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WHY DO MOST FISH PRODUCE SO MANY TINY OFFSPRING?

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Abstract.—A simulation model containing size-based rules for foraging, growth, and probability of survival was created to track the fates of pelagic larval fish. The relative success of cohorts comprised of equivalent initial biomass but containing different numbers and sizes of first-feeding larvae was compared in environments having different levels of patchiness and densities of food resources. In environments containing randomly distributed prey, the rate of growth and probability of survival were always greater, and duration of the larval stage was shorter for larger larvae due to the size-based rules. Broods comprised of fewer but larger first-feeding larvae resulted in the greatest number of survivors in low-prey-density environments. In prey-rich environments, broods containing the same initial biomass divided into greater numbers of small first-feeding larvae resulted in more survivors. This result occurred despite the fact that, on a per-individual basis, survival rate was much lower initially in larger broods. We used a negative binomial algorithm to generate encounter probabilities with patchily distributed prey on small spatial scales in which the previous day's experiences had no relationship to current probabilities for encounter. In prey-poor environments, the strategy of producing fewer large larvae was superior at all levels of small-scale prey patchiness. In prey-rich environments, broods containing larger numbers of smaller larvae resulted in more survivors in simulations for randomly distributed and moderately clumped prey. With greater clumping of prey, the greatest number of survivors resulted from the strategy of producing fewer but larger larvae. To examine the effect of large-scale prey patchiness, we solved for the percentage of a larval cohort that would have to settle and remain within a prey-rich patch, in order for a strategy of producing many small larvae to yield more survivors than a strategy of producing fewer larger larvae under the same conditions. When prey patches contained 200 prey/L (compared with 50 prey/L outside) and as few as 1% of the brood settled into the prey-rich patches, large broods comprised of 3-mm larvae yielded more survivors than small broods comprised of 10-mm larvae. Our simulations indicate that the superior evolutionary strategy is the investment in larger numbers of smaller eggs when resources are patchy on a relatively large spatial scale.

The literature on life history documents large variation among species in both clutch size and offspring size for most higher taxonomic groups. The trade-off between egg size and egg number has been addressed by a number of theoretical (see, e.g., Smith and Fretwell 1974; Sibly and Calow 1983; Lloyd 1987; Winkler and Wallin 1987) and empirical studies (see, e.g., Duarte and Alcaraz 1989; Elgar 1990; Fleming and Gross 1990; Hutchings 1991). Both types of studies have either assumed or shown that larger offspring generally have higher early survival, especially when larval or neonate resources are scarce. Therefore, a fixed amount of

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reproductive effort should be partitioned into many small offspring in resource-rich habitats or into a few large offspring in resource-poor habitats. Relatively few studies have dealt explicitly with the egg size/egg number trade-off in relation to variance in habitat quality. By assuming the minimal offspring size is smaller in "better" environments, McGinley et al. (1987) modeled the random settlement of offspring in patchy environments and showed that the production of small offspring is favored when differences in patch quality are large. Using a density- and frequency-independent model, Venable and Brown (1988) showed that patchy environments favor a smaller seed size and greater dispersal capabilities in plants.

Among animals, bony fishes (Osteichthyes) exhibit perhaps the greatest range of clutch sizes (Itô 1978; Winemiller 1992). For example, the ovoviviparous coelacanth (*Latimeria chalumnae*) produces a single neonate measuring a quarter of the female's body length (Balon 1984), whereas the ocean sunfish (*Mola mola*) produces tiny pelagic eggs that can number over 200,000,000 per clutch (Itô 1978). Rothschild (1986) noted that fishes are the only vertebrates that produce a superabundance of eggs. In other words, on the average, only a very small fraction of the eggs spawned need to survive in order to achieve a stable population (Svardson 1949). Production of large clutches of small pelagic eggs is the predominant strategy observed in fishes inhabiting offshore environments worldwide, as well as those inhabiting inland and coastal waters in temperate and polar latitudes (Duarte and Alcaraz 1989; Elgar 1990; Winemiller and Rose 1992).

Among pelagic larval fishes, body size appears to be a key characteristic influencing an individual's probability of recruitment into the year-class-1 population cohort (Miller et al. 1988; Houde 1989a; Pepin and Myers 1991). Both between and within fish species, smaller pelagic larvae are less likely to forage successfully, exhibit slower absolute growth, and are more likely to die from either starvation or predation than are larger larvae (Ware 1975; McGurk 1986; Miller et al. 1988; Bailey and Houde 1989; Houde 1989a, 1989b; Pepin 1991; Miller et al. 1992). If small size is almost universally detrimental to the individual fish's chances for survival in pelagic environments, then why is the production of large numbers of tiny eggs and larvae so predominant among fishes?

A number of investigators have proposed adaptive functions for the high fecundity/small egg life-history strategy in fishes. Itô (1978), Johannes (1978), Rothschild and DiNardo (1987), Sinclair (1988), and others have proposed that large clutches of pelagic eggs facilitate the placement of at least a portion of each brood into favorable conditions for larval development and survival. The broadcasting of large clutches is, in effect, a bet-hedging tactic for spatially heterogeneous environments that are to some extent unpredictable. In some cases, the *existence* of favorable environmental conditions for larval growth and survival can be predicted with a high degree of certainty, but the *location* of these favorable regions in time and space is highly uncertain. In marine pelagic environments, coastal currents, gyres, and convergence zones are spatiotemporally dynamic and can influence local patterns of productivity and community structure that influence larval fish feeding, growth, and survival (Laurence 1974; Lasker 1978; Lasker and Zweifel 1978; McGowan 1986; Brander and Hurley 1992; McFarlane and Beamish 1992). Laboratory studies have confirmed that larval fish growth and

survival are highly sensitive to food availability (Houde 1978; Buckley et al. 1987), lending support for Hjort's (1914) match/mismatch hypothesis for recruitment dynamics. Hjort was among the first to propose that recruitment of fishes with pelagic larvae may be determined by food availability during a critical period of the larval stage. Oceanic currents can also influence recruitment in fishes by transporting some pelagic larvae into favorable areas for larval or juvenile growth and survival and others into unfavorable regions (advection), a phenomenon that has been termed the membership/vagrancy hypothesis (Parrish et al. 1981; Sinclair 1988; MacCall 1990). Several field investigations have concluded that, depending on prevailing climatic conditions, fish populations may be influenced by either membership/vagrancy, match/mismatch, or the combined effects of both (Frank and Leggett 1982; Sherman et al. 1984; Fortier and Gagné 1990).

Several models dealing with the trade-off between offspring size and clutch size have examined the costs of reproduction and density-dependent selection in relation to parental fitness and the optimal size of offspring (see, e.g., Lack 1954; Pianka 1972; Smith and Fretwell 1974; Sargent et al. 1987; Nussbaum and Schultz 1989). Other models examine the demographic effects of trade-offs involving fecundity and survival in relation to different kinds of environmental variation, both density-dependent and density-independent (see, e.g., Cole 1954; Murphy 1968; Schaffer 1974; Boyce 1979; Lloyd 1987; McGinley et al. 1987; Winkler and Wallin 1987). These models incorporate aggregate population parameters, such as fecundity or survival at different age classes, and therefore lack sensitivity to deal with variable developmental and growth rates among individuals within age cohorts.

In this article, we employ a density-independent, size-based model of feeding, growth, and survival of pelagic larval fish to examine the effects of spatial variation in environmental quality on survival. The model is individual based (i.e., tracks the fates of simulated individual larvae). We examine the effects of patchy food resources (zooplankton prey) on the survival of broods adopting different strategies for initial size of larvae at first feeding. The simulation model integrates several strong, size-based relationships of early life stages with parental fitness. The model contains relatively few ecological assumptions, with most assumptions involving the size-dependent relationships summarized by a number of reviews (Blaxter 1986; Miller et al. 1988; Bailey and Houde 1989; Houde 1989a; Pepin 1991). We follow these authors in assuming that size-dependent ecological relationships observed among larvae across species are generally reflective of relationships within species. The precise form of these size-based relationships appears not to influence the qualitative results. Finally, we simulate larval encounters with both stochastic and patterned prey distributions at two different scales of spatial variance.

METHODS

Model Description

The model simulates prey encounters, growth, and mortality of individual larval fish within a cohort from the time of first feeding until 20-mm total length (L).

Two initial conditions were specified: the fixed biomass of spawn and the length of larvae at first feeding. Length at first feeding (mm total length) was converted to dry weight, W ($\mu\text{g dw}$), using a relationship derived from empirical data for larval fishes: $W = 0.1674 (L^{3.837})$ (B. Letcher, personal communication). Spawn biomass was then divided into numbers of first-feeding larvae based on the weight of an individual larva at first feeding.

Each larva was assumed to search a volume of water (L/d) that increases with its body length. The volume of water searched per hour (V) was a nonlinear function of total length and was estimated from empirical data appearing in Blaxter (1986). This relationship was

$$V = e^{-4.19 - 0.493L + 1.72(\ln L)^2}.$$

We also assumed that our larvae were visually oriented predators, that each larva searched for 13 h each day, and that searching volume increases with larval size because of increased swimming speeds and perceptive abilities.

The volume searched was multiplied by an assigned prey density to obtain the mean number of prey encountered during 1 d. The realized number of prey encountered by an individual larva was then generated from either a Poisson or negative binomial distribution. The Poisson distribution simulates larval encounters with prey that are randomly distributed in the environment. The negative binomial was used to represent patchily distributed prey (Owen 1989). The actual number of prey ingested was then determined as a random deviate from a binomial distribution: binomial(N , P_c), where N is the realized number of prey encountered, and P_c is the probability of capture.

The probability of capture (P_c) also increases with larval length (Miller et al. 1988; Houde 1989a). The following equation was used to determine the relationship between larval size and the probability of successful capture (ingestion) once prey were encountered:

$$P_c = 0.2 + \frac{0.927}{1.0 + (L/6.68)^{-2.76}}.$$

For a 3-mm larva P_c has a minimum value of 0.29 and increases with larval length as a sigmoidal function to a maximum of ~ 1.0 for a 20-mm larva. Similar curves for probability of capture have been documented for a variety of larval fish (Laurence and Lough 1985; Blaxter 1986). Simulation results should not be sensitive to the particular parameter values employed in generating the P_c curve, because all larvae use the same curve. Also, changing this curve merely shifts all prey capture probabilities up or down with respect to high or low prey densities, because the probability of prey capture is bounded between 0 and 1.0 and increases monotonically with size. Our simulations assume that there is no parental care following ovulation, that prey densities are unaffected by foraging larvae, and that larvae have no influence on one another (i.e., density independence).

Ingested prey were converted to biomass by assuming each prey weighs 0.8 $\mu\text{g dw}$, the approximate weight of individual copepod zooplankton (Durbin and Durbin 1981; MacKenzie et al. 1990). Growth of a larva was first computed in terms of weight gain assuming a gross growth efficiency (growth/ingestion) of

0.33 (Houde 1989a). The weight gain was then added to the weight of the larva and its new length recomputed using the L - W relationship. Assuming daily growth is limited by satiation and taking into account empirical growth estimates, individual larvae were not permitted to increase their length by more than 1.0 mm/d.

The probability of death for an individual larva was computed as $1 - \exp(-M)$, where $M = 0.68(L^{-0.68})$ (assuming 15°C; Pepin 1991). A random number between 0 and 1 was generated, and if the random number was less than the probability of dying, the model larva died. Pepin's (1991) size-dependent relationship is derived from field estimates and reflects both starvation and predation mortality. In our model, larval fish are not permitted to lose weight, so that predation is assumed to be the direct agent of mortality.

Comparison 1: Effects of Prey Density and Larval Size

Using the model, we designed a simulation in which the independent variables were the size of larvae at first feeding (3 mm [11 μ g dw], 5 mm [80 μ g dw], and 10 mm [1,150 μ g dw]) and prey density (50, 100, and 200 prey/L). This range of sizes for first-feeding larvae spans the range observed for first-feeding larvae of marine fishes with pelagic eggs and larvae (Miller et al. 1988; Houde 1989b). Typical zooplankton densities in estuaries and coastal waters range from 10/L to 100/L, with densities of >100/L occurring intermittently and densities of >500/L occurring infrequently (Miller 1983; Laurence and Lough 1985; MacKenzie et al. 1990).

In this first comparison, prey densities were assumed to be randomly distributed and constant over time under each condition. The total amount of spawned biomass to be allocated into larvae was held constant, so that smaller first-feeding larvae were always associated with a larger number of progeny. Each simulation was initiated with 11.0 g dw of spawn, which translated into 1×10^6 first-feeding larvae at 3 mm, 137,500 first-feeding larvae at 5 mm, and 9,565 first-feeding larvae at 10 mm. We repeated each of the nine combinations of the two independent variables five times using different random number seeds. Simulations were run until either all larvae in the cohort died or all had reached 20-mm length. The probability of survival (number surviving/initial number of first-feeding larvae) and number of survivors (i.e., parental fitness) were computed for each simulation.

Comparison 2: Effect of Small-Scale Prey Patchiness

Prey patchiness was examined using two different methods to represent the extreme conditions on a scale of spatial heterogeneity. The approach in comparison 2 assumes fine-scale prey patches such that an individual larva experiences different densities of prey on a day-to-day basis. This fine-scale patchiness was implemented in the model by generating realized encounter rates with prey from a negative binomial distribution. The negative binomial distribution has been used to represent spatial patchiness in zooplankton (Owen 1989).

Use of the negative binomial method for calculating larval encounters with prey simulates conditions in which larvae experience different spectra of prey densities on small spatial scales and, as a consequence, over the course of a day.

Several examples of results from the negative binomial method for the generation of realized prey encounters are illustrated in figure 1. Assuming an average encounter of 50, the frequency distribution of 1,000 realized encounters using the Poisson distribution and the negative binomial distribution with $K = 10.0$, $K = 1.0$, $K = 0.5$, and $K = 0.1$ are shown. A negative binomial distribution with $K = 10$ approximates a Poisson distribution. As K decreases we see higher frequencies of both low and high encounters with prey (fig. 1). Each simulation resulted in a mean number of encounters (based on the 1,000 realizations) near 50 (range = 49.5–52.1), but variance increased with decreasing values of K . In the model simulations, the negative binomial represents patchiness by having many larvae encounter fewer prey than the mean number of prey encounters and having few larvae experiencing more than the mean number of encounters (i.e., higher variance with the same mean).

The simulations involved four combinations of two first-feeding larval size classes (3 and 10 mm) and two prey densities (50 and 200 prey/L). These represent the extreme values of size at first feeding and prey density used in comparison 1. For each combination, we used four values for the contagion parameter ($K = 10, 1, 0.5, 0.1$) for calculations of the negative binomial distribution. Smaller values of K imply increasing degrees of prey patchiness. We used the value of $K = 10.0$ to approximate a Poisson distribution simulating encounters with randomly distributed prey. The values $K = 1.0$ and $K = 0.1$ are the median and minimum values of K estimated by Owen (1989) for zooplankton in the Southern California Bight.

As in comparison 1, we began all simulations with 11.0 g dw of spawn and repeated each of the 16 combinations five times using different random number seeds. Again, simulations were run until all larvae either died or attained 20-mm length, and the probability of survival and total number of survivors (i.e., parental fitness) were then determined.

Comparison 3: Effect of Large-Scale Prey Patchiness

This simulation compares larval fates when a cohort is distributed in different proportions within large patches of differing prey densities. We assumed that, once a larva entered a patch, it did not leave that patch for the duration of the larval stage. Large-scale circulation patterns, drift convergence zones, and marine upwelling zones exemplify this kind of large-scale spatial variation in marine pelagic environments (Lasker 1978; Lasker and Zweifel 1978; McGurk 1986; Sinclair 1988). We compared the fates of larval cohorts of different first-feeding sizes by solving, for each of two first-feeding size classes, the percentage of larvae that would have to be in the high-prey-density patch in order to achieve an equivalent number of survivors for both size classes.

The percentage of larvae required to be in the high prey patch in order for the number of survivors to be equal for small and large initial sizes at first feeding (X_e) is

$$X_e = \left(\frac{nP_L - (NR_L)}{n(P_L - P_H) - N(R_L - R_H)} \right) \cdot 100,$$

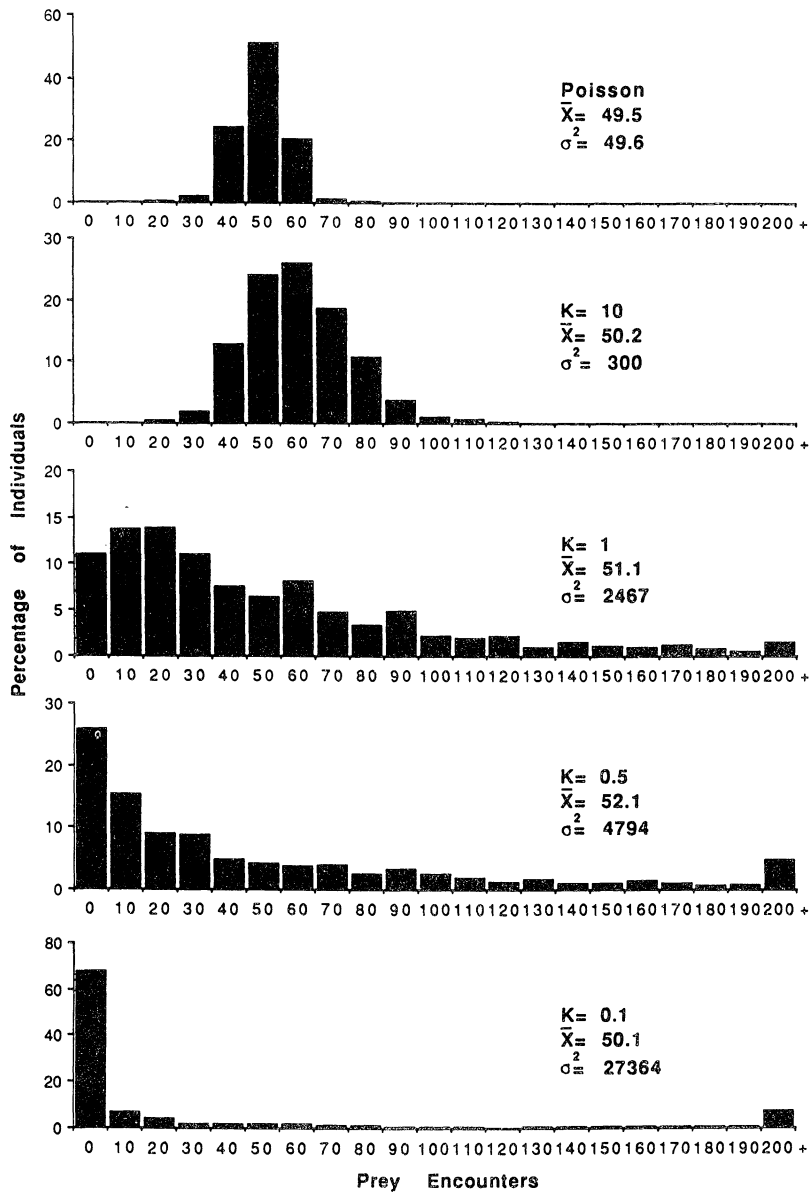


FIG. 1.—Distributions of daily encounters with planktonic prey for larval fishes based on the negative binomial algorithm. The contagion parameter, K , defines the level of prey patchiness, in which declining values simulate more clumped distributions that cause some individuals to encounter more than the mean number of prey and other individuals to encounter far fewer than the mean number of prey.

where n is the initial number of larvae for the small size at first feeding, N is the initial number of larvae for the large size at first feeding, P_L is the probability of survival for the small size at first feeding in low prey densities, P_H is the probability of survival for the small size at first feeding in high prey densities, R_L is the probability of survival for the large size at first feeding in low prey densities, and R_H is the probability of survival for the large size at first feeding in high prey densities.

When the percentages of larvae in the high-prey-density patch exceed X_c , broods with smaller first-feeding larvae produce more survivors than broods with larger larvae at first feeding. We use the average probabilities of survival for 3-, 5-, and 10-mm initial size at first feeding and densities of 50, 100, and 200 prey/L (comparison 1) as estimates of P_L , P_H , R_L , and R_H . This method is equivalent to randomly assigning individual larvae to different patches in different proportions for two or more broods and then contrasting average brood survival. Because larvae do not affect one another (i.e., no density dependence), results from earlier simulations can be combined without performing a new set of independent simulations. That is to say that if 10% survive in 50 prey/L and 20% survive in 100 prey/L and we assign 40% of the larvae to the low-prey-density patch, then 16% will survive on the average ($[0.4 \cdot 0.1] + [0.6 \cdot 0.2] = 0.16$).

RESULTS

Model predictions were highly repeatable from one random number seed to another (coefficients of variation [CVs] given in figs. 2, 3). We therefore compare the mean values from five simulations for each set of conditions.

Effects of Prey Density and Larval Size

At all three prey densities, the daily growth rate was higher, larval stage duration was shorter, and the probability of survival was greater for larger initial size of larvae (fig. 2). However, the absolute number of survivors depends on the combination of size at first feeding and prey densities (fig. 3). As prey densities increase from 50 to 200 prey/L, increasing numbers of survivors are produced from broods comprised of smaller first-feeding larvae. Under low prey densities (50 prey/L), the largest size at first feeding resulted in the greatest number of survivors. For our intermediate prey densities (100 prey/L), the intermediate size at first feeding resulted in the greatest number of survivors. At high prey densities (200 prey/L), the smallest size at first feeding produced the greatest number of survivors. Thus, while it is always better from an individual's perspective to begin life at a larger size, from the parental fitness perspective, it is more profitable to produce many small larvae in prey-rich environments.

Effect of Small-Scale Prey Patchiness

Results of the negative binomial method for calculating prey encounters with $K = 10$ were very similar to those obtained for the Poisson distribution. For 3-mm larvae and 50 prey/L, the Poisson method generated an average of 3.8 survivors, whereas the same initial conditions using the negative binomial method

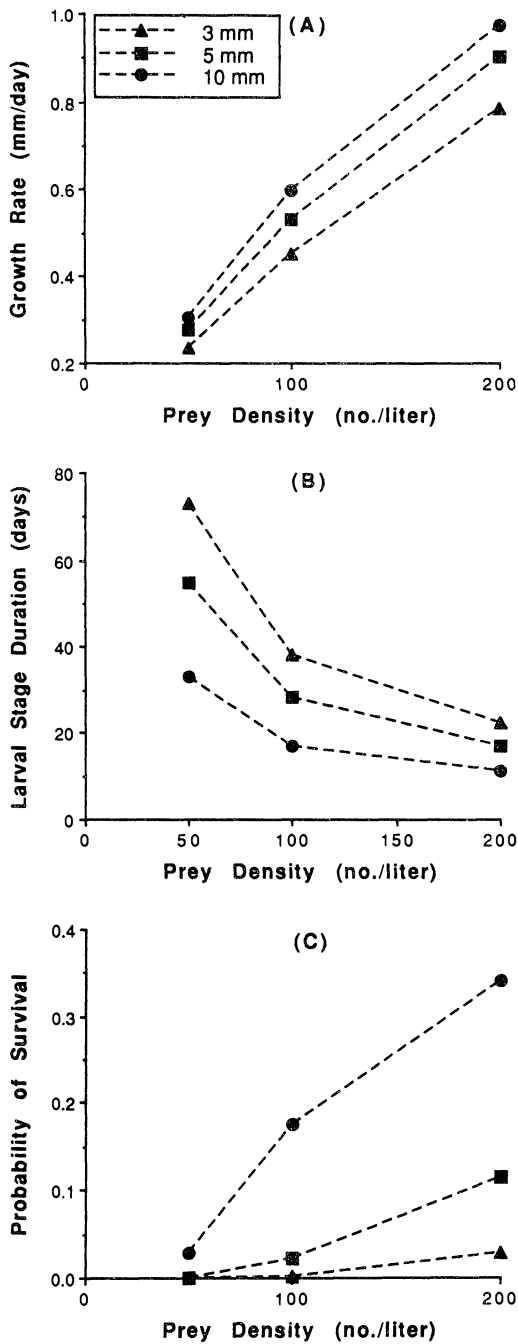


FIG. 2.—Daily growth rates (A), duration of the larval stage (B), and probabilities of survival of individual larvae (C) from model simulations using three different size classes of first-feeding larval fish. Each *point* represents the mean of five model simulations initiated with different random number seeds (CVs ranged between 0.006 and 0.25).

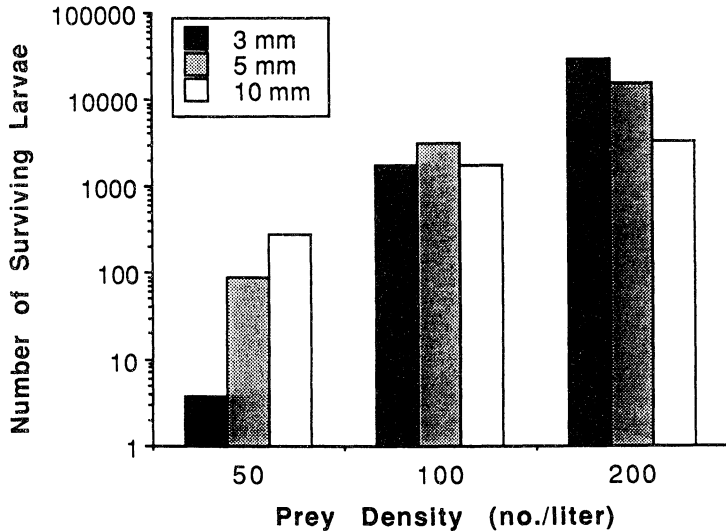


FIG. 3.—The number of surviving larvae at three densities of randomly distributed prey from simulations using a constant initial biomass for cohorts but different numbers and sizes of first-feeding larvae (3, 5, 10 mm). Each bar represents the mean of five model simulations initiated with different random number seeds. Variances were small (CVs < 0.33 for simulations with prey density = 50, CVs < 0.032 for prey density = 100, CVs < 0.008 for prey density = 200).

with $K = 10$ yielded an average of 3.6 survivors. For 10-mm larvae and 200 prey/L, the Poisson yielded an average of 3,257, and the negative binomial ($K = 10$) with same initial conditions produced an average of 3,119 survivors.

Simulations involving small larvae in environments with low prey densities resulted in very few survivors (range of mean survivors = 0.6–7.2) at all values of K , with the smallest values occurring at $K = 0.1$. Numbers of survivors decreased monotonically with increasing values of K for other combinations of size at first feeding and prey density (fig. 4). At 200 prey/L, decreases with lower values of K were greater for 3-mm first-feeding larvae compared with 10-mm larvae. This result is explained by the inability of very small larvae to survive several consecutive days of low encounters with prey that are highly clumped on a small spatial scale. Because there is no “memory” in the encounter probabilities calculated from the negative binomial method, both individuals encountering many prey and individuals encountering few or no prey on a given day are equally likely to encounter very few prey on the next day. According to our size-based rule for the probability of mortality, small larvae are more likely to perish than larger larvae under conditions of extreme prey clumping on a small spatial scale. Retarded growth due to chronic infrequent encounters with clumped prey resulted in increased mortality.

Larger first-feeding larvae yielded more survivors than smaller first-feeding larvae under conditions of low prey density (50 prey/L), and this was true for all values of K (fig. 4). Except for simulations with the highest level of prey patch-

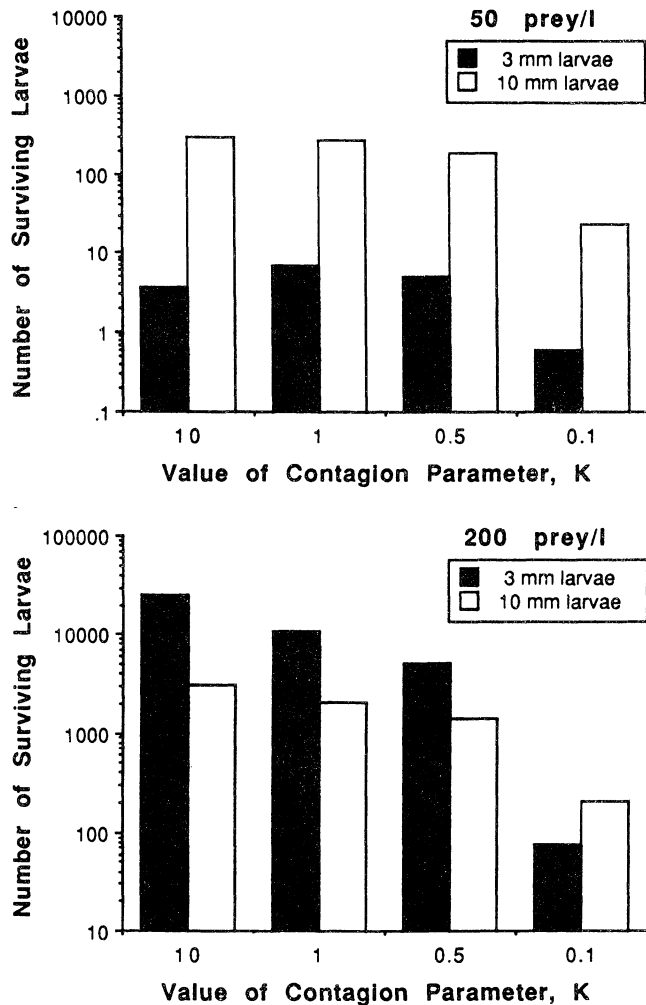


FIG. 4.—Comparisons of the influence of the contagion parameter, K , on the number of surviving fish larvae from cohorts of the same biomass but comprised of larvae of two different initial sizes (3 vs. 10 mm) in environments containing an average of 50 prey/L (*top*) and environments with an average of 200 prey/L (*bottom*). At low average prey densities, the smaller cohorts of 10-mm first-feeding larvae always yielded more survivors (*top*). At high average prey densities, larger cohorts of 3-mm larvae yielded more survivors except when prey were highly clumped ($K = 0.1$) (*bottom*).

iness ($K = 0.1$), smaller first-feeding larvae yielded more survivors than larger larvae under conditions of high prey density (200 prey/L). Lowering the value of K in simulations had a greater negative influence on the survival of smaller larvae (fig. 4). The results from simulations employing the negative binomial method for generating prey encounters (variation perceived on a day-to-day basis) appear to converge with the results from simulations based on randomly distributed prey (i.e., Poisson simulations) for all except the extremely patchy conditions: more

TABLE 1

THRESHOLD VALUES FOR PERCENTAGES OF LARVAE THAT MUST OCCUR IN DENSE PREY PATCHES IN ORDER FOR THE NUMBER OF SURVIVING SMALL LARVAE TO EXCEED THE NUMBER OF SURVIVING LARGE LARVAE

LARVAL SIZE AT FIRST FEEDING	PATCH PREY DENSITIES (no./L)		
	High = 100/Low = 50	High = 200/Low = 100	High = 200/Low = 50
3 mm vs. 5 mm	No solution*	9.49	.63
5 mm vs. 10 mm	11.92	No solution†	1.57
3 mm vs. 10 mm	91.26	No solution†	1.07

* $X_e > 100\%$.

† $X_e < 0\%$.

survivors result from broods comprised of smaller larvae only when prey are dense.

Effect of Large-Scale Prey Patchiness

Table 1 presents threshold values for the percentage of a larval cohort that must occupy high-density prey patches (X_e) in order for the smaller larvae strategy to result in a greater parental fitness. First, compare yields from broods of equal mass comprised of 3-mm versus 5-mm first-feeding larvae in patches of 200 prey/L versus 100 prey/L for background density. We find that X_e was 9.49, which implies that if more than 9.5% of the larvae settle into a patch with 200 prey/L, more survivors (and hence greater parental fitness) will result from the production of 3-mm larvae than 5-mm larvae (fig. 5).

Next, consider the threshold value for 3-mm versus 10-mm first-feeding larvae in large-scale patches with prey densities of 200 prey/L versus a background of 50 prey/L. Now X_e was 1.07%, which implies that if approximately 1% of the larvae are in a patch with 200 prey/L, more survivors will result from production of 3-mm larvae than production of 10-mm larvae (fig. 5). For example, if 5% of the larvae occupy patches of high prey density, broods comprised of 3-mm first-feeding larvae result in 867 survivors compared to 235 for broods comprised of 10-mm first-feeding larvae, a nearly fourfold difference in the number of survivors.

For some comparisons, there was no solution for X_e (i.e., values must be $>0\%$ and $<100\%$). For example, a comparison of broods with 3-mm versus 5-mm first-feeding larvae and prey-rich patches of 100 prey/L associated with 50 prey/L outside of the patches resulted in $X_e = -6.4\%$. The increase in survival of 3-mm larvae from 50 prey/L to 100 prey/L was not enough to compensate for the increase in survival of 5-mm larvae going from 50 prey/L to 100 prey/L.

DISCUSSION

According to our estimates of size-dependent probabilities of prey encounters and ingestion, small larvae (3–5 mm at first feeding) may require densities of prey

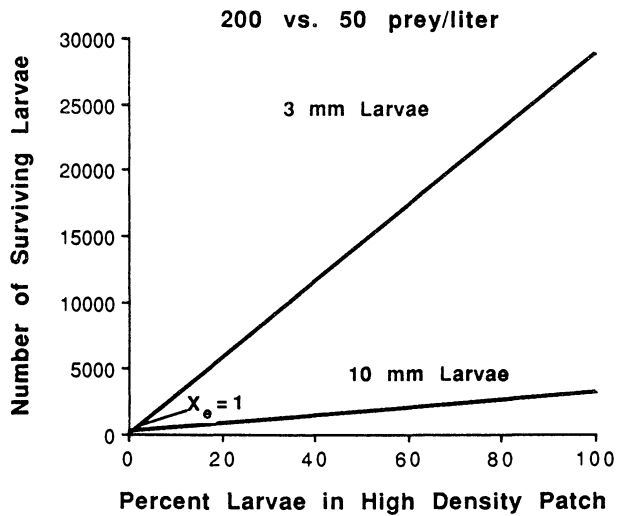
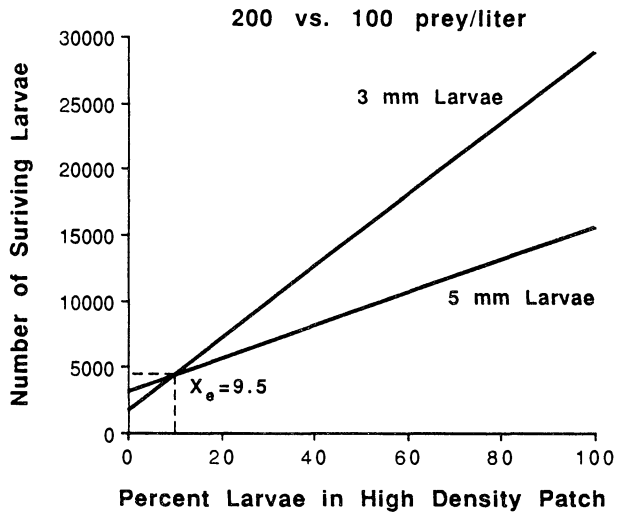


FIG. 5.—Comparisons of the number of surviving larvae from cohorts of equivalent biomass but different sizes of first-feeding larvae when different proportions of each cohort are placed in a large patch of high prey density. The *top graph* compares cohorts comprised of 3-mm vs. 5-mm larvae in environments with 200 prey/L patches in a background of 100 prey/L, and the *bottom graph* compares the cohorts of 3-mm vs. 10-mm larvae in environments with patches of 200 prey/L patches in a background of 50 prey/L. In each graph, X_e is the threshold for the percentage of larvae in the high-prey-density patch that yields more survivors from the cohort comprised of small larvae.

in the upper range of the reported field values in order to achieve high survival during the early stages of development. Our simulations used values for prey densities (50, 100, 200 prey/L) that are within the range of densities reported for marine pelagic zooplankton (Lasker 1978; Miller 1983; Sherman et al. 1984; Laurence and Lough 1985; McGowan 1986; MacKenzie et al. 1990). Houde (1978) reported that the mean weight of larvae of three marine fish species increased by 4.1 to 17.7 times during 16 d following hatching at prey concentrations of 100/L. Following the match/mismatch hypothesis, years of high recruitment (i.e., dominant age-class cohorts) arise from a concordance between the timing and placement of large numbers of larvae with the periodic occurrence of favorable climatic/environmental conditions (Shepherd and Cushing 1990). Strong recruitment in several marine fish populations has been attributed to temporal pulses of planktonic production (Sherman et al. 1984), and correlations have been found between larval fish condition or abundance and the spatial distribution and density of zooplankton (Laurence 1974; Lasker 1978; Frank and Leggett 1982; McGowan 1986).

Our finding that relatively high prey densities favor the division of reproductive biomass into smaller eggs and larvae and that low prey densities favor the production of a smaller number of larger larvae (i.e., given equal reproductive biomass) is consistent with observed fish life-history strategies in other ecosystems. Some fishes that produce relatively few large offspring are restricted to environments that contain chronically low densities of larval food resources. For example, North American cavefishes (Amblyopsidae) produce only 6–20 eggs at a time and brood the developing larvae in the branchial chamber for up to several months (Poulson 1963). Densities of planktonic invertebrates in a cave inhabited by *Chlorogaster agassizi* ranged from 0.006 to 0.019 individuals/L, and benthic dredge samples contained no invertebrates (Poulson 1963). Other fishes that produce relatively large eggs or neonates have trophic niches that may restrict a rapid transition from planktonic larval feeding to adult feeding. The coelacanth and many piscivorous elasmobranchs, sharks in particular, produce large advanced neonates. In the marine environment, this strategy of producing fewer but larger, more advanced offspring appears to be much more common in deep-sea, coral reef, and benthic habitats. Zooplankton prey in the marine pelagic environment appear to be exploited by early life stages of bony fishes irrespective of the adult trophic niche. Our model results may provide insights into why this is so. If high densities of zooplankton prey are regularly or periodically available year in and year out, the production of large numbers of small eggs and larvae is the optimal reproductive strategy.

Even if zooplankton prey are extremely patchy, which available evidence seems to suggest, the large clutch/small offspring strategy should yield higher fitness as long as the scale of patchiness is relatively large. In our simulations, large-scale patchiness is implied when an individual larva encounters the same average conditions over the course of many days. Our results show that small-scale patchiness can reverse the survival advantage of producing larger broods of smaller larvae versus smaller broods of larger larvae. Small-scale patchiness implies that the prey spatial distribution is locally clumped, so that daily encoun-

ters with prey may vary greatly. Because small larvae are less resistant to starvation than large larvae (Pepin 1991), high degrees of localized prey clumping results in many larvae experiencing several consecutive days of low prey encounters and captures. In effect, high amounts of small-scale clumping yields the same effect on the relative survival of larvae of different sizes as reducing prey densities (fig. 4). Again, if our parameter estimations are reasonably accurate, the model results strongly suggest that fitness in fishes with tiny eggs and larvae depends on the occurrence of relatively dense zooplankton patches or pulses of production on fairly large spatial scales.

Two key assumptions of our model were density independence and size-dependent mortality. First, prey densities were maintained at the assigned levels throughout the simulations without feedback between the amount of zooplankton ingested by larvae and subsequent zooplankton densities. In general, marine larvae are believed to be too sparse relative to their prey to have a substantial effect on prey population dynamics (Cushing 1983). The basic question of how density dependence would influence our results deserves further examination. Second, mortality is assumed to be a decreasing function of larval length following Pepin's (1991) regression. However, Pepin's analysis compared mortality rates across species rather than a single cohort or species population. Two observations lend support for Pepin's equation as a reasonable approximation of size-based mortality of individuals in a cohort. First, there is evidence that mortality rates decline as the size of larvae increases within fish populations (Anderson 1988; Bailey and Houde 1988; Rose and Cowan, in press). Second, the use of a less size-dependent mortality function would only increase the benefits of producing many small progeny in prey-rich environments. With Pepin's size-dependent mortality function, we have actually penalized smaller larvae by increasing their probability of dying. As the size dependence of mortality is reduced, it becomes less disadvantageous to be small.

We have demonstrated how the availability and distribution of larval food resources can influence the optimal reproductive strategy in fishes with pelagic larvae. Could patchiness in the probability of mortality result in a similar kind of directional selection for the initial size of larvae? We have not yet examined this possibility, but it seems likely, especially in light of Venable and Brown's (1988) findings for plants and Armstrong and Shelton's (1990) findings for marine fishes with planktonic larvae (discussed below). Predation intensity should be patchily distributed for many, perhaps most pelagic larval fishes. Large roving planktivorous fishes and invertebrates (e.g., jellyfishes) and schooling planktivorous fishes would produce patterns of high and low mortality threat on relatively large spatio-temporal scales. Larval mortality from advection by ocean currents would also produce a pattern of mortality on very broad spatial scales. We are currently exploring methods to simulate spatial and temporal variability in the probability of mortality for larval pelagic fishes.

Our comparative findings have strong implications for understanding the evolution of alternative life histories. Armstrong and Shelton (1990) used a Monte Carlo model to explore the demographic fates of clupeoid fishes in temporally varying environments. They found that serially spawning fishes with short life

spans achieved greater reproductive success than longer-lived pulse spawners in environments having greater within-season variation in conditions influencing larval growth and survival. Like our individual-based model simulations, Armstrong and Shelton's model assumed no density dependence. Results from Armstrong and Shelton's model stress the importance of spawners as the "samplers" of temporally varying environments, whereas our model results highlight larvae as samplers of spatial variation. To a large extent, the optimal adult sampling strategy for small-scale temporal variation (serial spawning of smaller clutches) trades off on the optimal strategy for dealing with large-scale spatial variation (pulsed production of larger clutches). Because any environment contains elements of both temporal and spatial variation, the optimal demographic strategy will represent a balance between selection on both adult and larval life stages (Southwood 1977).

In effect, many plants have adopted the same bet-hedging strategy in heterogeneous space as have fishes in the marine pelagic environment. Venable and Brown (1988) modeled the optimal seed size and dispersal capabilities in relation to environmental variability for plants. Their model simulations showed that increasing the number of patches on a landscape favored increased dispersal capability and decreased seed size. As the number of patches approached infinity, dispersal and small seed size began to lose their variance-reduction value in terms of optimal demographic strategies. They also determined that the optimal seed size decreased and dispersal capability increased as the probability of favorable environmental conditions increased in the model. In effect, two different simulation models (planktonic larvae and plant seeds) achieve similar qualitative results for the effect of large-scale environmental heterogeneity and patch quality on the optimal size of offspring. In terms of the fitness advantage of releasing large numbers of dispersive propagules into spatially patchy environments, the trophic status and mobility of the adult organism may have relatively little influence on this outcome. Given these general findings, it is possible that other taxa showing a predominance of the high fecundity/small offspring strategy (e.g., many higher plants, aquatic and marine invertebrates) may be exploiting similar patterns of heterogeneity in resources that influence the survival of early life stages.

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