PERSPECTIVES

Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework[1]

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Understanding the mechanisms controlling recruitment in fishes is a major problem in fisheries science. Although the literature on recruitment mechanisms is large and growing rapidly, it is primarily species specific. There is no conceptual framework to integrate the existing information on larval fish ecology and its relationship to survival and recruitment. In this paper, we propose an integrating framework based on body size. Although all larval fish are small relative to adult fish, total length at hatching differs among species by an order of magnitude. As many of the factors critical to larval survival and growth are size dependent, substantially different expectations arise about which mechanisms might be most important to recruitment success. We examined the evidence for the importance of size to feeding and starvation, to activity and searching ability, and to risk of predation. Regressions based on data from 72 species of marine and freshwater species suggest that body size is an important factor that unifies many of the published observations. A conceptual framework based on body size has the potential to provide a useful integration of the available data on larval growth and survival and a focus for future studies of recruitment dynamics.

La compréhension des mécanismes régissant le recrutement des poissons est un sujet important de l'halieutique. Bien que l'on dispose d'un grand nombre de documents sur les mécanismes du recrutement et que ceux-ci augmentent rapidement, il s'agit surtout d'un phénomène spécifique d'espèce. Il n'existe pas de cadre conceptuel pour intégrer les données existantes sur l'écologie des larves de poisson et son rapport avec la survie et le recrutement. Dans le présent article, nous proposons un cadre intégré fondé sur la taille. Bien que toutes les larves soient petites par rapport à l'adulte, la longueur totale à l'éclosion diffère d'un ordre de grandeur entre les espèces. Étant donné que plusieurs des facteurs critiques pour la survie des larves et leur croissance sont fonction de la taille, des hypothèses très différentes sont formulées relativement aux mécanismes qui pourraient être très importants pour le succès du recrutement. Nous avons étudié les données relatives à l'importance de la taille par rapport à l'alimentation et à l'inanition, à l'activité et à l'aptitude à chercher la nourriture, et le risque de prédation. D'après des régressions fondées sur des données provenant de 72 espèces de poissons marins et dulçaquicoles, la taille est un facteur important qui constitue un point commun dans plusieurs observations publiées. Un cadre conceptuel fondé sur la taille peut permettre une intégration utile des données disponibles sur la croissance et la survie des larves et constitue un sujet en vue d'autres études sur la dynamique du recrutement.

nterest in larval fishes and factors influencing recruitment variation has increased rapidly in recent decades (Blaxter 1974; Lasker and Sherman 1981). A field that had been dominated by a seemingly endless search for the "stock–recruitment" relationship has focused increasing effort on understanding *mechanisms* underlying recruitment, whether they be largely driven by environmental variation or biotic interactions. Recent interest in earlier life history stages was stimulated by the need to understand sources of variation in the adult

population size of exploited species. All larval fish are small relative to the size of adults, producing the perception that they will have similar ecological responses to important abiotic or biotic variables. Yet a careful analysis of the literature quickly reveals that larvae of different species differ widely in their response to these variables.

Historically, most studies of factors affecting larval fish survival and subsequent recruitment to the adult population have taken a single-species approach. In general, attempts to extend the results of such species-specific research to other larval fishes have met with limited success because these studies often reached conflicting conclusions regarding the key factors gov-

erning survival. For instance, some species appear highly vulnerable to starvation (Lasker 1975, 1978), while others are more likely controlled by predation or abiotic factors (Lett and Kohler 1976; Winters 1976; Hunter 1981; Bailey and Houde 1988).

Body size has long been recognized as an important variable influencing many aspects of the physiology, ecology, and behavior of living organisms (Thompson 1917; McMahon and Bonner 1983; Peters 1983; Calder 1984). While all larval fish are small, length at hatching varies among species by over an order of magnitude. Thus, initial weight may vary by three or more orders of magnitude. Moreover, while many fish increase in weight by more than five orders of magnitude over their life span, three orders of magnitude of this change may occur in the first year of life (Werner and Gilliam 1984; Houde 1987). If one were to allocate research effort to fishes scaled by weight stanzas (physiological time) rather than by years (calendar time), one would spend much less time on large adults (where body size does not change much) and would concentrate on dynamics in the first year of life.

If size-dependent processes are important, one should expect substantial differences in larval life histories based on differences among species in body size at hatching. Many factors influencing the behavior and physiology of larval fish are likely to be size dependent (Hunter 1981). Small larvae may be more susceptible to starvation because of the limited energy reserves in their yolk sac (Hunter 1981). In addition, small larvae may have short reactive distances and limited swimming abilities which will limit their searching ability (Blaxer 1986; Webb and Weihs 1986). The size of food particles ingested depends on both mouth gape and the ability to capture the particle, both of which clearly increase with larval size (Hunter 1981). Body size will also influence vulnerability to predators through differential encounter rates, escape ability, and predator gape limitation (Blaxter 1986; Zaret 1980). The effects of size-dependent processes acting on larval fishes may be profound. They must be considered comprehensively and the effects of various size-dependent mechanisms must be integrated to fully understand their role in survival and subsequent recruitment variability.

Generally, the implications of body size have been well investigated for larger juvenile and adult fishes. But these size-dependent relationships have not been thoroughly elaborated for larval fishes. The purpose of this paper is to examine the empirical evidence for the importance of size-dependent processes to the ecology of larval fish and to establish a conceptual framework that will integrate the available species-specific observations into a more general perspective. In this way, size-dependent ecological characteristics of particular species may be placed in a larger context, and work on the larval ecology of little studied species may profit more directly from previous research.

Methods

To start our investigation of the influence of body size on larval survival and subsequent recruitment, we hypothesized functional relationships between a number of life history traits and body length at hatching or at later points in the larval or juvenile stage. The traits we chose can be divided into four main categories related to feeding, activity, vision, and predation risk (Table 1). While all of the traits influence subsequent recruitment, for many the effect is indirect, acting through larval growth rate to influence the probability of larval survival.

To assess our proposed hypotheses, we surveyed the literature for relevant data, focusing our effort on papers published in the last 5 yr. We examined fisheries and aquatic journals as well as previously published reviews (Hunter 1981; Blaxter and Hunter 1982; Blaxter 1986). We only included studies on species that do not show significant parental care after hatching.

Total length was used as our measure of body size. Some of the traits we examined are probably more closely tied to weight than length, but weight is more difficult to measure and was rarely reported. We recognize that temperature is likely to affect some of these traits, particularly those related to metabolic rate. Unfortunately, the reviewed experiments were usually done at "typical" temperatures for the species being studied, rather than over a range of temperatures. Consequently, it was impossible to account for temperature effects using ANOVA techniques. For appropriate variables, we addressed the influence of temperature by repeating our analysis after standardizing results to 15°C using $Q_{10} = 2.3$ (Checkley 1984). This approach provides some indication of whether the size effects persist, independent of temperature. Other variables, including methodological differences among studies, are likely to contribute to variance in size-dependent relationships. However, as an initial step, using total length as a measure of size should be adequate to identify the generalities we seek.

We found information on 72 species of marine (54), freshwater (16), and anadromous (4) fishes from 30 different families (Table 2). The data included here are derived from 128 references out of more than 500 we examined.[2] The examined species provide a wide range of body size at hatching, thus enhancing our ability to detect size-related patterns in the data. Our analysis includes studies on species with egg diameters ranging from 0.8 to 9.7 mm (Fig. 1a) and length at hatching ranging from 1.6 to 17.6 mm (Fig. 1b). Although portions of the literature have previously been reviewed (Hunter 1981; Blaxter and Hunter 1982; Blaxter 1986; Webb and Weihs 1986), it has not been reviewed to examine a broad set of a priori hypotheses regarding the mechanisms controlling recruitment.

Criteria for inclusion of data from a particular species for each trait were decided prior to the review. Where possible, the original literature reference was used instead of later reviews. In most cases, data were derived from tables given in the original paper, but in some cases, data were interpolated from graphs. No single reference provided data on all traits for a particular species. If no larval hatching size was given in a reference, we substituted an average value from other references for that species. These averages were calculated from values given in as many references as possible. All other data were included as the original authors presented them; we did not judge the data or sort the results according to methods or "quality." All data were converted to standard units (Table 1). The data were analysed for the degree of fit to the hypothesized relationships using either a linear or simple exponential function. We report the function giving the best fit. In all cases the value of "n" quoted with the regression equation is the number of independent observations used by the analysis. Calculations were done using Statistical Analysis System (SAS Corporation, Cary, NC) at the Triangle Universities Computing Center.

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[2]A complete listing of the original references used in this review is provided in the Appendix. The data used to develop the regression relationships given below are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

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TABLE 1. Larval traits considered in this analysis, their definitions, and units of measurement.

Trait (units)	Definition
Yolk absorption (d)	Time taken to fully absorb the yolk from hatching
Point of no return (d)	Time after which the effects of starvation are irreversible, i.e. even if feeding is resumed, the larva still dies. It is defined for an individual, but can only be measured for a group
First possible feeding (d)	Time at which a larva is first physically or anatomically capable of feeding
First typical feeding (d)	Time at which larvae usually feed for the first time, defined for a group
Time to 50% mortality (d)	Time taken for half of the larvae in a group to die when starved
Sustained swim speed (cm/s)	Speed at which fish swim for extended period of time
Burst swim speed (cm/s)	Speed attained in short sprints, usually during prey capture attempts or in predator avoidance
Reactive distance (mm)	Maximum distance at which a potential prey item is recognized as such
Search volume (L/h)	Function of sustained swim speed and reactive distance: equivalent to the volume of water searched per unit time
% capture success	Percent of all "observed" capture attempts that were successful

Results

For each larval trait (Table 1), we first present our a priori hypothesis for its relationship with larval length and then the data from the literature to evaluate the hypothesis. Within each category, some traits relate directly to larval size at hatching, while others are general functions of body length for post-hatching larvae and juveniles.

Feeding and Larval Size

Initially, a larva obtains nutrition from its yolk, and later from food in the environment. To avoid starvation, a larva must be able to feed before its yolk supply is depleted. Accordingly, the importance of starvation in early life history depends upon the traits that govern access to both endogenous and exogenous sources of food.

Egg size sets a limit on the size of larva that can hatch from it (length at hatch = 1.96 + 1.89 egg diameter, $r^2 = 0.40$, $p < 0.0001$, $n = 100$). Within this limit, the partitioning of resources between larva and yolk supply may vary (Blaxter and Hempel 1963). An index of the amount of yolk available to a larva, relative to its energy demands, is the time to absorption of the yolk supply. The time to yolk absorption depends upon yolk volume, which is an exponential function of yolk sac diameter. Therefore, we hypothesized the time to yolk absorption to be an accelerating function of hatching length.

Time to yolk absorption did increase with larval length at hatching. Contrary to expectation, a linear model gave the best fit (Fig. 2). Times to yolk absorption varied from slightly longer than 1 d in 2.9-mm bay anchovy (*Anchoa mitchilli*) (Houde 1974) to 20 d in 9.9-mm *Coregonus wartmanni* (Braum 1967). Times to yolk absorption for marine, freshwater, and anadromous species were not significantly different (demonstrated by a nonsignificant habitat × length interaction, $F_{2,82} = 2.65$, $p = 0.079$), although the freshwater species we examined did tend to have longer times to yolk absorption. When standard-ized to 15°C to remove potential temperature effects, the strength of the size-dependent relationship increased, accounting for an additional 7% of the variation. This suggests a robust size-dependent relationship. The greater yolk supply of a large larva affords it greater flexibility in when it can shift to exogenous food than does the limited yolk of a small larva, even when the temperature differences are accounted for.

No larva can feed before it is functionally capable (i.e. its mouth and digestive system must have developed), but it must feed prior to reaching irreversible starvation or a "point of no return" (PNR). These limits define the period within which first feeding must occur if the larva is to survive. To understand size-dependent patterns in larval susceptibilities to starvation, one must understand how size influences first possible feeding and PNR. To assess these patterns, we proposed three hypotheses, summarized in Fig. 3.

Hypothesis 1
As large larvae are generally more developed at hatching than small larvae, we proposed that time to first possible feeding would be a negative function of larval size at hatching.

Hypothesis 2
Large larvae have more yolk and a larger body mass than small larvae. Therefore, we hypothesized that time to PNR would be a positive function of body length at hatching. Because PNR is likely related to the volume of the larva's energy reserves, we proposed an accelerating function.

Hypothesis 3
The difference between time to PNR and first possible feeding is an index of the flexibility allowed in timing of first feeding. In combination, the two previous hypotheses suggest that larvae hatching at large sizes experience a greater "window of opportunity" in which to first feed than larvae hatching at small sizes.

Hypothesis 1 was supported by the data, although the relationship is rather noisy (Fig. 4). Time to first possible feeding

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TABLE 2. Families and species of marine, freshwater, and anadromous fishes used in this study (listings are according to habits reported in the studies used). Numbers refer to references (Appendix) used to provide data for the analysis.

Marine

Ammodytidae
    Ammodytes hexapterus   92
Atherinidae
    Atherina presbyter, sandsmelt   90
    Leuresthes tenuis, grunion   81
Belonidae
    Belone belone. garfish   102
Blenniidae
    Coryphoblennius galerita, Montagu's blenny   30
Bothidae
    Paralichthys olivaceus   55
    Scopthalmus maximus, turbot   4, 8, 124
Carangidae
    Trachurus symmetricus, jack mackerel   2, 5, 113, 114, 115
Clupeidae
    Alosa sappidissima, American shad   58, 109
    Brevoortia patronus, gulf menhaden   38
    Brevoortia tyrannus, Atlantic menhaden   37, 38
    Clupea harengus, herring   9, 10, 12, 13, 76, 77, 83, 103, 108, 115, 116, 123
    Harengula pensacolae, scaled sardine   47
    Sardina pilchardus, pilchard   11, 13, 104
    Sardinops caerula, Pacific pilchard   1, 60, 65
Cottidae
    Ascelichthus rhodorus, rosylip sculpin   79
Cyprinodontidae
    Fundulus heteroclitus, mummichog   58, 95, 109
Engraulidae
    Anchoa mitchilli, bay anchovy   45, 48, 58
    Engraulis capensis, cape anchovy   17
    Engraulis japonica, japanese anchovy   33
    Engraulis mordax, northern anchovy   31, 51, 52, 54, 63, 66, 67, 84, 89, 115, 121, 122
    Engraulis ringens, Peruvian anchoveta   57, 101, 119
Gadidae
    Gadus morhua, Atlantic cod   8, 9, 61, 70, 115
    Merlangius melangus, whiting   40
    Melanogrammus aeglefinus, haddock   68, 70
    Merluccius productus, Pacific hake   3, 7
    Theragra chalcogramma, walleye pollock   88
Haemulidae
    Haemulon plumieri, white grunt   107
Labridae
    Lachnolaimus maximus, hogfish   20
Lophiidae
    Lophius piscatorius, angler   71
Percichthyidae
    Morone saxatilis, striped bass   58
Pleuronectidae
    Embassichthys bathybius, deepsea sole   98
    Hippoglossoides platessoides, American plaice   50
    Isopsetta isolepis, butter sole   99
    Limanda ferragunea, yellow tailed flounder   21, 49, 127
    Limanda limanda, dab   87
    Parophrys vetulus, English sole   64
    Platichthys flesus, flounder   10
    Pleuronectes platessa, European plaice   8, 9, 13, 82, 105, 106, 126
    Pseudopleuronectes americanus, winter flounder   18, 69
Sciaenidae
    Genyonemus luneatus, white croaker   120
    Leiostomus xanthurus, spot   93, 94
    Sciaenops ocellatus, red drum   74

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TABLE 2. (Concluded)

Scombridae	
Scomber japonicus, Pacific mackerel	53, 62
Serranidae	
Paralabrax clathratus, kelp bass	19
Paralabrax maculatofasciatus, barred sand bass	19
Paralabrax nebulifer, spotted sand bass	19
Soleidae	
Achirus lineatus, lined sole	45, 48
Solea solea. sole	13, 124
Sparidae	
Archosargus rhomboidalis, sea bream	45, 46, 48, 111
Lithognathus mormyrus	27
Sparus aurata, gilthead	128
Stenotomus chrysops, scup	34
Sphyraenidae	
Sphyraena borealis, northern sennet	44

Freshwater

Centrarchidae	
Lepomis macrochirus, bluegill	110, 117
Clupeidae	
Alosa pseudoharengus, alewife	36, 58, 59, 96, 109
Cyprinidae	
Aspidoparia morar, Indian carp	78
Danio rerio. zebra danio	32
Leuciscus leuciscus, dace	85, 124
Percidae	
Perca flavescens, yellow perch	23, 42, 43, 110
Stizostedion canadense, sauger	86
Stizostedion vitreum vitreum, walleye	43, 58, 75, 80, 86
Salmonidae	
Coregonus artedii. lake herring	23, 39, 56, 109, 124
Coregonus clupeaformis. lake whitefish	15, 23, 41, 109, 112
Coregonus hoyi, bloater	15, 97
Coregonus laverutus, Lake Syamozero whitefish	14, 15, 24
Coregonus pollan, pollan	25
Coregonus schiuzi	26
Coregonus wartmanni, Lake Constance whitefish	16
Salmo trutta. brown trout	6

Anadromous

Clupeidae	
Alosa sappidissima, American shad	22, 125
Gadidae	
Microgadus tomcod. Atlantic tomcod	91
Percichthyidae	
Morone saxatilis, striped bass	29, 100
Salmonidae	
Salvelinus alpinus, Arctic char	118

varied by a factor of 24 among larvae of different sizes. White croaker (*Geryonemus lineatus*), the species with the smallest larvae (1.8 mm at hatch), first fed after 3 d (Watson 1982). In contrast, the largest species, garfish (*Belone belone*), 13.5 mm at hatch, first fed after only 5 h (Rosenthal and Fonds 1973). The longest time to first possible feeding, 5 d, was shared by a variety of small marine, freshwater, and anadromous species.

Hypothesis 2 was also supported. Contrary to expectation, a linear model gave the best fit to the data (Fig. 4). In species for which we have data, times to PNR varied from an average of 3.4 d for the smallest (1.9 mm) lined sole (*Achirus lineatus*) (Houde 1974) to 18 d in the largest (9.4 mm) lake herring (*Coregonus artedii*) (John and Hasler 1956). Differences in temperature between studies could have a large effect on time to

PNR. However, when standardized to 15°C to remove temperature effects, the r^2 changed only slightly (Fig. 4). This suggests a robust size-dependent relationship independent of temperature effects. Large values of PNR may be underrepresented in the data set, as experiments on a number of larger species were ended after a set time, often before the larvae had reached their PNR. Data from such species could not be included in this analysis.

To evaluate hypothesis 3, we analysed the difference between PNR and first feeding using only those six studies that reported both variables. These restricted data conform to the general regression analysis for the first two hypotheses found in the entire data set (Fig. 4). Regression analysis indicated that the difference between PNR and first feeding increased signifi-
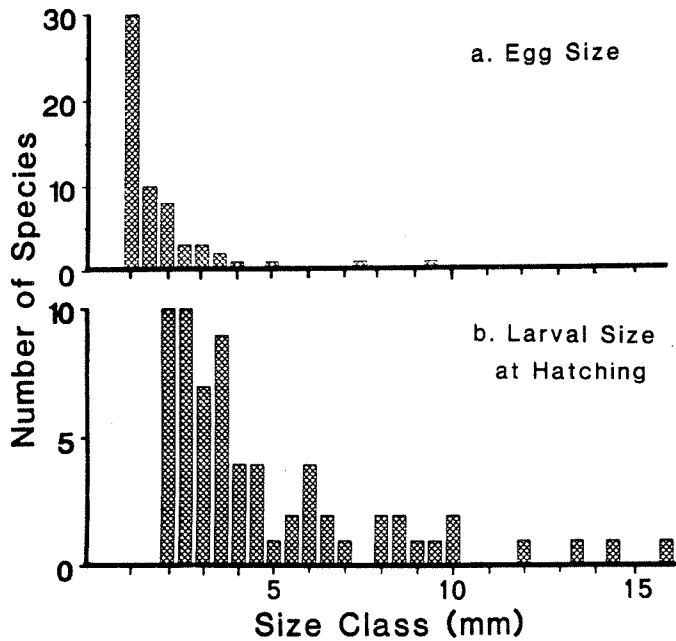
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FIG. 1. (a) Frequency distribution of egg diameter of 40 species of freshwater and marine fishes included in this analysis. (b) Frequency distribution of larval total length at hatching for 66 species of freshwater and marine fishes included in this analysis. In both cases, some species are represented more than once.
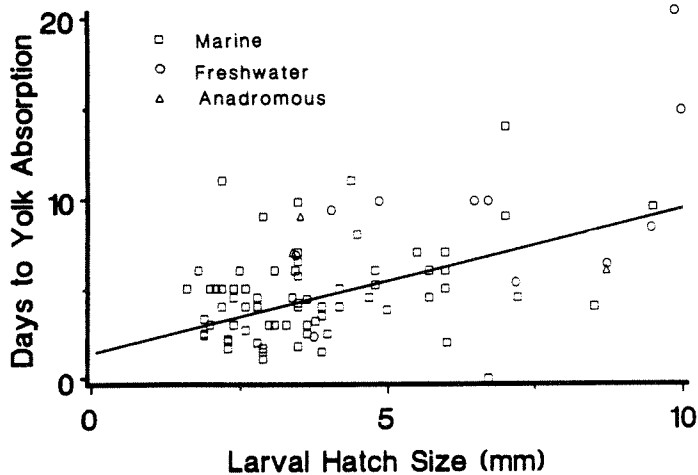

FIG. 2. Time to yolk absorption as a function of larval total length at hatching. Days to yolk absorption = $2.06 + 0.782$ length, $r^2 = 0.26$, $p < 0.0001$, $n = 88$ independent estimates of time to yolk absorption for 58 species. When standardized to 15°C: days to yolk absorption = $4.76 + 1.3$ larval length, $r^2 = 0.33$, $p < 0.0001$, $n = 88$.
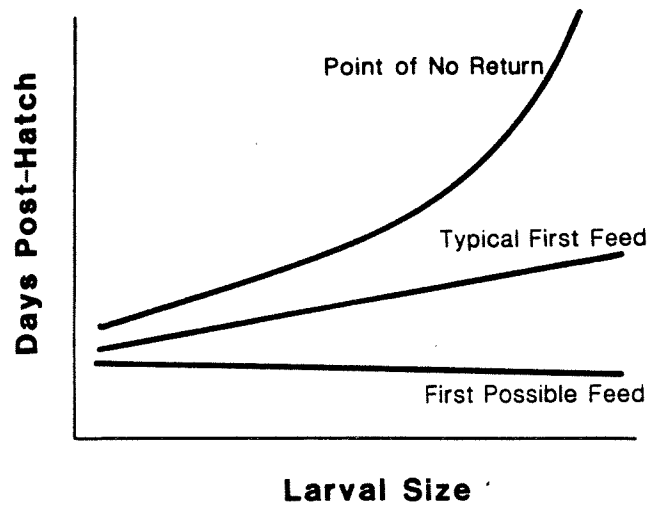

FIG. 3. Hypothetical relationship between different points in the feeding chronology of larval fish and larval length at hatching.
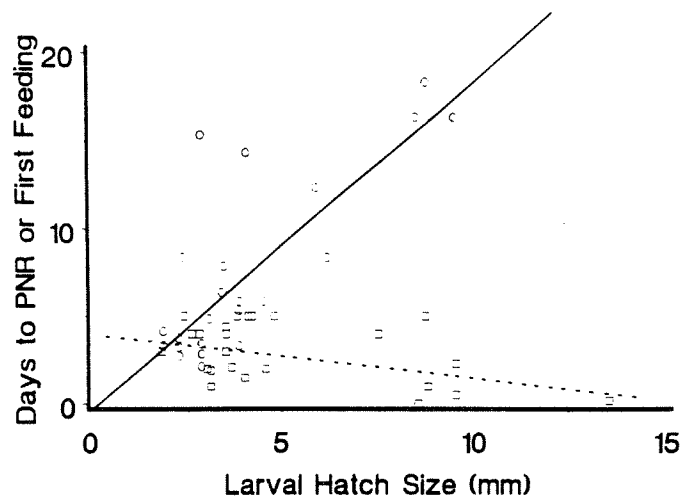

FIG. 4. Time to point of no return (circles) or to first possible feeding (squares) as a function of larval total length at hatching. Using all available data, the regression equations are as follows: days to first possible feeding = $4.09 - 0.237$ length, $r^2 = 0.169$, $p = 0.04$, $n = 25$ independent estimates based on 19 species (broken line); days to PNR = 1.82 length $- 0.19$, $r^2 = 0.61$, $p < 0.0001$, $n = 22$ independent estimates based on 16 species (solid line). When standardized to 15°C: time to PNR = $2.29 + 2.09$ length, $r^2 = 0.57$, $p < 0.0001$, $n = 25$. Regression equations were similar for six species for which both time to first possible feeding and PNR were measured: days to first possible feeding = $5.39 - 0.55$ length, $r^2 = 0.52$, $p = 0.10$; days to PNR = $0.58 + 1.90$ length, $r^2 = 0.69$, $p = 0.38$.

cantly with larval size ($y = 2.46$ length $- 4.809$, $r^2 = 0.89$, $p < 0.0044$, $n = 6$). Even small increases in body size at hatching apparently confer large benefits in terms of flexibility in time to first feeding. For every 0.1-mm increase in length at hatching, larvae gain about 6 h in which to find food; for each 1-mm increase in length at hatching, the "window of opportunity" to feed opens nearly 2.5 d. Larvae that hatch at a large size have a broad "window of opportunity" between the time to first possible feeding and the time to PNR during which they can find appropriate food.

Based on hypothesis 3, we hypothesized that the time when larvae first typically feed should increase and become more variable with increased hatching size (Fig. 3). The determina-

tion of time to first typical feeding in the literature is less precise than that for first possible feeding. Accordingly, our interpretation is more cautious. Measures of first typical feeding may depend as much upon when food was offered as upon when the fish were first able to feed. Nevertheless, this measure lends support to our hypothesis. We found a significant increase in typical times to first feeding with increased hatching size (time to first typical feeding = $2.14 + 0.678$ length, $r^2 = 0.178$, $p = 0.0006$, $n = 63$). More interestingly, species with large sizes at hatching also showed greater variance in timing of first feeding. To illustrate this point, the absolute value of the residuals of the predicted values in the time to first feeding regression increases significantly with hatching size ($r^2 = 0.658$, p
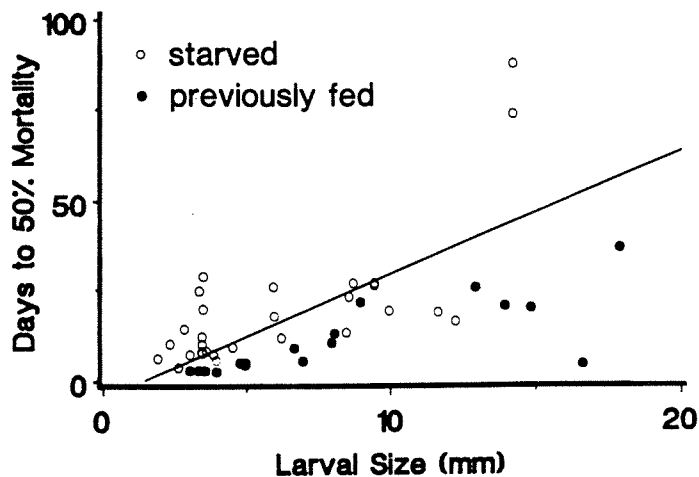
FIG. 5. Days to 50% mortality for a cohort of starved larvae as a function of larval total length at hatching. Days to 50% mortality = 3.60 length − 4.36, r^2 = 0.52, p < 0.0001, n = 29 independent estimates based on 21 species. When standardized to 15°C: time to 50% mortality = 1.27 + 4.17 length, r^2 = 0.58, p < 0.0001, n = 29.

< 0.0001, n = 63). This reinforces the expected increase in "window of opportunity" to first feeding with increases in larval size at hatching.

While time to PNR is a meaningful measure of larval ability to survive starvation, it is difficult to establish empirically. Instead of PNR, many investigators have measured response to starvation as the time to 50% mortality for a batch of larvae. These data showed the same trend as time to PNR; time to 50% mortality increased significantly with larval size (Fig. 5). Again, temperature may have a strong effect on time to 50% mortality. When we standardized the data to 15°C to account for these effects, a slightly improved fit was obtained. The standardized equation accounted for an additional 6% of the variation in the data. This suggests a robust size-dependent relationship, independent of temperature.

We have been emphasizing the importance of the first feeding in larvae because it is generally believed that once larvae have fed, the risk of death due to starvation is substantially reduced. This is the kernel of Lasker's (1975, 1978) interpretation of Hjort's (1914) critical period hypothesis. To assess this, we compared resistance to starvation in larvae that had already started to feed with those that had never fed. There was a significant interaction between prior feeding and length on time to 50% mortality ($F_{1,42}$ = 6.5, p = 0.015). Regardless of species, at any given length, we found equal or greater times to 50% mortality in those larvae that were relying on yolk reserves when compared with those that had fed and were subsequently starved (Fig. 5). This suggests that first-feeding larvae are no more vulnerable to starvation than larvae that are of a similar size which have previously fed and subsequently starve. Larvae appear more susceptible to starvation at first feeding only because that is when they are smallest! The influence of starvation or nutritional state on the performance of larval fish should be considered for larvae beyond the first feeding stage of their life history.

In summary, we suggest that a larger hatching size in fish confers resistance to starvation as a result of an increased time to 50% mortality, increased time to PNR, and increased flexibility in the timing of first feeding.
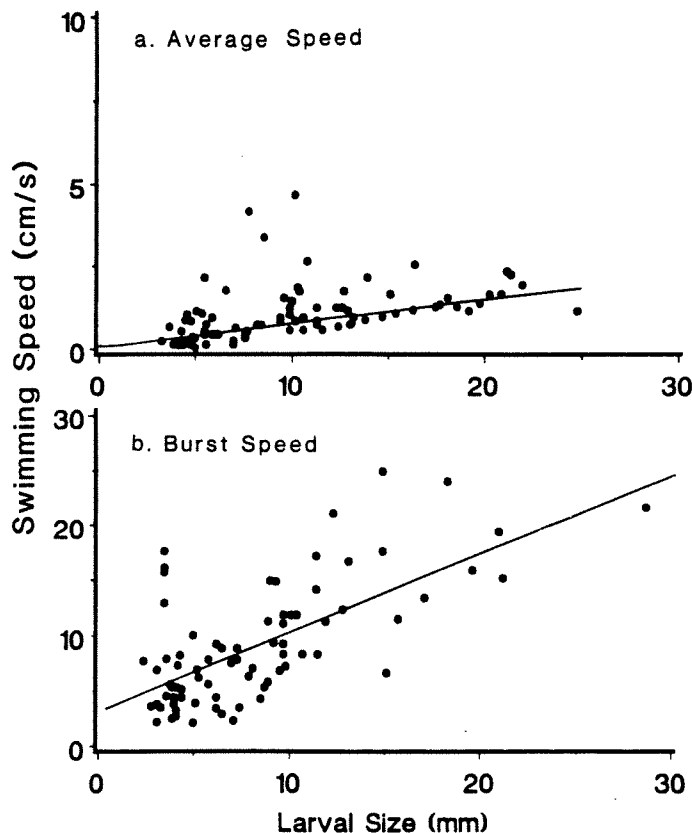
FIG. 6. (a) Average swimming speed as a function of larval total length. $\log_{10}$ speed = 1.07 $\log_{10}$ length − 1.11, r^2 = 0.46, p < 0.0001, n = 93 independent speed measurements on different sizes of larvae of nine species derived from 17 studies. (b) Burst swimming speed as a function of larval total length. Burst speed = 3.33 + 0.71 length, r^2 = 0.45, p < 0.0001, n = 76 independent speed measurements on different sizes of nine species derived from 17 studies.

Activity and Larval Size

Two potential determinants of larval survival are encounter rate with food (Laurence 1972) and ability to escape predators (Webb 1981). Both are influenced by larval activity. Consequently, the pattern and extent of larval activity may be an important factor in determining growth and survival of larvae (Webb and Corolla 1981; Weihs 1980).

Large larvae generally are more developed at hatching and have more energy reserves than small larvae. We therefore hypothesized that large larvae would become active earlier than small larvae. The data on larval activity are extremely limited but suggest that larvae that hatch at small sizes do have a longer time to maximum activity than do large larvae. Northern anchovies (2.9 mm) do not reach maximum activity until they are more than 4 d post-hatch (Hunter 1972); bloaters (9.5 mm) actively swim 100% of the time within 6 h of hatching (Rice et al. 1987a). Several other examples of small larvae generally agree with the anchovy data (Blaxter 1986), but we need additional data on the activity of species of intermediate and larger sizes to further assess the exact form of this relationship.

Larvae characteristically exhibit two types of swimming (Webb and Weihs 1986). Sustained swimming at almost constant speed is most common and is used primarily in searching for food (Hunter 1972). Larvae also swim in fast bursts which serve as both attack and escape responses and have a high energy requirement (Webb and Corolla 1981; Eaton and DiDomenico 1986). The size dependency of both swimming modes has long

been recognized (Bainbridge 1958: Webb 1975; Blaxter 1986). Following Blaxter (1969, 1986) and Hunter (1972, 1981), we proposed that both within and among species, sustained and burst speed would be accelerating positive functions of larval length.

In agreement with this hypothesis, sustained swimming speed was positively related to larval length (Fig. 6a). Burst swimming speed also increased with larval size (Fig. 6b), affording large larvae an advantage in the ability to gain food or escape predators. The swimming speed data we reviewed were variable. Differences in the swimming ability of species with substantially different morphologies at the same body size account for some of the observed variation (Webb and Weihs 1986). The differing times over which performance was measured may also account for some of the variation. In addition, a variety of methods have been used to estimate swimming speeds, such that the same species can be ascribed quite different abilities (e.g. herring, *Clupea harengus*) (Rosenthal and Hempel 1969; Blaxter and Staines 1971).

In summary, swimming ability is correlated with body size in larval fishes. Large larvae probably become active earlier than small larvae, affording them increased mobility. Moreover, not only can large larvae swim for longer periods of time, they also can swim faster. This greater speed is apparent both in sustained and burst performance. This implies that large larvae experience a higher encounter rate with food. Additionally, they will experience a higher encounter rate with potential predators (see de Lafontaine and Leggett 1988), but are likely better able to escape them once encountered.

Vision and Larval Size

Vision is an important sense in larval fish, influencing feeding ability and predator avoidance (Blaxter 1986). Changes in the complexity of the eye during development lead to increased visual performance as measured by reactive distance (Blaxter and Staines 1971), visual acuity (Rahmann et al. 1979; Neave 1984), and sensitivity to light (Blaxter 1968). At hatching, the eyes in many teleosts are nonpigmented and not fully functional. Consequently, the rate at which visual development occurs may well regulate survival by influencing when feeding begins. We hypothesized that reactive distance should increase with larval size because visual performance is related to larval development. Search volume, the product of reactive distance and swimming speed, should exhibit a similar increase with larval size.

The limited data available are completely summarized in Blaxter (1986) and support these expectations. The relationship between reactive distance and size is much stronger within a species in a particular study than across species. This may be due in part to investigators using different definitions of reactive distance. In some studies, the estimate of reactive distance used may more accurately be interpreted as a strike distance, and consequently, the distances may not be comparable from one study to another (e.g. Rosenthal and Hempel 1969; Blaxter and Staines 1971). Further, prey sizes were different between studies, also contributing to variation in the estimates of reactive distance (O'Brien 1979). In general, however, reactive distance increases significantly with larval length ($\log_{10}$ reactive distance $= 1.56 \log_{10}$ length $- 1.92$, $r^2 = 0.58$, $p < 0.0001$, $n = 31$ independent estimates based on three species derived from four studies).

Published data on search volume are also completely summarized in Blaxter (1986). Search volume also increased sig-
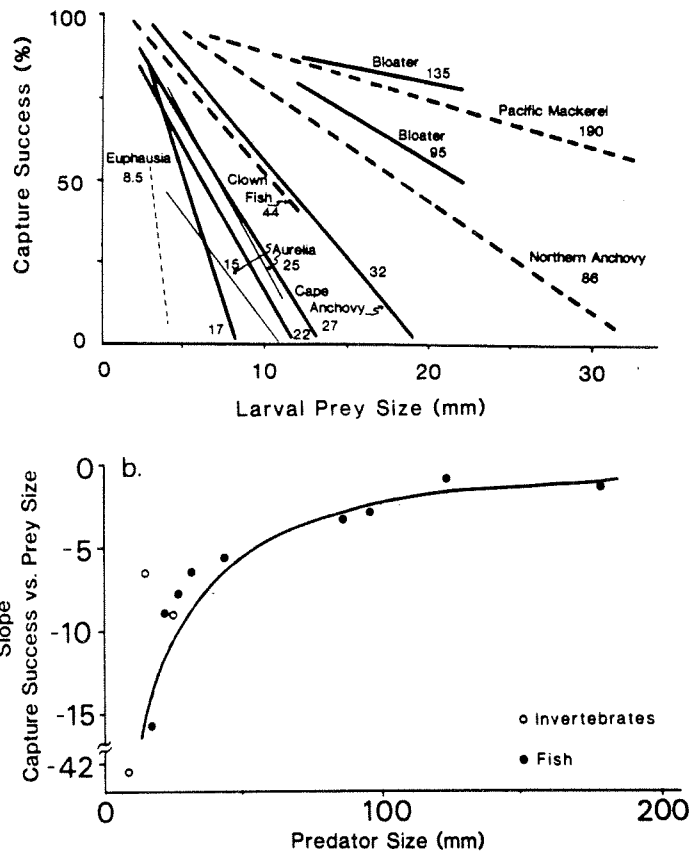

FIG. 7 (a) Capture success for different species and sizes of predators on different species and sizes of larval prey. Linear regressions were fit to the original data so that slopes could be compared. Predator species and sizes are listed adjacent to each line. Heavy lines indicate vertebrate predators; thin lines indicate invertebrate predators. Heavy solid lines for bloater and cape anchovy indicate cannibalism, light solid lines indicate larval herring as prey, and broken lines used northern anchovy as prey. All studies were done in relatively small aquaria with no alternative prey available. (b) Slopes of % capture success versus prey size regressions from Fig. 7a as a function of predator total length. Fish predators are indicated by solid circles; invertebrate predators are indicated by open circles. A large negative slope indicates a rapid decline in capture success with increasing prey size. The fitted equation is slope $= -((\text{predator size} + 63.8)/255)^{-2.53}$.

nificantly with larval length (search volume $= 0.307$ length $- 1.237$, $r^2 = 0.421$, $p < 0.0001$, $n = 51$ independent estimates based on seven species derived from eight studies). The limited range of reactive distances reported suggests that size-dependent swim speeds probably have a significant influence on search volume estimates (Blaxter 1986). In addition, laboratory studies may have underestimated swim speeds by up to 20% due to sensory deprivation (Westernhagen and Rosenthal 1979), which may increase the variability in the data. Nonetheless, general trends in the vision data among species are similar (Blaxter 1986).

In conclusion, large larvae should be better able to visually detect both food and potential predators, presumably affording them a higher probability of survival than small larvae.

Predation and Larval Size

Predation has frequently been cited as a significant cause of mortality in both fish eggs and larvae (Crowder 1980; Hunter 1981). The predators may come from a variety of taxa including
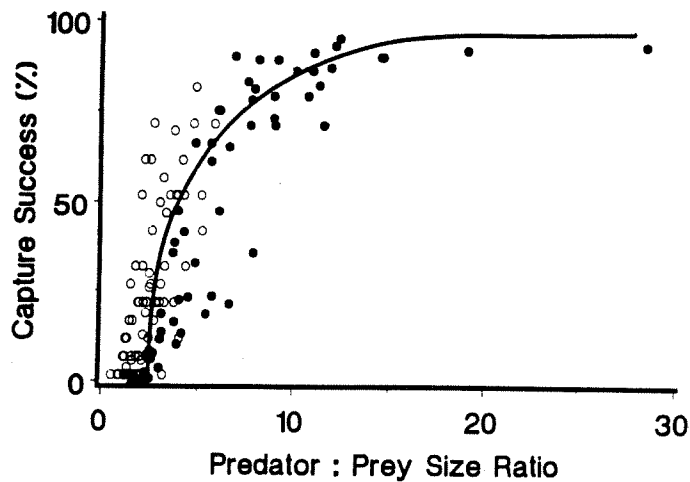
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FIG. 8. Capture success as a function of predator to prey length ratio. Points are original data from regressions included in Fig. 7a. Open circles represent invertebrate predators and solid circles represent fish predators. The equation for the fitted line is capture $= 100 - ((\text{ratio} + 3.37)/44.76)^{-2.28}$.

several phyla of marine invertebrates, other fishes, and even conspecifics (Hunter 1981; Brownell 1985). Although many factors influence the impact of predation, sizes of both predators and prey have been found to be important determinants of predation in aquatic systems (Brooks and Dodson 1965; Werner and Gilliam 1984; Kerfoot and Sih 1987). The ratio of predator size to prey size has been suggested as a reasonable scalar of predator–prey interactions (Werner and Hall 1974; Werner 1977; Werner and Gilliam 1984; Crowder 1985).

In general, we expected that probability of capture per attempt would decline with increasing larval length (Folkvord and Hunter 1986). When alternative prey are available, one might expect risk of predation by a predator of a particular size to depend upon the relative sizes of prey (Werner 1977; Werner and Gilliam 1984). Both small and large prey may be of lower utility (sensu Werner 1977) than those of intermediate sizes. In terms of optimal foraging theory, risk of predation for larval fish of a particular size should depend upon the size structure of the predator field and the abundance and utility of alternative prey. Unfortunately, few experiments on predation risk for larval fish have been performed with alternative prey (but see Pepin et al. 1987; de Lafontaine and Leggett 1988).

Published experimental studies on size-based patterns of predation on larval fish included predation by both invertebrates and other fish species, as well as cannibalism. We used capture success, the percentage of capture attempts observed that were successful, as a measure of size-based predation risk because few studies estimated predation rates or functional responses to prey density directly.

We investigated capture success of different sized predators as a function of prey size by fitting simple linear regressions to the published data for each predator–prey pair (Fig. 7a). Two features of the predator–prey interactions are evident. First, small predators are restricted to both smaller sizes and a narrower range of prey than large predators. Second, the capture success of small predators is influenced more dramatically by changes in prey size than is success of large predators. To demonstrate this, we plotted the slopes of the capture success regressions as a function of predator size (Fig. 7b). These slopes appear to describe one functional relationship despite the fact that they include different types and sizes of predators from

euphausiids (8.5 mm) to adult Pacific mackerel (*Scomber japonicus*) (20 times larger). A steep slope indicates a large change in capture success for a small change in prey size. As a predator's size increases, its expected capture success will be influenced less by prey size. For example, predators greater than 120 mm are affected little by the size of larval prey once encountered, yet for predators less than 50 mm the size of prey attacked is critically important in determining capture success. However, even though 190-mm Pacific mackerel have a high probability of capture for 10-mm northern anchovy larvae, they may not select these prey in the field if alternative prey are available.

To place these relationships in a more general context, we analyzed the relationship between capture success and the predator–prey size ratio using the raw data rather than the slopes of the relationships from individual studies. The results further underscored the importance of size in regulating predation processes as well as the generality of this dependence (Fig. 8). Capture success varied from zero in several cases to a maximum of 96% for 135-mm bloater eating 10.9-mm bloater larvae (Rice et al. 1987a). There was no substantial difference between the capture successes of similar sized vertebrate and invertebrate predators which included body forms as different as euphausiids and jellyfish. The analysis suggests that a predator 15–17 times larger than its prey would experience 100% success per attempt at capturing prey. Below this size ratio the relative sizes of predator and prey exert considerable influence on capture success. In fact, the smaller the size ratio, the greater the influence of changes in size in determining capture success.

In summary, the incidence of predation is affected by both predator size and prey size. Larvae may drastically reduce their susceptibility to smaller predators by outgrowing them. But there seems to be no larval size refuge from predators that are 15 or more times the size of the larval prey. Future studies should examine risk of predation with alternative prey, so that prey selectivity for larvae can be assessed in more realistic terms.

Discussion

Size-based scaling of physiological and ecological processes is well known from juvenile and adult fish (Brett and Groves 1979; Mittelbach 1981; Werner and Gilliam 1984) and has been broadly applied to other ecological questions (Peters 1983; Calder 1984). Until now, no analyses had been done for larval fish. We recognized that species of larval fish differ dramatically in morphology, developmental status at hatching, environmental temperature, and physiological or behavioral capabilities, so we questioned whether body size alone could integrate the existing data. Although body size alone clearly has limitations, we were pleased by how well the published data fit our general size-based expectations.

In particular, we view several of the results of this analysis as contributing new insights. Most important was the commonality of the relationships we found among fishes from diverse taxa and different habitats. Clearly, the importance of starvation as a factor in the recruitment of larval fish diminishes with increasing size. Larvae that are large at hatching are resistant to starvation, but more importantly, they have a greater flexibility (window of opportunity) in first feeding times. For example, herring from different geographic stocks hatch out at body sizes between 6 and 8.2 mm (Blaxter and Hempel 1963). If we ignore temperature, our analysis suggests that at this dif-

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ference in body size, the larger larvae would have about 5.5 d more time to find appropriate food before they reach a point of no return. This suggests that even small size differences of larvae at hatching can have significant ecological implications and that even within a species (e.g. herring), size at hatching might be an adaptive response to local geographic conditions.

We found no evidence to suggest that first-feeding larvae are any more vulnerable to starvation than larvae of a similar size which have been fed and subsequently starved (if anything, the reverse is true because the first-feeding larvae often still have yolk). This suggests that nutritional condition may be important for larvae at any stage; there is nothing "critical" about the first feeding period per se. Small larvae are simply more vulnerable to starvation than larger larvae. Not surprisingly, studies promoting the starvation hypothesis and a "critical period" at first feeding (Lasker 1975, 1978, 1981) involved relatively small marine larvae. If this work had been done with a larger larva, perhaps the current emphasis on the starvation hypothesis in the literature would not have been so strong.

The strong size dependence of capture success shown among predators from euphausiids to adult Pacific mackerel has substantial implications for understanding predation mortality of larvae. It suggests that if the size of a larva is known, some predators can be eliminated a priori as being too small to have much effect, while others which may be important can be identified from the extent of spatial overlap with appropriately sized predators. Surprisingly, the predators on larval fish need not be large or have a typical predator morphology. Most predators in our review could capture prey up to 40–50% of their body length. Probability of capture per attempt approaches 1.0 as the predator–prey length ratio approaches 15–17.

Further generalization regarding predator–prey interactions will become possible if two limitations can be addressed. First, the existing data are for probability of capture per attempt; there is little basis to model or predict the encounter rate between predators and larvae. Second, we know little about prey choice by predators once prey (larval fish) are encountered. The available experiments on predation on fish larvae generally were done without alternative prey (but see Pepin et al. 1987; de Lafontaine and Leggett, 1988). If we are to understand the potential effects of predators on larval fish recruitment, we need to be able to forecast prey choice in predators (i.e. will they select larval fish from among their alternatives?). We will also need estimates of consumption rates (e.g. functional responses of predators to larval fish density with and without alternative prey). Some of the current optimal foraging models (Werner 1977; Mittelbach 1981; Werner and Gilliam 1984) and bioenergetics models (Kitchell et al. 1977; Kitchell 1983) should prove helpful as starting points.

It is important to note that starvation and predation cannot be considered to be alternative (or independent) recruitment mechanisms. Because predation risk is size dependent, growth rates will directly influence the probability of mortality due to predation (Post and Prankevicius 1987). Starvation or poor nutrition can directly influence risk of predation by reducing swim speed or escape ability of larvae (Frank and Leggett 1982; Rice et al. 1987a). Reduced growth rates also prolong the period of vulnerability to gape-limited predators (Werner and Gilliam 1984), leading to reduced recruitment. Clearly, we need to better understand how feeding, growth rates, and risk of predation interact in the ecology of larval fishes.

Some of the relationships we demonstrate are neither new nor unexpected. Several previous workers have published sim-

ilar results (e.g. Blaxter 1986). Previously, however, the effect of size has not been comprehensively considered. It should be clear that many of the traits examined interact. An advantage in one leads to an advantage in another, forming a positive feedback loop. Consequently, even tiny initial size differences may translate into substantial differences in survival and subsequent recruitment (Adams and DeAngelis 1987). In light of this, we feel that it is important to focus research efforts on individuals rather than populations. Population statistics such as average growth rate or cohort mortality rates may contain less information than an analysis based on individual larvae (Rice et al. 1987b). As the average larval fish in a cohort dies in the first week of life, it is more relevant to know what is unique about the survivors.

Recently, several techniques have been developed that allow us to follow individuals. Otolith analysis, where possible, allows characterization of individuals. In this way, patterns of survival can be related to abiotic and biotic variability (Methot 1983; Crecco and Savoy 1985; Rice et al. 1987b). There is evidence that scale ageing could be used in a similar way (Healey 1982). The increased power of modern computers allows for growth and survival models that follow the fates of individuals. Huston et al. (1988) clearly demonstrated the advantages gained by using individual-based analyses. Such an analysis allows abiotic factors such as temperature and biotic factors such as food availability and predation to be integrated to forecast individual growth rates and survival (Kitchell et al 1977; Stewart and Binkowski 1986). Finally, new genetic techniques, such as those involving mitochondrial DNA, may afford a finer understanding of the pattern of reproductive success of individuals in a population (Wilson et al. 1987).

The approach we present here lends itself to addressing individual-based questions. It suggests strongly that even subtle differences in size between individuals may have profound effects on their fates. Not only is an average value important, but the variance around that average may have equal importance. Further, our approach implicitly recognizes the importance of interactions between factors controlling survival in larval fish.

The general size-based framework we have proposed is not meant to be the final statement, nor is it meant to be predictive for particular species. But it does seem useful as a general context in which to think further about the early life histories of fishes. If larval size at hatching is known, the relationships we report provide important insights into which factors are likely to be important to the survival and growth of individual larvae. But more importantly, there may be factors which can be disregarded a priori. Further, small differences in larval length at hatching can have profound implications for which recruitment mechanisms are likely to be important. This framework has already begun to assist us in addressing old conflicts in the literature; we hope it also admits new questions that more readily take advantage of the previous research on recruitment mechanisms in larval fishes.

Acknowledgements

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Appendix

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