

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/249530880>

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

Article in *Canadian Journal of Fisheries and Aquatic Sciences* · September 1988

DOI: 10.1139/f88-197

CITATIONS

1,335

READS

828

4 authors:



Thomas J. Miller

University of Maryland Center for Environmental Science

146 PUBLICATIONS 6,093 CITATIONS

SEE PROFILE



Larry B Crowder

Stanford University

336 PUBLICATIONS 31,738 CITATIONS

SEE PROFILE



James A. Rice

North Carolina State University

95 PUBLICATIONS 6,303 CITATIONS

SEE PROFILE



Elizabeth A. Marschall

The Ohio State University

93 PUBLICATIONS 4,516 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Global Seafood Market Studies [View project](#)



IOC Marine Spatial Planning Programme [View project](#)

Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework¹

Thomas J. Miller, Larry B. Crowder, James A. Rice, and Elizabeth A. Marschall

Department of Zoology, North Carolina State University, Raleigh, NC 27695-7617, USA

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45: 1657–1670.

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.

Received January 20, 1988

Accepted May 25, 1988

(J9551)

Reçu le 20 janvier 1988

Accepté le 25 mai 1988

Interest 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-

¹Paper No. 11677 in the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695, USA.

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 (Blaxter 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.

²A 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.

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 \times 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

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.

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

TABLE 2. (Concluded)

Scombridae	
<i>Scomber japonicus</i> , Pacific mackerel	53, 62
Serranidae	
<i>Paralabrax clathratus</i> , kelp bass	19
<i>Paralabrax maculatofasciatus</i> , barred sand bass	19
<i>Paralabrax nebulifer</i> , spotted sand bass	19
Soleidae	
<i>Achirus lineatus</i> , lined sole	45, 48
<i>Solea solea</i> , sole	13, 124
Sparidae	
<i>Archosargus rhomboidalis</i> , sea bream	45, 46, 48, 111
<i>Lithognathus mormyrus</i>	27
<i>Sparus aurata</i> , gilthead	128
<i>Stenotomus chrysops</i> , scup	34
Sphyraenidae	
<i>Sphyraena borealis</i> , northern sennet	44
Freshwater	
Centrarchidae	
<i>Lepomis macrochirus</i> , bluegill	110, 117
Clupeidae	
<i>Alosa pseudoharengus</i> , alewife	36, 58, 59, 96, 109
Cyprinidae	
<i>Aspidoparia morar</i> , Indian carp	78
<i>Danio rerio</i> , zebra danio	32
<i>Leuciscus leuciscus</i> , dace	85, 124
Percidae	
<i>Perca flavescens</i> , yellow perch	23, 42, 43, 110
<i>Stizostedion canadense</i> , sauger	86
<i>Stizostedion vitreum vitreum</i> , walleye	43, 58, 75, 80, 86
Salmonidae	
<i>Coregonus artedii</i> , lake herring	23, 39, 56, 109, 124
<i>Coregonus clupeaformis</i> , lake whitefish	15, 23, 41, 109, 112
<i>Coregonus hoyi</i> , bloater	15, 97
<i>Coregonus laverutus</i> , Lake Syamozero whitefish	14, 15, 24
<i>Coregonus pollan</i> , pollan	25
<i>Coregonus schiuzi</i>	26
<i>Coregonus wartmanni</i> , Lake Constance whitefish	16
<i>Salmo trutta</i> , brown trout	6
Anadromous	
Clupeidae	
<i>Alosa sappidissima</i> , American shad	22, 125
Gadidae	
<i>Microgadus tomcod</i> , Atlantic tomcod	91
Percichthyidae	
<i>Morone saxatilis</i> , striped bass	29, 100
Salmonidae	
<i>Salvelinus alpinus</i> , 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-

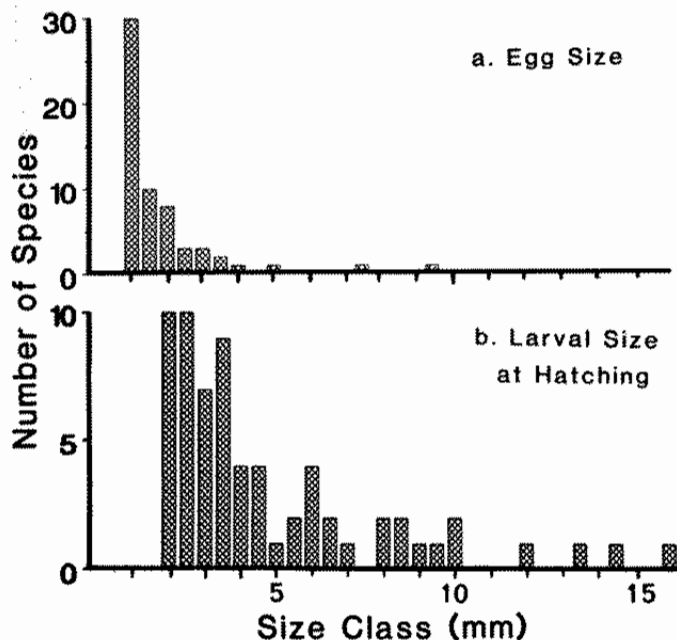


FIG. 1. (a) Frequency distribution of egg diameter of 40 species of freshwater and marine fishes included in this analysis. (b) Frequency distribution of larval total length at hatching for 66 species of freshwater and marine fishes included in this analysis. In both cases, some species are represented more than once.

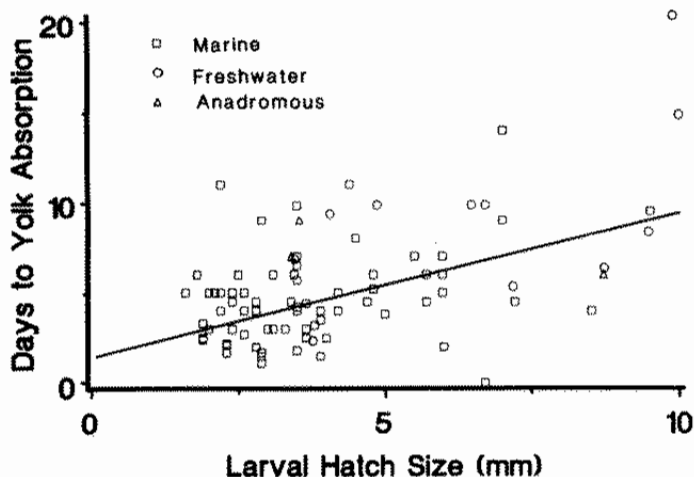


FIG. 2. Time to yolk absorption as a function of larval total length at hatching. Days to yolk absorption = $2.06 + 0.782 \text{ length}$, $r^2 = 0.26$, $p < 0.0001$, $n = 88$ independent estimates of time to yolk absorption for 58 species. When standardized to 15°C : days to yolk absorption = $4.76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

cantly with larval size ($y = 2.46 \text{ length} - 4.809$, $r^2 = 0.89$, $p < 0.0044$, $n = 6$). 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-

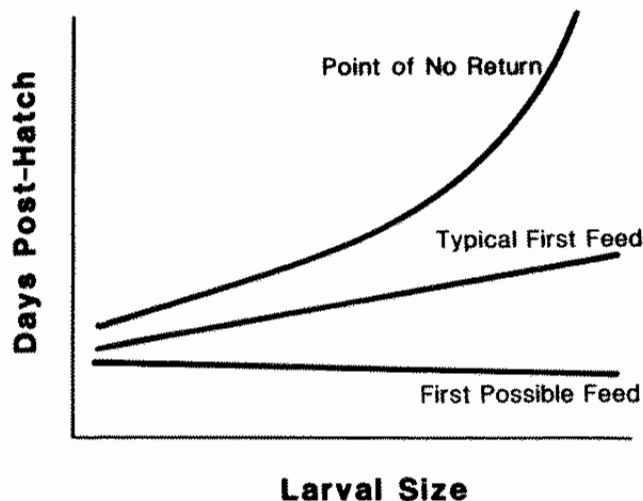


FIG. 3. Hypothetical relationship between different points in the feeding chronology of larval fish and larval length at hatching.

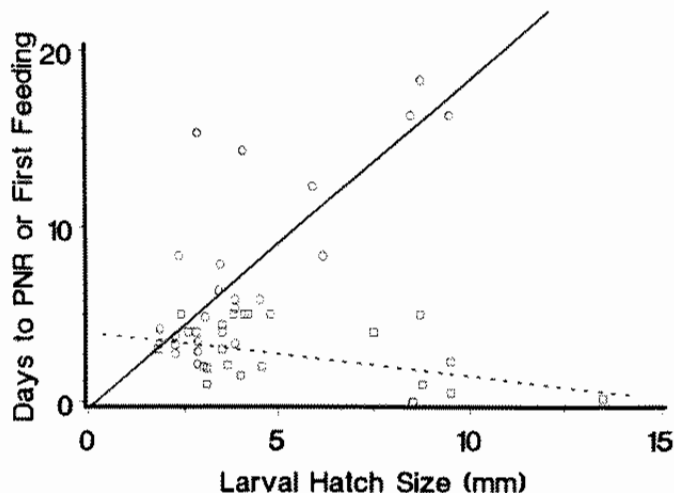


FIG. 4. Time to point of no return (circles) or to first possible feeding (squares) as a function of larval total length at hatching. Using all available data, the regression equations are as follows: days to first possible feeding = $4.09 - 0.237 \text{ length}$, $r^2 = 0.169$, $p = 0.04$, $n = 25$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

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 = $2.14 + 0.678 \text{ length}$, $r^2 = 0.178$, $p = 0.0006$, $n = 63$). 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

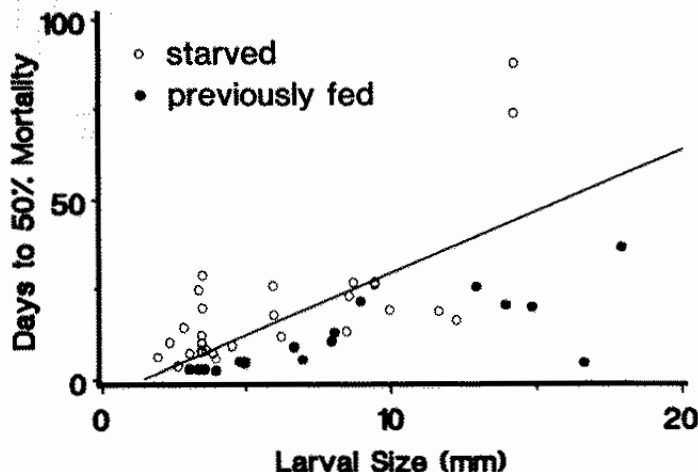


FIG. 5. Days to 50% mortality for a cohort of starved larvae as a function of larval total length at hatching. Days to 50% mortality = $3.60 \text{ length} - 4.36$, $r^2 = 0.52$, $p < 0.0001$, $n = 29$ independent estimates based on 21 species. When standardized to 15°C : time to 50% mortality = $1.27 + 4.17 \text{ length}$, $r^2 = 0.58$, $p < 0.0001$, $n = 29$.

< 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.

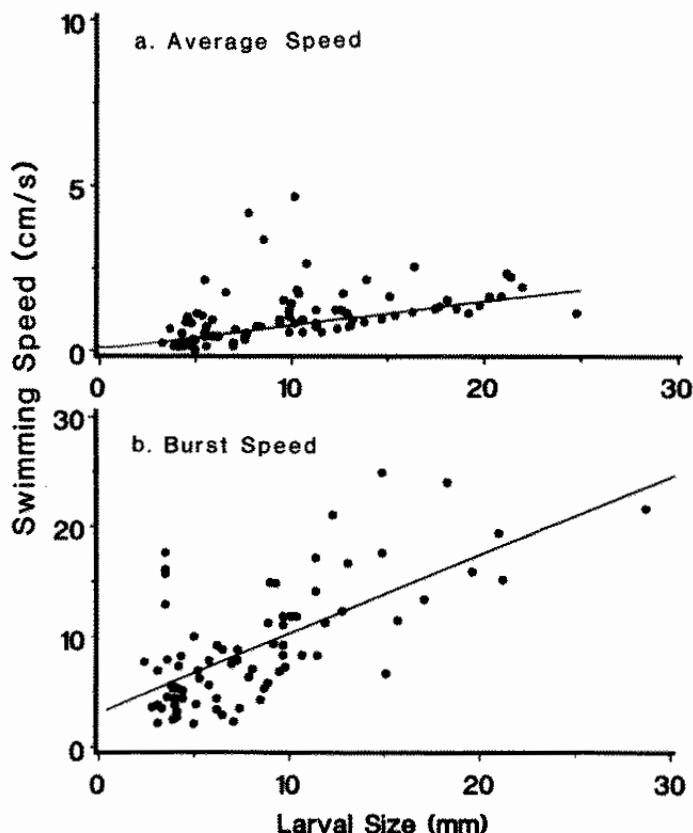


FIG. 6. (a) Average swimming speed as a function of larval total length. $\log_{10} \text{ speed} = 1.07 \log_{10} \text{ length} - 1.11$, $r^2 = 0.46$, $p < 0.0001$, $n = 93$ independent speed measurements on different sizes of larvae of nine species derived from 17 studies. (b) Burst swimming speed as a function of larval total length. Burst speed = $3.33 + 0.71 \text{ length}$, $r^2 = 0.45$, $p < 0.0001$, $n = 76$ 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-

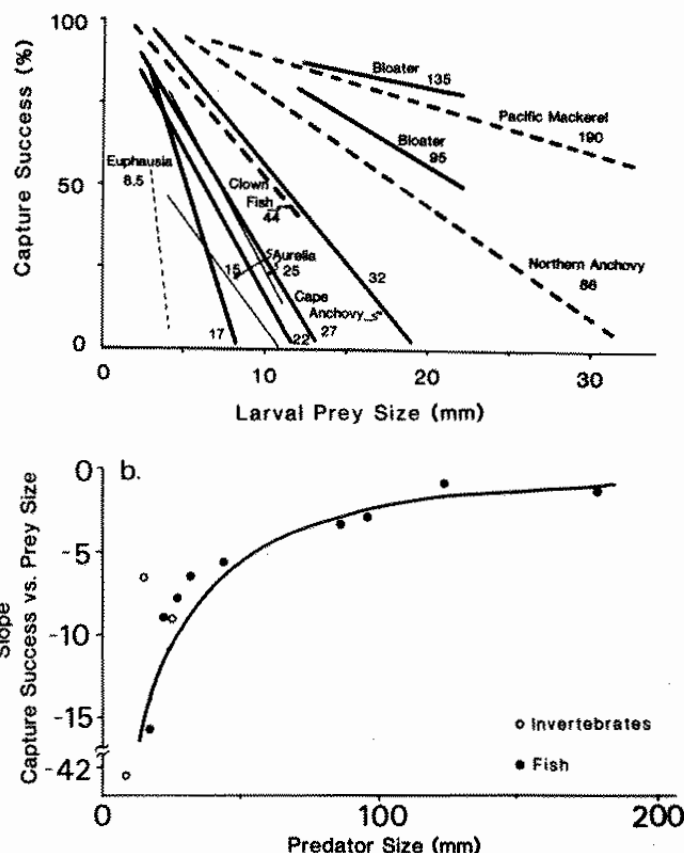


FIG. 7 (a) Capture success for different species and sizes of predators on different species and sizes of larval prey. Linear regressions were fit to the original data so that slopes could be compared. Predator species and sizes are listed adjacent to each line. Heavy lines indicate vertebrate predators; 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 $\text{slope} = -((\text{predator size} + 63.8)/255)^{-2.53}$.

nificantly with larval length (search volume = $0.307 \text{ length} - 1.237$, $r^2 = 0.421$, $p < 0.0001$, $n = 51$ 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

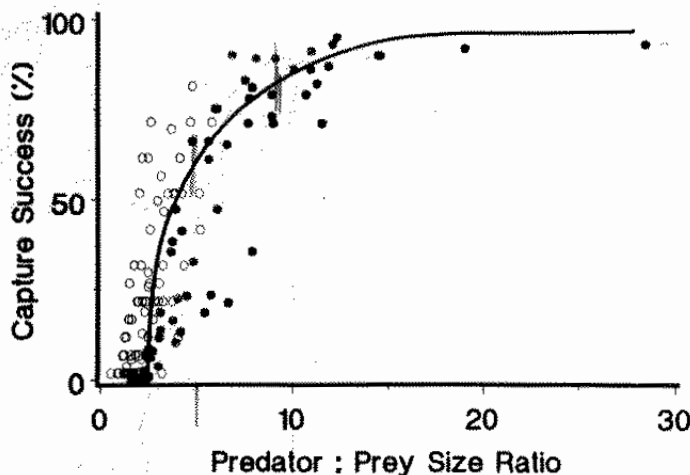


FIG. 8. Capture success as a function of predator to prey length ratio. Points are original data from regressions included in Fig. 7a. Open circles represent invertebrate predators and solid circles represent fish predators. The equation for the fitted line is $\text{capture} = 100 - ((\text{ratio} + 3.37)/44.76)^{-2.28}$.

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-

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 Prankevicus 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

An earlier version of this paper was presented at the Tenth Larval Fish Conference, American Fisheries Society, Miami, Florida, May 1986. We thank Ed Houde for the invitation to that meeting and the opportunity to elaborate these ideas. Kevin Bailey, Dave Checkley, Bob Francis, Gene Fritz, Ed Houde, John Hunter, Bill Leggett, Sam Mozley, and an anonymous reviewer provided useful discussions dur-

ing the development of this paper. Our research over the last decade has been supported by the University of Wisconsin Sea Grant College Program under grants from the Office of Sea Grant, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin, Federal Grant NA800AA-D-00086, Projects R/LR-15, R/LR-22 and R/LR-33. More recently, we have been supported by the University of North Carolina Sea Grant and the State of North Carolina, Federal Grant NA85AA-D-SG022, Projects R/ES-39 and R/MER-12, and by the University of North Carolina Marine Science Council. Computer funds were provided by the Department of Zoology at NCSU.

References

- ADAMS, S. M., AND D. L. DEANGELIS. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics, p. 103-117. In W. C. Kerfoot and A. Sih [ed.] Predation in aquatic ecosystems. University of New England Press, Hanover, NH.
- BAILEY, K. M., AND E. D. HOEDE. 1988. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. (In press)
- BAINBRIDGE, R. 1958. The speed of swimming fish as related to body size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35: 109-133.
- BLAXTER, J. H. S. 1968. Light intensity, vision and feeding in young plaice. J. Exp. Mar. Biol. Ecol. 2: 293-307.
1969. Swimming speeds of fish. FAO Fish Rep. 62. Vol. 2: 69-100.
1974. The early life history of fish. Springer-Verlag, Berlin. 765 p.
1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115: 98-114.
- BLAXTER, J. H. S., AND G. HEMPEL. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Int. Explor. Mer 28: 211-240.
- BLAXTER, J. H. S., AND J. R. HUNTER. 1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1-223.
- Blaxter, J. H. S., and M. E. Staines. 1971. Food searching potential in marine fish larvae, p. 467-485. In D. J. Crisp [ed.] Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.
- BRAUM, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply, p. 113-131. In S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.
- BRETT, J. R., AND T. D. GROVES. 1979. Physiological energetics, p. 279-352. In W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. 9. Academic Press, New York, NY.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation and body size and composition of plankton. Science (Wash., DC) 150: 28-35.
- BROWNELL, C. L. 1985. Laboratory analysis of cannibalism by larvae of the cape anchovy *Engraulis capensis*. Trans. Am. Fish. Soc. 114: 512-518.
- CALDER, W. A. III 1984. Size, function and life history. Harvard University Press, Cambridge, MA. 431 p.
- CHECKLEY, D. M. JR. 1984. Relation of growth to ingestion for larvae of Atlantic herring *Clupea harengus* and other fish. Mar. Ecol. Prog. Ser. 18: 215-224.
- CRECCO, V. A., AND T. F. SAVOY. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640-1648.
- CROWDER, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environ. Biol. Fishes 5: 225-233.
1985. Optimal foraging and feeding mode shifts in fishes. Environ. Biol. Fishes 12: 57-62.
- DE LAFONTAINE, Y., AND W. C. LEGGETT. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Can. J. Fish. Aquat. Sci. 45: 1173-1190.
- EATON, R. C., AND R. DiDOMENICO. 1986. Role of the teleost escape response during development. Trans. Am. Fish. Soc. 115: 128-142.
- FOLKVORD, A., AND J. R. HUNTER. 1986. Size-specific vulnerability of northern anchovy (*Engraulis mordax*) larvae to predation by fishes. Fish. Bull. 84: 859-869.
- FRANK, K. T., AND W. C. LEGGETT. 1982. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*) and its application to the match/mismatch hypothesis. Can. J. Fish. Aquat. Sci. 39: 691-699.
- HEALEY, M. C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Onchorhynchus keta*) during early sea life. Can. J. Fish. Aquat. Sci. 39: 952-957.
- HIORT, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in light of biological research. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 20: 1-228.
- HOEDE, E. D. 1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical fishes. Mar. Biol. 26: 271-285.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17-29.
- HUNTER, J. R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull. 70: 821-838.
1981. Feeding ecology and predation of marine fish larvae, p. 33-79. In R. Lasker [ed.] Marine fish larvae. Washington Sea Grant, University of Washington Press, Seattle, WA.
- HUSTON, M., D. L. DEANGELIS, AND W. POST. 1988. From individuals to ecosystems: a new approach to ecological theory. BioScience. (In press)
- JOHN, K. R., AND A. D. HASLER. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco, *Leucichthys artedii* LeSueur, in Lake Mendota, Wisconsin. Limnol. Oceanogr. 1: 176-194.
- KERFOOT, W. C., AND A. SIH. 1987. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH. 793 p.
- KITCHELL, J. F. 1983. Energetics, p. 312-338. In P. W. Webb and D. Weihs [ed.] Fish biomechanics. Praeger Publ., New York, NY.
- KITCHELL, J. F., D. J. STEWART, AND D. WEININGER. 1977. Application of a bioenergetic model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. 34: 1922-1935.
- LASKER, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the Californian Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173: 212-230.
1981. Factors contributing to variable recruitment of the northern anchovy, (*Engraulis mordax*), in the Californian Current: contrasting years 1975 through 1978. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178: 375-388.
- LASKER, R., AND K. SHERMAN. 1981. The early life history of fish: recent studies. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178: 607 p.
- LAURENCE, G. C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*M. salmoides*). J. Fish Biol. 4: 73-78.
- LETT, P. R., AND A. C. KOHLER. 1976. Recruitment: a problem of multispecies interaction and environmental perturbation, with special reference to the Gulf of St Lawrence Atlantic herring (*Clupea harengus harengus*). J. Fish. Res. Board. Can. 33: 1353-1371.
- MCMAHON, T. A., AND J. T. BONNER. 1983. On size and life. Scientific American Inc., New York, NY. 255 p.
- METHOT, R. D. JR. 1983. Seasonal variation in survival of larval *Engraulis mordax* estimated from the age distribution of juveniles. Fish. Bull. 81: 741-750.
- MITTELBACH, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.
- NEAVE, D. A. 1984. The development of visual acuity in larval plaice (*Pleuronectes platessa*, L.) and (*Scophthalmus maximus*, L.). J. Exp. Mar. Biol. Ecol. 78: 167-175.
- O'BRIEN, W. J. 1979. The predator-prey interaction of plantivorous fish and zooplankton. Am. Sci. 67: 572-581.
- PEPIN, P., S. PEARRE JR., AND J. A. KOSLOW. 1987. Predation on larval fish by Atlantic mackerel, *Scomber scombrus*, with a comparison of predation by zooplankton. Can. J. Fish. Aquat. Sci. 44: 2012-2018.
- PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK. 329 p.
- POST, J. R., AND A. B. PRANKEVICIUS. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 44: 1840-1847.
- RAHMANN, H., G. JESERICH, AND I. ZEUTZIUS. 1979. Ontogeny of visual acuity of rainbow trout under normal conditions and light deprivation. Behaviour 68: 315-322.
- RICE, J. A., L. B. CROWDER, AND F. P. BINKOWSKI. 1987a. Evaluating potential sources of mortality for larval bloater (*Coregonus hoyi*): starvation and vulnerability to predation. Can. J. Fish. Aquat. Sci. 44: 467-472.
- RICE, J. A., L. B. CROWDER, AND M. E. HOLEY. 1987b. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116: 703-718.

- ROSENTHAL, H., AND M. FONDS. 1973. Biological observations during rearing experiments with garfish *Belone belone*. Mar. Biol. 21: 203-218.
- ROSENTHAL, H., AND G. HEMPEL. 1969. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.), p. 344-364. In J. H. Steele [ed.] Marine food chains. University of California Press, Berkeley, CA.
- STEWART, D. J., AND F. P. BINKOWSKI. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling approach. Trans. Am. Fish. Soc. 115: 643-661.
- THOMPSON, D'A. W. 1917. On growth and form. Cambridge University Press, Cambridge, England. 1116 p.
- WATSON, W. 1982. Development of eggs and larvae of the white croaker *Geryonemus lineatus* Ayres (Pisces: Sciaenidae) off the southern California coast. Fish. Bull. 80: 403-418.
- WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190: 158 p.
1981. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. Fish. Bull. 79: 727-736.
- WEBB, P. W., AND R. T. COROLLA. 1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull. 79: 143-150.
- WEBB, P. W., AND D. WEIHS. 1986. Functional locomotor morphology of early life history stages of fishes. Trans. Am. Fish. Soc. 115: 115-127.
- WEIHS, D. 1980. Energetic significance of changes in swimming modes during growth of larval anchovy, *Engraulis mordax*. Fish. Bull. 77: 597-604.
- WERNER, E. E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111: 553-425.
- WERNER, E. E., AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15: 393-425.
- WERNER, E. E., AND D. J. HALL. 1974. Optimal foraging and size selection of prey by bluegills. Ecology 55: 1042-1052.
- WESTERNHAGEN, H. V., AND H. ROSENTHAL. 1979. Laboratory and in situ studies on larval development and swimming performance of Pacific herring *Clupea harengus pallasi*. Helgol. Wiss. Meeresunters. 32: 539-549.
- WILSON, G. M., W. K. THOMAS, AND A. T. BECKENBACH. 1987. Mitochondrial DNA analysis of Pacific Northwest populations of *Oncorhynchus tshawytscha*. Can. J. Fish. Aquat. Sci. 44: 1302-1205.
- WINTERS, G. H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence Atlantic herring, *Clupea harengus*. J. Fish. Res. Board Can. 33: 1751-1763.
- ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT. 187 p.

Appendix

The references used in the analysis are given below. They are sequentially numbered. The references that provided data for any species can be seen by cross-referencing the species with the reference numbers shown in Table 2.

1. AHLSTROM, E. H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wild. Serv. Spec. Sci. Rep. 23: 1-26.
2. AHLSTROM, E. H., AND O. P. BALL. 1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fish. Bull. 56: 209-245.
3. AHLSTROM, E. H., AND R. C. COUNTS. 1955. Eggs and larvae of the Pacific hake (*Merluccius productus*). Fish. Bull. 56: 295-429.
4. AL-MACHAZACHI, S. J., AND R. GIBSON. 1984. The developmental stages of larval turbot, *Scophthalmus maximus*, (L.). J. Exp. Mar. Biol. Ecol. 82: 35-51.
5. ARTHUR, D. K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull. 74: 517-530.
6. BAGENAL, T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. J. Fish Biol. 1: 349-353.
7. BAILEY, K. M. 1982. The early life history of the Pacific hake, *Merluccius productus*. Fish. Bull. 80: 589-598.
8. BAILEY, K. M. 1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Mar. Biol. 79: 303-309.
9. BAILEY, K. M., AND R. S. BATTY. 1984. Laboratory studies of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Mar. Biol. 83: 287-291.
10. BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. Fish. Bull. 53: 1-577.
11. BLAXTER, J. H. S. 1969. Experimental rearing of pilchard larvae, *Sardina pilchardus*. J. Mar. Biol. Assoc. U.K. 49: 557-575.
12. BLAXTER, J. H. S., AND K. F. EHRLICH. 1974. Changes in behaviour during starvation of herring and plaice larvae, p. 575-588. In J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, Berlin.
13. BLAXTER, J. H. S., AND M. E. STAINES. 1971. Food searching potential in marine fish larvae, p. 467-485. In D. J. Crisp [ed.] Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.
14. BOGDANOVA, L. S. 1980. The development and feeding of the larvae of the Lake Syamozero whitefish, *Coregonus lavaretus pallasi n exilis*, under different temperature conditions and feeding regimes. J. Ichthyol. 20: 66-73.
15. BOOKE, H. E. 1970. Speciation parameters in coregonine fishes: I. Egg size. II. Karyotype, p. 61-66. In C. C. Lindsey and C. S. Woods [ed.] Biology of the coregonid fishes. University of Manitoba Press, Winnipeg, Man.
16. BRAUM, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply, p. 113-131. In S. D. Gerking, [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.
17. BROWNELL, C. L. 1985. Laboratory analysis of cannibalism by larvae of the cape anchovy *Engraulis capensis*. Trans. Am. Fish. Soc. 114: 512-518.
18. BUCKLEY, L. J. 1980. Changes in ribonucleic acid, deoxyribonucleic acid and protein content during ontogenesis in winter flounder, *Pseudopleuronectes americanus*, and effect of starvation. Fish. Bull. 77: 703-708.
19. BUTLER, J. L., H. G. MOSER, G. S. HAGEMAN, AND L. N. NORDGREN. 1982. Developmental stages of three California sea basses (Parabrax, Pisces, Serranidae). Calif. Coop. Oceanic Fish. Invest. Rep. 23: 252-268.
20. COLIN, P. L. 1982. Spawning and larval development of the hogfish *Lachnolaimus maximus* (Pisces: Labridae). Fish. Bull. 80: 853-862.
21. COLTON, J. B., AND R. R. MARAK. 1969. Guide for identifying the common planktonic fish eggs and larvae of continental shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Biol. Lab., Woods Hole Mass. Lab. Ref. No. 69-9.
22. CRECCO, V., T. SAVOY, AND L. GUNN. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Can. J. Fish. Aquat. Sci. 40: 1719-1728.
23. CUCIN, D., AND D. J. FABER. 1985. Early life studies of lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*) in Lake Opeongo, Ontario. Ont. Fish. Tech. Rep. Ser. No. 16.
24. DABROWSKI, K. 1976. An attempt to determine the survival time for starving fish larvae. Aquaculture 8: 189-193.
25. DABROWSKI, K. 1981. The spawning and early life history of the pollan (*C. pollan* Thompson) in Lough Neagh, N. Ireland. Int. Rev. Gesamten Hydrobiol. 66: 229-326.
26. DABROWSKI, K., N. CHARLON, P. BERGOT, AND S. KAUSHIK. 1984. Rearing of coregonid (*Coregonus schinzi palea* Cuv. and Val.) larvae using dry and live food. I. Preliminary data. Aquaculture 41: 11-20.
27. DIVANACHI, P., AND M. KENTOURI. 1983. Preliminary data on production techniques, growth and survival of *Lithognathus mormyrus* larvae. Aquaculture 31: 245-256.
28. ELDRIDGE, M. B., J. A. WHIFFLE, AND M. J. BOWERS. 1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. Fish. Bull. 80: 461-474.
29. ELDRIDGE, M. B., J. A. WHIFFLE, D. ENG, M. J. BOWERS, AND B. M. JARVIS. 1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Trans. Am. Fish. Soc. 110: 111-120.
30. FIVES, J. M. 1980. An account of the eggs and developmental stages of Montagu's blenny, *Coryphoblennius galenia* (L.), with notes on the reproductive behaviour of the adults. J. Mar. Biol. Assoc. U.K. 60: 749-786.
31. FOLKVORD, A., AND J. R. HUNTER. 1986. Size-specific vulnerability of northern anchovy (*Engraulis mordax*) larvae to predation by fishes. Fish. Bull. 84: 859-869.

32. FUJMAN, L. 1986. Burst-swimming performance of larval zebra danios and the effects of diel temperature fluctuations. *Trans. Am. Fish. Soc.* 115: 143-148.
33. FUKUHARA, O. 1983. Development and growth of laboratory reared *Engraulis japonica* (Houttuyn) larvae. *J. Fish Biol.* 23: 641-652.
34. GRISWOLD, C. A., AND T. W. MCKENNY. 1984. Larval development of the scup, *Stenotomus chrysops* (Pisces: Sparidae). *Fish. Bull.* 82: 77-84.
35. HARDY, J. D. JR. 1978. Development of fishes of the mid-Atlantic Bight. Vol II: Anguillidae — Syngathidae. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.
36. HEINRICH, J. W. 1981. Culture, feeding, and growth of alewives hatched in the laboratory. *Prog. Fish-Cult.* 43: 3-7.
37. HETTLER, W. F. 1981. Spawning and rearing Atlantic menhaden. *Prog. Fish-Cult.* 43: 80-84.
38. HETTLER, W. F. 1984. Description of eggs, larvae, and early juveniles of gulf menhaden, *Brevoortia patronus*, and comparisons with Atlantic menhaden, *B. tyrannus*, and yellowfin menhaden, *B. smithi*. *Fish. Bull.* 82: 85-96.
39. HINRICH, M. A., AND H. E. BOOKE. 1975. Egg development and larval feeding of the lake herring, (*Coregonus artedii* LeSueur). The Museum of Natural History, University of Wisconsin, Stevens Point. Reports on Fauna and Flora of Wisconsin Number 10, 4: 75-86.
40. HISLOP, J. R. G. 1975. The breeding and growth of whiting, *Merlangius merlangus*, in captivity. *J. Cons. Int. Explor. Mer* 36: 119-127.
41. HOAGMAN, W. J. 1974. Vital activity parameters as related to the early life history of larval and post-larval lake whitefish (*Coregonus clupeaformis*), p. 547-558. In J. H. S. Blaxter [ed.] *The early life history of fish*. Springer-Verlag, New York, NY.
42. HOKANSON, K. E. F., AND CH. F. KLEINER. 1974. Effects of constant and rising temperature on survival and developmental rates of embryonic and larval yellow perch, *Perca flavescens* (Mitchill), p. 437-448. In J. H. S. Blaxter [ed.] *The early life history of fish*. Springer-Verlag, New York, NY.
43. HOUE, E. D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *J. Fish. Res. Board Can.* 26: 1647-1659.
44. HOUE, E. D. 1972. Development and early life history of the northern sennet, *Sphyræna borealis* Dekay (Pisces: Sphyrænidae), reared in the laboratory. *Fish. Bull.* 70: 185-195.
45. HOUE, E. D. 1974. Effects of temperature and delayed feeding on growth and survival of larvae of three species of subtropical fishes. *Mar. Biol.* 26: 271-285.
46. HOUE, E. D. 1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea bream *Archosargus rhomboidalis* (L.) (Sparidae). *J. Fish Biol.* 7: 115-127.
47. HOUE, E. D., AND B. J. PALKO. 1970. Laboratory rearing of the clupeid fish *Harengula pensacola* from fertilized eggs. *Mar. Biol.* 5: 354-358.
48. HOUE, E. D., AND R. C. SCHEKTER. 1980. Feeding by marine fish larvae: developmental and functional response. *Environ. Biol. Fishes* 5: 315-334.
49. HOWELL, W. H. 1980. Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea*, yolk sac larvae. *Fish. Bull.* 78: 731-740.
50. HOWELL, W. H., AND M. A. CALDWELL. 1984. Influence of temperature on energy utilization and growth of embryonic and prolarval American plaice, *Hippoglossoides platessoides* (Fabricius). *J. Exp. Mar. Biol. Ecol.* 79: 173-189.
51. HUNTER, J. R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. *Fish. Bull.* 70: 821-838.
52. HUNTER, J. R. 1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. *Calif. Coop. Oceanic Fish. Invest. Rep.* 19: 138-146.
53. HUNTER, J. R., AND C. A. KIMBRELL. 1980. Early life history of Pacific mackerel, *Scomber japonicus*. *Fish. Bull.* 78: 89-101.
54. HUNTER, J. R., AND G. L. THOMAS. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy *Engraulis mordax* Girard, p. 559-574. In J. H. S. Blaxter [ed.] *The early life history of fish*. Springer-Verlag, New York, NY.
55. ISHIBASHI, N. 1974. Feeding, starvation and weight changes of early fish larvae, p. 339-344. In J. H. S. Blaxter [ed.] *The early life history of fish*. Springer-Verlag, New York, NY.
56. IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CT. 302 p.
57. JOHN, K. R., AND A. D. HASLER. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco, *Leucichthys artedii* LeSueur, in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 1: 176-194.
58. JOHNSON, E. D. 1978. Development of fishes of the mid-Atlantic Bight. Vol IV: Carangidae — Ephippidae. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.
59. JONES, P. W., F. D. MARTIN, AND J. D. HARDY, JR. 1978. Development of fishes of the mid-Atlantic Bight. Vol. I: Acipenseridae — Ictaluridae. U.S. Fish and Wildlife Service, Washington, DC. p. 173-178.
60. KELLOGG, R. L. 1982. Temperature requirements for the survival and early development of the anadromous alewife. *Prog. Fish-Cult.* 44: 63-73.
61. KIMURA, M. 1970. Formation of a false annulus on scales of Pacific sardines of known age. *Calif. Coop. Oceanic Fish. Invest. Rep.* 13: 73-75.
62. KNUITSEN G. M., AND S. TILSETH. 1985. Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. *Trans. Am. Fish. Soc.* 114: 507-511.
63. KRAMER, D. 1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae, 1952-1956. *Fish. Bull.* 60: 393-438.
64. KRAMER, D., AND J. R. ZWEIFEL. 1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. *Calif. Coop. Oceanic Fish. Invest. Rep.* 14: 84-87.
65. LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG. 1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. *Fish. Bull.* 80: 93-109.
66. LASKER, R. 1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine, *Sardinops caerulea* (Girard). *J. Fish. Res. Board Can.* 19: 867-875.
67. LASKER, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull.* 73: 453-462.
68. LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY. 1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. *Mar. Biol.* 5: 345-353.
69. LAURENCE, G. C. 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. *J. Fish. Res. Board Can.* 31: 1415-1419.
70. LAURENCE, G. C., AND J. E. BEYER. 1980. A stochastic model of growth and mortality in winter flounder larvae (*Pseudopleuronectes americanus*) reared in the laboratory under experimental conditions. Symposium on the Early Life History of Fish, Woods Hole, Massachusetts, April 1979. *Rapp. P.-v. Réunion. Cons. Int. Explor. Mer* 178.
71. LAURENCE, G. C., AND C. A. ROGERS. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). *J. Cons. Int. Explor. Mer* 36: 220-228.
72. LEBOUR, M. V. 1925. Young anglers in captivity and some of their enemies. *J. Mar. Biol. Assoc. U.K.* 13: 721-734.
73. LEE, D. S., C. R. GILBERT, C. H. HOCUTT, R. E. JENKINS, D. E. MCALLISTER, AND J. R. STAUFFER, JR. 1980. Atlas of North American Freshwater Fishes. N.C. State Mus. Nat. Hist. Raleigh/i-r + 854 pp.
74. LEE, W. Y., G. J. HOLT, AND C. R. ARNOLD. 1984. Growth of red drum larvae in the laboratory. *Trans. Am. Fish. Soc.* 113: 243-246.
75. LI, S. AND J. A. MATHIAS. 1982. Causes of high mortality among cultured larval walleye. *Trans. Am. Fish. Soc.* 111: 710-721.
76. LILLELUND, K., AND R. LASKER. 1971. Laboratory studies of predation by marine gastropods on fish larvae. *Fish. Bull.* 69: 655-667.
77. LOUGH, R. G., M. PENNINGTON, G. R. BOLZ, AND A. ROSENBERG. 1982. Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine, Georges Bank region based on otolith growth increments. *Fish. Bull.* 80: 187-200.
78. MALHOTRA, Y. R., AND S. MUNSHI. 1985. First feeding and survival of *Aspidoparia morar* larvae (Cyprinidae). *Trans. Am. Fish. Soc.* 114: 286-290.
79. MATARESE, A. C., AND J. B. MARLIAVE. 1982. Larval development of laboratory reared rosy lip sculpin, *Ascelichthys rhodonus* (Cottidae). *Fish. Bull.* 80: 345-356.
80. MATHIAS, J. A., AND S. LI. 1982. Feeding habits of walleye juveniles: comparative laboratory and field studies. *Trans. Am. Fish. Soc.* 111: 722-735.
81. MAY, R. C. 1971. Effects of delayed initial feeding on larvae of grunion, *Leuresthes tenuis* (Ayres). *Fish. Bull.* 69: 411-425.
82. MAY, R. C. 1973. Larval mortality in marine fishes and the critical period concept, p. 3-19. In J. H. S. Blaxter [ed.] *The early life history of fish*. Springer Verlag, New York, NY.
83. MCGURK, M. D. 1984. Ring deposition in the otoliths of larval Pacific herring *Clupea harengus pallasii*. *Fish. Bull.* 82: 113-120.
84. METHOT, R. D., AND D. KRAMER. 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. *Fish. Bull.* 77: 413-423.

85. MILLS, C. A. 1982. Factors affecting the survival of dace, *Leuciscus leuciscus* (L.), in the early post-hatching period, J. Fish. Biol. 20: 645-655.
86. NELSON, W. R. 1968. Embryo and larval characteristics of sauger, walleye, and their reciprocal hybrids. Trans. Am. Fish. Soc. 97: 167-174.
87. NEWELL, G. E., AND R. C. NEWELL. 1963. Marine Plankton. Hutchinson Educational Ltd. 243 p.
88. NISHIMURA, A., AND J. YAMADA. 1984. Age and growth of larval and juvenile walleye pollack *Theragra chalcogramma* (Pallus), as determined by otolith daily growth increments. J. Exp. Mar. Biol. Ecol. 82: 191-205.
89. O'CONNELL, C. P., AND L. P. RAYMOND. 1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5: 187-197.
90. PALMER, C. J., AND M. B. CULLEY. 1984. The egg and early life stages of the sandsmelt, *Atherina presbyter* Cuvier. J. Fish Biol. 24: 537-544.
91. PETERSEN, R. H., P. H. JOHANSEN, AND J. L. METCALFE. 1980. Observations on early life stages of Atlantic tomcod *Microgadus tomcod*. Fish. Bull. 78: 147-158.
92. PINTO, J. M. 1984. Laboratory spawning of *Amnodytes hexapterus* from the Pacific coast of North America with a description of its eggs and early larvae. Copeia 1984(1): 242-244.
93. POWELL, A. B., AND A. J. CHESTER. 1985. Morphometric indices of nutritional condition and sensitivity to starvation of spot larvae. Trans. Am. Fish. Soc. 114: 338-347.
94. POWELL, A. B., AND H. R. GURDY. 1980. Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae). Fish. Bull. 78: 710-714.
95. RADTKE, R. L., AND J. M. DEAN. 1982. Increment formation in the otoliths of embryos, larvae and juveniles of the mummichog, *Fundulus heteroclitus*. Fish. Bull. 80: 201-216.
96. RICE, J. A. Unpublished data on alewife.
97. RICE, J. A. 1985. Mechanisms regulating survival of larval bloater *Coregonus hoyi* in Lake Michigan. Doctoral dissertation, University of Wisconsin-Madison, Madison, WI.
98. RICHARDSON, S. L. 1981. Pelagic eggs and larvae of deepsea sole *Embasiichthys bathybius* (Pisces: Pleuronectidae) with comments on genetic affinities. Fish. Bull. 79: 163-170.
99. RICHARDSON, S. L., J. R. DUNN, AND N. A. NAPLIN. 1980. Eggs and larvae of butter sole, *Isopsetta isolepis* (Pleuronectidae), off Oregon and Washington. Fish. Bull. 78: 401-418.
100. ROGERS, B. A., AND D. T. WESTIN. 1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. Trans. Am. Fish. Soc. 110: 100-110.
101. ROJAS DE MENDIOLA, B. 1980. Summary of the studies about food and feeding habits of the anchovy (*Engraulis ringens* J.). Workshop on the effects of environmental variation on the survival of larval pelagic fishes, Food and Agriculture Organization Intergovernmental Oceanographic Commission Workshop Report Number 28.
102. ROSENTHAL, H., AND M. FONDS. 1973. Biological observations during rearing experiments with garfish *Belone belone*. Mar. Biol. 21: 203-218.
103. ROSENTHAL, H., AND G. HEMPEL. 1969. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.), p. 344-364. In J. H. Steele [ed.] Marine food chains. University of California Press, Berkeley, CA.
104. RUSSELL, F. S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London.
105. RYLAND, J. S. 1963. The swimming speeds of plaice larvae. J. Exp. Biol. 40: 285-299.
106. RYLAND, J. S. 1966. Observations on the development of the plaice, *Pleuronectes platessa* L., in aquaria. J. Cons. Int. Explor. Mer 30: 177-195.
107. SAKSENA, V. P., AND W. J. RICHARDS. 1975. Description of eggs and larvae of laboratory-reared white grunt, *Haemulon plumieri* (Lacepede) (Pisces, Pomadasyidae). Bull. Mar. Sci. 25: 523-536.
108. SCHNACK, D. 1981. Studies on the mortality of Pacific herring larvae during their early development, using artificial in situ containments. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178: 135-142.
109. SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184.
110. SIEFERT, R. E. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner, and rainbow smelt. Trans. Am. Fish. Soc. 101: 219-225.
111. STEPIEN, W. P. 1976. Feeding of laboratory-reared larvae of the sea bream *Archosargus rhomboidalis* (Sparidae). Mar. Biol. 38: 1-16.
112. TAYLOR, W. W., AND M. H. FREEBERG. 1984. Effect of food abundance on larval lake whitefish, *Coregonus clupeaformis* Mitchell, growth and survival. J. Fish Biol. 25: 733-741.
113. THEILACKER, G. H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull. 76: 403-414.
114. THEILACKER, G. H. 1981. Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus*, larvae. Symposium on the Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp. P.-v. Réun. Cons. Explor. Mer 178: 432-400.
115. THEILACKER, G., AND K. DORSEY. 1980. Larval fish diversity, a summary of laboratory and field research. Workshop on the effects of environmental variation on the survival of larval pelagic fishes. FAO/Intergov. Oceanogr. Comm. Workshop Rep. No. 28: 105-142.
116. THEILACKER, G. H., AND R. LASKER. 1974. Laboratory studies of predation by euphausiid shrimps on fish larvae, p. 287-299. In J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY.
117. TOETZ, D. W. 1966. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. Invest. Indiana Lakes Streams 7: 115-146.
118. WALLACE, J. C., AND D. AASIORD. 1984. An investigation of the consequence of egg size for the culture of arctic char, *Salvelinus alpinus* (L.). J. Fish Biol. 24: 427-435.
119. WARE, D. M., B. ROJAS DE MENDIOLA, AND D. S. NEWHOUSE. 1980. Behaviour of first feeding anchoveta larvae *Engraulis ringens* J. Symposium on Early Life History of Fish, Woods Hole, Massachusetts, April 1979. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178.
120. WATSON, W. 1982. Development of eggs and larvae of the white croaker *Genyonemus lineatus* Ayres (Pisces: Sciaenidae) off the southern California coast. Fish. Bull. 80: 403-418.
121. WEBB, P. W. 1981. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. Fish. Bull. 79: 727-736.
122. WEBB, P. W., AND R. T. COROLLA. 1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull. 79: 143-150.
123. WERNER, R. G., AND J. H. S. BLAXTER. 1980. Growth and survival of larval herring (*Clupea harengus*) in relation to prey density. Can. J. Fish. Aquat. Sci. 37: 1063-1069.
124. WHEELER, A. 1969. The fishes of the British Isles and north-west Europe. Michigan State University Press, East Lansing, MI. 613 p.
125. WIGGINS, T. A., T. R. BENDER, JR., V. A. MUDRAK, AND J. A. COLL. 1985. The development, feeding, growth, and survival of cultured American shad larvae through the transition from endogenous to exogenous nutrition. Prog. Fish-Cult. 47: 87-93.
126. WYATT, T. 1972. Some effects of food density on the growth and behavior of plaice larvae. Mar. Biol. 14: 210-216.
127. YEVSEYENKO, S. A., AND M. M. NEVINSKY. 1981. On the development of the eggs and larvae of the yellow-tailed dab *Limanda ferruginea* Storer and their passive transport in the northwestern Atlantic. J. Ichthyol. 21: 15-74.
128. ZAKI, M. I. 1984. Artificial culture and early ontogeny of gilthead, *Spanus aurata*, of the Mediterranean Sea. J. Ichthyol. 24: 56-63.