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Review of Recruitment Variability in Exploited Marine

Fish Stocks and Survival During the Larval Stage

by

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Introduction

Recruitment variability in marine fish stocks has always been an issue of central importance in fishery science. Following the second world war fishing efforts of industrialized nations expanded causing a decline in the abundance of fish stocks throughout the Northwest Atlantic (Halliday and Pinhorn 1985). As fish stocks declined and conservation efforts intensified questions regarding recruitment variability and its causes gained prominence. In the early 1970's ICNAF (now NAFO) initiated two international studies to examine causes of recruitment variability in exploited fish stocks. On Georges Bank the study focused on the pelagic stock of Atlantic herring, and on Flemish Cap on demersal stocks of cod and redfish. Both studies have emphasized survival during the early life history stages.

Many research studies examining causes of recruitment variability have been carried out spanning several decades, yet few clear patterns have emerged. In the early 1980's planning for an International Recruitment Experiment Project (IREP) was initiated (Anon. 1982). However, following several years of discussions no clear course of action has emerged. A recent meeting of ICES Biological Oceanographic Committee concluded there was no adequate conceptual framework for pursuing the problem of studying recruitment (Sherman and Hansen MS1985). The purpose of this paper is to review and assess the existing hypotheses of recruitment variability in marine fish stocks. This review is followed by a closer examination of the growth-mortality hypothesis supported by observations from Flemish Cap.

Recruitment Theory in Fisheries

Recruitment variability in commercial fisheries is poorly understood. Measured fluctuations in recruitment, defined here as the age at which 50% or more of a year-class is mature, are large and few clear patterns have emerged from available time-series. The way in which recruitment depends on stock size is unresolved, yet compensatory stock-recruit relationships form the basis of current fisheries management. Recruitment is a continuous log-normal function in which the factors responsible for annual fluctuations occasionally combine to produce exceptionally large year-classes. The "recruitment problem" of fishery science (eg. Cushing 1982) concerns not so much annual variations in recruitment, but the occasional large year-class that typically recruits into a fishery every 4-11 years, or longer. These large recruitments sustain stock biomass for a number of years, depending on fishing effort, and may result from small stock sizes. Additionally, there is some belief these large year-classes can occur simultaneously in widely separated stocks (Templeman 1972, Koslow 1984). The question of recruitment, then, can be divided into two components: 1) what factors are responsible for annual fluctuations in recruitment, and 2) what factors are responsible for the less frequent very high levels of

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recruitment. The first question concerns itself with a clearer delineation of stock-recruit relationships. The second concerns itself with occasional large-scale effects that have a profound impact on fish stock size.

The concept of compensation is fundamental to the theory of fishery science. In a non-exploited state compensation ensures annual production (recruitment plus growth) approximately equals natural mortality, and fish density remains unchanged. In an exploited stock an increased (surplus) production occurs at stock densities below equilibrium biomass, due to compensatory responses. These responses are due to density dependent factors that increase production at lower densities, and may be a function of compensation by the mature fish (stock) and/or immature fish (pre-recruits). Stock responses at decreased densities might include: lower age of maturity, increased growth rate, increased fecundity, and decreased disease transmission. Pre-recruit responses might include: decreased intra-specific resource competition (food), increased growth rates, decreased predation, decreased cannibalism. These responses may compliment one another. In this way the stock response acts to increase production of fish eggs and the pre-recruit response acts to increase survival. These terms are synonymous with the growth and survival responses, respectively, of Walters et al. (1980) and similar to the concepts of stock-dependent and density-dependent processes as discussed by Harris (1975) and Ware (1980).

Empirical evidence in support of such responses are scattered and often circumstantial. Increases in growth rate of lake trout have been reported during population declines, together with a drop in female age at maturity (Walters et al. 1980). Changes in fecundity of marine fish with stock size is supported by Bagenal (1973), although precise data are lacking. Changes in fecundity with improved feeding conditions, which might reflect density-dependent processes, have been reported for a number of species (Ware 1980). Increased survival rates at lower stock densities are not well documented but it has been reported for North Sea plaice (Beverton 1962), Downs herring (Burd and Parnell 1973) and some examples exist for freshwater species (Backiel and LeCren 1967). Such observations support the concept of density-dependent responses in fish populations.

Due to the lack of a clear functional relationship between measured stock size and recruitment, a number of hypotheses have been proposed to explain recruitment variation that are independent of stock size. These density-independent hypotheses incorporate both biotic and abiotic factors. It should be made clear that these density-independent factors do not involve regulation of stock size. Regulation only occurs as a density-dependent feedback through the system. In this way mean stock size will increase or decrease independent of density-independent variation in recruitment about the mean.

Biotic factors affecting abundance might include: variations in food production and availability, variations in predation independent of stock density, inter-specific variations in resource competition (i.e. food). These factors, particularly food production, may be directly linked to physical conditions and may in fact be directly controlled by them. For example, in eastern boundary upwelling systems changes in wind conditions can result in different levels of primary production and subsequent food supply (Bakun and Parrish 1980) or, alternatively, can disrupt the concentration of food particles necessary for successful feeding (Lasker 1975).

Abiotic factors usually relate to the retention or dispersal of fish eggs and larvae into or out of oceanographic areas traditionally favourable for growth and survival. These include closed geographic areas such as bays or inland seas, individual fishing banks, inshore versus offshore areas, tidally mixed areas of continental shelves, and frontal regions. In each case the regions could vary in survivorship due to differences in food availability, physical characteristics such as temperature, and

conditions necessary for subsequent life history stages such as transition to a demersal or benthic mode of life. Abiotic factors are most important to the planktonic egg and early larval stages.

Existing Hypotheses

Survival in the marine environment is a complex process. Traditional approaches to studying causes of recruitment fluctuation in marine fishes are often based on the premise there is a single, clearly identifiable factor responsible for the annual production of marine fishes. These single-factor hypotheses have centered on studying survival during the first year of life, which is thought to determine year-class strength (Gulland 1965, Templeman 1972, Cushing 1974, Shepherd and Cushing 1981). The initial search for a unifying theory of causal mechanisms determining recruitment variability centered around the critical feeding period proposed by Hjort (1914). At the time this was considered the most promising theory that would explain recruitment variation in marine fishes (May 1974). Subsequently, a great deal of work was directed toward the demonstration of a critical period involving the transition from yolk sac to actively feeding larvae and successful feeding during the larval stage.

Inevitably other hypotheses relating to starvation of fish larvae have emerged, as well as hypotheses relating to predation and physical dispersal of fish eggs and larvae. Most studies have focussed on density-independent factors affecting recruitment, as a result of biological responses to physical processes. The major hypotheses can be considered under the headings: starvation (fish larvae), predation (pre-recruit stages), physical dispersal (eggs and larvae), cannibalism (pre-recruits), and disease (adults). A brief summary of hypotheses under these headings include:

STARVATION

Critical Period Hypothesis (Hjort 1914): The transition from the yolk sac stage to active first feeding is a critical period in the life history of fish, and the degree to which this successfully occurs each year will determine survival and eventual year-class strength. No specific reasons for why this would vary were specified.

Match-mismatch Hypothesis (Cushing 1975): Cushing observed that annual spawning time in fishes is constant, however, the onset of the annual primary production cycle is not constant but a result of changing physical conditions. Therefore, if the timing of the production cycle occurs too early or too late, then fish larvae will be variably 'matched' with the abundant food, resulting in varying levels of starvation and subsequently survival of the cohort.

This hypothesis is an elaboration of the critical period hypothesis that would explain why successful first feeding might vary annually. It is based on the premise that the variation in peak date of spawning for fish is low compared to the variability in timing of spring phytoplankton production. The theory was supported by the observation that cold winter temperatures delayed larval fish development which resulted in a better match with the food supply and the subsequent high survival of plaice during 1963. The controlling physical factors are proposed to be wind strength, wind direction, irradiance and heat, all of which affect the onset of spring production. This mechanism could act over very large scales, but it ignores many species whose spawning cycles do not coincide with the early spring production peak.

Food Limitation Hypothesis: The absolute magnitude of primary production varies annually, depending on certain physical conditions, such as temperature, wind mixing, retention zones, and vertical stratification. When production is

greater there is more available food for fish larvae, which increases survival as a result of less starvation. This is based, in part, on the critical period hypothesis but encompasses successful feeding conditions (i.e. non-starvation) throughout the pelagic larval stage. In this way it actually defines fish production as being resource limited on an annual basis in terms of its carrying capacity.

This hypothesis has not been clearly delineated and can be attributed to a number of authors describing conditions for different marine areas and different factors controlling production. Examples include eastern boundary currents where upwelling will increase production through increased nutrient supply (Bakun and Parrish 1980, Cushing 1982). On continental shelves circulation dependent on tidal currents may cause variation in the size of larval retention areas (Iles and Sinclair 1982). As these areas are ones of high productivity the size of the area relates directly to available food production and survival of fish larvae. Changes in annual freshwater runoff from the Canadian Arctic along the Labrador Coast has been related to lagged cod catches and, hence, recruitment variability (Sutcliffe et al. 1982). Mixing processes dependent on this runoff that would control production along this shelf were advanced as a possible controlling mechanism.

Vertical Stability Hypothesis (Lasker 1975): In the ambient environment average concentrations of planktonic food are too scarce to maintain fish larvae and must be concentrated at density discontinuity surfaces. If this stability structure is disrupted by mixing due to storms then food becomes too scarce and larvae starve. This can relate directly to the critical period hypothesis, but can also apply to successful feeding throughout the larval phase.

Resource Use Competition Hypothesis (Fraser 1970, van der Veer and Sadee 1984, Frank 1986): Annual variations in the abundance of gelatinous planktivore predators will significantly affect the amount of available food for ichthyoplankton. When competition is high survival of fish larvae will be low due to starvation. This can relate to the critical period hypothesis, but also to successful feeding conditions throughout the larval phase. Annual variations in ctenophores appear to be determined by overwintering conditions of ctenophores, primarily temperature.

Growth-Mortality Hypothesis (Ware 1975, Shepherd and Cushing 1980): Average growth rate of a fish species during the larval phase is directly related to predation survival. Therefore, conditions that determine growth rate during the larval phase, such as food availability and temperature, will ultimately determine survival.

PREDATION

Gelatinous Predator Hypothesis (Fraser 1970): Annual variations in the abundance of gelatinous zooplankton, particularly the ctenophore Pleurobrachia pileus, may significantly affect survival of fish larvae due to direct predation.

Fish Predator/Cannibalism Hypothesis (Oeistad 1985): Based on large enclosure experiments containing larvae with and without fish predators of the same and different species, it was hypothesized that fish predation and cannibalism was high enough to be a significant determinant of larval survival.

Juvenile Predation Hypothesis (Sissenwine 1985): Predation during the juvenile stage (i.e. post-larval to age of recruitment) is additive over several years and constitutes a significant proportion of total pre-recruit mortality. No specific mechanism was advanced to explain why predation would vary annually.

PHYSICAL TRANSPORT

Dispersal Hypothesis (Hjort 1914): Pelagic fish eggs and early larvae are part of the plankton and, therefore, subject to drift within prevailing currents. While fish are adapted to spawn in areas and times that will maximize their survival, annual variations in physical circulation patterns will result in variable survival.

Historically this mechanism has been given consideration in fishery studies but its occurrence has not been clearly demonstrated. It is assumed that eggs and larvae are passively carried within water masses and, therefore, this mechanism only applies to the passive drift stage of fish development. Recently, spawning patterns of pelagic fishes in the California Current have been classified as transport limited versus food limited, based on their spawning location in relation to major upwelling centres (Parrish et al. 1981).

DISEASE

Recently Sissenwine (1985) summarized possible effects of disease on variations in fish abundance. These can be summarized under two headings:

Transmission Hypothesis (Sindermann 1970): Transmission of contagious diseases within a population increases to critical levels at high population densities.

Temperature Hypothesis (Burreson 1981): Abnormally cold water temperatures become lethal due to physiological stress in fishes. This stress subsequently leads to disease outbreak.

Present Understanding

Recruitment studies have focussed on starvation hypotheses during the larval stage. Most have searched for density-independent biotic responses due to changing physical conditions that affect larval food supply and cause mortality due to starvation. Undoubtedly starvation occurs in the sea but the extent to which it occurs as a controlling mechanism of larval survival and subsequent recruitment has not been demonstrated. O'Connell (1980) measured 5-60% starvation in northern anchovy and overall classified 8% of the larvae as starving during what turned out to be a moderate year for recruitment. This was calculated as 3.6% of the total daily mortality rate, which is similar to the range of 3-23% estimated for Pacific herring in four cohorts over two years (McGurk 1985). This level of mortality due to starvation was not considered critical to the survival of these cohorts.

Under controlled laboratory conditions starvation of various larval species has been measured at 50-100 prey items per liter (O'Connell and Raymond 1970, Laurence 1974, 1977, Houde 1974, 1975). Such concentrations are well above those typically measured in the sea (Hunter 1981). This inconsistency has been attributed to the patchy distribution of prey and the averaging effect of integrated plankton sampling. In other words, standard sampling techniques do not adequately measure available prey concentrations. In addition, recent studies rearing larvae in large enclosures indicate that larvae can survive and grow at food concentrations ranging from 1-5 prey items per liter (Houde 1978, Oiestad 1985). Such observations bring into question the applicability of laboratory results of feeding and growth requirements to field conditions. While the indication is that starvation is not the sole controlling factor of larval survival the issue is still largely unresolved.

The extent to which larval survival is density-dependent is also unresolved. It has not been possible to correlate larval survival with recruitment for most fish species studied (Hunter 1976, Lough et al. 1986). This may be due to the high, and largely unknown, degree of sampling error for measures of both

larval survival and recruitment. Typically, measures of plankton abundance from replicate samples vary by factors of 3-5 (Anderson and Webster, 1986). Estimates from egg and larval surveys with this degree of variation are subsequently compared to recruitment that typically fluctuates by a factor of 2-8 for demersal stocks but can be much higher for pelagic stocks of herring and mackerel (Templeman 1982, Koslow 1984). In addition, these measures of recruitment are seldom made with estimates of sampling error, which will further obscure underlying relationships (Walters and Ludwig 1981).

In summary, there is little evidence to indicate: a) there is a critical period involving the transition from yolk sac to actively feeding larvae, b) that starvation is a significant determinant of larval survival, and c) that measured survival during the first year of life correlates with recruitment. This has led some to question the validity of past hypotheses pertaining to recruitment variability. Recently, attention has shifted to the role of predation as the significant determinant of survival leading to recruitment, and particularly during the post-larval to the pre-recruit period (eg. Sissenwine 1985).

Growth-Dependent Mortality

Perhaps it is not reasonable to search for a single, simple solution to the complex problem of recruitment, such as "larvae starve". As emphasized by Gulland (1965) simple correlates, once found, usually do not stand the test of time. A more rational approach would build upon existing ecological theory, and propose testable hypotheses. Seemingly overlooked by many researchers is the comprehensive growth and mortality theory. The concept that size-specific growth and mortality rates interact to determine survivorship in fish populations has long been a foundation of fisheries theory (Gulland 1965, Cushing and Harris 1973, Cushing 1974). These concepts were clearly summarized quantitatively by Ware (1975). In essence, the theory predicts survival of a cohort is directly related to the sum of individual growth rates during the pre-recruit stage. A similar derivation was summarized by Shepherd and Cushing (1980). These ideas have been further elaborated by Werner and Gilliam (1984) to incorporate ontogenetic habitat shifts based on a trade-off between growth and mortality. In their outline minimizing the mortality-to-growth ratio is a size-dependent function that determines habitat choice (shifts) as a fish grows and develops.

Ware (1975) hypothesized predation as the major cause of death and that predation mortality would be inversely related to growth rate. Qualitatively he linked growth rate to body size and food supply and survival rate to growth rate and abundance (density). Here the density-dependent response occurs due to food availability causing intra-specific competition affecting growth rate, which in turn affects body size. In this way one might expect an inverse relation between average body size and abundance during a given year, but such a relationship will be masked by density-independent variations in food supply (Ware 1975). Therefore, food availability is seen as the key factor determining survival and predation is primarily size dependent. Food availability may vary as a function of density-dependent and/or density-independent processes. Growth rate is the measure of this response in fish.

In summary, the growth-mortality hypothesis is important for several reasons:

1. It is based on bioenergetic principles of growth and ecological theory that can logically be extended to such concepts as maximum growth strategies and specific foraging strategies in fishes;
2. It treats successful feeding as a continuous function throughout the pre-recruit stage, and is not dependent on extreme conditions of starvation, which is only included as a special case;
3. It integrates the processes of feeding and predation in the same theory;

4. It predicts growth rate is directly related to survival, which is testable;
5. It can include density-independent processes affecting food supply.

This theory includes several qualitative predictions. Among them is that food supply, on average, is limiting to growth. Therefore, in the field growth rate is sub-maximum and any increase in food supply will increase growth rate. This would be expected to vary both spatially for any particular time, for different times during a cohort's growth and development, and among years for cohorts of a particular population. Conditions where food availability is greater would produce bigger larvae.

A second qualitative prediction is that survival increases through successive developmental stages. Therefore, survival is stage-dependent and there are one or more developmental stages during which recruitment is determined. In this way one would examine growth and survival through successive developmental stages of a particular species. These would include the first-feeding stage (prolarvae), the early planktonic larval stage, the later post-larval stage and eventually the juvenile stage(s).

The observation that patchiness, the heterogenous distribution of organisms, decreases with organism weight was recently extended into an hypothesis that patchiness may be linked to predation mortality (McGurk 1985). The rationale for this hypothesis is based on the underestimate of fish egg and larval mortality versus weight data, as published by Peterson and Wroblewski (1984), and the belief that predators aggregate on patches of fish eggs and larvae. Therefore, mechanisms that disperse eggs and larvae, such as spawning behaviour of adults and wind mixing of surface waters, will increase survival.

This hypothesis can be linked to the growth-mortality hypothesis. Increased larval patchiness results in greater density which should lead to decreased food availability and hence lower growth. The growth-mortality hypothesis predicts this would lead to increased predation as a result of more time spent at a smaller size and decreased larval condition. The patchiness-predation hypothesis advanced by McGurk (1985) extends this by predicting an increased aggregation of predators with increased larval patchiness. Whether or not increased patchiness results in food limitation or significant aggregation of predators is unknown at this time. Perhaps the most compelling aspect of this argument is that it introduces a spatial dimension to the concept of larval survival and focuses attention on examining relevant spatial scales. This has long been recognized as important, but only recently has attention shifted to examination of finer scales which may be the only viable approach to understanding survival in the sea (Rothschild and Rooth 1982).

Temperature Dependent Growth

A logical extension of the growth-mortality hypothesis would include temperature effects on growth. In a qualitative way the growth-mortality hypothesis includes both direct and indirect effects of temperature on successful feeding. One would predict that food and temperature conditions which maximized growth would also maximize survival. In numerous laboratory studies temperature has been shown to have a direct effect on metabolism and subsequently growth. When food (ration) is not limiting, growth rate in the young fish stages will increase with temperature to a maximum, above which growth rate will decrease (Ryland and Nichols 1967, Ryland et al. 1975, Williams and Caldwell 1978, Brett 1979, Boehlert 1981). As temperature increases standard metabolism, and hence maintenance ration, increases non-linearly (Brett 1979). Under natural conditions an increase in growth rate, as a result of temperature increases, will depend on the relative increase in the rate of food consumption versus digestion. When food is limiting, as may be the case in nature (Ware and Lambert 1985), growth rate will be less than maximum, may decrease and would be negative under conditions of starvation. As most species are found near their

optimum temperatures for maximum growth (reference) the direct effects of temperature on fish growth and survival may be important. Alternatively, temperature will affect the feeding and production rates of prey species, as well as fish predators. Therefore, one might also expect an interaction effect of temperature and food supply, or temperature and predation.

Predictions related to temperature effects, in the simplest case, might be that higher temperatures will increase growth rate and subsequent survival. This would assume that temperature, not food, is controlling growth. An alternative prediction might be that temperatures close to the average, long-term seasonal mean result in highest growth rates. In this way temperatures that are too low would reduce growth due to lower metabolic rates, and temperatures that are too high would also reduce growth if food demand exceeded supply.

Larval Redfish Growth and Survival on Flemish Cap

There is some indication that growth and mortality in larval redfish on Flemish Cap may be linked. Larval fish surveys were carried out on Flemish Cap from 1978-82. During these years abundances of larval redfish estimated each July, following a peak release in late April, indicated differences of two orders of magnitude, and greater (Anderson 1984). Catch per unit effort in the commercial redfish fishery during these years was relatively stable, ranging between 1.146-1.703 t/hr (Atkinson 1985), indicating the spawning stock was similar during these years.

Average mortality estimates for redfish larvae are only available in 1980 and 1981. Surveys in late May of each year indicated abundances were virtually identical. However, approximately two months later abundance in 1980 was almost an order of magnitude greater than 1981 (Anderson 1984). Average mortality estimated for this period during each year was 5.2%/d and 8.5%/d, respectively. Finally, in 1979 larval abundances surveyed during late April were near the maximum expected at this time of year, and similar to abundances measured, chronologically, eleven days later in May 1981. However, the July 1979 survey indicated the complete absence of these larvae in waters over Flemish Cap, indicating high mortality occurred during the spring and early summer 1979. Estimates of growth are also available from 1980 and 1981. Otolith analysis indicated average growth in 1980 was 0.156 mm/d, but in 1981 was significantly lower at 0.109 mm/d (Penney and Evans 1985).

In summary, observations on Flemish Cap during the spring and early summer demonstrated higher growth and survival occurred in 1980 than in 1981. Survival differences resulted from processes occurring in June and possibly July, during the period of highest growth (Penney and Evans 1985). The indication is that growth and survival may be directly related and that the critical period occurs during the time of peak growth rates.

The extent to which differences in growth are attributable to food availability is not known at this time. Temperatures measured during these years indicated monthly mean surface waters over Flemish Cap in 1980 were not significantly different than the long-term mean (Anderson 1984). However, in 1981 water temperatures during May and June were significantly warmer than the long-term mean (Ibid.). Therefore, warmer water temperatures are correlated with lower growth and survival. Significantly warm water temperatures in 1979 can also be compared to very low survival observed during that year, although no comparisons of growth rate are available.

Summary

Considerable research effort over the past two decades has not been successful in identifying clear causal mechanisms of recruitment in marine fish stocks. Studies matching food levels and year-class strength continue to provide indirect evidence that growth during the first year of life is dependent on food

supply. Starvation, however, does not appear to be a main causal mechanism controlling survival of fish larvae. It is argued here that food limited growth interacting with predation provides a realistic theoretical basis for future work. Studies examining the effects of food limitation on growth should be integrated across several developmental stages, ideally throughout the pre-recruit stage, and should incorporate temperature effects on growth. In addition, the spatial distribution of these organisms is important, both regarding the feeding success of larvae on their prey and also as this may affect the aggregation of predators on fish larvae. As such, this approach argues for studies at much finer sampling scales than have previously been carried out.

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