A Review of Size Dependent Survival During Pre-Recruit Stages of Fishes in Relation to Recruitment

John T. Anderson
Department of Fisheries and Oceans, Science Branch
Northwest Atlantic Fisheries Centre, P. O. Box 5667
St. John's, Newfoundland, Canada A1C 5X1

Abstract

The theory of recruitment in fishes and hypotheses pertaining to causes of recruitment fluctuation are summarized. In spite of considerable research effort over several decades there has been no significant improvement in identifying clear causal mechanisms of recruitment in marine fish stocks. Starvation has not been demonstrated to be a primary mechanism controlling survival of fish larvae. 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 and may be important in determining survival. The hypothesis that survival is a direct function of growth provides a rational theoretical framework for recruitment research and is suggested as a basis for future work. Growth rate must be studied as a function of both ration and temperature. Studies examining the relationship of growth rate to survival should be specific to each life history stage and ideally integrated throughout the pre-recruit period. It remains to be demonstrated that survival is a direct function of growth, mediated through size-dependent predation.

Introduction

Recruitment variability in marine fish stocks has been an important issue in fishery science for many years. 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 the International Commission for Northwest Atlantic Fisheries (now the Northwest Atlantic Fisheries Organization) initiated two studies to examine this problem. On Georges Bank the study focused on a pelagic stock of Atlantic herring and on Flemish Cap, demersal stocks of cod and redfish. Both studies have emphasized survival during the early life history stages, and in particular, understanding causal mechanisms affecting this survival and subsequent recruitment.

Results from the Georges Bank study over 8 years, 1971–78, failed to relate survival during the first year of life to subsequent recruitment (Lough et al., 1985). Associated with a decrease in daily mortality estimates during 3 years, 1974–76, was a shift in diet and an increase in the incidence of feeding larvae (Cohen and Lough, 1983). In addition, the mean length of larvae surviving the winter period increased each year, indicating either increased larval growth or differential survival of larger larvae. On Flemish Cap the abundance of redfish larvae measured over 5 years, 1978–82, were highly variable (Anderson, 1984). Estimates of average daily mortality increased from 5.2%/d in 1980 to 8.5%/d in 1981 and growth based on otolith analysis decreased significantly during these two years (Penney and Evans, 1985). Results from Georges Bank related increased feeding with higher survival and possibly growth, whereas results from Flemish Cap have related increased growth with higher survival.

In general, few clear patterns have emerged from the many studies examining causes of recruitment variability in marine fishes. Previously the emphasis has been on studying starvation during the first year of life, particularly in first-feeding larvae. However, starvation does not appear to be the sole determinant of survival. Recent reviews point to the significance of feeding and predation processes at finer scales during early life history stages (Leggett, 1986) and predation on juvenile stages (Sissenwine, 1984). Both reviews ignore the hypothesis that links growth directly to survival (Ware, 1975; Shepherd and Cushing, 1980), and fail to outline specific tests. Overall, there is no adequate conceptual framework for pursuing the problem of studying recruitment.

This paper summarizes existing hypotheses and evaluates their adequacy in the context of research on recruitment. The paper is divided into three sections. The first reviews the theory of recruitment in marine fishes followed by a summary of existing hypotheses relating to survival of pre-recruits and a brief evaluation of our present understanding. In the final section the

hypothesis that survival is directly related to growth is reviewed and re-stated to include the effects of temperature on growth and to emphasize feeding strategies in larval fishes. It is suggested this hypothesis forms a rational framework for future studies.

Recruitment Theory in Fisheries

Recruitment variability of commercial fisheries is poorly understood. Observed fluctuations in recruitment, defined here as the age at which 50% or more of a year-class 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 can be described as 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 (e.g. Cushing, 1982) concerns not so much annual variations in recruitment, but the occasional large year-class that typically occurs every 4–11 years, or longer. These large recruitments can sustain stocks for a number of years, depending on fishing effort, and may be produced by small stock sizes. Additionally, there is some evidence that these large year-classes occur simultaneously in widely separated stocks (Templeman, 1972; Koslow, 1984; Koslow et al., 1987). Therefore, the question of recruitment can be divided into two components: (1) factors responsible for annual fluctuations in recruitment, and (2) factors responsible for the less frequent very high levels of recruitment. The first is concerned with a clearer delineation of stock-recruit relationships and the interaction of density dependent processes with the environment. The second is concerned with occasional large-scale effects that have a profound impact on fish stocks and may be mediated by low-frequency events at global scales (e.g. Steele and Henderson, 1984).

The concept of compensation is fundamental to the theory of fishery science. In a non-exploited state, compensation ensures that annual production (recruitment plus growth) approximately equals natural mortality and stocks remain stable. 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). For the adult stock these responses may 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 and 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 of such responses are scattered and often circumstantial. Increases in growth rate of lake trout have been reported during periods of population decline, together with a reduced female age at maturity (Walters et al., 1980). Parrish and MacCall (1978) reported a reduction in the age of maturity of Pacific sardine from 2–3 years to 1 year at low stock densities. 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 have been reported for North Sea plaice (Beverton, 1962), Downs herring (Burd and Parnell, 1973) and some freshwater species (Backiel and LeCren, 1967). Such observations support the concept of density dependent responses in fish populations. However, Parrish et al. (1981) concluded that density dependent responses of fish stocks in the California Current are of a minor nature and are not responsible for observed fluctuations in recruitment.

Several hypotheses have been proposed to explain the apparent lack of a functional relationship between stock and recruitment. These density independent hypotheses incorporate both biotic and abiotic factors and do not involve natural regulation of stock size through feedback mechanisms. This only occurs due to density dependent responses.

Biotic factors which may effect abundance include: variations in food production, predation independent of stock density and inter-specific resource competition. These factors, particularly food production and availability, may be linked to physical conditions and be directly controlled by them. For example, in eastern boundary current systems changes in wind-driven Ekman transport can result in upwelling, nutrient renewal enhancing primary production and subsequently food supply (Bakun and Nelson, 1977; Bakun and Parrish, 1980). Alternatively, vertical mixing of the upper water column due to storms can disrupt the concentration of food particles necessary for successful feeding (Lasker, 1975).

Other abiotic factors relate to the retention or transport of fish eggs and larvae in areas considered to be favourable for growth and survival. These include

closed areas such as bays or inland seas, areas associated with retention such as anticyclonic gyres or other regions of convergent circulation, inshore *versus* offshore areas, tidally mixed areas of continental shelves, and frontal regions. In each case it is the successful transport of larvae to, or retention in, areas suitable for growth and survival to successive developmental stages that is deemed to be the controlling factor. Abiotic factors are most important in 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 that 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 (Hjort, 1914; Gulland, 1965; Templeman, 1972; Cushing, 1974; Shepherd and Cushing, 1974; Shepherd and Cushing, 1980). 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 (May, 1974). Subsequently, much effort 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 the starvation of fish larvae have emerged, as well as hypotheses relating to predation and physical dispersal of fish eggs, larvae and juveniles. Most studies have focused on density independent factors effecting recruitment, involving biological responses to physical processes. The major hypotheses can be considered under the headings: starvation (fish larvae); predation, which includes cannibalism (all pre-recruit stages); physical dispersal (eggs and larvae) 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 of success determines survival and eventual year-class strength. Hjort hypothesized that the timing of fish spawning relative to annual plant production could account for large differences in observed mortalities.

Match-mismatch hypothesis (Cushing, 1975). Cushing stated that while annual spawning time in fishes is constant the onset of the annual primary pro-

duction cycle is not constant but a result of changing physical conditions associated with Sverdrup's critical depth. 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 subsequent survival of the cohort. 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 hypothesis was the first to propose a mechanism that would explain why successful first-feeding might vary annually.

Food production 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 food available for fish larvae, which increases survival as a result of less starvation. Therefore, survival is resource limited on an annual basis due to changing carrying capacity.

This hypothesis has not been clearly delineated but can be attributed to a number of authors describing conditions for different marine areas and various factors controlling production. Examples include eastern boundary currents, where upwelling increases production through increased nutrient supply (Parrish and MacCall, 1978; 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 total size of the area relates directly to available food production and, therefore, survival of fish larvae. Changes in annual freshwater runoff from the Canadian Arctic along the Labrador Coast have been related to lagged cod catches and, hence, recruitment variability (Sutcliffe *et al.*, 1983). It was hypothesized that nutrient supply to surface waters would be dependent on vertical mixing as a function of the annual runoff. Such a variation in nutrient supply would ultimately control fish production.

Vertical stability hypothesis (Lasker, 1975; 1978). Ambient concentrations of planktonic food are too low, on average, to sustain first-feeding fish larvae and must be concentrated, particularly at the pycnocline. If this structure is disrupted by vertical mixing due to storms or wind-driven upwelling, then food of the correct size is dispersed, or possibly the food type becomes inappropriate, and larvae starve.

This relates directly to the critical period hypothesis, but can also apply to successful feeding throughout the larval phase.

Resource use competition hypothesis (Fraser, 1970; Veer and Sadee, 1984; Frank, 1986). Annual variations in the abundance of gelatinous planktivore predators will significantly affect the amount of food available 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.

Growth-mortality hypothesis (Ware, 1975; Shepherd and Cushing, 1980). Predation decreases with increasing size, therefore, survival during the larval phase is directly related to growth. Conditions that determine growth rate during the larval phase, such as food availability, will ultimately determine survival.

This hypothesis is not limited to starvation, which occurs as a special case and, in addition, includes factors effecting predation.

Predation

Gelatinous predator hypothesis (Fraser, 1970). Annual variations in the abundance of gelatinous zooplankton, particularly the ctenophore *Pleurobrachia pileus*, may significantly effect survival of fish larvae by direct predation.

Fish predator/cannibalism hypothesis (Oiestad, 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 were high enough to be a significant determinant of larval survival.

Juvenile predation hypothesis (Sissenwine, 1984). Predation during the juvenile stage (i.e. post-larval to age of recruitment) accumulates over several years and constitutes a significant proportion of total pre-recruit mortality. No specific mechanism was advanced to explain why predation should vary annually.

Physical dispersal

Transport-retention hypothesis (Hjort, 1914; Parrish et al., 1981; and others). Pelagic fish eggs and early larvae are part of the plankton and drift within prevailing currents. While fish are adapted to spawn in areas and at times that will maximize their survival, annual variations in physical circulation patterns will result in variable survival due to physical processes effecting larval retention in, or downstream transport to, suitable growth areas.

Disease

Sissenwine (1984) reviewed 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 could subsequently lead to disease outbreak.

Present Understanding

Starvation

Many studies of recruitment have focused on starvation hypotheses during the larval stage. Most have searched for density independent biotic responses to changing physical conditions that effect larval food supply and cause mortality due to starvation. Undoubtedly starvation occurs in the sea but the extent to which it acts as a controlling mechanism of larval survival and subsequent recruitment is uncertain. O'Connell (1980) classified 8% of larvae sampled 1 year as starving, during what turned out to be a moderate year for recruitment. McGurk (1985) estimated starvation mortality of 3–23%/d for recently hatched Pacific herring in four cohorts sampled over 2 years. This level of mortality due to starvation was not considered critical to the survival of these cohorts. However, recent estimates for Northern anchovy and jack mackerel off California indicate that starvation mortality of first-feeding larvae was high in offshore waters being 70%/d up to 100%/d (Hewitt et al., 1985; Theilacker, 1986). These mortality estimates were not related to subsequent estimates of recruitment, but the high estimates of daily mortality during first-feeding were considered to be important to the ultimate success of the year-class. In general, however, studies have not conclusively linked starvation and year-class size.

An important observation pointing to starvation as a significant source of mortality is the disparity between laboratory estimates of minimum prey densities necessary for larval survival compared with concentrations measured in the field. It is argued that ambient food concentrations, on average, are too low to support larval growth and survival. Typical estimates of food concentrations to ensure 10–20% survival range from 100 to 1,000 nauplii/l for first-feeding larvae, and higher (O'Connell and Raymond, 1970; Hunter, 1972; Saksena and Houde, 1972; Wyatt, 1972; Laurence, 1974, 1977; Houde, 1978) although some species, such as sea bream (*Archosargus rhomboidalis*), can survive at concentrations of 50 nauplii/l (Houde, 1978; Houde and Schekter, 1981). Copepod nauplii, a major food source, measured in 5 field studies ranged from 13 to 36 nauplii/l (Hunter, 1981). Concentrations in coastal and estuarine areas tend to be higher, in the order of 50–100

nauplii/l, but are still well below laboratory estimates deemed necessary for survival (Houde, 1978).

This inconsistency may be due to the patchy distribution of prey and the averaging effect of plankton net tows. Therefore, standard sampling techniques underestimate locally available prey concentrations. However, Owen (1981) reported concentrations from 15 to 58 nauplii/l for replicate samples taken off California at 0.2 m sample spacing. Similarly, using a pumped sampler in Long Island Sound, Monteleone and Peterson (1986) measured concentrations at specific depths during peak abundances in March of 124 nauplii/l. Such observations indicate copepod nauplii concentrations may not exceed 100–200 nauplii/l.

A second reason for the discrepancy between laboratory and field results may be that laboratory estimates of larval feeding are not realistic. For example, based on observed growth of 10 mm sandlance larvae (*Ammodytes* sp.), and assuming 30% gross growth efficiency, daily ration was estimated to be 60–70 μg/d (Monteleone and Peterson, 1986). This growth rate was estimated for larvae within ambient concentrations of 100 nauplii/l. However, laboratory estimates of sandlance feeding rates at this prey concentration underestimated the required daily ration by 80%. In addition, cod larvae (*Gadus morhua*) reared in large enclosures had 10–20% survival from hatching through to metamorphosis at low prey concentrations ranging from 1–8 up to 110 nauplii/l (Oiestad, 1985). Such observations question the direct application of laboratory data to field conditions and indicate laboratory estimates of feeding rates often may be too low.

Predation

Predation is undoubtedly an important source of mortality in fishes but its role in regulating year-class strength is not known (Hunter, 1984; Bailey and Houde, 1988). Due to the relative scarcity of fish larvae in the plankton, their importance as food to predators such as ctenophores (Veer and Sadee, 1984) or planktivorous fish (Pepin et al., 1987) may be negligible. Consequently, the predation on fish eggs and larvae might be considered to vary as a function of the density of invertebrate plankton species, independent of larval density (Pepin, 1987). However, given that fishes are ultimately the most important predators of fish larvae (Pepin, 1987; Bailey and Houde, 1988), and planktivorous fishes may positively select fish larvae as prey, particularly as they grow (Pepin et al., 1987), then to assume density independent predation may be unreasonable.

It has been postulated that predation may be most important during post-larval stages acting through cumulative mortality during this longer period (Sissenwine, 1984). Density dependent growth during the pre-recruit period has been reported for a number of fish stocks (examples cited in Ware, 1980; Zijlstra et al.,

1982; Peterman and Bradford, 1987). For populations at high densities, experiencing slow growth, predation should act in a compensatory way to reduce population abundance. However, it is not clear how low levels of predation during the pre-recruit period would explain the occasional occurrence of very large year-classes. Such a mechanism would argue for a significant reduction in predation on young fish during one or more of the post-larval, pre-recruit stages.

Only during the larval stage has a possible mechanism been proposed whereby predation could be significantly reduced. This would occur if alternate prey densities increased, thereby reducing predation mortality on larval fish (Pepin, 1987). However, such a mechanism implies a general increase in the zooplankton community that has no direct effect on larval fish feeding, growth and survival, which seems unlikely.

Predation rates on fish larvae are difficult to measure in the field due to a wide variety of potential predators, the rapid digestion of fish larvae by predators and sampling difficulties relating to the patchy distribution of predators. Previously, predation mortality has been estimated indirectly, either as the difference between total mortality and starvation mortality (Hewitt et al., 1985; Theilacker, 1986) or based on laboratory estimates of growth and condition while starving (O'Connell, 1980; Leak and Houde, 1987). It has been, and no doubt will be, difficult to study the specific role of predation as a regulator of year-class size in fish.

Summary

The issue of what factors control fish survival prior to recruitment remains largely unresolved. Attempts to correlate larval survival with recruitment indices for many fish species have been unsuccessful (e.g. Hunter, 1976; Crecco and Savoy, 1984; Lough et al., 1985). The role of physical advection of fish eggs and larvae from, or retention within, areas favourable to survival remains largely speculative. Recently, Myers and Drinkwater, (MS 1987) related Gulf Stream ring activity to recruitment in Northwest Atlantic groundfish stocks. However, it was not possible to conclude from this study that lower recruitment was a direct result of physical transport of fish eggs and larvae off the shelf. Lower recruitment may have been due to other mechanisms. In summary, there is little convincing evidence for rejection of any hypotheses pertaining to recruitment in marine fishes.

Growth and Mortality

Size dependent mortality

It may be unreasonable to search for singular solutions to the complex problem of recruitment, such as "larvae starve". As noted by Gulland (1965) simple correlates usually do not stand the test of time. A more

rational approach would be to build upon existing eco-
logical theory, and propose testable hypotheses. The
concept that size-specific growth and mortality rates
interact to determine survivorship in fish populations
has long been a foundation of fisheries theory (Gul-
land, 1965; Cushing and Harris, 1973; Cushing, 1974).
This concept was clearly summarized by Ware (1975)
and a similar derivation was presented by Shepherd
and Cushing (1980). Simply stated, the theory predicts
that survival of a cohort is directly related to growth
rates during the pre-recruit period. These ideas have
been further elaborated by Werner and Gilliam (1984)
to incorporate size dependent shifts in habitat based on
a trade-off between growth and mortality. In their out-
line, minimizing the mortality-to-growth ratio is a size
dependent function which determines habitat choice
as a fish grows through successive life history stages.
They conclude that growth is a sensitive index of avail-
able resources and is probably the parameter through
which intra- and inter-specific competition is
expressed.

Ware (1975) hypothesized predation would be the
major cause of death and that mortality due to preda-
tion would be inversely related to growth rate for differ-
ent species, within their respective ranges of growth
and mortality. Qualitatively he linked growth rate to
body size and food supply, and survival rate to growth
rate and abundance (density). Here a density depend-
ent response would occur due to changes in food avail-
ability, causing intra-specific competition effecting
growth rate, which in turn effects body size. Implied in
this hypothesis is that growth, on average, is sub-
maximum and those feeding conditions that maximize
growth will minimize mortality. In addition, feeding
conditions may change significantly due to density
independent factors that will have a direct effect on
growth.

In general, mortality rates decrease with size for
marine organisms (Peterson and Wroblewski, 1984)
and this is thought to be true for fish as they grow and
enter successive life history stages. Decline in mortality
as fish grow has been reported for a number of marine
fish species (Zijlstra et al., 1982; Hewitt et al., 1985;
Folkvord and Hunter, 1986; Veer, 1986). Decreasing
mortality with increasing size is based on the premise
that developing fish pass through various predatory
fields and, as they do so, both the number of potential
predators declines and the mortality rate decreases for
any particular predator. The phenomenon of the preda-
tory field has been clearly demonstrated for Northern
anchovy by Folkvord and Hunter (1986). They demon-
strated that the percentage of larvae escaping attack by
various predators increased with increasing larval size,
and the escape response was species specific, with
escape from some predators quickly increasing to
100% as larvae grew. In addition, they observed that
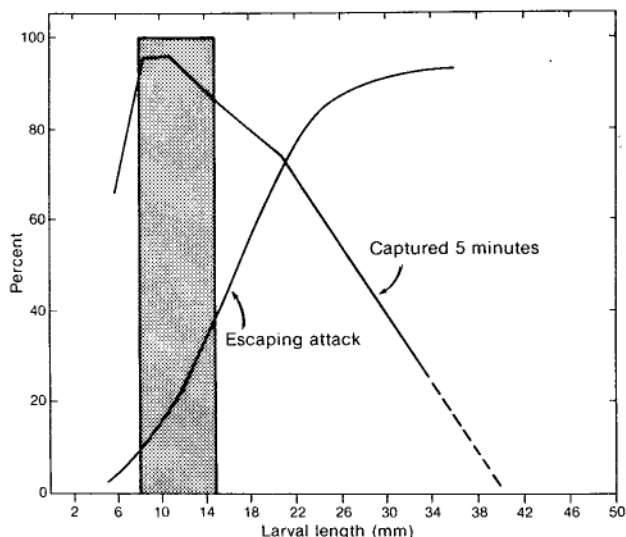vulnerability of larval anchovy to predation by adult

Fig. 1.   Mean percentage of northern anchovy larvae escaping attack
and percentage eaten in 5 minutes by adult northern anchovy,
as a function of larval length. Shaded area represents the
length range of highest predation rate. (Adapted from Folk-
vord and Hunter, 1986.)

Northern anchovy was highest for larvae 8.5–15 mm in
length, attributed to larvae of this length being more
visible to the adults but still having a low escape
response (Fig. 1). Thus, larval anchovy move through a
definite size window where their vulnerability to canni-
balism is highest. Pepin et al. (1987) have demonstrated
this is generally true for vertebrate and invertebrate
predators.

The hypothesis that survival is directly related to
growth includes several qualitative predictions. Among
them is that food availability, 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. Differential food availability can occur
between areas at any particular time or at different
times during a cohort's growth and development,
resulting in different growth rates and subsequent
survival.

The prediction of food limited growth is supported
by empirical observations. Laboratory studies repeat-
edly show that increasing food concentrations result in
higher growth and increases in survival from 10 to 80%.
Only at very high food concentrations, >500–1000 nau-
plii/l, does survival level off due to a saturation of feed-
ing rates (Wyatt, 1972; Laurence, 1974, 1977; Houde,
1978; Houde and Schekter, 1980). An enclosure study
demonstrated higher growth and survival of capelin
larvae when in association with surface waters contain-
ing abundant food in the 0.040–0.051 mm size range,
versus subsurface waters with inadequate food (Frank
and Leggett, 1986). In the field, increased incidence of
feeding has also been related to higher growth and
better condition of fish larvae (Shelbourne, 1957;

Gadomski and Boehlert, 1984; Crecco and Savoy, 1984; Ware and Lambert, 1985; Buckley and Lough, 1987). As detailed feeding studies were not carried out simultaneously, the direct impact of food on growth and survival is less clear. However, Buckley and Lough (1987) did observe higher prey abundance at their two stations which had higher growth and condition. Changes in food types among years for fish larvae has been observed (Wyatt, 1974; Gadomski and Boehlert, 1984; Peterson and Ausubel, 1984) but the impact on growth and survival has not been demonstrated.

Survival, while increasing through successive life history stages, will be dependent on conditions specific to each stage. This recognizes that factors effecting growth and survival change as fish grow, and these changes are most dramatic with a change from one life history stage to the next. An obvious change, for instance, is at metamorphosis from the larval to juvenile stage. This is associated with the formation of bony parts and can, as with flatfish, involve dramatic changes in body shape and habitat. The degree to which survival is stage dependent has been demonstrated for North Sea plaice where daily mortality rate decreased from 0.068 to less than 0.01 from the egg stage to post-settled fish during the first year of life (Fig. 2, Zijlstra et al., 1982). When the transition to the next stage is size dependent, rapid growth will increase survival. Therefore, it is important to study growth and survival specific to each life history stage, for it will be during one or more of these stages that year-class size is determined. These stages would possibly include: the egg, the yolk-sac larvae (prolarvae), the first-feeding larvae, the later planktonic larvae (postlarvae), the first juvenile stage immediately following metamorphosis and one or more later juvenile stages.

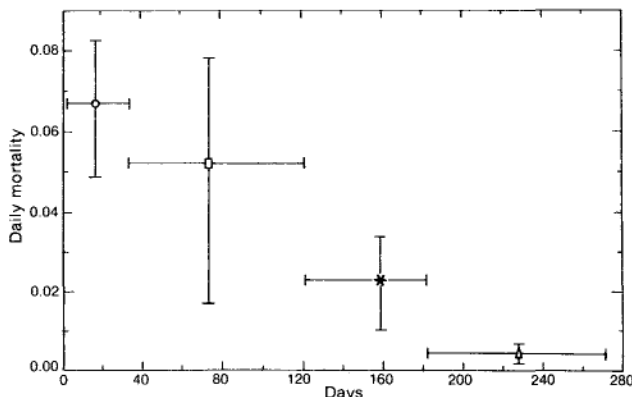As fish larvae grow and develop their diet changes to accommodate changing metabolic demands and presumably changing habitats. This concept has recently been reviewed by Werner and Gilliam (1984). In general, they select an ever wider range of prey organisms (Checkley, 1982; Gadomski and Boehlert, 1984; Ware and Lambert, 1985) and also may select food organisms on the basis of nutrition (Houde, 1978; Checkley, 1982). One might also expect a dietary shift at meatamorphosis, but this has received little attention. Unfortunately, most studies on fish feeding have been restricted to the examination of stomach contents and have not related diet to food availability. However, recently attention has shifted to an examination of prey selection, but these studies have been restricted in both time and space (Kane, 1984; Peterson and Ausubel, 1984; Monteleone and Peterson, 1986). Only Cohen and Lough (1983), studying herring larvae, have examined food and feeding over more appropriate time and space scales. Their results indicated that increased incidence of feeding over 3 years was related to increased survival and possibly growth. However, their limited sampling for larval prey prevented any conclusions regarding the effect of food supply on survival.

In summary, the growth-mortality hypothesis provides a reasonable framework upon which to base future research studies. In this regard it is important for several reasons:

1. It is based on bioenergetic principles of growth and ecological theory that include such things as strategies to maximize somatic growth (as immature fish) and predictions of optimal foraging theory;

2. It treats successful feeding as a continuous function throughout the pre-recruit period and is not dependent on the extreme condition of starvation, which is 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 includes density independent processes effecting changes in food supply, in addition to density dependent effects.

Temperature dependent growth

A logical extension of the growth-mortality hypothesis for poikliotherms 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 limited,

Fig. 2. Mean and range of daily mortality rate of eggs (o), larvae (▢), settling juveniles (✳) and post-settled juveniles (Δ) of North Sea plaice in relation to approximate day of peak abundance and duration of each life history stage. (Adapted from Zijlstra et al., 1982.)
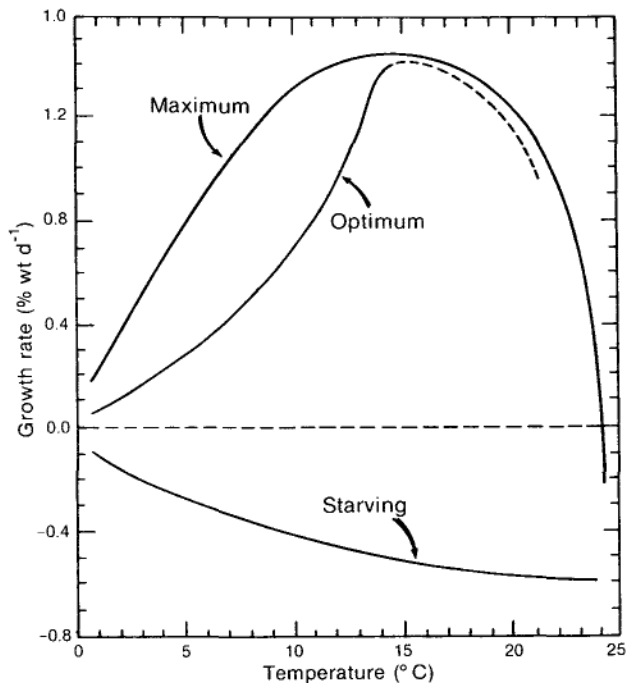
Fig. 3.   Relationship of expected growth rate for salmon fry as a
function of temperature for maximum, optimum and starving
rations. Growth rate for optimum ration is hypothesized
based on the escalating maintenance cost with increasing
temperature. The dashed line at zero growth represents
maintenance ration. (Taken from Brett, 1979.)

growth rate in the young fish stages will increase with
temperature to a maximum, above which growth rate
will decrease (Fig. 3) (Ryland and Nichols, 1967;
Ryland et al., 1975; Williams and Caldwell, 1978; Brett,
1979; Boehlert, 1981). Higher temperatures increase
standard metabolism nonlinearly and, therefore, will
similarly increase maintenance ration (Brett, 1979).
Under natural conditions as temperature increases, a
corresponding increase in growth rate will depend on a
sufficient food supply. This results from the relative
increase in the rate of food consumption versus diges-
tion. If food is limited to growth, as may be the case in
nature (e.g. Ware and Lambert, 1985), growth rate will
be sub-maximum. If temperature then increases with
no increase in food supply then growth rate will
decrease, seemingly independent of food, and would
be negative under conditions of starvation. As most fish
species are found near their optimum temperatures for
maximum growth (Jobling, 1981) the direct effects of
temperature on fish growth and survival may be impor-
tant. In addition, temperature will effect the feeding and
production rates of prey species, as well as fish preda-
tors. Therefore, one might also expect a strong interac-
tion effect of temperature with food supply and growth
rate, and/or temperature with predators and mortality
rate.

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. Crecco and Savoy (1984) correlated an
increase in the incidence of feeding and larval survival
of American shad (Alosa sapidissima) with tempera-
ture during 4 years. However, there was no clear rela-
tionship of feeding incidence with zooplankton
concentrations nor did they study specific changes in
diet that might have occurred.

An alternative prediction might be that tempera-
tures close to the long-term seasonal mean, and there-
fore, optimum temperatures, result in highest growth
rates. Thus, below average temperatures would limit
growth, regardless of food availability, due to lower
metabolic rates, and above average temperatures
would also reduce growth if food demand exceeded
supply. Ware and Lambert (1985) found a negative
correlation of survival in Atlantic mackerel (Scomber
scombrus) over 4 years with the rate of the seasonal
increase in water temperature. However, they sug-
gested this may be due to a change in the spatial distri-
bution of their prey as a result of the higher
temperatures and rate of warming (i.e. an interaction
effect).

Conclusions

Little progress has been made in solving the deter-
minants of pre-recruit survival in fish since Hjort (1914)
first proposed possible mechanisms so many decades
ago. It now appears that a single clearly defined event
does not determine year-class success, such as starva-
tion during first-feeding. However, there is insufficient
evidence upon which to reject any of the many hypo-
theses relating to survival mechanisms of fish. It is
suggested here that progress will best be made by
proposing hypotheses with testable predictions and,
specifically, that the growth-mortality hypothesis pro-
vides a rational framework upon which to base future
studies. This approach emphasizes a size-indexed
demography studying process known to be important
to growth in fishes, in addition to size-specific mortality
and fecundity rates (Werner and Gilliam, 1984). Studies
should not be limited to one stage in a fish's life. It is
important to emphasize that growth and survival will be
specific to each life history stage with density depend-
ent regulation occurring throughout a cohort's
existence.

Recognizing the ultimate goal is to maximize fit-
ness, fish are expected to choose between minimizing
mortality and maximizing growth. For immature fishes
living in temperate waters, one prediction might be that
fish always will choose to maximize growth, over min-
imizing mortality. Maximizing surplus energy by the
end of the first growing season should be an important
strategy of temperate water fishes toward surviving
their first winter. MacLean et al. (1981) found that size
following the first summer feeding period and duration

of the winter were important factors determining recruitment in smallmouth bass. They concluded that winter mortality was a result of size-selective starvation mortality; bigger fish had higher winter survival due to greater energy reserves.

An apparent contradiction to the growth-mortality hypothesis is the prediction that a large year-class would be expected to result in density dependent reduction of growth and survival. The important question is, however, at what stage does density dependence occur? For instance, if survival is high during the larval stage due to conditions which maximize feeding and growth it is possible that predators simply cannot respond quickly enough, functionally or numerically, to reduce larval fish abundance. Thus, there would be a lag in predation such that a density dependent response does not occur until one or more stages following the larval stage in which the large year-class is formed. It has been demonstrated for North Sea plaice that density dependent growth and mortality occurs during the settlement period, but that year-class size has been established already during the planktonic drift stage (Zijlstra *et al.*, 1982; Veer, 1986). Such observations emphasize the key processes responsible for establishing large year-classes probably occur during very specific stages early in life. Compensatory density dependent responses in subsequent life history stages would then act to regulate population size throughout the remainder of a cohort's existence.

Certain relationships must be demonstrated in the field. First, is survival directly related to growth rate during one or more life history stages of pre-recruits? Measures of growth rate are relatively easy to make, as opposed to absolute estimates of abundance, while estimates of annual recruitment are routinely available for commercial fish stocks. If survival is a function of growth then we have an important tool with which to begin examining the mechanisms effecting recruitment in marine fishes. An important component of this is to determine the extent to which predation rate is size dependent. Much empirical evidence indicates that it is.

Second, is growth rate in pre-recruit fishes food limited? This differs from the question: Does food limitation result in starvation mortality? Here starvation is a special case of food limited growth. The important factors relating to growth will be a function of processes effecting successful feeding and the direct and indirect effects of temperature on growth. Successful feeding would be a function of the foraging behaviour of the species in question, which would be expected to vary due to food abundance of the right size and/or the correct type. Conditions for successful feeding will change as a fish grows and this could be critical at the time of transition from one life history stage to the next.

To examine processes related to growth and feeding of poikliotherms without regard to the effects of temperature would be meaningless. Ricker (1979) concluded a general mathematical relationship combining growth, ration and temperature will not be found except for small temperature ranges. In the field the range of temperatures experienced by each life history stage may be fairly narrow, and interannual differences similarly may be relatively small. It is important to recognize, however, that the effect of temperature on growth may change across a small temperature range. This was true for brown trout (*Salmo truta*) for a change of less than 1° C (Elliot, 1975). Estimates of temperature specific ration that maximizes growth for each species are important prerequisites to determine the degree to which food is limited in nature. However, relating growth to food availability and temperature must be made in the field and not be simply extrapolated from laboratory measurements. In addition, it is possible that temperature effects might be manifested through an interaction with a fish's food.

Future research must rely on better field estimates of growth and survival during specific life history stages of fish. Experience dictates that such studies must occur at finer scales than in the past (Leggett, 1986) but also, that sampling scales be appropriate to the processes being studied. As a conceptual framework it is hoped this review will serve to focus attention on important questions and testable predictions originating from the theory of size dependent survival as a direct function of growth. It is hoped that by a broader theoretical treatment of the problem of determining fish survival, progress will be made in a meaningful way.

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