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

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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’alimentation marine. 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 poissons 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’inclusion 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 dulciaquicoles, 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.

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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 concept 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-
ering survival. For instance, some species appear highly vuln-
erable to starvation (Lasker 1975, 1978), while others are more
likely to be affected by predation or abiotic factors (Lett and Koh-

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 fish sizes 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 differ-
ences 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 sacs (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 Welts 1966). 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 differenti-
ating encounter rates, escape ability, and predator gape limitation
(Blaxter 1986; Zaret 1980). The effects of size-dependent pro-
cesses 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 pro-
cesses 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 the 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 stages. The traits we chose are those divided into four
categories related to feeding, activity, vision, and predation risk
(Table 1). While all of the traits influence subsequent recruit-
ment, 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 litera-
ture 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 spe-
cies 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 impos-
sible to account for temperature effects using ANOVA tech-
niques. For appropriate variables, we addressed the influence
of temperature by repeating our analysis after standardizing
results to 15°C using Q10 = 2.3 (Checkley 1984). This approach
provides some indication of whether the size effects persist,
independent of temperature. Other variables, including meth-
odological differences among studies, are likely to contribute
to variance in size-dependent relationships. However, as an ini-
tial step, using total length as a measure of size should be ade-
quate to identify the generalities we seek.

We found information on 72 species of marine (54), fresh-
water (16), and anadromous (4) fishes from 30 different fami-
lies (Table 2). The data included here are derived from 128
references out of more than 500 we examined.3 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 that have previously been reviewed (Hunter 1981;
Blaxter and Hunter 1982; Blaxter 1986; Webb and Welts 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 origi-
nal 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 refer-
ences 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 func-
tion. We report the function giving the best fit. In all cases the
value of "r" 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.

3A 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 0Z2.
TABLE 1. Larval traits compared in this analysis, their definitions, and units of measurement.

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<tr>
<th>Trait (units)</th>
<th>Definition</th>
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<tr>
<td>Yolk absorption (d)</td>
<td>Time taken to fully absorb the yolk from hatching</td>
</tr>
<tr>
<td>Point of no return (d)</td>
<td>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</td>
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<tr>
<td>First possible feeding (d)</td>
<td>Time at which a larva is first physically or biochemically capable of feeding</td>
</tr>
<tr>
<td>First typical feeding (d)</td>
<td>Time at which larval usually feed for the first time, defined for a group</td>
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<tr>
<td>Time to 50% morality (d)</td>
<td>Time taken for half of the larvae in a group to die when starved</td>
</tr>
<tr>
<td>Sustained swim speed (cm/s)</td>
<td>Speed at which fish swim for extended period of time</td>
</tr>
<tr>
<td>Burst swim speed (cm/s)</td>
<td>Speed attained in short sprints, usually during prey capture attempts or in avoidance attempts</td>
</tr>
<tr>
<td>Reactive distance (mm)</td>
<td>Maximum distance at which a potential prey item is recognized as such</td>
</tr>
<tr>
<td>Search volume (L/h)</td>
<td>Function of sustained swim speed and reactive distance: equivalent to the volume of water searched per unit time</td>
</tr>
<tr>
<td>% capture success</td>
<td>Percent of all &quot;observed&quot; capture attempts that were successful</td>
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Results

For each larval trait (Table 1), we first present our prior 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 posthatching 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 starvations 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 hatching = 1.96 + 1.89 egg diameter, r² = 0.40, p < 0.0001, n = 100). Within this limit, the partitioning of resources between larval and yolk supply may vary (Ballin and Hemphel 1983). 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 warcesgenii (Bream 1967). Times to yolk absorption are, as we have seen, freshwater and anadromous species were not significantly different (demonstrated by a nonparametric Kruskal–Wallis × length interaction, F₁,₈ = 2.65, p = 3.079), 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" (PNN). These limits define the period within which first feeding must occur if the larva is to survive. To understand size-dependent patterns in larval susceptibility to starvation, one must understand how size influences first possible feeding and PNN. 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 PNN would be a positive function of body length at hatching. Because PNN is likely related to the volume of the larval's energy reserves, we proposed an accelerating function.

**Hypothesis 3**
The difference between time to PNN 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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**Freshwater**

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**Anadromous**

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Varied by a factor of 24 among larvae of different sizes. White croaker (Corynorhamphus analis), the species with the smallest larve (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 15.4 d for the smallest (1.9 mm) lined sole (Acrina lineata) (Hoede 1974) to 18 d in the largest (9.4 mm) lake herring (Coregonus arcticus) (John and Hester 1956). Differences in temperature between studies could have had a large effect on time to PNR. However, when standardized to 15°C to remove temperature effects, the r² changed only slightly (Fig. 4). This suggests a robust size-dependent relationship independent of temperature effects. Large values of PNR may be underestimated 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 is 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 length, \( r^2 = 0.26, p < 0.0001, n = 48 \) 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, \( r^2 = 0.166, p = 0.04, n = 25 \) 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 + 2.99 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 - 0.53 length, \( r^2 = 0.52, p = 0.10; \) days to PNR = 0.58 + 1.90 length, \( r^2 = 0.69, p = 0.38 \).

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-

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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, \( r^2 = 0.32, p < 0.0001, n = 29 \). 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 re
tains 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 shared 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 (\( F_{1,6} = 5.5, p = 0.015 \)). Regardless of species, at any given length, we found equal or greater times to 50% mortality in those larvae that were depending 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 starved. 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 = 3.01 log 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 Corrila 1981; Weiss 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); bluestreaks (9.5 mm) actively swim 100% of the time within 6 h of hatching (Rice et al. 1987). 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 characteristic possess two types of swimming (Webb and Welts 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 Corrila 1981; Eaton and DiDomenico 1980). The size dependency of both swimming modes has long
been recognized (Rainbridge 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 Weith 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 larval 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 LaFontaine and Leggett 1988), and 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 active distance (Blaxter and Staines 1971), visual acuity (Rahmann et al. 1979; Neave 1984), and sensitivity to light (Blaxter 1968). At hatching, the eyes are many telocysts 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-
several phytes 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 Sib 1997). 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 1983).

In general, we expected that probability of capture per attempt would decline with increasing larval length (Folkevold 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 (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
eugoniasids (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 blunter eating 10.9-mm blunter larvace (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 eugoniasids 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 larvace can be assessed in more realistic terms.

**Discussions**

Size-based scaling of physiological and ecological processes is well known from juvenile and adult fish (Brett and Groves 1979; Mittlebach 1981; Werner and Gilliam 1984) and has been broadly applied to other ecological questions (Peters 1983; Calder 1984). Until now, no studies had been done for larval fish. We recognize 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 important, 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 4.2 mm (Blaxter and Hempel 1963). If we ignore temperature, our analysis suggests that at this
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 lar-
vae 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 vul-
nerable to starvation than larger larvae. Not surprisingly, stud-
ies promoting the starvation hypothesis and a ‘‘critical period’’ at first feeding (Lasker 1975, 1978, 1981) involved relatively small marine larva. 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 sub-
estantial 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 iden-
tified 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 to the predator-prey length ratios 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 larva. Second, we know little about prey choice by predators once prey (larval fish) are encountered. The avail-
able experiments on predation on fish larvae generally were done without alternative prey (but see Pepin et al. 1987; de Lafontaine and Leggett, 1988). We are 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 need also estimate 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 bi-
energetics 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 Frankevicius 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 bet-
ter 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-
lar 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 feed-
back loop. Consequently, even tiny initial size differences may translate into substantial differences in survival and subsequent recruitment (Adams and DoAngelis 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 infor-
mation than an analysis based on individual larva (Rice et al. 1967b). 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 Savy 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 tech-
niques, 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 indi-
vidual-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 impor-
tance. Further, our approach implicitly recognizes the impor-
tance of interactions between factors controlling survival in lar-
val 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 con-
text 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 dis-
regarded 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 read-
ily take advantage of the previous research on recruitment mechanisms in larval fishes.

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