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WHY DO FISH POPULATIONS VARY?*

by

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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 a) use an inappropriate proxy for recruitment, b) are data exploration exercises that are not based on a plausible a priori hypothesis, c) do not consider, simultaneously, physical variables and spawning biomass, and/or d) 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, namely, 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, b) lack of evidence of starvation for field collected larvae, c) a high survival rate of larvae in large, predation-free, enclosures, d) the high mortality rate of eggs and yolk-sac larvae which are not subject to starvation, and e) the identification of fish and invertebrates as predators of egg, larval, and post-larval stages.

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At least for some systems, fish consume most of their own production. Two important implictions 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.

INTRODUCTION

The dynamics of a fish population are determined by the balance between increases due to recruitment and growth, and losses due to fishing and natural mortality. This paper concerns the biological mechanisms and physical factors that control recruitment, growth, and natural mortality. Broadly speaking, this is most of fishery science. Herein, I only attempt to highlight ideas from some of the most important and recent literature.

Population size may vary in either a density-independent or density-dependent manner. Density-independent means that population growth per unit size (i.e., numbers or biomass) is unrelated to population size; density-dependent means that there is a relationship. A density-dependent relationship is referred to as compensatory if population growth per unit size is inversely related to population size (all other factors remaining constant), or depensatory if there is a direct relationship.

The terms density-dependence and -independence are often taken literally to imply numbers or biomass per unit area or space. While this may be the case, these terms are used in the context of population size without regard to local density.

Physical factors are usually considered to have a density-independent influence since their potential effect on each member of the population is the same regardless of population size. On the other hand, biological mechanisms are usually density-dependent. For example, the constraining effect of competition increases with the size of the population competing for a limiting resource. Yet, physical factors may act indirectly as density-dependent (e.g., physical changes may affect the environment's carrying capacity, thus exacerbating competition). So, too, may biological processes be density-independent. Predators may consume a constant proportion of their prey independent of prey population size. Depensation occurs when predators consume a constant amount (or increasing proportion) of their prey as prey population size decreases.

The theory of fishing depends on the existence of compensation. The theory is that an unexploited fish population remains in a quasi-equilibrium with no surplus production (i.e., recruitment plus growth minus natural mortality). Fishing reduces population size, resulting in a compensatory response with a surplus production available for harvest. Compensation may involve an increase in recruitment or growth rate as population size decreases, or a decrease in natural mortality rate. Unfortunately, density-dependent responses of fish populations (particularly involving recruitment) are often obscured by variability, presumably due to the density-independent effect of fluctuating environmental factors.

RECRUITMENT, GROWTH, AND NATURAL MORTALITY

The growth rate of a fish depends on its consumption rate and the efficiency of the conversion of food energy to body tissue (i.e., growth efficiency). Compensation in growth occurs when fish reduce the abundance of their prey as their own population size increases. When this happens, there is less prey available for consumption and more energy is required to search for and/or capture it. Compensatory growth may also result from competition for habitat space. In this case, the "interference" effect of an increase in population size per unit space reduces consumption rate or growth efficiency. Growth rate is also affected by physical factors. Temperature has a density-independent effect. Physiological processes (e.g., metabolism) that determine growth efficiency are a function of temperature.

There is ample evidence that growth rate varies. Compensation in growth rate is indicated for Pacific halibut (26), Baltic Sea sprat (45) and Georges Bank haddock (15). Yet, there are also examples of remarkable little change in growth rate in spite of large changes in population size (e.g., North Sea haddock; (46)).

Natural causes of death of fish are predation, starvation, lethal environmental conditions, and disease. Starvation of post-recruit fish has rarely been documented. Furthermore, the generally precise relationship between length and weight argues against the significant proportion of a population suffering from starvation. Fish on the verge of starvation would be expected to have an anomalously low weight at specific length, yet such anomalies are infrequent.

Disease is probably always a source of natural mortality, although routine monitoring of fish from the waters off the northeastern USA indicate that gross pathology and anomalies (e.g., ambicoloration, fin rot, lymphocystis, skeletal anomalies, and ulcers) are relatively infrequent (25). It is clear that epidemics occasionally devastate some populations. Northwest Atlantic herring populations were ravaged by periodic epizootics of a systemic fungus pathogen. Outbreaks occurred in the Gulf of Maine in 1932 and 1947, and in the Gulf of St. Lawrence in 1898, 1916, 1940, and 1955 (80, 81). The effect of contagious disease is probably density-dependent since transmission efficiency increases with density.

Disease and physical factors may act synergistically. Burreson (11) provides convincing evidence that virtually all of the juvenile summer flounder within the Chesapeake Bay were killed during the winter of 1980-81 by the combined effect of anomalously low temperatures and a hemoflagellate parasite. The parasite only became lethal when the fish were stressed by the low temperature.

There are numerous predators of fish, e.g., marine mammals, marine birds, and larger fish. As will be domonstrated later in this paper, predation is probably the major cause of natural mortality, although other factors (e.g. stravation) may increase vulnerability to predation.

Unfortunately, it is very difficult to estimate natural mortality rate on average, much less its variability. MacCall and Methot (64) attempt annual estimates of natural mortality of northern anchovy, but their results are confounded with variability in estimates of biomass. Nevertheless, an increase in estimated mortality in the late 1970's coincided with an increase in the abundance of Pacific mackerel, a known predator.

Natural mortality is usually estimated by relating it to life span or other life history characteristics such as growth and age at maturity (69).

Fisheries scientists have focused on the relationship between recruitment and spawning biomass (referred to as S-R relationship). They have done so because most production to the fishery results from recruitment, and ultimately population persistence requires replacement in numbers by the recruitment process.

There are numerous biological mechanisms that result in a compensatory S-R relationship. Ricker (72) noted several mechanisms including competition for breeding sites or living space, competition for food resulting in starvation, increased susceptibililty to disease from crowding, cannibalism, and compensatory growth coupled with size-dependent predation mortality. Some of these mechanisms lead to characteristic mathematical relationships between spawning biomass and recruitment. The best known of these relationships are the Ricker (72) and Beverton and Holt (5) functions. The underlying differential equation model of the dome-shaped Ricker function assumes that mortality rate of offspring is proportional to the number of spawners. This relationship could result from cannibalism by spawners. According to Shepherd (79), based on a personal communication from R. May), it may also result from depletion of a key food resource due to the stock itself. The asymptotic Beverton and Holt function results from a differential equation model with mortality rate of offspring proportional to their own number. This relationship results from intracohort cannibalism or competition.

Unfortunately, neither function or other S-R functions proposed in the literature (e.g., (20)) account for the variation in typical stock-recruitment data (e.g. Figs. 1-2). It is usually hypothesized that the unexplained variability in recruitment results from the density-independent effects of environmental fluctuations.

In most cases, spawning biomass is estimated with the assumption that age at maturity and fecundity are constant and independent of density. This assumption is frequently invalid and it may contribute to the apparent lack of a relationship between spawning biomass and recruitment.

Recruitment variability is the central problem of fishery science and a major source of uncertainty in fishing management (84). Only projections of abundance based on year classes already recruited to the fishery are possible until recruitment variability is understood. Sustainable yield strategies depend on quantifying density dependence in the S-R relationship.

There are two general approaches to the variable "recruitment problem", empirical- and process-oriented. The empirical approach involves fitting statistical relationships between recruitment (or proxies for it) and physical, and sometimes biological, variables. Presumably, these relationships can be used to predict recruitment. The process-oriented approach involves identifying the causes of prerecruit mortality (egg, larval, and post-larval, i.e., a portion of the juvenile stage) and the factors that cause prerecruit mortality to vary. The process-oriented approach can be applied holistically to several species or to functional units as an aggregate.

EMPIRICAL APPROACH TO THE RECRUITMENT PROBLEM

Ultimately, the spatial distribution and abundance of fish is controlled by climate, e.g., there are no parrot fish in boreal waters, nor are there codfish in the tropics. Jones and Martin (47) found that the fisheries for demersal species relative to pelagic species became more prevalent in the Atlantic as bottom water temperature decreased. Therefore, it is only natural to try to correlate changes in abundance of fish with changes in climate.

Templeman and Fleming (92) considered long-term changes in hydrographic conditions and corresponding changes in abundance of fishery resources in the waters off of Newfoundland and Labrador. They note similar trends in climate (as indicated by air temperature) and abundance (as indicated by catch or sightings) for mackerel, lobster, squid, billfish, capelin, and cod. Taylor et al. (91) examined climatic trends and the distribution of fishery resources off of New England. They noted a general warming trend from 1900 to 1940. They relate landings statistics for mackerel, lobster, whiting, menhaden, and yellowtail flounder to air temperature and water temperature records. They also relate range extensions to the warming trend.

Cushing and Dickson (23) examined variations in atmospheric and marine climate ranging from changes over a century in duration to changes occurring within a year. They speculate that long-term changes in fisheries (e.g., herring fisheries since 1400 A.D.) have been in response to climate. In particular, they cite the correlation between the periods of the Atlanto-Scandian herring and periods of ice cover north of Iceland (6). Cushing and Dickson (23) conclude that climatic changes occur on a worldwide scale and biological events in one region can be related to those in another. Likewise, Garrod and Colebrook (32) conclude that fish communities respond to climate on the "pan-Atlantic scale."

It is important to understand the nature of changes in fish communities that occur over a time scale of decades so that long-term fisheries expectations are not unrealistic. Yet the success of fisheries management also depends on understanding inter-annual variability in fish abundance. The empirical approach has been used frequently to examine this scale of variability (see (1) for a more complete review than is given herein).

Many of these attempts have demonstrated correlations between catch and environmental factors (usually temperature). Dow (27) compared landings of lobster, scallop, and shrimp with annual average water temperature at Boothbay Harbor. Lags between variables were inspected until a relationship was found. Similarly, Dow (28) considered Maine lobster, in more detail, for the period from 1905. He found that the optimum center of catch moved southward as temperature decreased. Flowers and Saila (30) and Dow (29) correlated several water temperature records (both surface and bottom) with lobster catch from the Gulf of Maine region and found a direct relationship.

Gunter and Edwards (36) found a correlation between the catch of white shrimp from the Gulf of Mexico and rainfall in Texas that year and two years earlier. Sutcliffe et al. (90) correlated the catch of seventeen species of fish from New England with water temperature. The correlations were improved by considering fishing effort and select time lags. Ulanowicz et al. (93) found that an appreciable portion of the annual variation in catch of seven commercially important fisheries of Maryland could be linked to fluctuations in the past physical environment.

These studies use catch as a proxy for abundance and, presumably, as a proxy recruitment a short time prior. The validity of this substitution depends on the degree of variability in fishing effort and the degree of dependence of the fishery on annual recruitment. In the case of the lobster, the fishery is almost totally dependent on annual recruitment, and fishing effort is relatively stable (30). Therefore, catch is a reasonable proxy for recruitment. On the other hand, substitution of catch for recruitment is questionable for several of these correlations.

There are many examples where physical factors are correlated directly with recruitment (instead of with a proxy). Carruthers (12) correlated computed winds with recruitment of haddock, herring, cod, and hake of the northern North Sea. Sissenwine (82) correlated recruitment of southern of New England yellowtail flounder with air temperature. In order to minimize the chances of a spurious relationship, Sissenwine tested correlation coefficients fit to each half of the data base separately and determined that there was no statistically significant difference between them. In this case, air temperture was shown to be a reasonable proxy for surface and bottom water temperature. Hayman (38) modeled Dover sole and English sole recruitment of populations off the Oregon Coast of the USA using numerous environmental variables (i.e., temperature, sea level, barometric pressure, index of offshore and alongshore transport, offshore divergence index, wind speed, solar radiation, Columbia River discharge, water quality, number of wind direction shifts, storm frequency, and storm duration).

A major shortcoming on most of the studies cited above are that they are primarily examples of data exploration exercises. The correlations cannot be viewed as a test of a previously stated hypothesis and nominal levels of statistical significance are misleading due to multiply testing. At best, they serve as a basis for establishing a future hypothesis.

Some empirical studies have been based on a plausible reason for expecting a correlation between recruitment and a physical variable in advance of the analysis. Walford (96) correlated Pacific sardine recruitment for 1934-1941 with salinity. Salinity was taken as an index of upwelling which would affect production of food suitable for larval fish.

Chase (13) hypothesized that the loss of haddock pelagic larvae from Georges Bank should be related to norhtwesterly winds as derived from pressure measurement. He achieved a relatively good correlation ($r^2 = 0.59$) by taking account of the effects of temperature fluctuations on spawning time.

Bakun (2) and Bakun and Nelson (3) used longshore wind stress data to calcualte monthly upwelling indices and surface layer divergence indices for the California Current area. Coastal upwelling is always associated with positive nearshore divergence, but the intensity and sign of offshore divergence depends on the rotaion of the wind field, i.e., wind stress curl (Fig. 3, (4)). These indices of upwelling and divergence have been used to examine fluctuations in recruitment of several species (including Dover and English sole, cited above). Bakun and Parrish (4) review several of these applications (e.g., for coho salmon, dungeness crab, rockfish, bonito, hake, sardine, mackerel, and anchovy). In particular, poor upwelling in 1947-1952 was associated with recruitment failures of anchovy, mackerel, sardine, and bonito. Although some of these analyses were primarily data exploration exercises.

So far, we have focused on empirically-derived relationships between recruitment and physical variables, ignoring the relationship with spawning biomass. There are some noteworthy investigations that consider both.

Bakun and Parrish (4) model Pacific sardine recruitment per unit spawning biomass as a multiplicative function of indices of upwelling and divergence at 30°N, and 39°N, spawning stock size, and a linear trend. There was a statistically significant fit, with a positive dependence on upwelling, a negative dependence on divergence, a negative dependence on stock (implying compensation), and a negative trend. They speculate that the negative trend is due to competition with anchovy.

Parrish and MacCall (70) present a number of empirical models of Pacific mackerel recruitment. They consider several compensatory stock recruitment functions (i.e., Ricker, Beverton and Holt, Cushing), physical variables (i.e., sea surface temperature at two locations, barometric pressure, wind speed, sea level height, upwelling index, and surface layer divergence index), and a variety of combinations of monthly values of the physical variables. In some cases, they excluded a portion of the data time series from parameter estimation procedures for use in testing the predictive value of the models. They were able to explain 76% of the variability in recruitment for the period 1946-1968, and 59% for 1931-1968 (Fig. 4).

Nelson et al. (66) fit a Ricker stock recruitment model to Atlantic menhaden year class strength data for 1955-1970. Deviations from the relationship were used to calculate a "survival index," and these were correlated with several environmental variables; 84% of the variations in the survival index was explained. Zonal Ekman transport, which acts to transport larvae from offshore spawning grounds to inshore nursery grounds, was the most statistically significant physical variable.

Csirke (19) hypothesized that recruitment of the Peruvian anchovy was dependent on the density of spawners, as well as their absolute biomass. Presumably, the amount of suitable spawning area varies as a result of environmental fluctuations, and this affects density, which in turn affects the rate of cannibalism. Csirke modified the Ricker S-R function to include a variable "concentration index." He calculated the index by comparing commercial catch-per-unit data with spawning biomass estimates. His analysis provides a family of S-R functions depending on the concentration index (Fig. 5).

Sissenwine (83) developed simulation models of the southern New England yellowtail flounder fishery. Catch was simulated based on age and size structured models, with variable fishing effort, and the effects of temperature variations (82) superimposed on underlying S-R functions. Reminiscent of the classic debate between Clark and Marr (14), recruitment was modeled as independent of the spawning biomass (Marr's position) and linearly dependent on spawning biomass (quasi Clark's position). The models explained 83 and 85% variability in catch, respectively (Figs. 6-7) and appear to have predictive value, since only information up to 1965 was used to fit parameters, yet they continued to predict after that date.

While it appears that much progress has been made using the empirical approach, the approach has some serious limitations. Empirical methods do not demonstrate "cause and effect." There is always a concern about spurious correlations, particularly when several combinations of variables are considered (35). In only a few cases have some data been excluded from the fitting procedure for use in model testing (e.g., (70,82)). The predictive value of empirical models beyond the date of publication is usually unknown. I am aware of some models, which were based on plausible hypotheses about the effects of physical factors, which have failed to predict post-publication events (e.g., (13, 66)). I suspect that post-publication failure of empirical models is not infrequent.

Perhaps an even more important limitation of empirical models is that they may not be useful for quantifying density dependence. The influence of physical variables may be so dominant that it may not be possible to distinguish between fundamentally different S-R models (e.g., Figs. 6-7, (83)).

PROCESS-ORIENTED APPROACH

Hjort (40) hypothesized that Atlanto-Scandian herring recruitment fluctuated according to the availability of food to early stage (first-feeding) larvae. This hypothesis is known as the "critical period hypothesis." Although Hjort was never able to test it, the hypothesis remains attractive today. Most process-oriented research is focused on starvation of larvae.

Since Hjort's work, two important corollaries have evolved. One is that recruitment depends on water currents which maintain pelagic eggs and larvae in, or transport them to, areas where food is concentrated. This hypothesis is the basis of many of the empirical studies reviewed earlier (e.g., (13,66)). The second corollary is referred to as the "match-mismatch" hypothesis (21). According to this hypothesis, recruitment depends on the match or mismatch of the annual reproductive cycle of fish and the annual production cycle of larval fish prey. Cushing and Dickson (23) give several examples of unique events that could be explained by the match-mismatch hypothesis. They note that the 1963 year class of southern North Sea plaice was the largest ever recorded. They speculate that an unusually cold winter delayed egg and larval development, resulting in a better match with production of prey.

One of the first attempts to investigate the "critical period hypothesis" was described by Sette (78). Sette began egg and larval surveys off New England in 1926. By 1932 he had developed the necessary quantitative techniques to estimate larval growth and mortality rates and describe egg and larval drift. The 1932 year class turned out to be poor. Mortality was high (10-14% per day) throughout the egg and larval stages, but not especially high for the small yolk sac and first-feeding larvae. The highest mortality appeared to have been connected with the transition from larval to post-larval stages. Sette attributed this to the particular drift pattern caused by dominant winds, which left the larvae further from their nursery grounds along the southern New England Coast than usual. Unfortunately, Sette was unable to continue his study and compare the 1932 year class with more successful year classes that followed. The research vessel...."ALBATROSS II was withdrawn from service as a government economy measure."

Lasker (49-51) qualitatively compared year class strength to prey density for three year classes (1975, 1976, 1978) of northern anchovy of the California current area. Larval anchovy require a "threshold" concentration of prey particles in order for them to feed and survive.

This concentration is substantially higher than the average, and Lasker hypothesized that necessary concentrations occur in small-scale layers that form in inshore waters during periods of water column stability. He observed that these layers could be dispersed by storms and by intense upwelling. These observations led Lasker (51) to hypothesize that anchovy year class strength depended on the stability of the environment. A complicating factor in 1975 was that the dominant food particle in the environment of larval anchovy was a dinoflagellate which is nutritionally inadequate (77). The 1976 spawning season was characterized by stable conditions.

Consistent with Lasker's "stability" hypothesis, the 1975 year class was poor, the 1976 was outstanding. The 1978 year class was predicted by Lasker (50) to be of intermediate strength due to the onset of stable conditions and food aggregations during the latter part of the spawning season. Methot (65) showed that juveniles of the 1978 year class were, in fact, survivors from the latter half of the spawning season. He used daily growth rings of otoliths to determine birth date. In 1979, the birth date distribution of juveniles corresponded more closely with the seasonal distribution of larval production (Fig. 8). In fact, the 1978 year class seems to be one of the largest ever (64). In general, water column stability has not proved to be a good predictor of year class strength.

Lasker's investigation of the relationship between anchovy year class strength and larval prey density is supplemented by a simulation model. Vlymen's (95) model showed the importance of the microstructure of larval prey. He treated the spatial distribution of prey as negative binomial. His simulation indicated that extremely different larval growth rates could occur at the same average concentration of prey as a function of contagion. The highest growth rate was at an intermediate level of contagion.

Lasker and Zweifil (53) modified Vlymen's model to simulated growth and survival of first feeding larvae on different prey sizes and concentrations. Their stimulation was based on laboratory and field data. They showed that at nominal capture efficiency of 20-30%, there is a threshold of 30 to 50 small particles (45-50 microns in diameter) per ml necessary for substantial survival and growth. This threshold concentration is found in inshore areas during periods of environmental stability.

The relationship between larval survival and prey concentration and distribution has also been the focus of process-oriented research concerning coastal waters off the northeastern USA. Georges Bank haddock and cod are the target species. Laurence (54,55)) determined their laboratory growth, respiration, and survival rates in relationship to prey concentration and temperature. Laurence (56) and Lough (59) described a sampling strategy for determining fine to microscale vertical distribution of fish larvae. Their initial results are pertinent to Lasker's stability hypothesis. In 1981, they observed the vertical distribution of cod and haddock larvae and copepod prey on Georges Bank, before and after a storm (Figs. 9-10). Before the storm, a thermocline was established and fish larvae and copepods were found in greatest density at about the thermocline depth. After the storm, the water column was well mixed (isothermal) and copepods were dispersed throughout the water column. The peak density of larvae was at the mid-depth. The implication is that the concentration of prey in the immediate environment of the fish larvae was nearly an order-of-magnitude lower following the storm. The actual impact of the storm on larval growth and survival is unknown.

There have been a series of stochastic larval growth simulation models (7,8,57) used to evaluate the importance of prey concentration. The most recent version of the model treats the following as stochastic: a) prey encounter frequency conditional on prey concentration (poisson distribution), b) prey size frequency (Poisson distribution), c) larval size frequency at hatching (normal distribution), and d) daily variation in prey concentration (uniform distribution). Individual larvae are simulated and their growth and survival is determined based on their stochastic feeding rate compared to laboratory determined energy requirements.

Laurence (56,57) concludes that haddock require a mean prey concentration of 50 per liter for 50% survival through their 42 day larval period, while cod larvae require about 20 per liter for 50% survival. Lough (54) reports prey concentrations of 10-65 per liter on Georges Bank in the vicinity of larval cod and haddock. Laurence (57) concludes that, although starvation mortality is important, it does not appear to be the single controlling mortality factor under normal ranges of prey density.

This conclusion is supplemented by RNA/DNA ratios of field collected larval fish. Buckley (10) showed that the RNA/DNA ratio increases with growth rate of laboratory reared larval fish. Since then, the Northeast Fisheries Center (National Marine Fisheries Service, Woods Hole, Massachusetts, USA) has monitored RNA/DNA ratios of larval fish collected in the field. To date, these studies indicate that most field collected larval fish have a high growth rate and are not on the verge of starvation.

What about the effects of larvae on their prey? Laurence (56,57) and Cushing (22) address this question. Laurence concludes that larvae are too dilute to affect the concentration of their prey. Cushing bases his analysis on several of Laurence's results and confirms that at least early stage larvae are too dilute to affect the concentration of their prey, although this may not be the case as larvae approach metamorphosis.

The effect of larvae on their prey is an important aspect of the recruitment problem. If they have no effect, then starvation mortality is density-independent since the density of prey does not change in response to larval density. Thus, even if fluctuations in recruitment are a result of varying amounts of starvation mortality, additional processes are necessary if the existence of a compensatory stock-recruitment relationship is to be confirmed.

Cannibalism is a source of density-dependent mortality (72). Hunter and Kimbrell (43) estimate that cannibalism by adults accounts for 32% of the daily egg mortality of northern anchovy. By comparing the number of eggs in anchovy stomachs and the density in the same area, they estimate that the consumption rate of eggs increases as the 1.6 power of egg concentration. One hypothesis is that at low concentration eggs are consumed incidentally during filter feeding, whereas at higher concentrations eggs contribute to stimulating feeding (63).

MacCall (63) and Lasker and MacCall (52) considered density-dependent effects of cannibalism for a population which expands and contracts its range with changes in abundance. This behavior is clearly demonstrated by the distribution and abundance of anchovy larvae off southern California. MacCall (63) developed a model that indicated that this geographic behavior is a consequence of density-dependent habitat selection under the following assumptions: a) spawning habitat is most favorable near the center of the range, b) local spawning habitat becomes less favorable as spawning intensity increases, and c) fish individually attempt to spawn in the most favorable location. Cannibalism is one mechanism that could make local spawning habitat less favorable as spawning intensity increases, as in assumption b.

An important consequence of the geographic expansion-cannibalism model is that the stock recruitment relationship will be less dome-shaped than would result from cannibalism alone. This conclusion is consistent with stock-recruitment data for the California sardine and anchovy (61, 62). It is also consistent with Csirke's ((19), described earlier in this paper) stock-recruitment model of Peruvian anchovy, which took account of density of spawners.

Hunter (42) considers, in general, the importance of predators as a cause of egg and larval mortality. He rejects the hypothesis that starvation is the largest cause of mortality. He cites evidence that growth rates "in situ" are about the same as growth rates when larvae are fed a high ration in laboratories. He cites histological studies that indicate that the starvation rate, based on the frequency of detection of starving larvae, is much lower than observed mortality rates. He notes that high mortality rates of eggs and yolk sac larvae could not result from starvation and concludes that predation is the major cause of mortality.

There are numerous potential invertebrate and vertebrate predators of fish eggs and larvae. Hunter (42) speculates that pelagic fish are the most important predator. There are numerous examples of fish predation on eggs and larvae (e.g., (37,43)). One reason for hypothesizing that fish are the most important predator is that egg and larval mortality remains high over a broad size range. Fish are capable of consuming prey over a broader size range than are small invertebrate predators. Hunter notes that a serious problem that limits research on predation is that eggs and particularly larvae are digested beyond recognition in the gut of fish within a short period (about an hour).

Results of enclosure studies support Hunter. Øiestat (67) conducted experiments with cod, herring, capelin, and plaice larvae in enclosures in Norway and found a very high survival potential to metamorphosis in systems without predators (e.g., 70% for herring, 50% for cod), even at marginal feeding conditions where growth rate was reduced. Survival was markedly reduced when predators were introduced to the system. He notes that post-larval fish can be important predators of larval fish of their own and other species.

It should now be apparent that the recruitment problem is extremely complex. Recruitment is probably influenced by both starvation and predation, and the modifying effects of physical factors. This was the conclusion of meeting of experts during 1982 (i.e., Fish Ecology III, (73)). In fact, several of the important (42,56) works cited above were presented during Fish Eoclogy III. The meeting represents a turning point in the scientific attack on the recruitment problem. Several plans for future research were developed.

Fish Ecology III gave little consideration to processes that occur during the post-larval (but prerecruit) stage. I next review a more holistic approach which reflects on the importance of the post-larval stages.

A HOLISTIC APPROACH

The holistic approach has been used to examine the roles of starvation and predation for Georges Bank. Georges Bank and the surrounding region have been the focus of intensive ecological studies (31,33,85). The results of these investigations have been summarized in the form of an energy budget of Georges Bank (86). The energy budget is most certain for primary productivity and fish production. Estimates of primary productivity are based on a three-year study with samples collected throughout the year (61). Estimates of fish abundance, production, and consumption are based on extensive bottom trawl surveys and fisheries statistics. While estimates of other components (e.g., macrozooplankton) are less certain, conclusions based on the entire energy budget are generally robust. This rebustness results from the bounding effect of the more precise information at the lowest (primary productivity) and the higher (fish) trophic levels.

Average biomass, annual consumption, and annual production estimates of finfish of Georges Bank for the periods 1964-1966 and 1973-1975 were calculated by Grosslein et al. (34). The former period was one of increasing fishing pressure from distant-water-fleets in response to high fish abundance. The latter period was one of low abundance, following a decade of excessive fishing pressure. Pre-exploitable fish (individuals which were either too small or young to be captured by commercial or research vessel bottom trawl survey gear) are not represented in these traditional estimates of abundance. Nevertheless, they are important components of the ecosystem.

Relatively little is known about the population dynamics of these small fish, particularly after the late larval stage and before they grow large enough to be captured in trawls. However, some valuable information is available. The initial number and biomass of the cohort of pre-exploitable fish can be estimated from the abundance of adults, the proportion of the total adult production used for reproduction, and the average size of an egg. As the young fish reach exploitable size, their number and biomass can be determined for traditional stock assessments based on trawl surveys and fisheries statistics. With these beginning and end points known for the pre-exploitable fish, a simple model can be used to calculate estimates of average biomass, production, and consumption. The model assumes that growth of individual fish and of the entire cohort of pre-exploitable fish is exponential. While pre-exploitable fish are only 10% of the biomass of exploitable fish, their consumption is nearly as great and their production is two and a half times as high (86).

Extensive stomach content investigations indicate that fish consume macrozooplankton (e.g., by herring, mackerel, and redfish), benthos (e.g., by haddock and flounder), and fish (e.g., by cod and silver hake). Sissenwine et al. (86) noted that consumption of fish by silver hake and cod accounted for 40 to 50% of the total consumption by the demersal component of the fish community. For the purposes of this discussion, we assume that approximately 50% of demersal consumption is fish.

The Georges Bank energy budget is summarized in Table 1. Estimates of particulate phytoplankton, zooplankton, and benthic production are form Cohen and Grosslein (16).

Fish production was 1.2% to 2.1% of particulate primary productivity. Considering the complexity and number of trophic levels of the food web, trophic efficiency must be high relative to traditional thinking (10%, (88)). One implication of the result is that the energy budget is "tight," and fish production is ultimately limited by their food resource. In fact, Table 1. indicates that fish consume from 30 to 50% of the production of suitable prey types. This is remarkably high considering that microzooplankton (about 60% of the zooplankton production) is a suitable food for only a brief period during the life cycle of fish, and that consumers other than finfish and squid are dependent on the components of the ecosystem which have been labeled in Table 1. as potential fish prey.

Table 1. also indicates that fish consume most of their own production (61-93%). Other consumers are marine mammals, birds, large pelagic migratory fish (e.g., sharks) and humans. Estimates of their consumption are also included in Table 1. The estimated total consumption of fish ranges from 83 to 130% of production for the two periods considered. The deviations of these estimates from 100% are considered within the level of precision of available data. Although this shows that predation is the major cause of mortality of fish in terms of biomass, it does not necessarily follow that most fish (in terms of numbers) are victims of predation. Most mortality occurs during the egg and larval stage, but these stages account for relatively little biomass. With respect to starvation, there is generally enough food for the fish community in aggregate, but food probably limits production of some species or life stages, particularly when fish biomass was higher prior to overfishing. Density-dependent growth (as observed in juveniles and adult fish) seems likely.

It is noteworthy that most of the predation of fish was by silver hake. The primary prey of silver hake are post-larval, pre-exploitable fish. In fact, silver hake consume most of the production of the pre-exploitable component. The implication is that predation must cause a high post-larval mortality. This predation probably affects recruitment. If post-larval mortality is high, then there exists a potential that year class strength is not established until this life stage since only small variations in mortality would be necessary to account for large changes in recruitment.

There is clearly a biological basis for expecting compensation in production by the Georges Bank finfish community. They modify their own abundance by predation (cannibalism at the community level). It seems likely that this mechanism operates at the species as well as community level. Some species are cannibalistic (e.g., silver hake); furthermore, an abundance of fish as prey may enhance production of predators, ultimately resulting in compensation.

There is also the potential for depensation. Sissenwine et al. (87) speculate that the marine mammals contributed to the demise of herring on Georges Bank, although overfishing was certainly the primary cause. The estimated biomass of marine mammals in the range of the Georges Bank herring is sufficient to have consumed the entire population that was estimated to remain after the last commercial harvest in late 1977. There has been virtually no evidence of the population of herring since that time.

Cohen and Grosslein (16) compared Georges Bank to other Continental Shelf ecosystems. These comparisons indicate that Georges Bank is not unique in its efficient conversion of primary productivity to fish production. For example, fish production is about 1% of particulate primary productivity for the North Sea (24), and about 3% for the East Bering Sea (58). These ecosystems are also "tight" like Georges Bank, and probably food limits their overall production as well. Furthermore, North Sea and East Bering Sea fish also consume a significant proportion of their own production.

DISCUSSION

The focus of this paper has been variability. While variability is generally the case, recruitment of some populations is relatively stable (e.g., North Sea plaice, (94)). Ursin (94) hypothesized that this stability results from space limitation during the post-larval stage. Competition for space is, potentially, a strong compensatory mechanism that will stabilize recruitment. The mechanism appears to be particularly important for species depending on coastal areas where space is measured in a linear scale.

It is clear that there should be more emphasis on predation mortality of early life stages, including post-larvae. It is ironic that post-larvae have been nearly ignored since there is an obvious clue that year class strength may not be established until this stage. It is widely recognized that year class strength is not correlated with larval abundance (e.g., (4,31,41,74,75,89)). For this reason, stock assessment working groups of the Internation Council for the Exploration of the Sea (ICES) use egg and larval surveys to back-calculate spawning biomass of certain species (e.g., (18)) and use young fish (primarily age one) surveys to predict recruitment (e.g., (17)). Apparently, year class strength is established somewhere between. Saville and Schnack (75) argue that the lack of correlation between larval abundance and year class strength probably indicates a problem of quantitative sampling, not the time at which year class strength is established. If this were the case, then larval abundance should not correlate with spawning stock biomass.

One reason why the egg and larval stages have received so much emphasis is that mortality rates (M) are very high, and presumably only a small change is necessary to account for large changes in year class strength. But year class strength is determined by the product of M and the duration of the time period (t) during which M applies (assuming the initial number is constant). It is more logical to compare Mt between life stages, in order to evaluate the sensitivity of year class strength to prerecruit mortality, than it is to compare M alone. Sissenwine et al. (86) compared egg and early larval Mt to late larval and post-larval Mt for several species of Georges Bank. They found that the latter was always higher, but since they did not examine size composition data, the distinction between early and late stage larvae is unclear.

Mt for the entire prerecruit stage is $-\log_e(R/E)$, where R is the number of recruits and E is the number of eggs spawned. For values of R and E reported in Sissenwine et al. (86), Mt is 12.6 and 13.5 for prerecruit herring and haddock, respectively. Lough et al. (60) applied catch-curve analysis to larval herring length frequencies from Georges Bank. By comparing day and night catches, they were able to take account of the bias that would result from an increase in net avoidance with length. Using the catch-curve analysis and larval growth data, Lough et al. estimated that M ranged from 0.022 to 0.047/day for the first 150 days of life (to about 30 mm length) for 1971-1978. This amounts to an egg and larval mortality of about 5.2 (0.35 x 150). By substraction, the post-larval, prerecruit Mt is estimated as 7.4.

Unpublished larval length frequencies and larval growth data for Georges Bank haddock indicate a mortality rate of 0.094 to 0.131/day for a 50-day period for 1977-1982. The average was 0.108/day (Morse, personal communication, National Marine Fisheries Service, Sandy Hook, New Jersey, USA). Assuming that pelagic eggs suffer the same mortality rate for 14 days, Mt for eggs and larvae is 6.9. Therefore, the post-larval Mt is 6.6. In the case of haddock, larval mortality rate was certainly overestimated since no correction was made for an increase in net avoidance with length.

Thus, post-larval mortality is at least comparable to egg and larval mortality for two of the principal species on Georges Bank. This is not surprising in light of the energy budget evidence that most production of post-larval fish is consumed by larger fish. We suspect that Georges Bank is not unique. If predation mortality of post-larval fish has a major role in the determination of year class strength, then why is year class strength so variable? The number of recruited fish that are predators of post-larval fish is certainly less variable than recruitment. Fogarty et al. (31) noted that although year class strength is highly variable, it is autocorrelated for several species of Georges Bank. This indicates that the factor (s) controlling year class strength has a tendency to persist between years. This would be characteristic of predation by recruited fish.

Although the number of fish predators of post-larvae may not be very variable (in a relative sense), their diet composition may be. For example, the percentage (by weight) of fish in the stomachs of silver hake collected on Georges Bank during spring 1973-1979 was 23.7, 57.9, 88.2, and 68.6%, respectively (9). Variability in diet composition could have a significant effect on post-larval mortality, and predator switching could be a compensatory mechanism.

It is almost axiomatic that variability in recruitment is caused by fluctuations in physical factors. In spite of the pitfalls of empirical studies, there are enough correlations to indicate that physical factors are certainly important. There are numerous possible mechanisms associated with physical factors that could influence starvation of early life stage larvae. It is less apparent how predation, particularly on post-larval fish, is influenced by the physical environment, although growth rate is effected by environmental factors like temperature, and this in turn effects vulnerability to predation.

Future hypotheses about the effects of physical factors on recruitment should be compatible with certain statistical characteristics of the frequency distribution of year class strength. The distribution is usually skewed towards poor recruitment (39)). The implication is that research should focus on physical factors that explain occasional "bonanzas," not disasters."

Recruitment is frequently auto-correlated. As noted above, this could be associated with the effects of predation by recruited fish or auto-correlation of spawning potential. If it is associated with a physical variable, then the physical variable must also be auto-correlated. The average of physical variables is more likely to be auto-correlated the longer the period included in the average (e.g., annual average temperature is more likely to be auto-correlated than average temperature of a specific day of the year). There is a coherence in recruitment between stocks over broad geographic areas (32,48)). Therefore, if a physical factor determines recruitment, it must occur over a broad area.

There are numerous reasons why fish populations vary. Predation plays a much greater role than had been hypothesized until recently. As a result of predation by fish on their own and other species, and a limited amount of food potentially available to them, fish populations are able to compensate for some fishing pressure. Recruitment is likely to be a multiplicative function of highly variable processes occurring throughout the first year of life, including the post-larval stage. The more we learn about it, the better able we are to ask the right questions in the future.

REFERENCES

(1) Austin, H.M., and Ingham, M.C. 1979. Use of environmental data in the prediction of marine fisheries abundance. In Climate and Fisheries, pp. 93-118. Kingston,RI: University of Rhode Island.

(2) Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. NOAA Tech. Rept. NMFS SSRF-671. Washington, D.C.: U.S. Dept. of Commerce.

(3) Bakun, A., and Nelson, C.S. 1977. Climatology of upwelling related processes off Baja, California. CA Coop. Oceanic Fish. Invest. Rept. 19: 107-127.

(4) Bakun, A., and Parrish, R. 1980. Environmental inputs to fishery population models for eastern boundary current. In Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes, ed. G.D. Sharp, pp. 67-1-4. Intergovernmental Oceanographic Commission, UNESCO.

(5) Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Min. Agric. Fish., Fish. Invest. (Ser. 2) 19.

(6) Beverton, R.J.H., Lee, A.J. 1965. Hydrographic fluctuations in the North Atlantic Ocean and some biological consequence. In The Biological Significance of Climatic Changes in Britain, eds. C.G. Johnson and L.P. Smith, pp. 79-107. Symposia No. 14, London: Institute of Biology.

(7) Beyer, J., and Laurence, G.C. 1980. A stochastic model of larval fish growth. Ecol. 8: 109-132.

(8) Beyer, J., and Laurence, G.C. 1981. Aspects of stochasticity in modelling growth and survival of clupeoid fish larvae. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 178: 17-23.

(9) Bowman, R.E. 1980. Silver hake's regulatory influence on the fishes of the Northwest Atlantic. NMFS, NEFC Woods Hole Lab. Ref. Doc. 80-85.

(10) Buckley, L.J. 1979. Relationships between RNA-DNA ratio, prey density and growth rate in Atlantic cod (Gadus morhua) larvae. J. Fish. Res. Board Can. 36: 1497-1502.

(11) Burreson, E. 1981. Effects of mortality caused by the hemoflagellate (Trypanoplasma bullocki) on summer flounder populations in the Middle Atlantic Bight. Int. Cons. Explor. Sea. C.M. 1981/G: 61.

(12) Carruthers, J.N. 1951. An attitude on "fishery hydrography." Mar. Res. 10 (1): 101-118.

(13) Chase J. 1955. Winds and temperatures in relation to the brood strength of Georges Bank haddock. J. Cons. perm. int. Explor. Mer 21: 17-24.

(14) Clark, F.N., and Marr, J.C. 1955. Population dynamics of the Pacific sardine. CA Coop. Ocean Fish. Invest. Progr. Rept: 11-48.

(15) Clark, S.H., Overholtz, W.J., and Hennemuth, R.C. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. 3: 1-27.

(16) Cohen, E.B., and Grosslein, M.D. 1984. Total ecosystem production on Georges Bank: comparison with other marine ecosystems. In Georges Bank, ed. R. Backus. MIT Press, in press.

(17) Corten, A. 1980. Report of ICES young fish survey, 1980: herring data. Int. Cons. Explor. Sea., C.M. 1980/H: 35.

(18) Corten, A. 1980. The use of larval abundance data for estimating the stock size of North Sea herring (II). Int. Cons. Explor. Sea., C.M. 1980/H: 37.

(19) Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 177: 307-313.

(20) Cushing, D.H. 1973. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33 (3): 340-362.

(21) Cushing, D.H. 1973. Recruitment and parent stock in fishes. University of Washington, Seattle.

(22) Cushing, D.H. 1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 5 (6): 847-854.

(23) Cushing, D.H., Dickson, R.R. 1976. The biological response in the sea to climatic changes. In Advances in Marine Biology, eds. Russell and Younge, vol. 14. New York: Academic Press.

(24) Daan, N. 1983. The ICES stomach sampling project in 1981: aims, outline and some results. Northw. Atl. Fish. Organ. Sci. Res. Doc. 83/IX/93, 23 pp.

(25) Depres-Patanjo, L., Ziskowski, J., and Murchelano, R.A. 1982. Distribution of fish diseases monitored on stock assessment cruises in the Western North Atlantic. Int. Cons. Explor. Sea., C.M. 1982/E: 30.

(26) Deriso, R.B. 1983. Management of North Pacific halibut fishery. II. Stock assessment and new evidence of density dependence. Inter. Pac. Halibut. Comm., unpublished.

(27) Dow, R.L. 1964. A comparison among selected species of an association between sea water temperature and relative abundance. J. Cons. Perm. Int. Explor. Mer 28: 425-431.

(28) Dow, R.L. 1969. Cyclic and geographic trends in sea-water temperature and abundance of American lobster. Science. 146: 1060-1063.

(29) Dow, R.L. 1977. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. J. Cons. Perm. Int. Explor. Mer 37 (3): 274-280.

(30) Flowers, J.M., and Saila, S.B. 1972. An analysis of temperature effects on the inshore lobster fishery. J. Fish. Res. Bd. Can. 29: 1221-1225.

(31) Fogarty, M.J., Sissenwine, M.P., and Grosslein, M.D. 1984. Fisheries research on Georges Bank. In Georges Bank, ed. R. Backus. MIT Press, in press.

(32) Garrod, D.J., and Colebrook, J.M. 1978. Biological effects of variability in North Atlantic Ocean. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 173: 128-144.

(33) Grosslein, M.D., Brown, B.E., and Hennemuth, R.C. 1979. Research, assessment, and management of a marine ecosystem in the Northwest Atlantic: a case study. In Environmental Biomonitoring, Assessment, Prediction, and Management - Certain Case Studies and Related Quantitative Issues, eds. J. Cairns, Jr., P. Patil, and W.E. Waters, pp. 289-357. Fairland, MD: International Co-operative Publishing House.

(34) Grosslein, M.D., Langton, R.W., and Sissenwine, M.P. 1980. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relationship to species interaction. Rapp. P.-v. Reun. Cons. int. Explor. Mer 177: 374-404.

(35) Gulland, J.A. 1952. Correlations on fisheries hydrography. Letters to the editor. J. Cons. Perm. Int. Explor. Mer 18: 351-353.

(36) Gunter, G., and Edwards, J.C. 1967. The relation of rainfall and freshwater drainage to the production of the Penaeid shrimps (Penaeus anviatillis and P. aztecus) in Texas and Louisiana waters. Proceedings of the World Sciience Conference on Biology and Culture of Shrimps and Prawns. FAO Fish Repts. 57 (3): 875-892.

(37) Harding, D., Nichols, J.H., and Tungate, D.S., 1978. The spawning of plaice (Pleuronectes platessa L.) in the southern North Sea and English Channel. Rapp. P.-v. Reun. Cons. int. Explor. Mer 172: 102-113.

(38) Hayman, R.A. 1977. The relationship between environmental fluctuation and year-class strength of Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus) in the fishery off the Columbia River. Master's Thesis, Oregon State University, Corvallis, OR.

(39) Hennemuth, R.C., Palmer, J.E., and Brown, B.E. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northw. Atl. Fish. Sci. 1: 101-111.

(40) Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer 20: 1-228.

(41) Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. In Marine Fish Larvae, ed. R. Lasker, pp. 33-79. Seattle: University of Washington Press.

(42) Hunter, J.R. 1982. Predation and recruitment. Fish Ecology, III CIMAS, University of Miami, September 7-10, 1982.

(43) Hunter, J.R., and Kimbrell, C.A. 1980. Egg cannibalism in the northern anchovy, Engraulis mordax. Fish. Bull. (USA) 78: 811-816.

(44) ICES. 1983a. Report of the Arctic Fisheries Working Group. Int. Cons. Explor. Sea., C.M. 1983/Assess: 2.

(45) ICES. 1983b. Report of the Working Group on Assessment of Pelagic Stocks in the Baltic. Int. Cons. Explor. Sea. C.M. 1983/Assess: 13.

(46) Jones, R. 1979. Relationship between mean length and year-class strength in North Sea haddock. Int. Cons. Explor. Sea., C.M. 1979/G: 45.

(47) Jones, R. and Martin, J.H.A. 1981. The relationship between demersal fish landings and bottom temperature. Int. Cons. Explor. Sea, C.M. 1981/G: 44.

(48) Koslow, A.J. 1984. Recruitment patterns in Northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci., in press.

(49) Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll layers and successful first feeding. Fish. Bul. (USA) 73: 453-462.

(50) Lasker, R. 1978. Ocean variability and its biological effects - regional review - Northeast Pacific. Rapp. P.-v. Reun. Cons. int. Explor. Mer 173: 168-181.

(51) Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (Engraulis mordax) in the California current: contrasting years, 1975 through 1978. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178: 375-388.

(52) Lasker, R., and MacCall, A. 1982. New ideas on the fluctuations of the clupeoid stocks off California. In CNC/SCOR Proceedings of Joint Oceanographic Assembly 1982 - General Symposia, pp. 110-120. Ottawa, Ont.: Canadian National Committee/Scientific Committee on Ocean Research.

(53) Lasker, R., and Zweifel, J.R. 1978. Growth and survival of first-feeding northern anchovy larvae (Engraulis mordax) in patches containing different proportions of large and small prey. In Spatial Pattern in Plankton Communities, ed. J.H. Steele, pp. 329-354. New York: Plenum.

(54) Laurence, G.C. 1974. Growth and survival of haddock (Melanogrammus aeglefinus) larvae in relation to plankton prey concentration. J. Fish. Res. Board Can. 31: 1415-1419.

(55) Laurence, G.C. 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (Gadus mahua) and haddock (Melanogrammus aeglefinus) as influenced by temperature during laboratory studies. Mar. Biol. 50: 1-7.

(56) Laurence, G.C. 1982. Nutrition and trophodynamics of larval fish - review concepts, strategic recommendations and opinions. Fish Ecology, III CIMAS, University of Miami, September 7-10, 1982.

(57) Laurence, G.C. 1983. A report on the development of stochastic models of food limited growth and survival of cod and haddock larvae on Georges Bank. NOAA, NMFS, NEFC, Narragansett Lab. , Unpublished.

(58) Laevastu, T., and Larkins, H.A. 1981. Marine fisheries ecosystems: Farnham Survey, England: Fishing News Books Ltd.

(59) Lough, R.G. 1984. Larval fish trophodynamic studies on Georges Bank: Sampling strategy and initial results. In E. The Propagation of Cod, Gadus morhus L., Fløddevigen rapportser, eds. E. Dahl., D.S. Danielssen, E. Moksness, and P. Solemdal.

(60) Lough, R.G., Bolz, G.R., Pennington, M.R., and Grosslein, M.D. 1980. Abundance and mortality estimates for sea herring (Clupea harengus L.) larvae spawned in the Georges Bank-Nantucket Shoals area, 1971-1978 seasons, in relation to spawning stock and recruitment. NAFO SCR Doc. 80/IX/129 (Revised): 1-59.

(61) MacCall, A. 1979. Population estimates for the waning years of the Pacific sardine fishery. CA Coop. Oceanic Fish. Invest. Rep. 20: 72-82.

(62) MacCall, A. 1980. Population models for the northern anchovy (Engraulis mordax). Rapp. P.-v. Reun. Cons. int. Explor. Mer 177: 292-306.

(63) MacCall, A. 1980. The consequences of cannibalism in the stock-recruitment relationships of planktivorous pelagic fishes such as Engraulis. Intergov. Oceanogr. Comm. Workshop Rep. 28: 202-220.

(64) MacCall, A.D. and R. Methot 1983. Historical spawning biomass estimates and population model in the 1983 anchovy Fishery Management Plan. U.S. National Marine Fisheries Service, SW Fisheries Center, Adm. Rep. LJ - 83-17. 53 pp.

(65) Methot, R.D., Jr. 1981. Growth rates and age distribution of larval and juvenile northern anchovy, Engraulis mordax, with influences on larval survival. Ph.D. dissertation, University of California, San Diego, CA.

(66) Nelson, W.M., Ingham, M., and Schaaf, W. 1977. Larval transport and year class-strength of Atlantic menhaden, Brevoortia tyrannus. US Fish. Bull. 75 (1): 23-41.

(67) Øiestad, 1983. Predation on fish larvae as a regulatory force illustrated in enclosure experiments with large groups of larvae. Northw. Atl. Fish. Organ. Sci. Res. Doc. 83/IX/73. 14 pp.

(68) O'Reilly, J.E., and Busch, D.A. 1984. The annual cycle of phytoplankton primary production (netplankton, nannoplankton and release of dissolved organic matter) for the Northwestern Atlantic Shelf (Middle Atlantic Bight, Georges Bank and Gulf of Maine). Rapp. P.-v. Reun. Cons. int. Explor. Mer 183., in press.

(69) Pauly, D. 1981. On the interrelationship between natural mortlaity, growth parameters, mean environmental temperature in 175 fish stocks. J. Cons. Perm. int. Explor. Mer 39 (2): 175-192.

(70) Parrish, R.H., and MacCall, A.D. 1978. Climatic variations and exploitation in the Pacific mackerel fishery. CA Dep. Fish. Game, Fish. Bull. 167.

(71) Powers, K.D. 1984. Estimates of consumption by seabirds on Georges Bank. In Georges Bank, ed. R. Backus. MIT Press.

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

(73) Rothschild, B.J. and Rooth, C. 1982. Fish ecology III. University of Miami Tech. Rep. No. 82008. 389 pp.

(74) Saville, A. 1977. Survey methods of appraising fishery resources. FAO Fish. Techn. Paper 171: 76.

(75) Saville, A., and Schnack, D. 1981. Overview - some thoughts on the current status of studies of fish eggs and larval distribution and abundance. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178: 153-157.

(76) Scott, G.P., Kenney, R.D., Thompson, T.J., and Winn, H.E. 1983. Functional roles and ecological impacts of the cetacean community in the waters of the Northeastern U.S. continental shelf. Int. Cons. Explor. Sea, C.M. 1983/N: 12.

(77) Scura, E.D., and Jerde, C.W. 1977. Various species of phytoplankton as food for larval northern anchovy, Engraulis mordax, and relative nutritional value of the dinoflagellates Gymnodinium splendens and Gonyaulax polyedra. Fish. Bull. USA 75: 577-583.

(78) Sette, O.E. 1943. Biology of the Atlantic mackerel (Scomber scomberus) of North America. Fish. Bull. 50 (38): 149-237. Fish and Wildlife Service of the U.S. Dept. of Interior.

(79) Shepherd, J.G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. int. Explor. Mer 40 (1): 67-75.

(80) Sindermann, C.J. 1963. Disease in marine populations. Trans. N. Am. Wildl. Conf. 28: 221-245.

(81) Sindermann, C.J. 1970. Principal Diseases of Marine Fish and Shellfish. New York: Academic Press.

(82) Sissenwine, M.P. 1974. Variability in recruitment and equilbrium catch of the southern New England yellowtail flounder fishery. J. Cons. Perm. int. Explor. Mer 36: 15-26.

(83) Sissenwine, M.P. 1977. A compartmentalized simulation model of the southern New England yellowtail flounder (Limanda ferruginea) fishery. Fish. Bull. USA. 73 (3): 465-482.

(84) Sissenwine, M.P. 1984. The uncertain environment of fishery scientists and fishery managers. Mer Resource Econ. 1 (1): 1-29.

(85) Sissenwine, M.P., Brown, B.E., Grosslein, M.D., and Hennemuth, R.C. 1984. The multispecies fisheries problem: a case study of Georges Bank. Lecture Notes Math. Biol., in press.

(86) Sissenwine, M.P., Cohen, E.B., and Grosslein. 1984. Structure of the Georges Bank ecosystem. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183: 243-254.

(87) Sissenwine, M.P., Overholtz, W.J., and Clark, S.H. 1984. In search of density dependence. In Proceedings of the Workshop on Marine Mammal Fishery. Interactions of the East Bering Sea., ed. B.R. Melteff. University of Alaska Sea Grant, Report 84-1: 119-139.

(88) Slobodkin, L.B. 1961. Growth and Regulation of Animal Populations. New York: Holt, Rinehart and Winston.

(89) Smith, P.E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v. Reun. Cons. int. Explor. Mer 1973: 117-127.

(90) Sutcliffe, W.H., Jr., Drinkwater, K., and Muir, B.S. 1977. Correlations of fish catch and environmental factors in the Gulf of Maine. J. Fish. Res. Bd. Can. 34: 19-30.

(91) Taylor, C.C., Bigelow, H.B., and Graham, H.W. 1957. Climate trends and the distribution of marine animals in New England. Fish. Bull. 57: 293-345.

(92) Templeman, W., and Fleming, A.M. 1953. Long term changes in the abundance of marine animals. Int. Comm. Northwest Atl. Fish. Annual Proc. 3: 78-86.

(93) Ulanowicz, R.E., Ali, M.L., Vivian, A., Heinle, D.R., Rickus, W.A., and Summers, J.K. 1982. Identifying climatic factors influencing commercial fish and shellfish landings in Maryland. Fish. Bull. USA. 80 (3): 611-619.

(94) Ursin, R. 1982. Stability and variability in the marine ecosystem. Dana 2: 51-67.

(95) Vlymen, W.M. 1977. A mathematical model of the relationship between larval anchovy (Engraulis mordax) growth, prey micro-distribution and larval behavior. Env. Biol. Fish. 2 (3): 211-233.

(96) Walford, L. 1946. Correlation between fluctuations in abundance of the Pacific sardine (Sardinops caerulea) and salinity of the sea water. J. Mar. Res. 6 (1): 48-53.

TABLE 1 - Components of Georges Bank energy budget. Based on Sissenwine et al. (86) Powers (71), Scott et al. (76), Cohen and Grosslein (16), average catch for 1968-1982. Range of values is for 1973-1975 (low) and 1964-1966 (high).

	Kcal/m²yr	
Production		
Phytoplankton (particulate)	3780	
Macrozooplankton	496	
Benthos	106	
Fish (exploitable)	13-17	
(pre-exploitable)	29-52	
(total)	42-69	(1.3-2.1% of Phytoplankton Production)
Potential Fish Prey	644-671	
Fish Consumption		
All Prey	197-344	(31-50% of Potential)
Of Fish	39-42	(73-61% of Their Own Production)
Consumption of Fish		
By Fish	39-42	
By Birds	2.0	
By Mammals	5.4	
By Large Pelagics	2.0	
By Humans	6.1	
Total	54.6-57.6	(130 and 83% of Fish Production, Respectively)

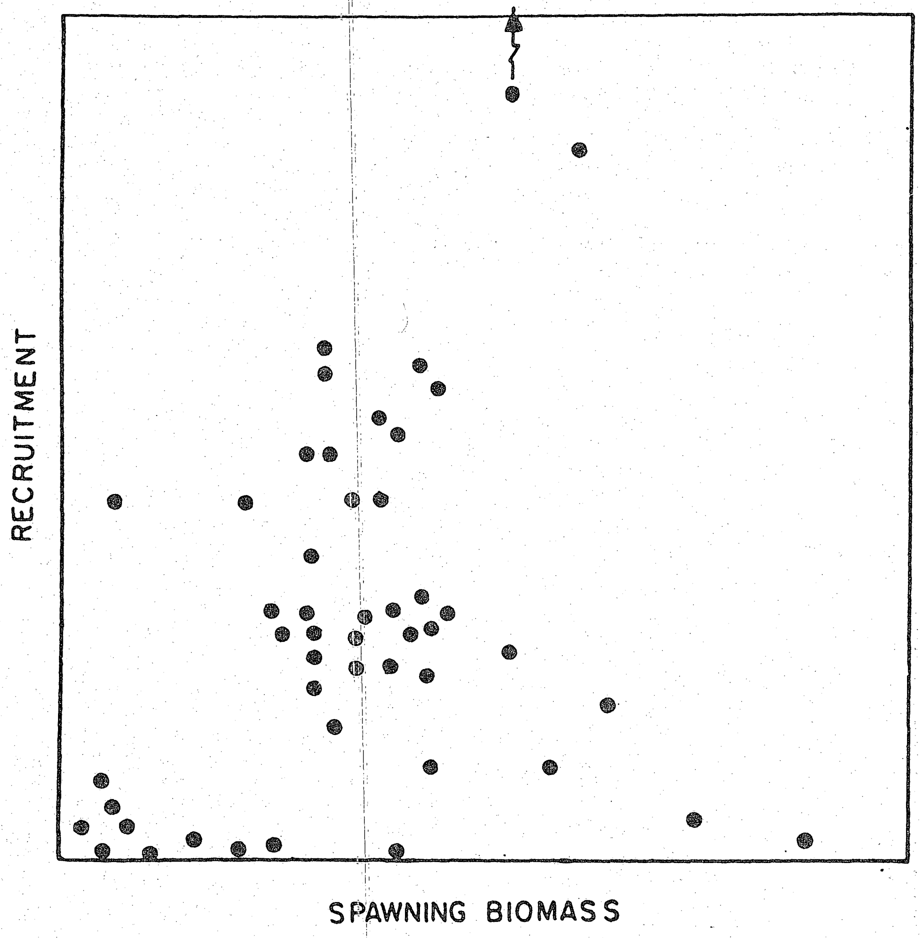

Figure 1. Stock-recruitment data for Georges Bank haddock (15).

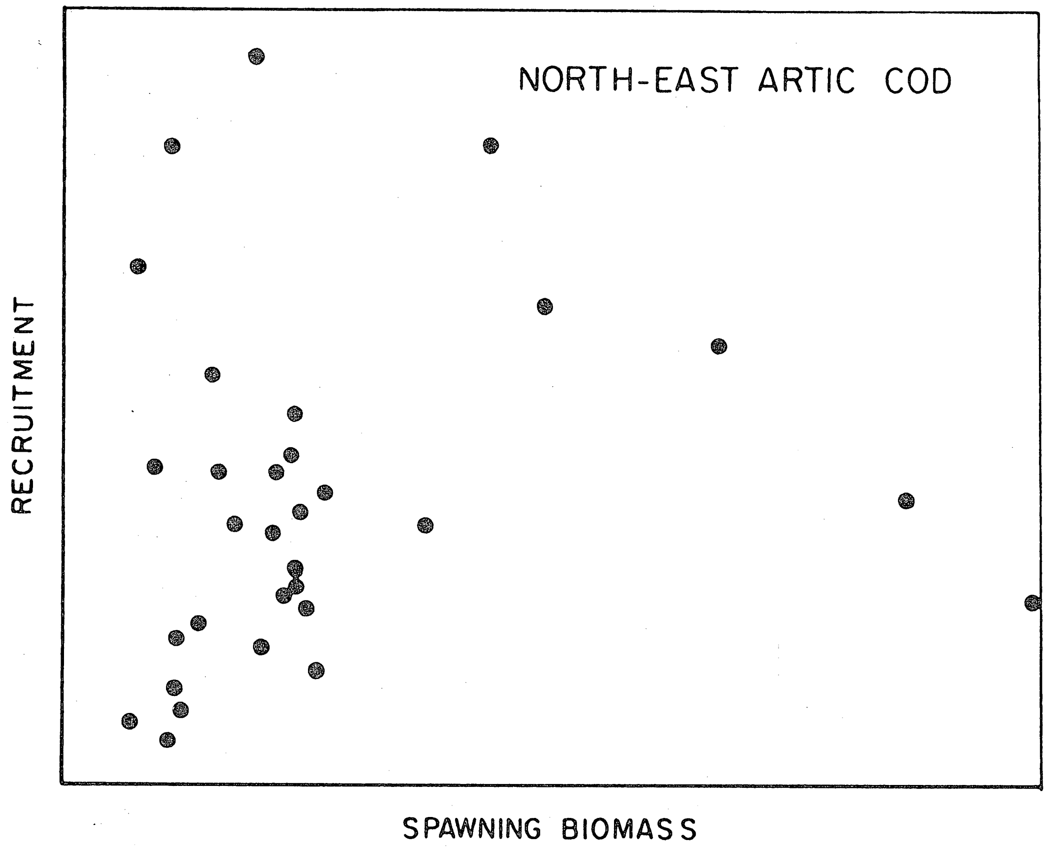

Figure 2. Stock-recruitment data for Northeast Arctic cod (44).

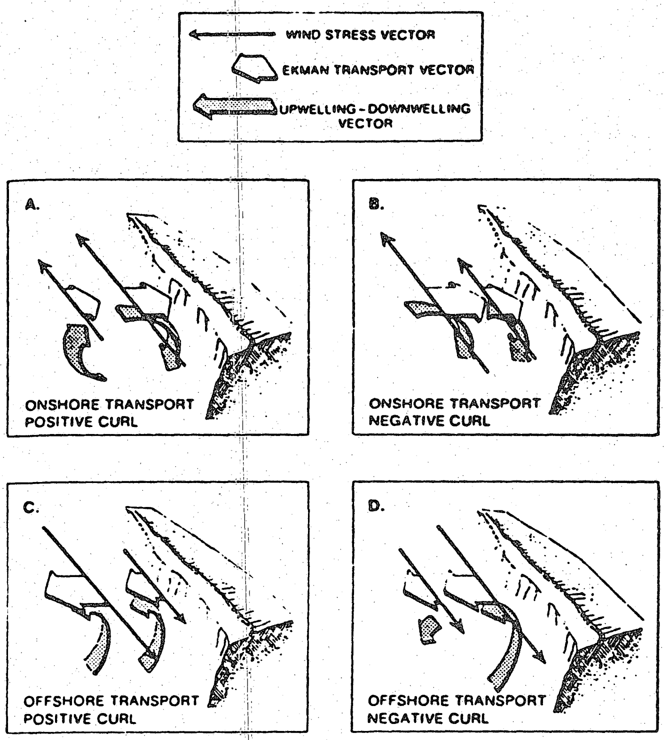

Figure 3. Types of couplings between surface convergence or divergence at the coast (due to the onshore-offshore component of Ekman transport) and that (due to wind stress curl) occurring offshore of the coastal boundary zone. A. Convergence and downwelling at the coast, divergence and upwelling offshore. B. Convergence and downwelling at the coast, continued convergence offshore. C. Divergence and upwelling at the coast, continued divergence offshore. D. Divergence and upwelling at the coast, convergence offshore. After Bakun and Nelson (3).

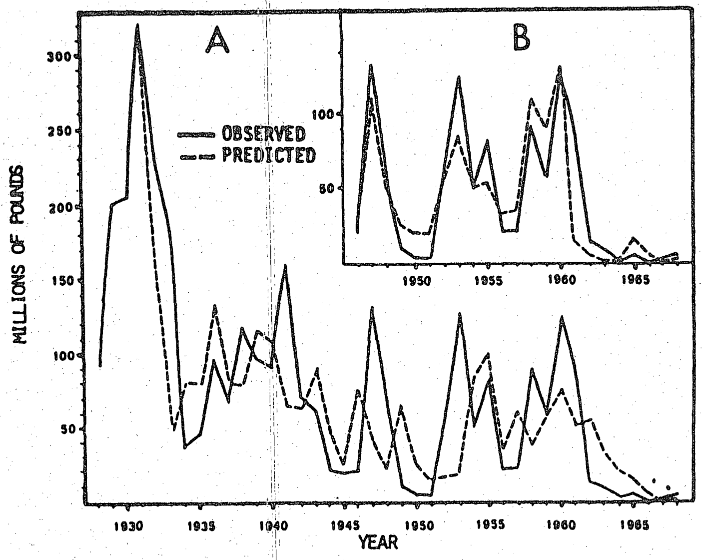

Figure 4. Observed and predicted recruitment for Pacific mackerel (69).

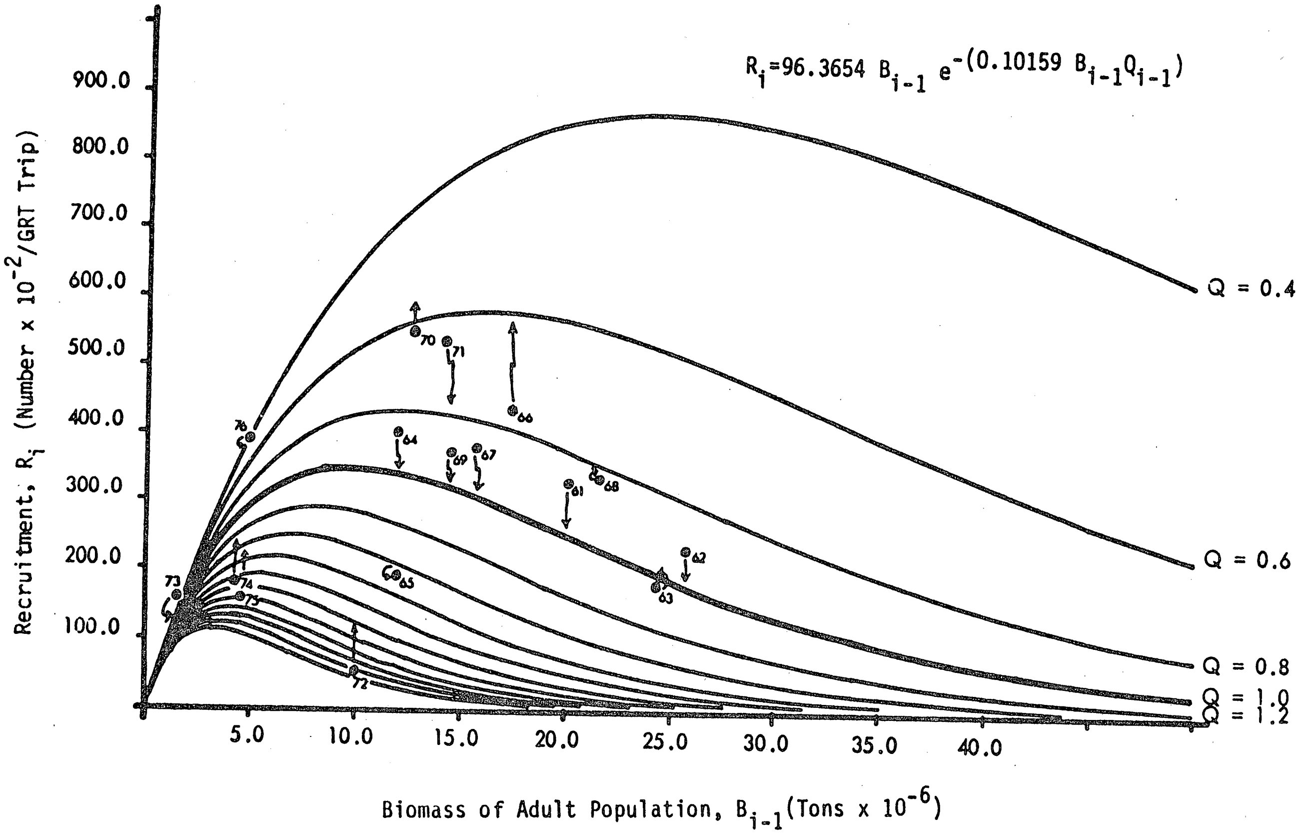

Figure 5. Family of recruitment functions for Peruvian anchovy depending on density of spawners (19).

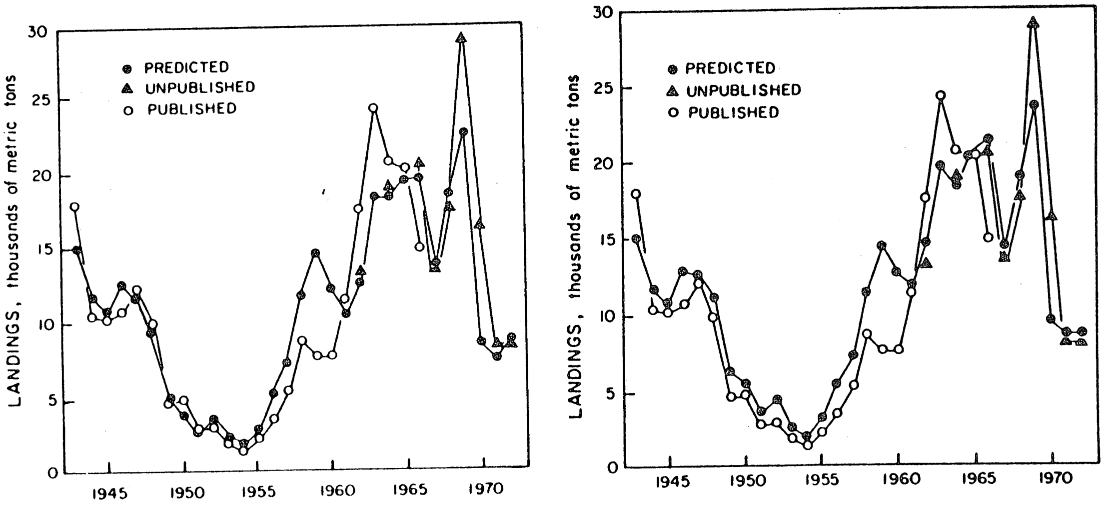

Figure 6-7. Simulation of Southern New England yellowtail flounder with recruitment independent (left) or linearly dependent (right) on spawning biomass (83).

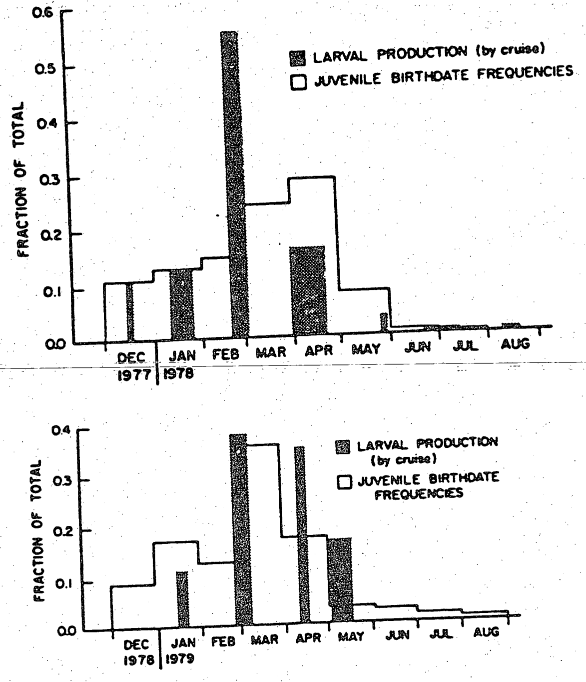

Figure 8. Birthdate frequencies of juvenile anchovies compared to the larval production. Hatched bars indicate each of seven cruises (after (65)). Top, December 1977-August 1978; Bottom, December 1978-August 1979.

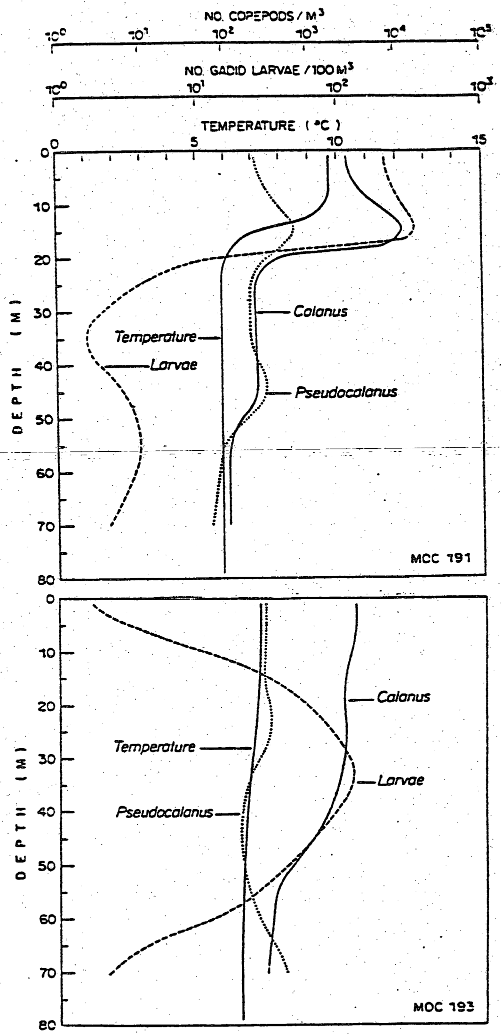

Figure 9-10. Vertical distribution for Georges Bank before (21 May 1981, top) and after (24 May 1981, bottom) storm (59).