

RECRUITMENT IN MARINE FISHES: IS IT REGULATED BY STARVATION AND PREDATION IN THE EGG AND LARVAL STAGES?

W.C. LEGGETT and E. DEBLOIS*

Department of Biology, McGill University, 1205 Dr. Penfield, Montreal, Canada H3A 1B1

**Current address: Northwest Atlantic Fisheries Centre, White Hills, St. John's, Newfoundland, Canada A1C-5X1*

ABSTRACT

We used literature reports to evaluate the hypotheses that: 1. year-class strength in marine fishes is determined by mortality operating during the pre-juvenile stage of the life history, and 2. recruitment in marine fishes can be regulated by starvation and predation in the egg and larval stages. The available evidence is largely consistent with the first hypothesis, although mortality operating during the juvenile and post-juvenile stage may moderate the variation induced at the pre-juvenile stage. The hypothesis that recruitment can be regulated by starvation during the larval stage was assessed in relation to Hjort's 'critical period' and Cushing's 'match-mismatch' hypotheses. The available evidence does not support a major link between food abundance at the time of first feeding, and recruitment (Hjort's 'critical period'). The hypothesized relationship between recruitment and the coincidence between the seasonal timing of plankton production and the seasonal abundance of larvae (Cushing's 'match-mismatch') is generally supported. However, the relationships are weak and the importance of the strength of the coupling between seasonal cycles in plankton and larval abundance appears to be weaker than had previously been surmised. Recent evidence, which suggests that failure to distinguish between food abundance in the environment and the availability of food to individual larvae may have compromised the evaluation of these hypotheses, is reviewed. The relationship between mortality due to predation and its potential effects on recruitment was evaluated with reference to two emerging paradigms, the 'bigger is better' and the 'stage duration' hypotheses. We conclude that failure to fully evaluate the assumptions underlying these hypotheses may have led to erroneous generalizations regarding the importance of size at age/stage and growth rate on the probability of death due to predation. Neither the 'bigger is better', nor the 'stage duration' hypotheses is unequivocally supported.

1. INTRODUCTION

Recruitment variation in marine fishes is enormous, and has major biological and economic implications for the management of commercial fisheries. This reality underlies the interest in the causes of recruitment variation in marine fishes. For most of the 20th century, researchers have operated on the belief that year-class strength (and recruitment) in marine fishes is regulated during the larval stage. The principal agents of this regulation are hypothesized to be food and predation-mediated mortality occurring during the egg and larval stages. In this paper we explore the justification for this hypothesis. This paper is a contribution to the Second International Flatfish Symposium, Texel 1993. Other papers in this series concentrate more specifically on the ecology of the flatfishes. We have opted for a broader view primarily because the egg and larval stages of most flatfishes are pelagic. Consequently, the processes governing the dynamics of these stages should be similar to those of other pelagic spawning species.

2. THE TIMING OF YEAR-CLASS FORMATION

Credible evidence that year-class size is principally determined by the end of the larval stage is fundamental to any analysis of the importance of predation and/or starvation during the early life to recruitment variation in the adult stock. Such evidence is, by its very nature, difficult to develop (Taggart & Frank, 1990; Bradford, 1992). The scarcity of significant direct correlations between egg and/or larval abundances and recruitment have lead many to a question the importance of these early life stages to recruitment (May, 1984; Sissenwine, 1984; Smith, 1985; Peterman *et al.*, 1988; Wooster & Bailey, 1989; Taggart & Frank, 1990).

However, a body of data and analysis does suggest a link between events during the pre-juvenile life stage and recruitment (see Cushing, 1990). Bradford (1992) analysed the relationship between egg abundance, early and late larval abundance, and recruitment. He concluded that correlations between the abundance of egg and early larval stages of marine

fishes and recruitment were too weak to justify a conclusion that recruitment was regulated at these stages in the early life history. Correlations between abundances of late larvae, recently metamorphosed juveniles, and recruitment were, however, quite strong. These data suggest that numbers regulation occurs sometime between late larval phase and the metamorph phase. Meekham, Fortier & Desbiens (Laval University, Quebec, pers. comm.) determined, from birthdate frequency analyses, that recruitment patterns in Canadian Scotian Shelf cod were largely determined by the time the larvae had reached the age of 30 days. Additional support is provided by Myers & Cadigan (1993b), who studied the magnitude and causes of variability in juvenile mortality in 14 populations of demersal marine fishes from 5 species. They found little or no interannual variability in the density-independent component of juvenile mortality. This finding led them to conclude that the variability of relative year-class strength in these demersal species is usually determined in the larval stage. Density-dependent juvenile mortality, in these and other populations, was significant, and was judged sufficient to attenuate fluctuations in abundance induced during the pre-juvenile stage (see Myers & Cadigan, 1993a; Myers *et al.*, 1994; Bailey, 1994). These findings are consistent with Gulland's (1965) hypothesis of coarse control of recruitment during the pre-juvenile stages, and fine control during later life stages. Table 1 provides a summary of species for which links between larval abundance/survival and recruitment have been identified.

The link between recruitment and abundance/survival during pre-juvenile life stages of marine fishes is sufficiently well documented to justify a continued

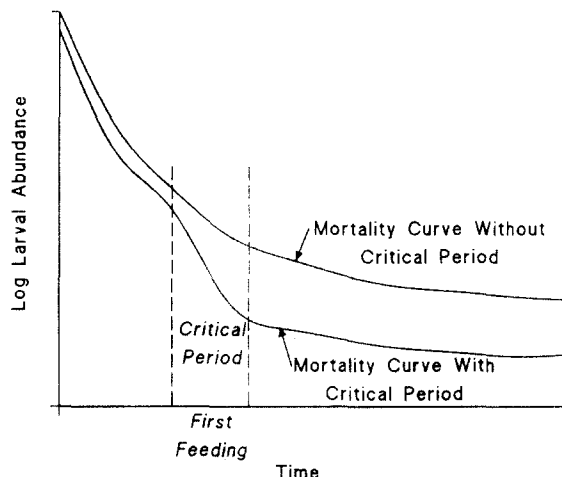


Fig. 1. Schematic representation of Hjort's 'critical period' hypothesis illustrating the proposed link between survival at the time of first feeding (mediated by food abundance at this time) and subsequent year class size.

interest in factors regulating survival and abundance in the egg and larval stages. It should be noted, however, that processes operating during the post-larval stages can significantly moderate, and may regulate, recruitment in some fishes, or under some circumstances (see Bailey, 1994). Thus, search for a fuller understanding of recruitment processes in fishes will clearly require a broader exploration of regulatory processes than has been common to date (see Beyer, 1989; Bradford, 1992; Myers & Cadigan, 1993a).

3. STARVATION

The hypothesis that starvation during the larval stage of fishes is an important regulator of recruitment to the adult population has a long and illustrious history. In this paper we focus on two hypotheses that have dominated most of the thinking, and much of the research, on this question. Allied hypotheses are treated as special cases of these larger views.

3.1. HJORT'S CRITICAL PERIOD HYPOTHESIS

Hjort (1914, 1928) appears to have been the first to formally propose a causal link between feeding, larval survival and recruitment. His 'critical period' hypothesis (Fig. 1) explicitly linked larval survival, and subsequent recruitment, to food abundance during the transition of larvae from endogenous (yolk sac) to exogenous feeding. He proposed that when food was limiting during this transition a high proportion of the larval population would die from starvation. In contrast, when food was abundant at this time, survival would be high. He proposed that variation in the intensity of starvation during this transition to exoge-

TABLE 1

Studies indicating a link between recruitment and larval abundance or survival.

species	location	reference
herring	North Sea	Cushing, 1990
sardine	California	
herring	Finland	
capelin	Newfoundland	
American shad	Connecticut	Crecco & Savoy, 1984, 1987 Bradford, 1992
cod	NW Atlantic	
anchovy	California	Myers & Cadigan, 1993a, b
herring	NW Atlantic	
cod	North Sea	
	NW Atlantic	
	Baltic Sea	
haddock	North Sea	
	Barents Sea	
whiting	North Sea	
plaice	North Sea	

nous feeding could explain the enormous fluctuations in year-class strength observed in North Sea fishes.

In the years since the publication of Hjort's hypothesis, and in particular since the 1960's, an extensive literature based on laboratory data has developed on the relationship between food abundance (and quality) at the time of the transition to exogenous feeding, and the survival of larvae. The time to first feeding under a wide range of conditions simulated in laboratory settings has been documented for a large number of species. Similarly, the rates of survival of laboratory reared larvae under a wide range of food levels and types, and following varying intervals of starvation, have been documented (see Miller *et al.*, 1988; Pedersen *et al.*, 1990). These laboratory investigations have demonstrated that first feeding and early post-first feeding larvae are very vulnerable to starvation.

However, unequivocal field evidence of a relationship between food abundance and/or quality at the time of first feeding and either larval survival or year-class strength/recruitment has been elusive. Dahlberg (1979) and May (1974) reviewed the literature on the subject and found it inconclusive. To quote May (1974): 'The available data do not allow one to answer the question of whether or not mortality is concentrated at the end of the yolk-sac stage in natural populations.' Leggett (1986) and Anderson (1988) reached similar conclusions. Leggett (1986) identified several sampling problems which had compromised the conclusions that could be drawn from these field investigations and cautioned against outright rejection of the critical period concept on the strength of the evidence available at that time. Several additional studies designed to evaluate the critical period hypothesis have now been published.

Fortier & Leggett (1984, 1985) show that larval mortality at first feeding in capelin (*Mallotus villosus*) is related to food abundance but that variability in this mortality is perhaps too small to impact on subsequent recruitment. Similarly, Peterman & Bradford (1987) found that mortality in larval anchovy (*Engraulis mordax*) is related to wind activity, presumably through its effect on food concentration, but that this mortality does not affect recruitment to the juvenile stage (Fig. 2). Butler (1991) compiles a large dataset and adds strength to Peterman & Bradford's (1987) conclusion. Counter to the above, Taggart & Leggett (1987) found no relationship between mortality of larval capelin (*Mallotus villosus*) and food abundance. Crecco & Savoy (1984, 1987) reported that mortality in larval American shad (*Alosa sapidissima*) was not related to food abundance. Crecco & Savoy (op. cit.) did find, however, that larval survival and year-class strength were related to feeding success as measured through gut fullness. Bradford (1992) reviewed recruitment in cod, herring, anchovy and plaice. He found that correlations between egg and early larval abundances and recruitment were weak. This too

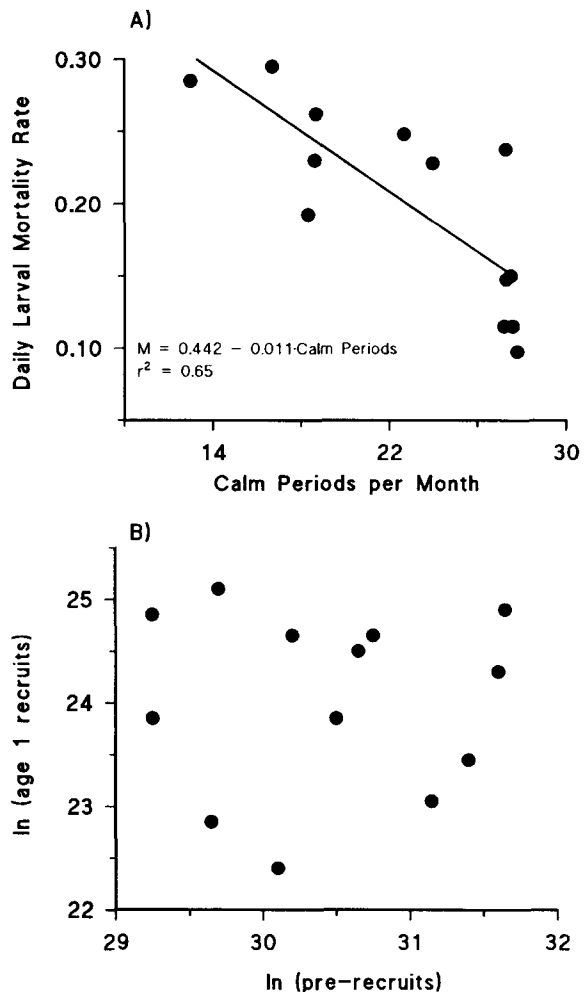


Fig. 2. A. Relationship between average instantaneous mortality rate (M) of northern anchovy larvae and the weighted average number of calm four-day periods per month during the main spawning season for 13 years (redrawn Peterman & Bradford, 1987); B. Relationship between prerecruit abundance and resulting abundance of age 1 recruits of northern anchovy for the 1965-1985 year classes (redrawn from Peterman *et al.*, 1988).

suggests that food levels at first feeding do not contribute strongly to year-class strength. Correlations involving the abundance of later stage larvae and metamorphosis were stronger.

Overall, little unequivocal evidence of a causal link between the availability of food at first feeding and larval survival and/or recruitment has been reported. Moreover, in those cases where evidence does exist, the magnitude of the effect appears to be small. We conclude that the available evidence does not support Hjort's 'critical period' as an important general contributor to recruitment variation in marine fishes.

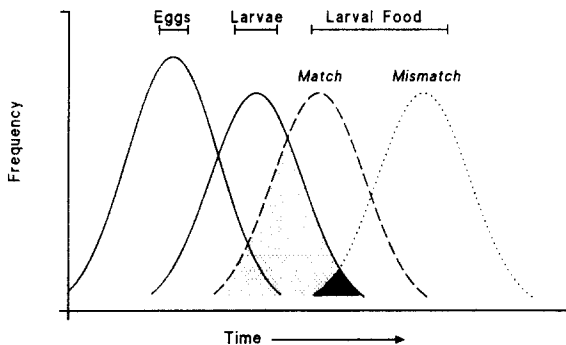


Fig. 3. Schematic representation of Cushing's 'match-mismatch' hypothesis (after Cushing, 1990) illustrating variability in the degree of overlap between the timing of the spring peak in plankton production and the occurrence of larval fishes which is hypothesized to regulate feeding success, and year-class formation, in fishes. The stippled area indicates a condition of high overlap (and predicted high survival), the darkened area indicates a condition of low overlap (and predicted low survival).

3.2. CUSHING'S MATCH-MISMATCH HYPOTHESIS

Hjort's 'critical period' was generalized by Cushing (1972, 1973). His 'match-mismatch' hypothesis (Fig. 3) removed the restriction that food-mediated mortality leading to recruitment variability would be restricted to a particular 'critical' stage in larval development. In Cushing's model the survival of a larval cohort (and ultimately recruitment to the adult population) is hypothesized to be causally linked to the abundance of food during the period of larval drift from the spawning to the nursery area—an interval encompassing most of the larval period. This, in turn, is argued to be related to the magnitude of the temporal overlap between the production of larvae (without specific reference to the timing of first feeding) and the seasonal production cycle of the plankton.

The direct implication of this hypothesis is that food limitation during the entire larval period is a major regulator of larval survival, and of recruitment. Further, the role of abiotic factors as regulators of the timing and intensity of the seasonal cycle of plankton production, and hence of the abundance of food for larval fishes, is explicitly recognized in the Cushing hypothesis (Cushing, 1972). It is important to note, however, that the hypothesis does not operationally relate 'overlap' to recruitment. Hence direct tests are difficult.

Cushing (1990) reviewed recent literature in an attempt to compile evidence in support of his hypothesis. Numerous examples of relationships between physical processes known to be linked to production (upwelling, spring overturn, wind events etc.) and fish population traits such as the timing of spawning, the abundance of larvae, their survival, and in some cases recruitment, are given. Combined, this evi-

dence, while indirect, is broadly consistent with the expectations derived from the hypothesis. However, when each study is considered individually, the strength of much of the evidence presented by Cushing (1990) in support of a direct relationship between food level and survival is equivocal. Frequently, Cushing's evidence is no more compelling than that cited by Sinclair (1988) as counter to Cushing hypothesis. Indeed, both authors use some of the same studies to either support or refute Cushing's theory. Since then, five more recent studies have addressed the 'match-mismatch' hypothesis.

Fortier & Gané (1990) examined the dispersion, growth and survival of two cohorts of larval herring (*Clupea harengus*) in the St. Lawrence estuary in relation to the 'match-mismatch' and the 'member/vagrant' hypotheses (Iles & Sinclair, 1982). The development of the spring larval cohort was matched to the development of suitable prey. Further, larval abundances decreased more slowly in the spring than the fall cohort which hatched in a period of low food abundance. However, both cohorts grew at approximately one-half the maximum rate. The authors note that differences in advection out of the estuary may have contributed to the differential reduction in larval numbers. Hence a clear distinction between the importance of 'match-mismatch' and 'member/vagrant' influences could not be drawn. The authors speculate that a combination of energetic (match-mismatch) and retention (member/vagrancy) factors may interact to define larval survival and recruitment.

Ellertsen *et al.* (1989) monitored the abundance and distribution of eggs and first feeding larvae of cod (*Gadus morhua* L.), and their prey off the Lofoten Islands, Norway, from 1976 to 1986. They found, as have others, that poor year classes of cod were consistently associated with cold years. In warm years, either strong or weak year classes may be produced. Timing of cod spawning was largely independent of temperature (see also Hutchings & Myers, 1993), whereas the timing of spawning of its principal prey, *Calanus finmarchicus*, was highly temperature-dependent. Naupliar production was later in colder years. Strong evidence of a temporal mismatch between the production of larvae and prey is presented (Fig. 4). However, high variability in recruitment was also observed in years during which temperatures should have resulted in a strong match in the production cycles of larvae and their prey. The authors suggest that in these years when recruitment does not match the temperature/production cycle other abiotic and/or biotic factors may dominate in regulating recruitment.

Brander & Hurley (1992) found a south to north trend in spawning times of cod on the Scotian Shelf of the Northwest Atlantic of the Canadian Nova Scotia coast. This caused maximum egg abundance in all areas to be approximately concurrent with the *Calanus*

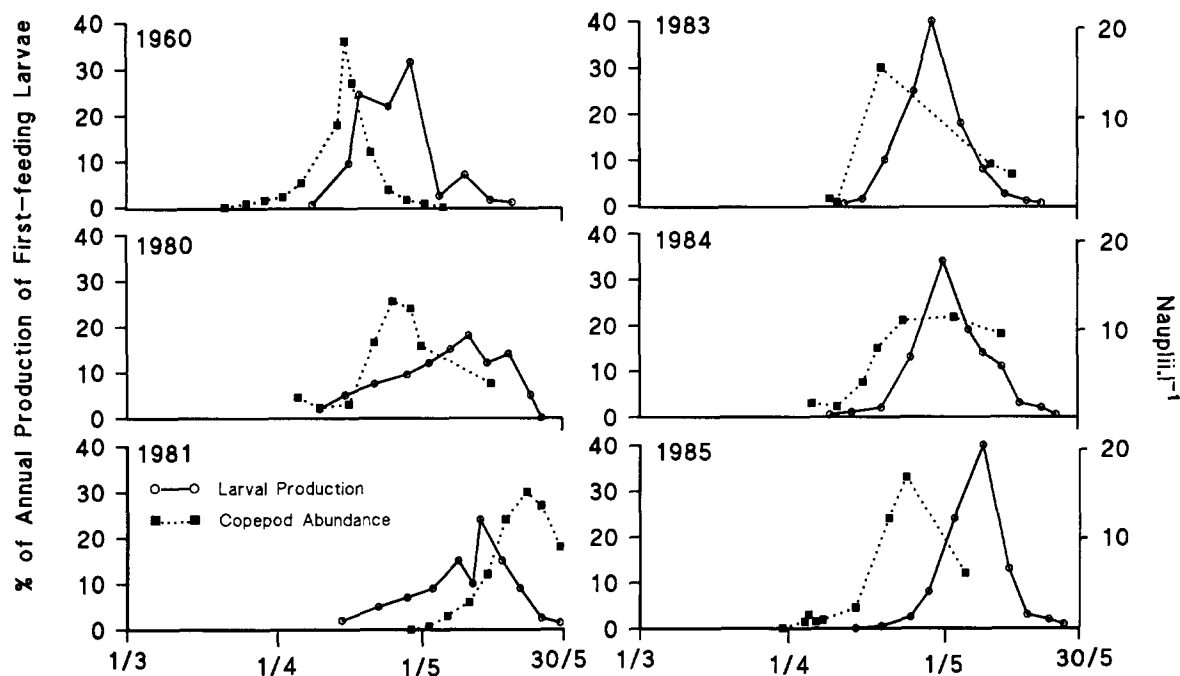


Fig. 4. Match and mismatch between the abundance of larvae of northeast Arctic cod and that of their principal prey *Calanus finmarchicus* (redrawn from Ellersten *et al.*, 1989).

nus peak. However, Myers *et al.* (1993) observed no such pattern in northern Northwest Atlantic cod populations. In fact, spawning times in the north of their study area were earlier than those of the more southern stocks studied by Brander & Hurley (op. cit.). However, consistent with Cushing's hypothesis cod spawning consistently occurred prior to the *Calanus* peak indicating a coincidence between spawning and production (Myers *et al.*, op. cit.) possibly regulated by a common environmental signal. They concluded that a very general rather than a precise correspondence between larval production and planktonic food abundance was sufficient to assure reproductive success in Northwest Atlantic cod. They also observed that this appears to be true for the North Sea species considered by Cushing (1990).

Myers *et al.* (1993) conclude by noting that 'the sufficiency, for larval viability, of a general match implies that recruitment will not be strongly influenced by changes in the timing of the plankton peak, contrary to the assertions of the full match-mismatch hypothesis'.

To summarize, much of the evidence available is broadly consistent with the hypothesized existence of a relationship between the overlap in seasonal food production/larval abundance and larval survival. However, as pertains to recruitment, the evidence in favour of the 'match-mismatch' hypothesis is only marginally more compelling than for the 'critical period' hypothesis. Moreover, recent studies (cited

above) suggest that the precision of this coupling may be less important than has previously been assumed, and that other factors may dominate the dynamics of larval survival and recruitment.

3.3. FOOD ABUNDANCE VS FEEDING SUCCESS

Much of the field and laboratory research stimulated by the above hypotheses has been predicated on the supposition that food abundance would directly influence survival and recruitment. Hence, the overwhelming focus of field and laboratory studies conducted to date on the interaction between prey abundance, feeding success, survival and recruitment. The broad and often uncritical acceptance of the existence of such a causal link has been fostered by the frequent observation that minimum food densities necessary to support larval growth and survival in laboratory settings are frequently much higher than prey densities commonly observed in nature (Leggett, 1986).

Several recently developed lines of evidence suggest that a direct causal link between food abundance and these variables may be weak, or even absent. Crecco & Savoy's (1987) observation that cohort mortality rates in American shad were positively correlated with larval feeding success but unrelated to the abundance of zooplankton prey led them to conclude that mortality of larval shad and the subsequent production of juveniles was strongly linked to hydro-

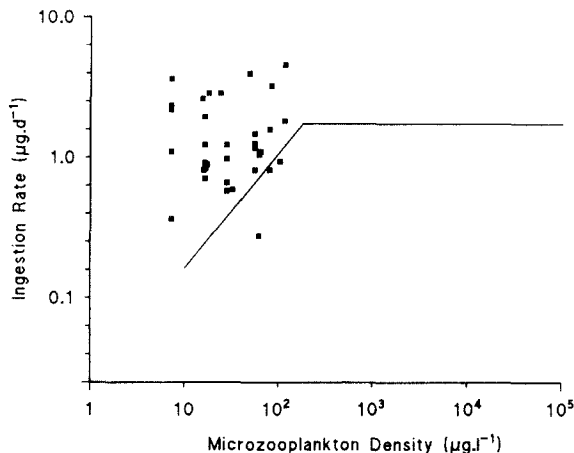


Fig. 5. Laboratory-based relationship between microzooplankton density and larval fish ingestion rates (solid line) and estimates of *in situ* ingestion rates (redrawn from MacKenzie *et al.*, 1990). Note that the majority of the *in situ* estimates exceed the rates predicted from laboratory experiments at equivalent prey densities.

graphic and meteorological conditions which affected feeding rate and capture success independently of prey abundance.

MacKenzie *et al.* (1990), following a review of the available laboratory and field data on larval fish ingestion rates, have seriously questioned the applicability of laboratory derived relationships between prey abundance and larval ingestion rates in wild larvae. Their analyses indicate that *in situ* larval ingestion rates are frequently higher than would be predicted from laboratory studies. Field estimates of feeding rates are commonly at or near satiation levels, and appear to be largely independent of food density (Fig. 5).

Several factors could contribute to this apparent anomaly. Zooplankton abundance estimates may underestimate prey availability because they neglect zooplankton production which is typically in the size range required by young stages of fish larvae (Hunter, 1981; Frank & Leggett, 1986; Checkley *et al.*, 1988). Production typically ranges from 0.5 to 2.0 $\mu\text{g}\cdot\text{dm}^{-3}\cdot\text{d}^{-1}$ in shelf ecosystems (Middlebrook & Roff, 1986; McLaren *et al.*, 1989) and may be consumed as quickly as it is produced in some systems. Zooplankton is known to be patchily distributed on the spatial scale searched by feeding larval fish (metres to hundreds of metres—see Owen, 1989). Traditional estimates of zooplankton abundance, where values were integrated over large vertical and horizontal scales, would probably under-estimate the effective concentrations of zooplankton available to larvae if these larvae have the ability to exploit micro-scaled food patches. To date, the distributions of larval fishes have not been shown to be coherent with that of their

prey at these scales (Courtois *et al.*, 1982; Fortier & Leggett, 1984; Taggart & Leggett, 1987). Moreover, wild larvae are known to swim faster than larvae confined in laboratory tanks (Von Westerhagen & Rosenthal, 1979). Higher routine swimming speeds may cause wild larvae to search larger volumes, thereby increasing their probability of encounter with prey. Finally, census estimates of prey density also fail to incorporate the potential positive effects of small-scale turbulence on encounter rates between larval fishes and their zooplankton prey (Rothschild & Osborn, 1988).

MacKenzie & Leggett (1991) used Rothschild and Osborn's (1988) turbulence/encounter rate model to predict encounter rates that could be expected under natural turbulence levels and prey densities, and under both homogenous and patchy distributions of larvae and prey. They conclude that failure to consider the influence of small-scale turbulence when prey densities are $< 35 \text{ ind}\cdot\text{dm}^{-3}$ could result in up to an 11-fold underestimation of encounter rates at conditions typical of fronts in waters over the northwest European continental shelf during the summer. Moreover, underestimates of up to 112% are possible for larvae at a depth of 20 m during turbulence typical of that generated by wind velocities of $5 \text{ m}\cdot\text{s}^{-1}$ (Fig. 6). The magnitude of these underestimates increases as prey densities decline, and when prey are heterogeneously distributed. The analyses also suggest that turbulence may slow the rate of starvation because weakened, slow-swimming individuals are more likely to benefit from the effect of turbulence than are faster-swimming larvae.

MacKenzie *et al.* (in press) have subsequently shown that the probability that larvae will successfully capture a prey once encountered declines nonlinearly with turbulence. This effect, combined with the increase in encounter probability with turbulence pre-

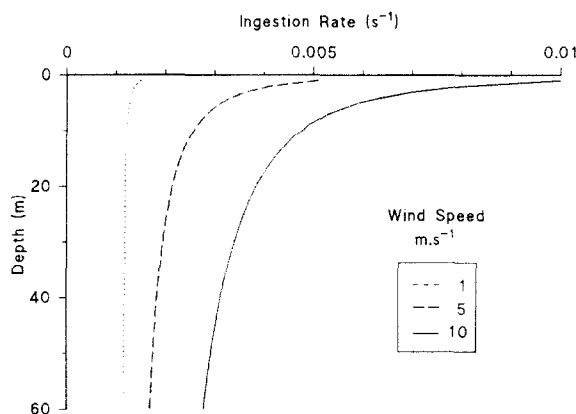


Fig. 6. Effect of turbulence on encounter rates of larval fishes with zooplankton prey (redrawn from Mackenzie & Leggett, 1991). The relationship shown is for larvae of 6 mm feeding at a prey density of $5 \text{ nauplii}\cdot\text{dm}^{-3}$.

dicted by Rothschild & Osborn (1988), results in a dome-shaped response of ingestion rate to increasing turbulence (Fig. 7). Landry *et al.* (1994) conducted a direct experimental test of prediction of a dome-shaped response of ingestion rate to turbulence and report findings consistent with expectation. Maximum ingestion is thus likely to occur at intermediate turbulence levels. The negative influence of turbulence in these simulations begins to be expressed at turbulent velocities induced by wind speeds (and hence turbulence levels) comparable to those commonly observed in nature (MacKenzie & Leggett, 1993). This, together with dissipation of vertical or horizontal structure in prey concentrations (Wroblewski & Richman, 1987; MacKenzie *et al.*, 1990; Maillet & Checkley, 1991), could contribute to the diminished larval feeding rates reported during storms (Maillet & Checkley, 1991) and high river discharges (Crecco & Savoy, 1987).

Upwelling systems, too, generate significant micro-scale turbulence (MacKenzie & Leggett, 1991). Curry & Roy (1989) demonstrated a dome-shaped relationship between wind-generated turbulence and recruitment in Eckman-type upwelling systems with maximum recruitment at approximately 5 to $6 \text{ m}\cdot\text{s}^{-1}$. This is consistent with the optimum wind speed predicted by MacKenzie *et al.* (in press) (Fig. 7); given the known effects of prey density, larval size, and pursuit time on the position of this maximum. It is not clear, however, whether the increased recruitment reported by Curry & Roy (1989) is related to enhanced feeding success due to the turbulence associated with upwelling.

Sundby & Fossum (1990) provide the only direct field evidence to date of the positive influence of small-scale turbulence on ingestion rates in larval fishes. Their data indicate the optimal level of wind-generated turbulence for larval cod would exceed $6 \text{ m}\cdot\text{s}^{-1}$. MacKenzie *et al.* (in press) predicted a maximum at $8.9 \text{ m}\cdot\text{s}^{-1}$ given an estimated pursuit time of 1.7 s and swimming speeds and prey densities reported by Sundby & Fossum (1990).

The apparent anomaly between the positive relationship between the frequency of 4-day periods having wind speeds $<10 \text{ m}\cdot\text{s}^{-1}$ ('Lasker events') and survival of first feeding larvae, and the absence of a relationship between the numbers of first feeding larvae and recruitment to age 1 in northern anchovy (Peterman & Bradford, 1987; Peterman *et al.*, 1988), deserves further consideration in the light of these findings. It is possible that the advantage of calm periods for first feeding larvae is offset by reduced feeding success in later stage larvae which do not rely on the subsurface chlorophyll maximum, and fail to benefit from increases in feeding success resulting from turbulence.

We assessed this possibility using the relationship between ingestion rate and turbulence for first feeding larvae (mean size 4 mm) and for later stage lar-

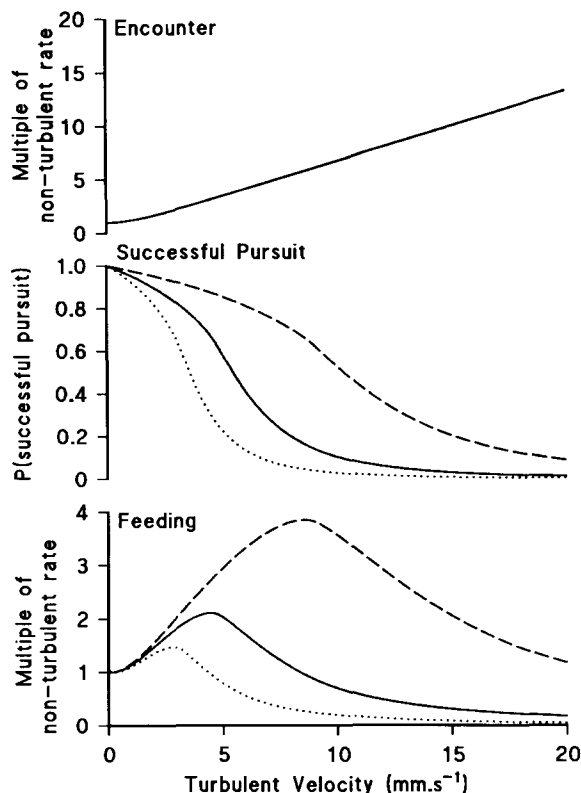


Fig. 7. The influence of turbulence on encounter, the probability of successful pursuit and ingestion. The effect illustrated is for a cod larvae having a reactive distance of 8 mm , and a swimming speed of $2.0 \text{ m}\cdot\text{s}^{-1}$. Prey density = $5 \text{ ind}\cdot\text{dm}^{-3}$, prey swimming speed = $0.2 \text{ mm}\cdot\text{s}^{-1}$. Three larval reaction times are shown (redrawn from MacKenzie *et al.*, in press).

vae (mean size 12 mm) using the MacKenzie *et al.* (in press) model. Reaction distances were set at 6 mm and 16 mm for 4 mm and 12 mm larvae, respectively. The simulations suggest that first feeding larvae would achieve maximum ingestion at wind speeds approximating $6 \text{ m}\cdot\text{s}^{-1}$. At these speeds the maximum ingestion rate is estimated to be three times the rate of ingestion under calm conditions. In contrast, the maximum ingestion rates for 12 mm larvae occur at higher wind speeds ($16 \text{ m}\cdot\text{s}^{-1}$), and approach eight times the rates predicted under calm conditions. These results suggest that in years in which wind conditions are favourable for feeding and survival of first feeding larvae, feeding rates for later stage larvae will be suboptimal and *vice versa*. Hence high survival in first feeding larvae could be diminished or negated by reduced survival in the later stages. Such abiotically regulated reciprocal trends in survival in early and later stage larvae could diminish or eliminate any relationship between survival in the early larval stages and subsequent recruitment, as reported

by Peterman *et al.* (1988).

Owen *et al.* (1989) report that growth and mortality rates and the incidence of starvation in northern anchovy larval were similar at two sites at which food densities differed by two fold. The low food site was reported to be 'much more energetic, as seen by its greater wind speed, current speed, mixed layer depth, and depth of maximum stability'. This finding is fully consistent with the proposed mediating effect of turbulence on feeding success and survival.

It is quite unlikely that the relationship between wind-driven turbulence and larval survival is as simple as the MacKenzie *et al.* (in press) analyses suggest (see Wroblewski & Richman, 1987; Wroblewski *et al.*, 1989). In fact, the added complexity introduced by Wroblewski's models could help to explain the high variability in mortality rates characteristic of later stage larvae (Peterman *et al.*, 1988). The MacKenzie *et al.* (in press) analyses do, however, highlight the reality that the dynamics of feeding and survival in larval fishes can be complex, and quite independent of simple measures of food abundance and distribution.

Given these findings, a more detailed investigation of the relationship between hydrographic conditions, prey densities and ingestion rates seems warranted. Clearly, the potential for erroneous conclusions based on the simple assumption of a direct link between *in situ* prey density and feeding success is high. It would thus appear to be unwise to conclude, as did Cushing (1990), that 'the dichotomy of positive/negative links between upwelling and recruitment **do not indicate a dependence on food or a lack of it**'. Upwelling- and wind-generated turbulence may, in fact, be major regulators of the true availability of food to larval fishes, and of their growth, survival and recruitment.

4. PREDATION

The literature on predation on eggs and larvae of marine fishes has recently been comprehensively reviewed by Bailey & Houde (1989). In contrast with the literature on the potential effects of food on recruitment, relatively few studies have yet attempted, or claimed, to directly quantify the contribution of predation to observed recruitment variation. With few exceptions those that do exist have been effectively summarized by Bailey & Houde (1989). We will not repeat that exercise here. It is generally assumed that predation is the major source of egg mortality in marine fishes. Reliable data on egg mortality rates in general, and on the contribution of predation to these rates in particular, are very limited. There is no direct empirical evidence of the contribution of egg predation to recruitment variation (Bailey & Houde, 1989).

Rijnsdorp & Jaworski (1990) hypothesized that the higher mortality rates of cod eggs in the southern North Sea, relative to rates observed in plaice, resulted from differential mortality related to egg size

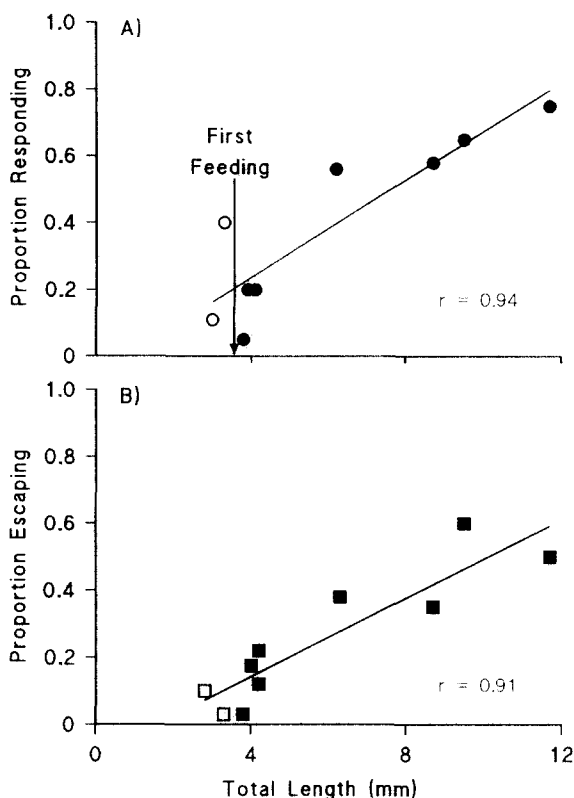


Fig. 8. Relationship between the length of northern anchovy larvae and (A) the proportion responding to an attack by clown fish (B) and the proportion escaping an attack (redrawn from Webb, 1981).

differences between the species, cod eggs being on average smaller. They attempted to test this hypothesis by examining the changes in the mean diameter of the egg populations of the two species between fertilization and hatching. Mean egg size increased with season consistent with their expectation leading them to conclude that the result was due to higher rates of mortality in smaller eggs. Similar findings were reported for sole (Rijnsdorp & Vingerhoed, 1994). While the changes in mortality and egg size noted in these studies could be related to predation, alternative explanations are possible and should be considered. First, hatching time is generally shorter for small eggs. Hence, the higher mortality rates observed in small eggs could result from confusion of differential losses to the smaller egg pool due to hatching with mortality. Second, T. Miller (Dept. of Biology, McGill University, Montreal, Canada) (pers. comm.) reports a similar increase in egg size with season in cod on the Canadian Scotian shelf. However, in this instance, the positive trend results from two distinct spawnings by different stocks or groups of individuals having different demography and egg sizes. Importantly, within each group, egg size

decreases with time—a trend opposite to that reported by Rijnsdorp & Jaworski (1990). Finally, linking of the higher mortality rates reported in small eggs by Rijnsdorp & Jaworski (1990) with predation is inconsistent with the considerable body of literature (reviewed below) which suggests that predators will typically select larger prey when confronted with a choice. Pepin & Myers (1991) and Pepin (1991) have concluded from comparative analyses of many species that egg size is unrelated to daily or cumulative mortality. However, Pepin & Miller's (1993) caution against inferring within population inferences drawn from comparative studies applies here as well. Pepin's (1991) multi-species analyses indicate that egg mortality rates are positively related to temperature. This result could be related to a corresponding increase in predator foraging rate with temperature (see Bailey & Houde, 1989) but this link has not been empirically demonstrated.

In commenting on the relative importance of predation *versus* food-mediated processes to larval fish dynamics Bailey & Houde (op. cit.) conclude that 'the question of whether starvation or predation is more important as a cause of early life mortality remains unresolved, and there may be no unequivocal answer because the situation may vary with species, area, and year.' We concur fully with this assessment. In fact, the either/or determination is likely to be impossible for a more fundamental reason. Food-mediated changes in larval growth, condition and performance are likely to alter both the frequency, and the intensity, of predation on post-yolk-sack stages of most, if not all, marine fish larvae (see Frank & Leggett, 1981; Owen *et al.*, 1989). Moreover, eggs and larvae are integral elements of the planktonic ecosystem. Hence, changes in the relative abundance of other organisms in the plankton, be they predators, prey, competitors for common prey, or alternate prey for

potential predators of fish eggs and larvae, are certain to alter the intensity, timing, and impact of predation on the early life stages of fishes (for examples of such interactions see: Frank, 1986; Frank & Leggett, 1983a, 1983b, 1985; Fortier & Harris, 1989 and Gotceitas & Brown, 1993).

The reality of these interactions, and of their potential impact on recruitment processes, is now becoming widely recognized. Predictably, new hypotheses are emerging and these have begun to shape both the nature of the studies being undertaken, and the interpretation of their findings. In the balance of this paper we focus on two such hypotheses which, for convenience, we shall refer to as the 'bigger is better' and the 'stage duration' hypotheses. It will become apparent that they, like food and predation effects, are not cleanly separable. It is true, also, that both have enjoyed significant gestation periods in arriving at their present state, and that they are rapidly approaching the status of dogma.

4.1. THE 'BIGGER IS BETTER' HYPOTHESIS

The 'bigger is better' concept holds that larger larvae are less susceptible to predation. Hence the prediction is that larvae which hatch at larger sizes, or grow at faster rates, thereby achieving larger body size at a given age, should be less vulnerable to predation. A significant body of experimental and field data support this thesis. Examples are provided in Figs 8 and 9. The vast majority of this literature deals with the relationship between size and the ability of individual larvae to detect, react to, avoid and/or escape predators (for full review see: Bailey & Houde, 1989, pp 16-22) and it is from these findings that the 'bigger is better' hypothesis has grown. It is important to note, however, that the only comprehensive comparative test of the 'bigger is better' hypothesis to date (Pepin & Myers, 1991) indicates that neither egg size nor size at hatching are correlated with recruitment variability. Our concern with this hypothesis is not with the data used to support it, but rather with the larvae-centric view that has helped to generate and sustain it.

The act of predation involves several stages. These include behavioural responses by both predator and prey. Specifically, a successful act of predation is the product of the combined probabilities of encounter, attack and capture (O'Brien, 1979; Fuiman, 1989). As noted above, studies of the vulnerability of larval fishes to predation conducted to date have focused almost exclusively on the probability of capture (or more specifically, the ability of larvae to escape predators once encountered) as a function of size.

A considerable body of evidence suggests that encounter probabilities should increase with larval size, although the exact form of this relationship is unclear. Larval swimming speed (Fig. 10) and ambit (Fig. 11) increase with larval size thereby increasing

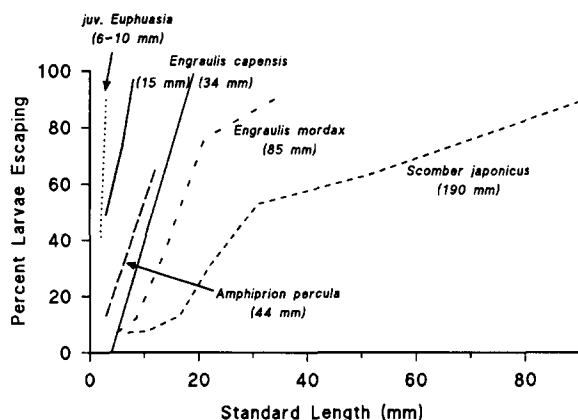


Fig. 9. Percentage of larval and juvenile anchovies escaping attacks by various predators as a function of length (redrawn from Bailey & Houde, 1989).

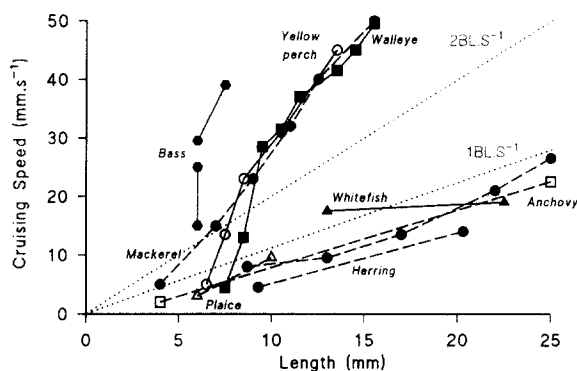


Fig. 10. Larval swimming speeds as a function of length (redrawn from Blaxter, 1986).

the probability of their encounter with a predator. Encounter probabilities may be enhanced by increases in the reactive field of the predator for larvae of greater size (Gerritsen & Strickler, 1977; O'Brien, 1979). Within species both coloration and movement increase with larval size (Fig. 12). For visual predators, increased coloration and movement of prey are known to increase their reactive distance (Ibrahim & Huntington, 1989).

A substantial body of theoretical and empirical literature also suggests that the probability of attack will be size dependent. Optimal foraging theory predicts that predators should selectively pursue prey that maximize their energy cost benefit ratio (reviewed in: Stephens & Krebs, 1986). This suggests that larger larvae may be preferred even though their probability of escape (foraging cost) is higher. Brooks & Dodson (1965) were the first to document the selective reduction of larger members of the zooplankton due to predation. Stein *et al.* (1988) provide additional evidence

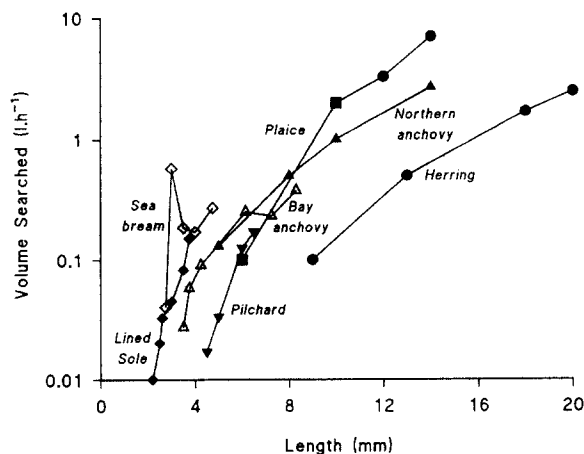


Fig. 11. Search volume of larval fishes as a function of length (redrawn from Blaxter, 1986).

of this effect. Oiestad (1985), De Lafontaine & Leggett (1988), Fuiman (1989), Litvak & Leggett (1992), and Pepin *et al.* (1992) have reported similar findings for larval fish based on mesocosm studies.

The potential advantage of size, in relation to the probability of predation, thus resolves itself to a question of the relative importance of the size-dependent probabilities of encounter and capture.

In an attempt to distinguish between these processes, Litvak & Leggett (1992) have shown that interpretations of the results of earlier experimental studies on size-related vulnerability of larval fishes may have been biased by failure to distinguish between size and age effects, and by experimental designs which excluded the potential for predator choices between larger and smaller prey. In nature, predators foraging on a cohort of larvae are confronted with prey which vary considerably in both age and size. Moreover, there is considerable variability in the size of larvae of similar age, and *vice versa*. This variability is the template upon which selective predation operates, and its character and magnitude is likely to significantly influence the nature of predator choice, and hence the outcome of predation. As noted by Litvak & Leggett (1992), in both laboratory and mesocosm experiments, the probability of capture by both jellyfish (*Staurophora mertensi*) and stickleback (*Gasterosteus aculeatus*) predators decreased with age when age treatments were tested in separate trials. These results are consistent with those of earlier studies. However, contrary to the prevailing view, when predators were offered a mixture of larvae of different ages, and hence a choice such as would occur in nature, the probability of death by predation was higher for older larvae. Further, when predators were offered a choice of larvae of similar age but varying in size, no preference in prey size was observed. However, once again, contrary to current thinking, (but as predicted from theory) when the predators were exposed to a cohort of similar-aged larvae having a distribution of sizes, larger larvae were selectively consumed.

Litvak & Leggett (1992), following Greene's (1985) example, proposed a conceptual model which incorporates the effects of age and size related changes in encounter, attack and capture on gross vulnerability to predation (Fig. 13). In the model the probabilities of attack and capture of large and small larvae were assumed to be reciprocal (large larvae being preferentially attacked by predators, but having higher escape probabilities) leading to a common declining susceptibility to predation with age for both large and small larvae. Encounter probabilities are assumed to be higher for larger larvae. The empirical and theoretical basis for these assumptions are detailed above.

The Litvak & Leggett (1992) model predicts that the gross vulnerability of larval fishes to predation will be a dome-shaped function of age (and hence size). The exact form of this interaction will depend on the form

of the encounter, attack and capture functions which are likely to vary with predator type (Bailey & Houde, 1989). However, the similarity of the outcomes of the experiments conducted by Litvak & Leggett (1992), which employed both active and passive predators, suggests that these differences may not be as great as expected.

The findings reported by Litvak & Leggett (1992) and supported by Pepin *et al.* (1992) suggest that, contrary to most assumptions being drawn from the 'bigger is better' hypothesis, for individual members of a cohort of larvae being smaller at a given age could, under some conditions, and at certain stages of development, confer a survival advantage. This difference in perspective derives from an explicit recognition of the reality that, in nature, individual larvae exist, and are preyed upon, as members of a population characterized by evolving distributions of ages, sizes and sizes at age. Hence, individual vulnerability will be a function of the structure of these distributions, and of the predators' response to them.

For all of the above reasons, many of the inferences currently being drawn from the 'bigger is better' hypothesis require careful rethought. In particular, the often hypothesized inverse relationship between feeding and growth rates and predation losses requires re-examination. If the relationships illustrated in Fig. 13 prove valid, the impact of predation on larval survival (and potentially on recruitment) will depend significantly on the timing of that predation relative to the developmental stage of individuals within a population of larvae and on the frequency distribution of individual sizes relative to that developmental stage. The latter is likely to depend, in turn on the feeding history of the larvae at earlier ages.

For example, if predation is most intense early in larval development, differential predation on larger individuals within a population consisting of a mixture of several cohorts could negate any survival advantage accruing from favourable feeding conditions experienced by members of individual cohorts at earlier stages (including the period of transition to exogenous feeding). Such an effect could, for example, explain the absence of a relationship between feeding success in the early larval stages of northern anchovy and recruitment to age 1 as reported by Peterman *et al.* (1988). In contrast, if predation is most intense at later stages in larval development when the gross vulnerability of large and small larvae within a cohort is more similar no such effect would be expected. This expectation is supported by the work of Bertram (1993), who controlled for the interactive effects of size and age in predation trials involving recently metamorphosed winter flounder exposed to the predatory shrimp *Crangon septemspinosa*. He found, as predicted by the Litvak & Leggett (1992) model, no evidence of size or age related bias in gross vulnerability to predation in recently metamorphosed flounder.

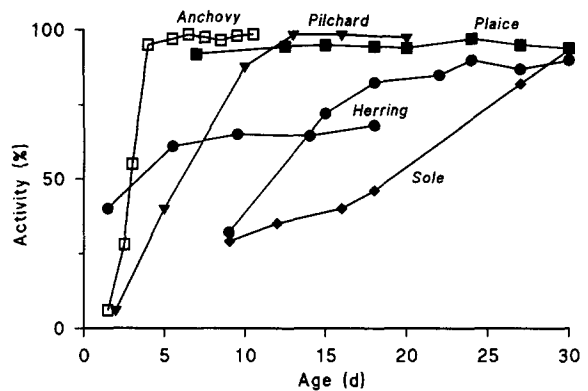


Fig. 12. Relationship between age (size) and the percentage of time spent in active behaviours by larval fishes (redrawn from Blaxter, 1986).

It is likely, too, that the shape of the dome-shaped function, and the age of maximum vulnerability of large and small larvae, will be species, or at least group (clupeoid, gadoid, etc.), specific. Moreover, as Bailey & Houde (1989) have noted, the form of the vulnerability vs age function can be expected to vary in relation to the feeding mode of the predator and, in particular, the way in which feeding mode influences susceptibility (measured as the combined probability of attack and capture) to predation.

4.2. THE 'STAGE DURATION' HYPOTHESIS

The 'stage duration' hypothesis, also known as the

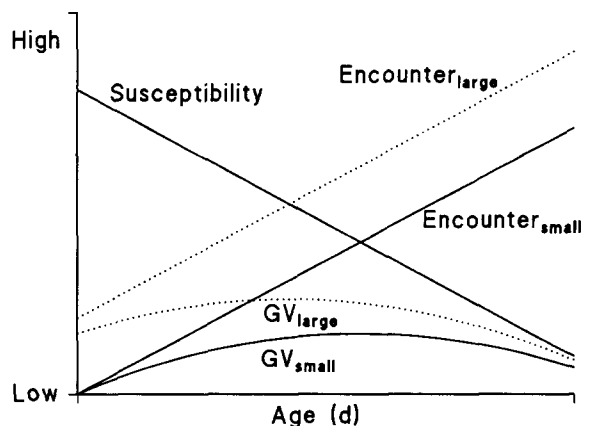


Fig. 13. Conceptual model of the influence of size and of age related changes in encounter, attack and capture probabilities on gross vulnerability of larval fishes to predation. (redrawn from Litvak & Leggett, 1992). $Encounter_{large}$ = probability of encounter of large larvae as a function of age. $Encounter_{small}$ = probability of encounter of small larvae as a function of age. GV_{large} = gross vulnerability of large larvae as a function of age. GV_{small} = gross vulnerability of small larvae as a function of age.

'single process' (Cushing, 1975), predicts that larvae which experience favourable feeding conditions, and therefore grow quickly, will achieve metamorphosis at earlier ages and experience lower cumulative mortality due to predation during the larval stage when mortality rates are known to be high. This expectation is supported by the finding that variance in sizes at metamorphosis in larval fishes is lower than variance in sizes at intermediate ages between hatching and metamorphosis, thereby implying a 'target size' for metamorphosis (Chambers *et al.*, 1988). Ages at metamorphosis are much more variable than size at metamorphosis, and are more plastic to manipulations of temperature, food level and crowding (Chambers & Leggett, 1987).

Chambers & Leggett (1987) and Houde (1987) examined the implications of the observed variability in time to metamorphosis in larval fishes and concluded, independently, that such variability could result in up to 100-fold changes in the numbers of larvae surviving to the juvenile stage. Luecke *et al.* (1990) have recently drawn similar conclusions from their simulation modelling of the effects of predation by alewife (*Alosa pseudoharengus*) on larval bloater (*Coregonus hoyi*). Solid empirical support for the hypothesis is, however, limited.

Bertram (1993) recently reviewed 42 papers in which a positive relationship between rapid growth and high survival through the larval period was inferred. Only three provided data which clearly supported the proposed interaction. Perhaps the most compelling evidence for a positive relationship between growth rate and survival to date has been developed within the Cod Recruitment Program of the Ocean Production Enhancement Network (OPEN). Meekan, Fortier & Desbiens (Laval University - Quebec, pers. comm.) have shown, through otolith analyses, that larvae which lived more than 80 days were, on average, growing faster and were larger at age than the rest of the population at earlier ages. These findings are consistent with Pepin & Myers' (1991) finding that recruitment variability was positively correlated with the difference in size at hatching and size at metamorphosis (which they inferred to be equivalent to larval stage duration) when these parameters were assessed across 86 stocks representing 21 species. Their assumption that the difference in hatching and metamorph sizes equates to the duration of the larval period (*i.e.* that growth rates during the larval stage are equal in all species considered) requires validation before this generalization is fully justified. In addition, Pepin & Miller (1993) have correctly cautioned against inferring within-species patterns from cross species comparisons. In their analysis of the potential effects of variation in stage duration, both Chambers & Leggett (1987) and Houde (1987) assumed that instantaneous mortality rates during the larval period were constant with respect to size, age and growth rates. However, as

noted above, Oiestad (1985), De Lafontaine & Leggett (1988), Fuiman (1989), Litvak & Leggett (1992) and Pepin *et al.* (1992) have reported higher rates of predatory losses among larger or faster-growing larvae in mesocosms. Such differential mortality could counter, or even negate, the potential advantages of reduced stage duration.

Bertram (1993) used the model developed by Luecke *et al.* (1990) to re-examine the implications of size and or age related variability in larval mortality rates on the stage duration hypothesis. In formulating their model, Luecke *et al.* (1990) made the assumption that encounter rates do not vary with prey size. While valid for bloater and alewife, which were the subject of their analysis, this assumption is not readily generalizable to other species. Incorporation of a size-dependent encounter rate function into the model completely reversed the outcome. Whereas Luecke *et al.* (op. cit.) concluded that faster growing larvae would experience lower cumulative mortality during the larval stage (Fig. 14a) as predicted by the 'stage duration' hypothesis, Bertram's (1993) analysis indicated a higher cumulative larval stage mortality to a given age for faster growing larvae (Fig. 14b).

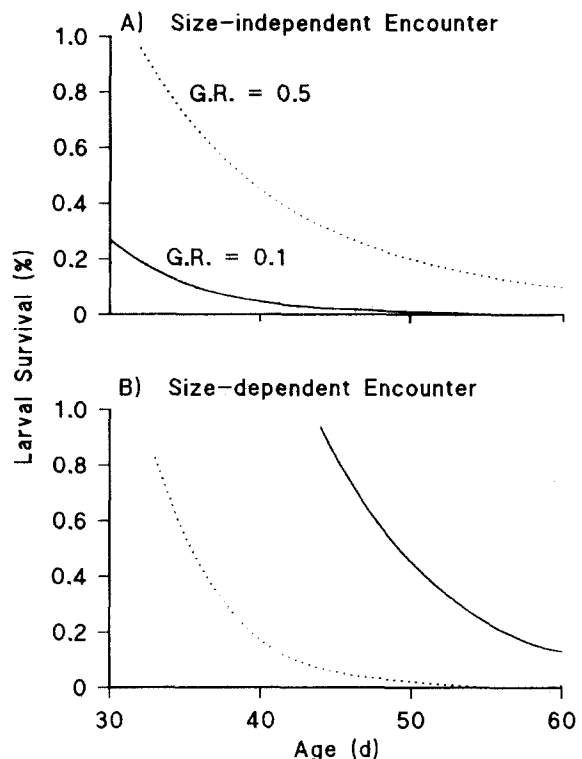


Fig. 14. Percent cumulative survival to 60 d for fast and slow growing larvae as determined from simulation models in which encounter rates were: A. constant and independent of larval size; B. curvilinear and positive with respect to larval size (redrawn from Bertram, 1993).

However, given that metamorphosis in larval fishes tends to be size- rather than age-related (Chambers & Leggett, 1987), the cumulative mortality to metamorphosis could be higher in slower-growing larvae even if their cumulative mortality to a given age were lower than that of fast-growing larvae. In a second series of simulations Bertram (1993) examined this possibility. He found that if encounter probabilities increase as a function of growth rates the survival benefits of rapid growth are diminished, and could render cumulative survival to a common size (metamorphosis) equivalent in fast- and slow-growing larvae. Further analytical and experimental study of the form and magnitude of size, age, and growth-dependent mortality during the larval stage is clearly needed given the demonstrated importance of these functions to the validity of predictions derived from the 'bigger is better' and the 'stage duration' hypotheses.

5. CONCLUSION

Notwithstanding the conflicting and often indirect nature of the information currently available on the role of food and predation as regulators of early life stage survival in marine fishes, a conclusion that recruitment in marine fishes is not regulated by starvation and predation in the egg and larval stages does not appear to be justified at this time.

This conclusion is supported by the recent work of Myers & Cadigan (1993a, 1993b) and by a substantial body of direct and indirect evidence of positive relationships between recruitment and egg and larval abundance, larval survival, and by plausible causal links between food and/or predation and these relationships.

It is also important to note that the failure, to date, to find consistent relationships between food abundance and/or predation on the one hand, and egg and larval survival and/or recruitment on the other, is not strong evidence in favour of the alternate hypothesis, currently gaining popularity, that interannual variability in survival during the juvenile life stage is the most important contributor to recruitment variability (May, 1984; Smith, 1985; Sale, 1990). As has been detailed above, several of the fundamental assumptions related to the dominant hypotheses of the era are now in need of careful re-examination.

It is also becoming increasingly obvious that the either/or approach to food vs predation as the primary cause of variability in larval survival is flawed. Feeding conditions may influence larval survival and recruitment directly. However, the scarcity of evidence supporting this causal link suggests that the major influence of food may be indirect, and may operate principally through its regulation of the timing and intensity of mortality due to predation. Critical experimental and field based tests of the assumptions underlying the hypotheses that have dominated thinking in this field, and creative exploration of the

potential of alternative hypotheses that are emerging, are prerequisites to advancement in this field.

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