O. Box 13687
Savannah, GA 31416

Institute of Geophysics
University of Hawaii
Library Room 252
2525 Correa Road
Honolulu, HI 96822

Library
Chesapeake Bay Institute
4800 Atwell Road
Shady Side, MD 20876

MIT Libraries
Serial Journal Room 14E-210
Cambridge, MA 02139

Director, Ralph M. Parsons Laboratory
Room 48-311
MIT
Cambridge, MA 02139

Marine Resources Information Center
Bldg. E38-320
MIT
Cambridge, MA 02139

Library
Lamont-Doherty Geological Observatory
Columbia University
Palisades, NY 10964

Library
Serials Department
Oregon State University
Corvallis, OR 97331

Pell Marine Science Library
University of Rhode Island
Narragansett Bay Campus
Narragansett, RI 02882

Working Collection
Texas A&M University
Dept. of Oceanography
College Station, TX 77843

Library
Virginia Institute of Marine Science
Gloucester Point, VA 23062

Fisheries-Oceanography Library
151 Oceanography Teaching Bldg.
University of Washington
Seattle, WA 98195

Library
R.S.M.A.S.
University of Miami
4600 Rickenbacker Causeway
Miami, FL 33149