Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment

James H. Cowan, Jr, Edward D. Houde, and Kenneth A. Rose

Twenty-day simulations of responses by a larval fish cohort were investigated with an individual-based model of predation by ctenophore, medusa, and planktivorous fish predators. Results indicate that the relationship between larval size and vulnerability to predation was generally dome-shaped for invertebrate predators and could be dome-shaped for fish predators if they foraged optimally by size, and depended upon attributes of both predators and larval fish prey. For the predators that did not forage optimally, cohort-specific mortality generally decreased as the mean length of larvae in a cohort increased, but bigger or faster-growing larvae within a cohort were not always most likely to survive. Until larvae grew through a ''window'' of vulnerability and reached a threshold length when susceptibility to the predators decreased more rapidly with larval length than encounter rate increased, mean length or growth rate of surviving larvae on each day was slightly lower, or not different from those that died in most of the simulations. After the threshold length was reached, predators began to catch smaller larvae, which resulted in larger survivors. The time necessary to grow through the window and reach the threshold length depended on growth rate of the larvae, size of the predators, and the variance structure of these parameters. These results indicate that size and growth rate of fish larvae are partially decoupled by the predation process and, ultimately, act differentially to determine cohort survival rate, although both may be most important after larvae have reached the threshold length. In these simulations, the threshold length was reached after a significant portion (56–99%) of total larval mortality had occurred; time to reach the threshold was generally shorter for the faster growing cohorts. Initially, both fast- and slow-growing individuals within a larval cohort differed little in size and, therefore, were nearly equally vulnerable to predation. However, reduced risk of predation occurred when all members of a cohort had reached the threshold length, which suggests that mean growth rate of individuals within a cohort, not their size, is probably the more important parameter affecting cumulative mortality, especially when the rate is high. We propose that characteristics of larval survivors may be more influenced by attributes of the predators to which they were exposed in early life, rather than by their initial status within a cohort with respect to length at hatching and potential growth rate.

© 1996 International Council for the Exploration of the Sea

Key words: predation, larval fish, vulnerability, individual-based model.

James H. Cowan, Jr: Department of Marine Sciences, University of South Alabama, Marine Environmental Sciences Consortium, Dauphin Island Sea Lab., P.O. Box 369-370, Dauphin Island, AL 36688, USA. Edward D. Houde: University of Maryland System, Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, Solomons, MD 20688, USA. Kenneth A. Rose: Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 38731, USA.

Introduction

Fluctuations in abundances of fish stocks occur because of variability in the level of recruitment, which is largely attributable to variable mortalities of early life stages (Cushing, 1975; Sissenwine, 1984; Houde, 1987). With the exception of catastrophic environmental events, factors affecting the survival of larval and juvenile fish are believed to be related by what Cushing (1975) called the ''single process'', which infers that as the length of time

that larvae spend in a stage vulnerable to high mortality increases, the time over which the mortality operates also increases, thereby increasing cumulative mortality (Dahlberg, 1979; McGurk, 1986; Houde, 1987). Moreover, it is clear that small changes in larval growth and mortality rates can generate order of magnitude or greater differences in annual recruitments (Shepherd and Cushing, 1980; Houde, 1987, 1989; Davis *et al.*, 1991) and that relationships among larval size, growth rate, and behavioral processes such as foraging and predator avoidance are critical in determining survival (Bailey and Houde, 1989). Although causes of *in situ* mortality are rarely known explicitly (Sissenwine, 1984; Houde, 1987), factors that control predation rates can ultimately affect recruitment success. Although data are scarce, a generally accepted paradigm and intuition imply that large individuals are usually less susceptible to predation or other sources of mortality and thus more likely to survive (Peterson and Wroblewski, 1984; McGurk, 1986; Anderson, 1988; Miller *et al.*, 1988; Pepin, 1989a,b, 1991; Cowan and Houde, 1992; Rice *et al.*, 1993).

Predation is a major cause of high and variable mortality of egg and larval stages in marine fish (Hunter, 1984; McGurk, 1986; Bailey and Houde, 1989; Heath, 1992; Cowan and Houde, 1993). The role of predators and their potential to influence fish recruitment through mortality of larvae has been well demonstrated in large enclosure (mesocosm) experiments in which fish eggs and larvae, their predators, and alternative prey for predators are stocked at abundance levels near those in the sea (Øiestad, 1985, 1988; deLafontaine and Leggett, 1987, 1988; Gamble and Fuiman, 1987; Fuiman and Gamble, 1988; Fuiman, 1989; Gamble and Hay, 1989; Cowan and Houde, 1992). Recently, Cowan and Houde (1993) combined results from mesocosm experiments with field data on the abundance and distribution of fish and gelatinous zooplankton to estimate probable predation in Chesapeake Bay, USA, with good agreement between estimated *in situ* predation potential (20–40% d^{-1}) and larval anchovy *Anchoa mitchilli* mortality rates (0.29–0.32 d^{-1}; Loos and Perry, 1991; Houde, unpubl.).

Between-predator differences in consumption of ichthyoplankton may be related to variability in encounter rates with prey, probability of attack, capture efficiency, predator size, prey size and abundance, and presence of alternative prey for predators. Consequently, species-specific characteristics of predators and prey, as well as environmental conditions in which they occur (deLafontaine and Leggett, 1988), define the predation process at each location. Some enclosure experiments have indicated that the size-dependent predation paradigm occurs; cohort-specific mortality rate generally decreases as the mean age or size of members of the cohort increases. Recent results and

conceptual arguments, however, suggest that the process is more complex because, under some circumstances, larger or faster growing larvae within a cohort are more vulnerable to predators than smaller larvae (Fuiman, 1989; Pepin *et al.*, 1992; Litvak and Leggett, 1992; Cowan and Houde, 1992).

Cowan and Houde (1992) used results of experiments in 3.2 m^3 mesocosms that enclosed predatory ctenophores *Mnemiopsis leidyi*, scyphomedusae *Chrysaora quinquecirrha*, and planktivorous fish *Anchoa mitchilli* preying upon pelagic bay anchovy (*A. mitchilli*) eggs and naked goby *Gobiosoma bosc* larvae (Cowan and Houde, 1990, 1992, 1993) to empirically derive parameter estimates in a predator–prey encounter model (Gerritsen and Strickler, 1977; Bailey and Batty, 1983; Fuiman and Gamble, 1989), with good agreement between mesocosm and model results. In Chesapeake Bay, these predators are abundant, co-occur and are major consumers of fish eggs and larvae, but they differ greatly in morphological and behavioral attributes, e.g. size, swimming speed, search pattern, all of which are known to affect predation potential. Experimental and modelling results (Cowan and Houde, 1992) indicated that while susceptibility to predation declines with larval size, individual vulnerability is a trade-off (as described by Fuiman, 1989; Fuiman and Gamble, 1989) between increasing encounter rate and decreasing susceptibility as size increases, especially if larval swimming speed is high relative to that of the predator. Cowan and Houde (1992) hypothesized that the ''general'' relationship of decreasing vulnerability to predation with increasing larval size may be incorrect or, at least, may vary significantly with predator type.

In this paper, we apply the estimates of static model parameters of Cowan and Houde (1992) in a stochastic, individual-based model (IBM) to describe general properties of a larval cohort's vulnerability to the ctenophore (small, slow swimming, cruising stealth invertebrate), medusa (larger, tentacled, cruising invertebrate) and planktivorous fish (raptorial fish) predators. The potentials of the predators are compared with respect to predator size and the length, growth rate, and variability in growth rate of individual larval prey within a single cohort. Formulations in the predation IBM are based, to the extent possible, on empirical data and observations from laboratory or mesocosm experiments of predation on bay anchovy and/or naked goby early life stages (Cowan and Houde, 1990, 1992, 1993; Cowan *et al.*, 1992). In some cases, however, when data for bay anchovy eggs or naked goby larvae were not available, general relationships observed for other larvae were substituted and modified before the IBM was tuned to generate results that closely resembled the outcome of our mesocosm experiments (Cowan and Houde, 1990, 1992, 1993).

Methods

Model description

The individual-based model tracks the daily growth and survival of individual members of a larval cohort over 20 d as they are exposed to predation by individual ctenophore, medusa, or planktivorous fish predators, as well as the three predator types combined. On the first day of a simulation, each larval fish was randomly assigned an initial length (L_L, mm) and growth rate (G_L, mm d^{-1}) and each individual predator was assigned an initial length (L_P, mm) from normal distributions with specified means, standard deviations, and minimum and maximum values. Minimum and maximum values were specified to eliminate unrealistic random deviates from the distributions of length and growth rates and to simulate the two- to three-fold variation in growth rates observed within cohorts in large enclosures stocked at near natural densities of larvae and zooplankton prey (Cowan and Houde, 1990; Secor and Dean, 1992; Folkvord *et al.*, 1994). Larvae maintained their assigned growth rate throughout the simulation.

On each day of the simulation, the length of each larva was incremented by its assigned growth rate and then evaluated to determine whether it had encountered and been captured by a predator. The probability of attack by predators was assumed to be unaffected by the presence of alternative zooplankton prey nor did the predators become satiated when feeding on the ichthyoplankton (Cowan and Houde, 1992, 1993). Encounter rate was determined using the Gerritsen-Strickler formulation (Gerritsen and Strickler, 1977) modified to account for the non-negligible size of fish larvae prey (Bailey and Batty, 1983). Both encounter and capture were treated as stochastic processes. The mean number of encounters in a day (E) between the ith larva and the jth individual predator was computed by:

$$E = \pi(R_L + R_P)^2 C(10^{-9}/V) \tag{1}$$

$$C = \begin{cases} \dfrac{D_L^2 + 3D_P^2}{3D_P} & \text{if } D_P > D_L \\[2ex] \dfrac{D_P^2 + 3D_L^2}{3D_L} & \text{if } D_P < D_L \end{cases} \tag{2}$$

where: C=foraging rate (mm s^{-1}); R_P=encounter radius of the predator (mm); R_L=encounter radius of the larva (mm); D_P=distance swum in a day by the predator (mm); D_L=distance swum in a day by the larva prey (mm); and, V=modelled volume (l).

E is the mean number of times in a day that the encounter volume of the larva enters the encounter volume of the predator. Equation (1) was derived under the following assumptions: (1) predators and prey are randomly distributed in the small volume modelled; (2)

swimming by predators and prey is random in direction; (3) encounter volume of the predator is a cylinder with its base having a radius equal to the encounter radius of the predator and its height equal to the distance swum by the predator in a day; (4) encounter volume of a larva is a sphere with radius equal to its encounter radius; and, (5) the planktivorous fish does not search for prey below its body, i.e. its encounter volume is a half-cylinder (Rosenthal and Hempel, 1970; Fuiman and Gamble, 1989). The actual number of encounters was generated for each larva and predator from a Possion distribution with mean=E. Finally, the number of encounters that resulted in a successful capture of a larva was determined from a binomial distribution with the actual number of encounters used as the number of trials and the empirically-determined larval susceptibility as the probability of capture success. For each larva, this process was repeated for each of the individual predators. If an encounter between a larva and predator resulted in a capture, the larva was "eaten" and was removed from the cohort. Lengths of surviving larvae were updated for the next day based upon their assigned growth rates. Daily accounting of numbers, lengths, and growth rates of surviving larvae and those that died were repeated for 20 d.

Encounter model parameters

Encounter radius for the gelatinous predators (R_P) was the radius of the bell (scyphomedusa) or the radius of the whole cylindrical body (ctenophore). Encounter radius of a fish larva (R_L) is given as $2L/\pi^2$ where L is length of the larva in mm (Bailey and Batty, 1983) and the distance swum (D_L) by a larva in a day is 1.5 L_L 46 800 s. D_L (mm) is based on an assumed larval swimming speed of 1.5 body lengths s^{-1} (Blaxter, 1986) for 13 of 24 h d^{-1}, including rest periods; larvae were assumed to be motionless at night (Cowan, unpubl.).

Search velocities and distances swum by the predators were estimated from measurements in the laboratory and from determinations (24-h experiments in 3.2 m^3 mesocosm enclosures) of clearance rates (1 d^{-1} predator^{-1}) of fish eggs by each of the predator types of known size, assuming that immobile fish eggs had a capture probability of 1.0 (Table 1). To estimate larval susceptibility (here is a *realized* capture probability and includes an unknown probability of attack (P_a) plus predator error), predators were allowed to feed in the 24-h mesocosm experiments on goby larvae ranging from 2 to ≤10 mm total length. Because the mean number of larvae consumed by each predator type in each 1 mm larval length class was known, susceptibility by our definition was the ratio of the number of larvae eaten in each size class to the number of probable encounters between predators and larvae in the length class (Table 1).

Table 1. Encounter characteristics and susceptibility equations for each of the predator types used in the individual-based model simulations (from Cowan and Houde, 1992). L_P is the total length of the predator (for ctenophores and planktivorous fish, bell diameter for medusa) in mm. L_L is length of the larval prey in mm. 86 400 = seconds per day.

Predator type	Encounter radius (R_P)	Distance swam (D_P)	Realized capture probability (susceptibility)
Ctenophore	$0.5 \times$ diameter of cylindrical body	$0.025\ L_P \times 86\ 400$ s	$0.813 - 0.074\ L_L$
Medusa	$0.5 \times$ bell diameter	$(1.2 + 0.04\ L_P) \times 86\ 400$ s	$0.505 + 0.082\ L_L - 0.020\ L_L^2 + 0.0008\ L_L^3$
Planktivorous fish	$0.8\ L_P$	$3.0\ L_P \times 86\ 400$ s	$0.180 + 0.015\ L_L - 0.003\ L_L^2 + 0.0001\ L_L^3$
Optimally-foraging fish	$0.8\ L_P$	$3.0\ L_P \times 86\ 400$ s	$0.029 + 0.040\ L_L - 0.003\ L_L^2$

Simulations

The initial number (N_L, 5000 larvae) and lengths of fish larvae, individual predators (N_P, 600 ctenophores, 50 scyphomedusae, 10 planktivorous fish), and the volume of the modelled system (V, 200 m^3) were defined to provide densities and size distributions of larvae and predators that are typical for Chesapeake Bay (Dovel, 1971; Brownlee and Jacobs, 1987; Dalton, 1987; Horwitz, 1987; Olson, 1987), and to yield sufficient numbers of surviving larvae at the end of the simulations to permit a meaningful interpretation.

All model simulations were initiated with a cohort of fish larvae having identical size distributions, with larvae ranging in length from 1.8–2.2 mm total length ($\bar{X} = 2.0$ mm TL). Larval growth rate distributions in simulations were of three types: (1) slow, mean growth rate = 0.30 mm d^{-1} and standard deviation (s.d.) = 0.20; (2) fast, mean growth rate = 0.50 mm d^{-1}, s.d. = 0.20; and, (3) fast but variable, mean growth rate = 0.50 mm d^{-1}, s.d. = 1.0. Predator size distributions in simulations were specified as small or large individuals (Table 2), except for the planktivorous fish which had a single size distribution.

Table 2. Attributes of predators in individual-based model simulations. Medusae sizes are bell diameters, ctenophore and planktivorous fish sizes are total lengths (s.d. = standard deviation).

Predators	Min size	Max size	Mean initial	s.d.
Ctenophore				
Small	7.5	22.5	15.0	5.0
Large	30.0	60.0	45.0	10.0
Medusae				
Small	17.5	32.5	25.0 mm dia	5.0
Large	60.0	90.0	75.0	10.0
Planktivorous fish				
	25.0	45.0	35.0 TL	5.0

To examine the consequences of changes in larval growth rate to predation by an optimally-foraging fish predator, we made probability of attack (P_a) by the planktivorous fish increase with size of prey. Now the product of P_a and the slowly declining susceptibility curve for the planktivorous fish resulted in a susceptibility to the new predator (optimally-foraging fish) that increased until larvae became difficult for the predator to capture (Table 1), and decreased to 0 when larvae approached the predator's gape limit (33% of predator length, this gape limit was used in all fish simulations). We then repeated the fish model runs with the optimally-foraging predator, keeping all other attributes of the fish predators (Table 2) and their larval prey (see above) as in other simulations.

The numerical experiment consisted of a series of simulations that resulted in all combinations of the predator-type/prey-size and growth rate attributes. To illustrate predator effects on characteristics of surviving and dead larvae, some simulations were defined based on empirical estimates of predation potential (Cowan and Houde, 1993) to insure similar mortality rates ($\simeq 10\%$ d^{-1}) attributable to each predator over the 20-d run. For the comparison of survivors, we used 5000 larvae and 225 large ctenophores, or 25 large medusae or 19 optimally-foraging fish. For the comparison of dead larvae, simulations were run with 5000 larvae and 100 ctenophore, 12 medusa, and 9 fish predators combined. Simulation results (Table 3) are means of three runs of the stochastic model. Results of individual runs varied by less than 10%. Data from representative, individual runs are presented in Figures 2–9 for illustrative purposes.

Results

In nearly all of the model simulations, the results indicated that faster-growing cohorts of larvae had lower mortality rates than cohorts with slower growth rates, regardless of predator type (Table 3). Bigger survivors which had experienced faster growth generally

Table 3. Summary of 20-d individual-based model simulation results. Lengths and growth rates are means for larval survivors and those that died on the final day of the simulations. Day of threshold=the day in the simulation that the threshold length was reached at which susceptibility to the predators decreased more rapidly with larval size than did encounter rate increase. Percentage mortality before threshold=relative to total mortality. Final length ratio=the ratio of mean size of the larvae that died on the last day to those that were alive on the last day in the simulations. Data are means of three model runs.

Predator type	Nominal mean larval growth rate (mm d^{-1}) (s.d. in parentheses)	20 d survival (%)	Day of threshold	Percentage of mortality before threshold	Survivor final mean length (growth rate in mm d^{-1})	Dead larval final mean length (growth rate in mm d^{-1})	Final length ratio
Small ctenophore	0.30 (0.20)	38	13	76	8.13 (0.31)	5.88 (0.20)	0.73
	0.50 (0.20)	45	10	56	12.57 (0.53)	7.93 (0.30)	0.63
Large ctenophore	0.30 (0.20)	<01	15	99	7.84 (0.39)	6.02 (0.20)	0.77
	0.50 (0.20)	03	9	96	15.34 (0.67)	8.15 (0.33)	0.53
	0.50 (1.00)	04	8	92	17.23 (0.76)	5.00 (0.11)	0.29
Small medusae	0.30 (0.20)	63	16	81	7.98 (0.30)	6.29 (0.22)	0.79
	0.50 (0.20)	67	10	59	12.25 (0.51)	7.57 (0.28)	0.62
Large medusae	0.30 (0.20)	<01	10	92	10.26 (0.41)	9.84 (0.38)	0.96
	0.50 (0.20)	03	7	84	14.29 (0.61)	8.72 (0.46)	0.61
	0.50 (1.00)	04	7	84	16.93 (0.75)	6.10 (0.24)	0.36
Planktivorous fish	0.30 (0.20)	07	12	88	8.71 (0.33)	7.04 (0.25)	0.81
	0.50 (0.20)	11	10	82	13.66 (0.58)	9.73 (0.39)	0.71
	0.50 (1.00)	14	10	82	14.91 (0.66)	5.38 (0.16)	0.36
Optimally-foraging fish	0.30 (0.20)	10	—	—	6.86 (0.24)	7.75 (0.29)	1.13
	0.50 (0.20)	09	12	81	12.81 (0.54)	10.05 (0.40)	0.78
Combined predators	0.30 (0.20)	05	10	85	8.39 (0.32)	7.23 (0.26)	0.87
	0.50 (0.20)	07	8	83	13.56 (0.58)	9.18 (0.36)	0.68

were favored (Figs 2–5). However, the degree of size selection and resulting cohort survival rate to 20 d, which increased by a two-fold average when growth rate of larvae was increased from 0.30 to 0.50 mm d^{-1}, varied greatly depending on predator types and sizes. Moreover, effects of growth rate on cohort survival rate in high and low growth rate simulations increased as mortality rate increased.

Cruising invertebrate predators

In model runs with invertebrate (gelatinous) predators, the results indicated only a weak overall predator selection for prey size that resulted in the consumption of smaller, slower-growing larvae (Table 3). The mean length and growth rate of survivors within a cohort during the first 7–16 d was not substantially different, and occasionally slightly less, than larvae which were eaten. Later, larger or faster-growing individuals became more likely to survive. This occurred when larvae grew through a length range or "window" of vulnerability to attain a threshold length after which susceptibility decreased more rapidly than encounter rate increased in relation to larval size. Swimming speeds of the invertebrate predators were slow relative to the larval prey and changed little in relation to predator size. Encounter rates between these predators and larvae changed primarily as a consequence of prey growth and an increase in their swimming speed. In this circum-

stance, vulnerabilities (the product of, and trade-off between, susceptibility and encounter probabilities) were dome-shaped and generally increased until larvae were 5–7 mm TL, before slowly declining. Figure 1 shows theoretical vulnerability curves for different invertebrate and fish predator types compared with the observed vulnerabilities derived from our mesocosm experiments (Cowan and Houde, 1992) and used in these simulations. The observed vulnerabilities for the gelatinous predators did not conform strictly to either the ambush raptorial or cruising invertebrate predators of Bailey and Houde (1989), which probably represent points (perhaps endpoints) in a continuum of vulnerability relationships. Thus, the observed vulnerabilities were intermediate in the continuum and the predators exhibited attributes of both of the theoretical types. This result occurred because the ctenophore and medusae are slow-swimming (relative to their larval prey), cruising invertebrate predators, and the resulting relationship between larval size and vulnerability well illustrates the trade-off described above.

Variability in length of the window of larval vulnerability (and the number of days needed to grow through it), and the consequence of the trade-off between increasing encounter rate and decreasing susceptibility as larval length increased, are illustrated by comparing simulations with the two gelatinous predators. When small ctenophores were predators, small larvae within a slow-growing cohort were slightly less vulnerable to

Theoretical
vulnerability

Observed
vulnerability

Ambush raptorial invertebrate   Ctenophore

Cruising invertebrate   Medusae

Filter-feeding fishes   Planktivorous fish

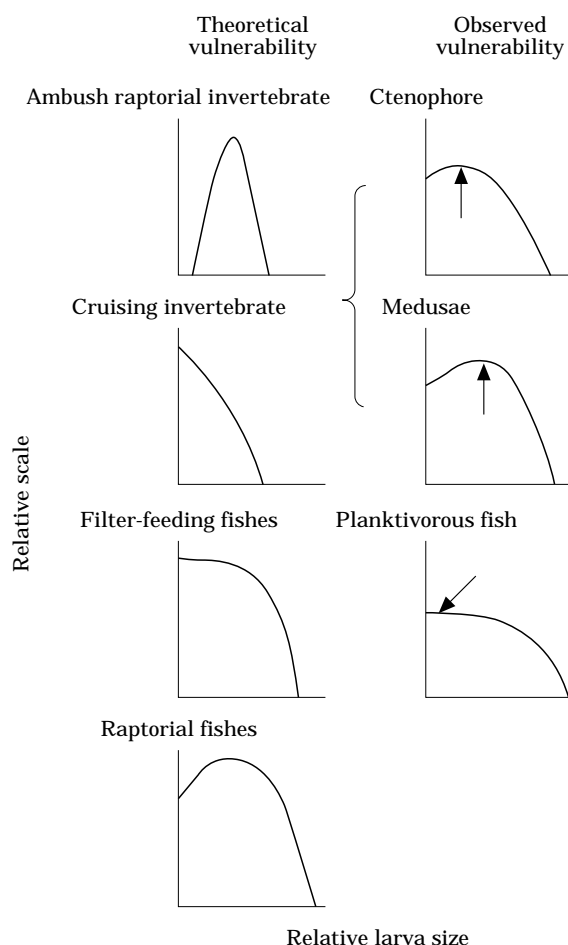Raptorial fishes

Relative scale

Relative larva size

Figure 1. Vulnerability of fish larvae to different types of predators. Theoretical relationships are redrawn from Bailey and Houde (1989). Observed relationships are redrawn from Cowan and Houde (1992). Arrows indicate the relative size of maximum larval vulnerability to the predators.

20 d and length differences between survivors and larvae that were consumed by large ctenophores, were less than for small ctenophores (Fig. 2c, Final length ratio in Table 3) because a higher percentage (99%) of the total mortality occurred before larvae reached the threshold length. An increase in larval growth rate to 0.50 mm d^{-1} shortened the window of vulnerability (Fig. 2d), and resulted in a three-fold increase in survival of the larval cohort as well as increased size selection (i.e. larger survivors and smaller Final Length Ratio).

In small medusae simulations when larval growth rates were slow, the mean lengths and growth rates of survivors were less than those of larvae that died during the first 15 d (Fig. 3a). The window of vulnerability before the threshold was prolonged, and many of the faster-growing, larger larvae within a cohort were eaten, a consequence of higher encounter rates with the small, relatively slow medusae as swimming speeds of the larval prey increased with growth. The length of survivors to 20 d was less and the Final length ratio was greater (i.e. less size selection) than in simulations when small ctenophores were predators (Table 3). Increasing the larval mean growth rate to 0.50 mm d^{-1} (Fig. 3b) produced a result similar to that in simulations with ctenophore predators, i.e. the period of relatively high vulnerability of faster-growing larvae was shortened and a survival advantage for larvae larger than the threshold length was more evident. Overall mortality rates were low when small medusae were predators. The increase in larval growth rate only increased survival to 20 d by 4%.

When large medusae were predators, mortality rates of larvae were high and results of the trade-off between encounter rate and susceptibility were dramatic. The slow-growing larval cohort experienced increased encounter rates, a function of the combined swimming speeds of predators and prey, coupled with slowly declining susceptibilities of larvae, which prolonged the period of high vulnerability to predation. Consequently, both fast- and slow-growing larvae were nearly equally vulnerable to predation in all 20 d of the simulation (Fig. 3c). Many individual larvae within the slow-growing cohort which had higher than average growth rates were consumed before significant length differences could be established. Lengths of larval survivors were almost indistinguishable from those that died each day throughout the simulation (Table 3, Fig. 3c).

When mean growth rate was increased from 0.30 to 0.50 mm d^{-1}, the cohort of larvae grew more quickly through the period and length range when susceptibility to the predator declined little and, as a consequence, the period of vulnerability of larger larvae was shortened (Fig. 3d). As a result, less of the total mortality occurred before larvae reached the threshold length and the apparent size selection resulting in large survivors with rapid growth rates was strong (Table 3). In this
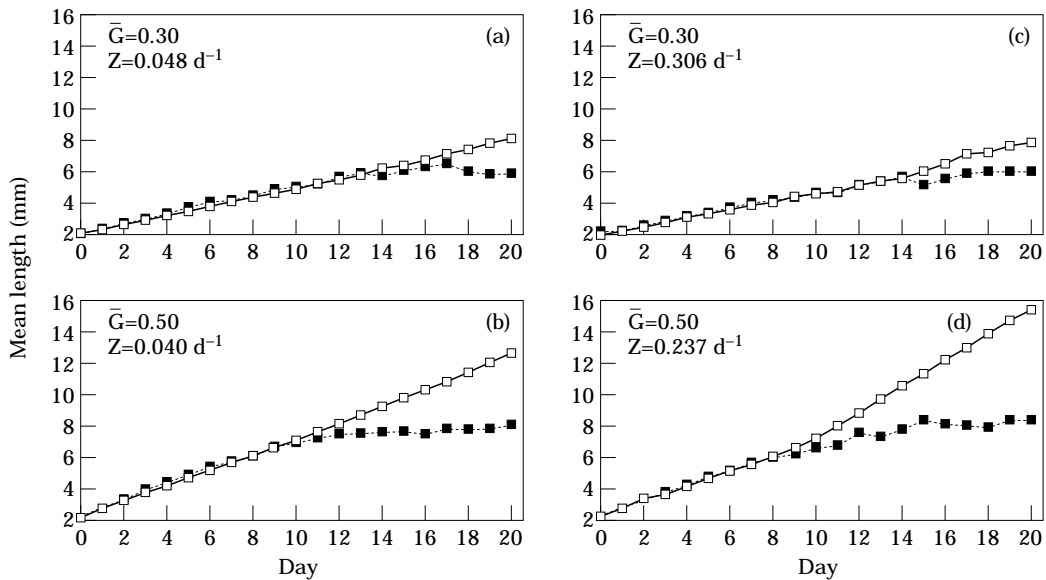
predation for the first 13 days (Fig. 2a), a period in which 76% of the total larval mortality occurred (Table 3). Because susceptibility to the ctenophore declined linearly (Table 1), and small ctenophores swam slowly relative to their larval prey, an increase in mean growth rate of larvae from 0.30 to 0.50 mm d^{-1} caused vulnerability to decrease more rapidly, especially for the faster-growing individuals within the cohort. Consequently, many larvae reached the threshold length at a younger age (Fig. 2b), after only 56% of the larvae had been consumed. At the 0.50 mm d^{-1} growth rate, mean length of survivors at 20 d was greater, while survival of the cohort increased by 7% (Table 3).

When larger ctenophores were simulated, mortality rate of the larval cohort was high because young larvae were consumed more rapidly due to higher encounter rates with the faster predators. Consequently, at the 0.30 mm d^{-1} growth rate, mean length of survivors at

Figure 2. Plots of daily mean lengths of larval survivors (S, □) compared with those that died (d, ■) in 20-d individual-based model simulations employing a ctenophore predator preying on a cohort of fish larvae. Results in (a) and (b) are for small ($\bar{X}=15$ mm) and (c) and (d) are for large ($\bar{X}=45$ mm) ctenophore predators. Note that growth rates (mm d^{-1}) of the larval cohorts vary between simulations.
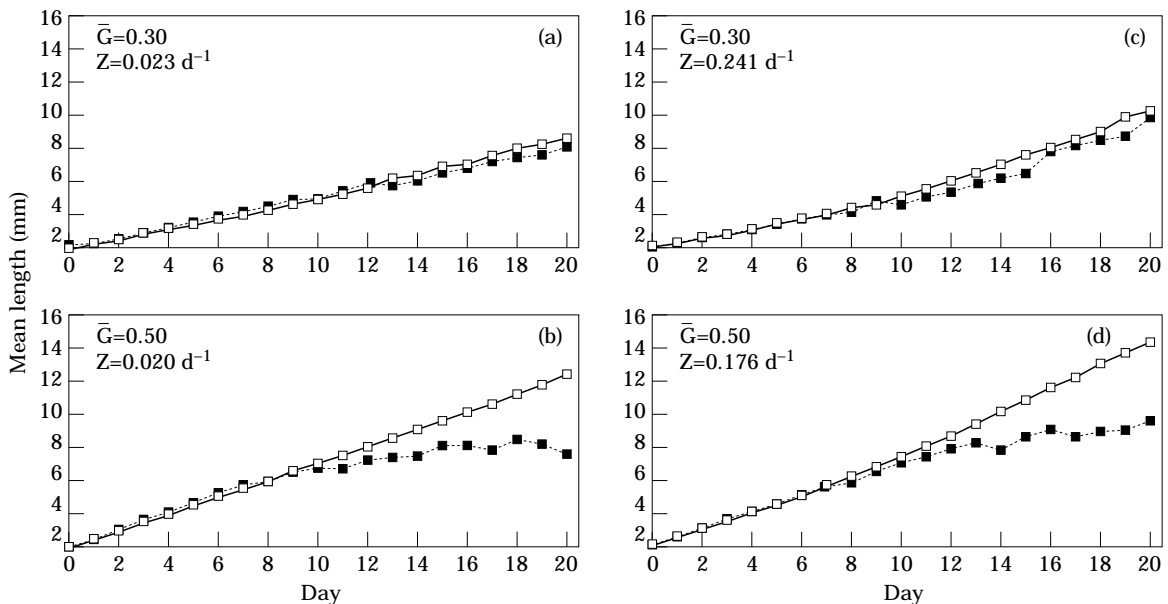

Figure 3. Plots of daily mean lengths of larval survivors (S, □) compared with those that died (d, ■) in 20-d individual-based model simulations employing a medusa predator preying on a cohort of fish larvae. Results in (a) and (b) are for small ($\bar{X}=25$ mm) and (c) and (d) are for large ($\bar{X}=75$ mm) medusae predators. Note that growth rates (mm d^{-1} of the larval cohorts vary between simulations.

situation, cohort survival was 3.7 times higher than that in the slow growth rate simulations.

In model runs with large medusae ($\bar{X}=75$ mm) in which larval prey had fast but highly variable growth rates (Table 3), size selection increased (Fig. 4). Surviv-ing larvae at 20 d were larger and had higher mean growth rates, but there was only a small increase in larval survival rate and no change in the duration of the period before the threshold length was reached. An impressive increase in size-selective predation when
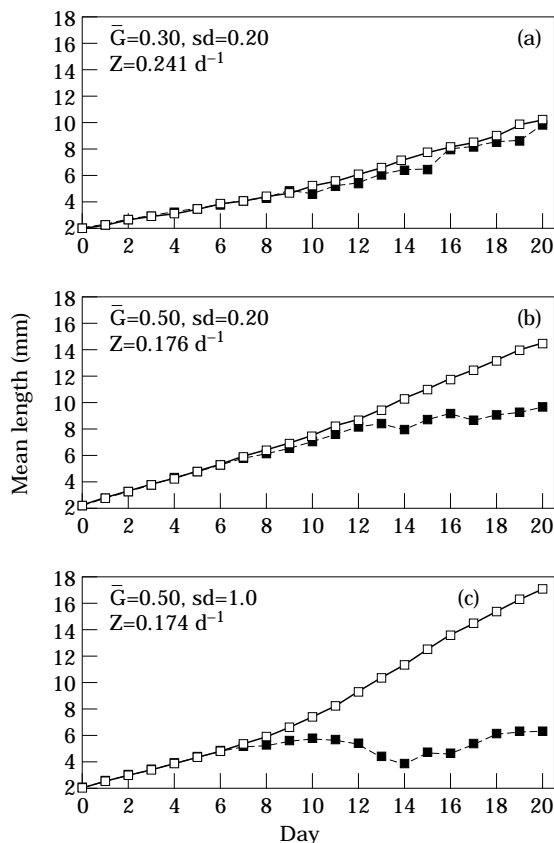
Figure 4. Plots of daily mean lengths of larval survivors (S, □) compared with those that died (d, ■) in 20-d individual-based model simulations employing a large ($\bar{X}=75$ mm) medusa predator preying on a cohort of fish larvae. Results in (a) are for a larval cohort growing at a mean rate of 0.30 mm d^{-1}, (b) for larvae growing at a mean rate of 0.50 mm d^{-1}, and (c) for larvae growing at 0.50 mm d^{-1} but with an increase in growth-rate variability.

Figure 5. Plots of daily mean lengths of larval survivors (S, □) compared with those that died (d, ■) in 20-d individual-based model simulations employing a planktivorous fish predator (35 mm) preying on a cohort of fish larvae. Results in (a) are for a larval cohort growing at a mean rate of 0.30 mm d^{-1} and (b) for larvae growing at a mean rate of 0.50 mm d^{-1}.

variability in larval growth rate increased was common to all of the predators (Table 3). When growth rate was variable, size selection by each predator increased, despite only small differences in mean survival rates. Survivors on day 20 were derived from larvae with growth rates in the upper 25% of the initial distribution of rates.

Raptorial fish predators

Encounter rates between the planktivorous fish and the larval prey were determined primarily by the rapid swimming speeds of the predators (3 body lengths s^{-1}), making smaller larvae slightly more vulnerable than larger larvae until larval length approached the predator's gape limit (33% of predator length). Thus, the mean lengths of survivors in the fish predator simulations were never less than those that died. Strong size
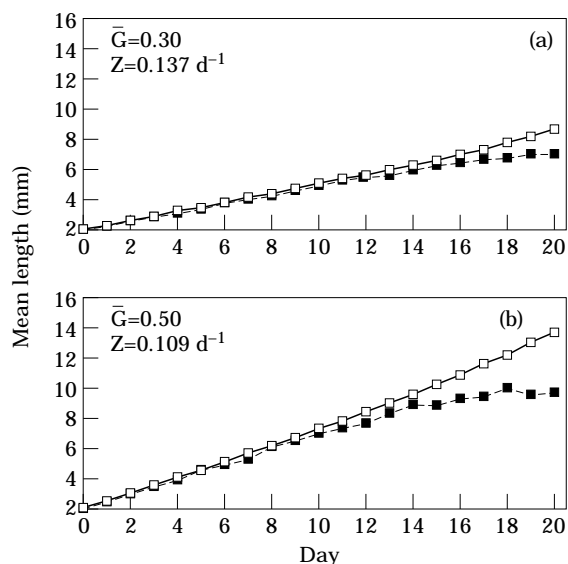
selection became evident after 10–12 d (Fig. 5). This result occurred because the relationship between larval size and vulnerability derived from the Cowan and Houde (1992) mesocosm experiments with a fish predator (Fig. 1), and used in these simulations for the planktivorous fish, resembled the theoretical relationship given by Bailey and Houde (1989) for a filter-feeding predator which does not select based on size of its prey.

Size-selective predation by the planktivorous fish was less evident for the slower-growing cohort because encounter rate between the predators and prey varied little as a function of the prey's swimming speeds and susceptibility declined slowly with larval length (Fig. 5). An increase in larval growth rate from 0.30 to 0.50 mm d^{-1} caused significant increases in size selection (Fig. 5b), survival, and mean length of survivors on day 20 (Table 3). An increase in growth rate variability of larval prey increased size selection by the fish predator and, in contrast to results for the gelatinous predators, substantially increased (by 1.3-fold) the survival rate of the larval cohort.

The simulations with an optimally-foraging fish (similar to the raptorial fish of Bailey and Houde, 1989; see our Fig. 1) preying on a slow-growing (0.30 mm d^{-1}) cohort caused slightly but consistently higher consumption rates of larger larvae over the 20-d period (Fig. 6a). Under this circumstance, cohort survival was increased substantially over the simulation of slow-
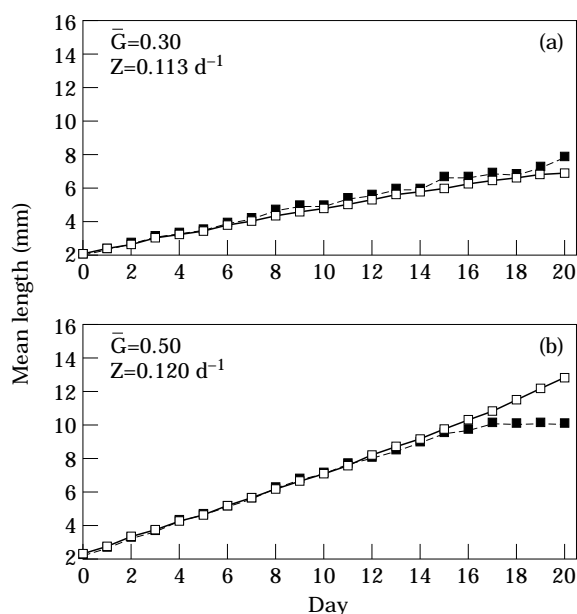
Figure 6. Plots of daily mean lengths of larval survivors (S, □) compared with those that died (d, ■) in 20-d individual-based model simulations employing an optimally-foraging fish predator preying on a cohort of fish larvae. Results in (a) are for a larval cohort growing at a mean rate of 0.30 mm d^{-1} and (b) for larvae growing at a mean rate of 0.50 mm d^{-1}.
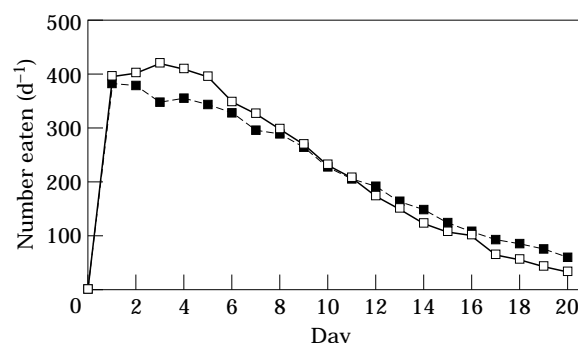

Figure 7. Number of larvae eaten each day in a 20-d individual-based model simulation employing an optimally-foraging fish predator preying on a cohort of fish larvae. □=Fast (0.50 mm d^{-1}); ■=slow (0.30 mm d^{-1}).
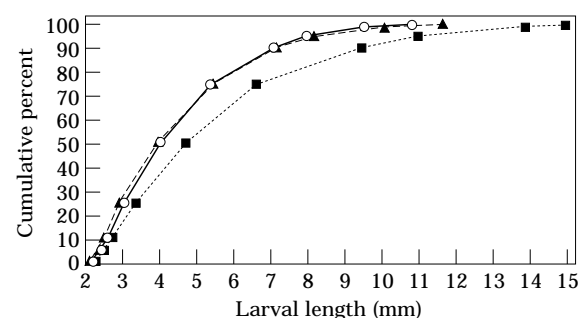

Figure 8. Cumulative percent-frequency of lengths of members of a fast-growing larval cohort which were consumed by each predator type in a simulated predator field comprised of large ctenophores, large medusae and optimally-foraging fish. Each predator contributed $\simeq 5\%$ d^{-1} to total larval mortality. ○=ctenophores; ▲=medusae; ■=optimally-foraging fish.

growing larvae without optimal foraging because larvae were less vulnerable to the predator when they were small. Moreover, under the optimal foraging alternative, mean length of survivors on day 20 was lowest of all the simulations in our numerical experiment (Table 3). When growth rate of the larval cohort was increased to 0.50 mm d^{-1}, results of simulations with the optimally-foraging predator resembled those for fish predators without optimal foraging (Fig. 6b), i.e. stronger size selection became evident on day 12, after which larger survivors were favored. This simulation also produced an unexpected result of decreased survival of the cohort (Table 3). The outcome occurred because faster-growing larvae were selected during the first 10 d (Fig. 7) as these larvae, while still abundant, quickly grew into lengths that made them preferable to the predator. After day 10, relatively few larvae in the faster-growing cohort were consumed by the optimally-foraging fish as the larvae quickly became less susceptible to the predator.

Characteristics of survivors and dead larvae

To demonstrate the potential for predator type to determine characteristics of dead larvae, we exposed a cohort at the 0.50 mm d^{-1} growth rate to a simulated predator field comprised of large ctenophores, large medusae and optimally-foraging fish at densities such that each accounted for a similar fraction of the total larval

mortality ($\simeq 5\%$ predator^{-1} d^{-1}). In these simulations, the threshold length was reached early (day 8) after 83% of total larval mortality had occurred (Table 3). Cumulative percent-frequency of lengths of larvae consumed by the three predators differed (Fig. 8). Larvae which had encountered and were eaten by optimally-foraging fish had experienced a larger window of vulnerability and were larger than those eaten by the medusa, which generally were larger than those eaten by the ctenophore, although larvae consumed by the ctenophore were slightly larger than those eaten by the medusae when larvae were small. Thus, larvae that survived to 20 d had faced a variety of predation pressures, growing less vulnerable to one predator while growing more vulnerable to another. In addition, under the circumstance of fast larval growth, predation rate by gelatinous predators was reduced while predation rate by optimally-foraging fish was simultaneously increased. Despite this complexity, survival rate of the cohort still increased by 1.7-fold when growth rate was increased from 0.30 to 0.50 mm d^{-1} (Table 3).

To illustrate the potential for predator type to affect characteristics of larval survivors, we exposed a cohort growing at the 0.50 mm d^{-1} rate to large ctenophores, large medusae or optimally-foraging fish singly, but each at densities necessary to produce $\simeq 10\%$ predator^{-1} d^{-1} larval mortality. In these simulations, differences in length distributions of survivors that developed over time (Fig. 9) reflect previously mentioned differences in length of windows of vulnerability (Fig. 8) to, and morphological and behavioral attributes of (Tables 1 and 2), individual predator types because all cohorts of larvae were initially identical.

All but the slowest-growing larvae in the cohort grew quickly through the window of vulnerability to the slow-swimming ctenophore, which resulted in large survivors ($\bar{X}=14.54 \pm 3.04$ mm, $s^2=10.61$) with relatively low length variability on day 20. When large medusae were predators, many of the potentially fastest-growing larvae were consumed while still small due to increased encounters during a prolonged window of vulnerability, resulting in smaller ($\bar{X}=13.31 \pm 3.24$ mm, $s^2=11.09$) and more variable survivors on day 20 (Fig. 9). This trend is dramatically illustrated by results for the optimally-foraging predator. Because vulnerability of larvae to this predator increased rapidly with length until they became difficult to capture, the largest and fastest-growing larvae were selectively removed by the predators from the cohort for much of the simulation, leaving behind small survivors ($\bar{X}=12.08 \pm 3.76$ mm, $s^2=14.11$) with a high variability in length on day 20 (Fig. 9).

Discussion

It has been hypothesized that increased larval size should improve an individual's probability of survival because of increased foraging ability (Miller *et al.*, 1988; MacKenzie *et al.*, 1990) or reduced susceptibility to predation (Miller *et al.*, 1988; Bailey and Houde, 1989). Yet, it also has been proposed that the theoretical relationship between vulnerability to predation and larval size should be dome-shaped, with highest vulnerability at some intermediate size (Fuiman, 1989; Bailey and Houde, 1989; Pepin *et al.*, 1992). The two arguments seem contradictory. In attempts to deduce how predators affect larval fish, several recent studies in mesocosm enclosures (Fuiman, 1989; Cowan and Houde, 1992; Litvak and Leggett, 1992; Pepin *et al.*, 1992) have demonstrated that larger larvae in a cohort may in fact be more vulnerable to predation for a period during the first few days after hatching. However, these studies have usually been limited to single (or a few) predator types and sizes, and prey lengths, thus making the generality of the results difficult to infer.

To explore the possible significance of the recent mesocosm results with respect to potential effects on recruitment, we have applied an individual-based model to simulate a variety of predator types consuming larval fish prey distributed over a wide size range. Our numerical experiment was realistic, being based on mesocosm results (Fig. 1). We recognize, however, the potential for error if some of our parameter estimates, or assumptions made about predator and prey behaviors and capabilities, are incorrect. For example, the larval susceptibility curves that we derived include probability of capture success, plus an unknown probability of attack, and predator error, which can be as high as 10–20% for fish predators feeding on larval fish prey (Fuiman, 1989; Fuiman and Batty, 1994). This is undoubtedly why our *realized* capture probabilities (susceptibilities) are considerably lower than expected, based on empirical model predictions of capture success derived from ratios of predator and prey lengths (Pepin *et al.*, 1987; Miller *et al.*, 1988; Fuiman, 1994). This is true for our fish predators where *realized* capture probabilities were never higher than 20% in our mesocosm experiments (Cowan and Houde, 1992). We interpreted this result to mean that fish predators did not attack every larval fish that they encountered.

In addition, we have represented predator–prey dynamics in a relatively small modelled volume because the Gerritsen-Strickler formulation used to generate numbers of encounters in our mesocosms and, in these simulations, assumed that predators and prey were randomly distributed in space. While this assumption may be true over relatively small spatial scales, larval fish feeding and mortality rates are dependent on mesoscale patchiness of prey and predators (McGurk, 1986), the patchy distribution of larvae themselves (Frank and Leggett, 1985; Houde *et al.*, 1989; Cyr *et al.*, 1992), and changes in predator behavior upon locating a patch of prey (Shipley and Spalinger, 1992; Noda *et al.*, 1994). Consequently, while it is unlikely that our model results represent between-patch dynamics well, the simulated consequences of variability in composition of potential predators and larval fish prey within patches may be realistic.

In most of our simulations, size-dependent predation was an *a priori* condition in the model (i.e. larvae susceptibility decreased with larval length, except to optimally-foraging fish). However, the simulation results indicate that effects of length and growth rate of fish larvae, relative to the predation process, may be most important when the larvae are larger or older and after a significant portion (54–99% in these simulations) of the total larval mortality in a 20-d experiment has occurred. The outcome was observed because fast- and slow-growing members of a cohort are initially nearly the same length and are nearly equally vulnerable to predation. Within-cohort, selective mortality, as we have represented it, develops in response to variability in a larval cohort's length distribution, which requires time to develop as a cohort of newly-hatched larvae grows,
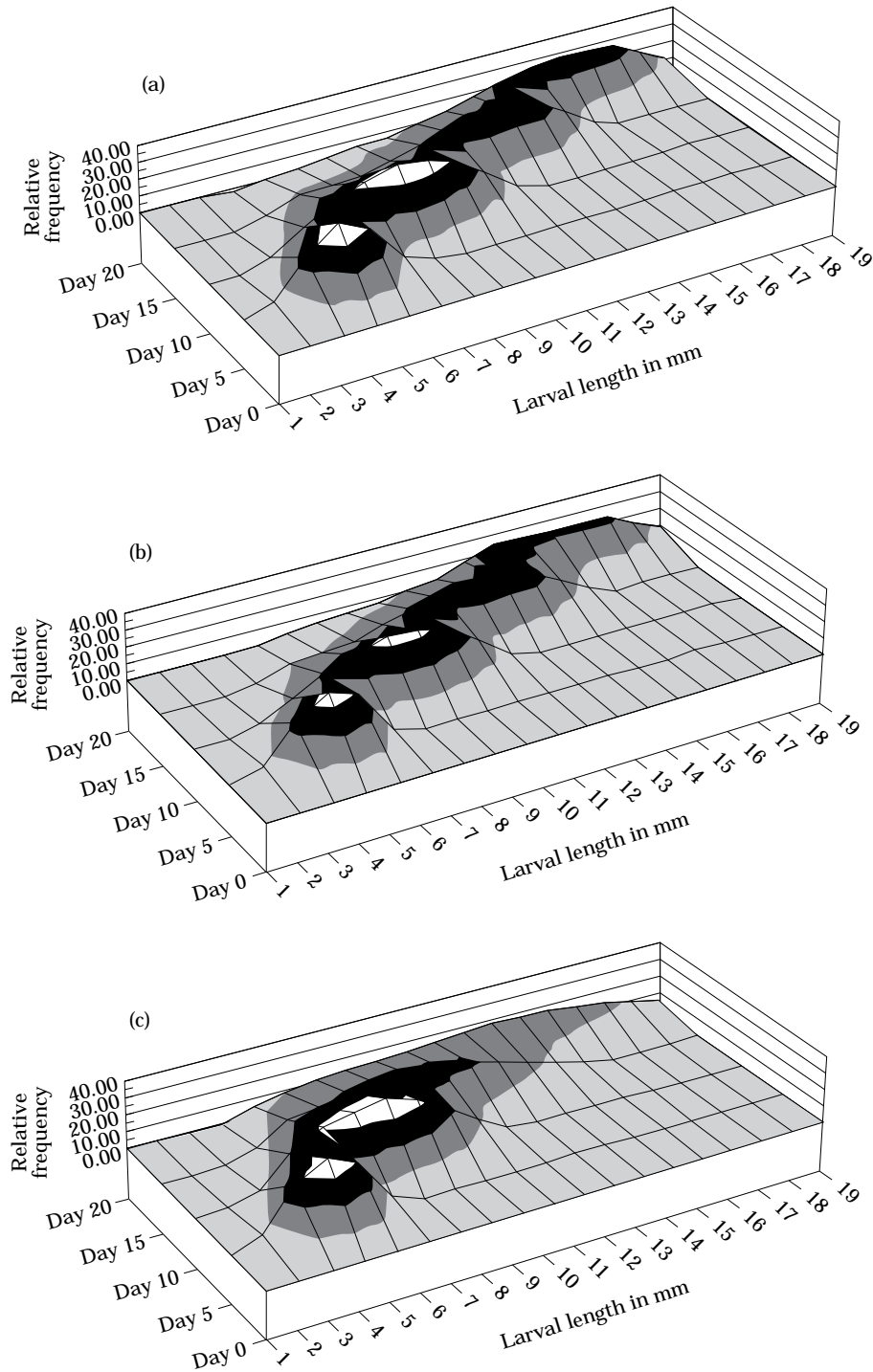
Figure 9. Response surfaces of the relative frequency of lengths of larval survivors exposed to (a) large ctenophores, (b) large medusae and (c) optimally-foraging fish predators on days 5, 10, 15 and 20 in model simulations. The combined predators consumed $\simeq 10\%$ d^{-1} of the larvae present.

rather than in response to variability in growth rate *per se* (Rice *et al.*, 1993).

Stronger size selection by predators on a larval cohort was indicated when mean growth rates were high and variable in the face of high predation pressure. Strong size selection usually was accompanied by a substantial increase in survival rate. When cohort growth rates were slow, or predation pressure was less, size-selective mortality was weaker. However, when variability in growth rate of the larval prey was increased without a concomitant increase in mean growth rate, most of our simulations again indicated strong size selection, but little change in survival rate of the larval cohort. This result demonstrates how increased growth rate variability, in the absence of increased mean cohort growth rate, can produce strong size-dependent predation at the individual level without benefits to the population of increased survival (Beyer, 1989; Pepin, 1989a,b; Rice *et al.*, 1993).

For the planktivorous fish predator, increased variability in prey growth rate did result in a lower overall predation rate. This result is similar to simulation results of Rice *et al.* (1993) who reported an increase in the numbers of larger survivors and a four-fold increase in survival rate of larval bloater *Coregonus hoyi* cohorts being preyed upon by hypothetical 90 mm SL alewife *Alosa pseudoharengus* predators when larval growth rate variability, but not mean growth rate, was increased. Our susceptibility relationship (Table 1) for the fish predator is based upon a linear extrapolation extended for larvae from 10 to 15 mm from data for larvae $\leqslant 10$ mm, the larger value being the estimated length at which larvae should become invulnerable to predation by even the largest predators. If probability of capture actually declines faster in larvae that are longer than those we tested in the mesocosm experiments ($\simeq 10$ mm), as Fuiman (1989) found for herring juveniles (*Clupea harengus*) feeding on herring larvae, then the degree of size selection and increase in cohort survival may have been affected more dramatically by increases in both mean growth rate and growth rate variability of the larval cohort (Rice *et al.*, 1993). On the other hand, if raptorial fish predators forage optimally or can detect and preferentially consume the largest individuals of a young or slower-growing cohort, as indicated by our simulations and by results of experiments with sticklebacks *Gasterosteus aculeatus* feeding on capelin *Mallotus villosus* larvae (Pepin *et al.*, 1992; Litvak and Leggett, 1992), vulnerability to predation by some fishes may also be best described by a dome-shaped relationship, with vulnerability decreasing after an intermediate maximum as larger larvae become better able to avoid capture by the predator (Fig. 1, also see Bailey and Houde, 1989).

Because it is likely that members of most cohorts of larvae *in situ* are exposed to predation during early life,

and the mix of predator types and sizes is highly variable, it seems unlikely that a simple conceptual model relating prey size to predation vulnerability will apply. Moreover, vulnerability relationships that appear to be similar in form, such as those for the gelatinous predators and optimally-foraging fish, may be mechanistically different, and result from a combination of dissimilar attributes that are unique to predator–prey combinations. However, our simulation results strongly suggest that increased mean growth rate of a larval cohort, in most cases, results in lower cumulative mortality of the cohort, especially if predators do not forage optimally and if predation pressure is high. When data from all simulations of slow-growing cohorts are considered, the range of daily mean lengths of larval survivors at 20 d (6.86–10.26 mm) was higher than those that died (5.88–9.84 mm) but overlapped considerably. However, when mean growth rate was increased, mean survival rates of cohorts increased and larval survivors were considerably larger (12.25–15.34 mm) than those that died (7.57–10.05 mm). We interpret this to indicate that reduced cumulative risk of predation at the population (cohort) level is reached when the smallest or slowest-growing members of the cohort become invulnerable, and that the time necessary for all to grow through a window of vulnerability and reach the threshold length depends upon the minimum growth rate in the cohort. The degree to which this interpretation is general, however, probably depends upon preferred prey size and the degree to which predators are able preferentially to consume prey based on size. Under these circumstances, one adaptive strategy for increasing survival rate may be the production of cohorts with highly variable growth rates or potentials, including, for example, negatively correlated rates during different periods of early life (Bertram *et al.*, 1993).

Another complexity for many fish species is the day-to-day influx of new cohorts of small, abundant larvae as spawning occurs over a protracted season. Thus, no single cohort, but rather a distribution of cohorts, is present at any one time. Under this circumstance, larger, faster-growing members of a younger cohort may be as vulnerable to predators that exhibit dome-shaped relationships between prey size and vulnerability as smaller, slower-growing members of an older cohort. While a conceptual model relating prey size to vulnerability would be complex in this case, our simulation results indicate that increased mean growth rates of all, or any, of the larval cohorts present would probably result in a higher population survival rate, hence recruitment, especially if predation pressure is high.

This does not imply, however, that survivors from among a cohort exposed to predation are likely to be exceptional individuals with respect to size or growth rate, a notion that has been inferred (Crowder *et al.*,

1992), because the ''average'' fish dies soon after hatching (Sharp, 1987; Houde, 1987). This ''parsimonious'' view has placed great emphasis on larval size as a factor in predation vulnerability, which has lead to an oversimplification or misinterpretation of the mechanics of predation. This has resulted in the discussion of connate ideas such as ''bigger is better'' and ''stage duration'' as conflicting hypotheses (Leggett and DeBlois, 1994). Our simulation results demonstrate that, while mean growth rate of members of a cohort probably controls cumulative predation risk, the day-to-day risk of individuals within the cohort may be more a function of the predator to which to cohort is exposed than the size of individuals. Predation pressure that imposes strongly dome-shaped vulnerabilities will probably result in relatively small survivors with a high variability in length, because large, and fast-growing individuals within a cohort are initially more likely to be consumed. As time passes, larvae of intermediate length become most vulnerable, which may ultimately result in a bimodal distribution in lengths of survivors if mortality rates are high.

In summary, depending upon the combination of attributes assigned to both predators and larval prey, evidence for size-selective mortality based on characteristics of survivors at the end of our numerical experiment was sometimes difficult to find because encounter rate also was size-dependent but inversely related to susceptibility. Many of the larvae ''consumed'' by the predators in these simulations were encountered and eaten before strong size selection occurred because fast- and slow-growing larvae within a cohort are initially similar in size. Variability in the time necessary to reach the threshold length, if it occurs, indicates that the nature of the size-dependent relationship is predictable but specific to predator-type/prey combinations and depends upon growth rate and, to a lesser extent, size of the larval prey. In all of our simulations, survival benefits of larger larval size were only evident after 7–16 d, suggesting that small changes in larval size and growth rate may be more important to the predation process and resulting cohort survival after larvae are a few days to a few weeks old (Litvak and Leggett, 1992; Rice *et al.*, 1993), and after a significant fraction of the total mortality has occurred. Our results also indicate that knowledge of variability in growth rate may be as important as knowledge of changes in mean growth rate, if inferences are to be made about relative survival potential between larval cohorts or individuals within cohorts (Rice *et al.*, 1993). We propose that characteristics of individual larval survivors may be more influenced by attributes of the predators to which they were exposed in early life than by their initial sizes within the cohort and their potential growth rate.

Acknowledgements

References

Anderson, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fisheries Science 8: 55–66.

Bailey, K. M., and Batty, R. S. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. Marine Biology 72: 295–310.

Bailey, K. M., and Houde, E. D. 1989. Predation on early developmental stages of marine fishes and the recruitment problem. Advances in Marine Biology 25: 1–83.

Bertram, D. F., Chambers, R. C., and Leggett, W. C. 1993. Negative correlations between larval and juvenile growth rates in winter flounder: implications of compensatory growth for variation in size-at-age. Marine Ecology Progress Series 96: 209–215.

Beyer, J. E. 1989. Recruitment stability and survival – simple size-specific theory with examples from the early life dynamics of marine fish. Dana 7: 45–147.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Transactions of the American Fisheries Society 115: 98–114.

Brownlee, D. C., and Jacobs, F. 1987. Mesozooplankton and microzooplankton in Chesapeake Bay. Chapt. 12. *In* Contaminant Problems and Management of Living Chesapeake Bay Resources, pp. 217–269. Ed. by S. K. Majumdar, L. W. Hall, Jr and H. W. Austin. Pennsylvania Academy of Science.

Cowan, J. H., Jr, and Houde, E. D. 1990. Estimates of relative predation potential by medusae, ctenophores and fish on ichthyoplankton in Chesapeake Bay. International Council for the Exploration of the Sea C.M. 1990/L: 2. 24 pp.

Cowan, J. H., Jr, and Houde, E. D. 1992. Size-dependent predation on marine fish larvae by ctenophores, scyphomedusae, and planktivorous fish. Fisheries Oceanography 1: 113–126.

Cowan, J. H., Jr, and Houde, E. D. 1993. The relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95: 55–65.

Cowan, J. H., Jr, Birdsong, R. S., Houde, E. D., Priest, S., Sharp, B., and Mateja, G. 1992. Enclosure experiments on growth and survival of black drum eggs and larvae in lower Chesapeake Bay. Estuaries 15: 492–502.

Crowder, L. W., Rice, J. A., Miller, T. J., and Marschall, E. A. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. *In* Individual-based models and approaches in ecology, pp. 237–255. Ed. by D. L. DeAngelis & L. J. Gross. Chapman and Hall, New York, London.

Cushing, D. H. 1975. Marine Ecology and Fisheries. Cambridge Univ. Press, Cambridge. 278 pp.

Cyr, H., Downing, J. A., Lalonde, S., Baines, S. B., and Pace, M. L. 1992. Sampling larval fish populations: choice of sample number and size. Transactions of the American Fisheries Society 121: 356–368.

Dahlberg, M. D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessment. Marine Fisheries Reviews, March 1979: 1–12.

Dalton, P. 1987. Ecology of *Anchoa mitchilli* eggs and larvae in the mid-Chesapeake Bay. M.S. Thesis, University of Maryland, College Park. 104 pp.

Davis, C. S., Flieri, G. R., Wiebe, P. H., and Franks, F. J. S. 1991. Micropatchiness, turbulence and recruitment in plankton. Journal of Marine Research 49: 109–151.

deLafontaine, Y., and Leggett, W. C. 1987. Evaluation of in situ enclosures for larval fish studies. Canadian Journal of Fisheries and Aquatic Sciences 44: 54–65.

deLafontaine, Y., and Leggett, W. C. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Canadian Journal of Fisheries and Aquatic Sciences 45: 1173–1190.

Dovel, W. L. 1971. Fish eggs and larvae of the upper Chesapeake Bay. Natural Resources Institute, University of Maryland Special Report 4. 71 pp.

Folkvord, A., Øiestad, V., and Kvenseth, P. G. 1994. Growth patterns of three cohorts of Atlantic cod larvae (*Gadus morhua* L.) studies in a macrocosm. ICES Journal of Marine Science 51: 325–336.

Frank, K. T., and Leggett, W. C. 1985. Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation? Canadian Journal of Fisheries and Aquatic Sciences 42: 1841–1849.

Fuiman, L. A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. Marine Ecology Progress Series 51: 291–299.

Fuiman, L. A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. Journal of Fish Biology 45: 55–79.

Fuiman, L. A., and Batty, R. S. 1994. Susceptibility of Atlantic herring and plaice larvae to predation by juvenile cod and herring at two constant temperatures. Journal of Fish Biology 44: 23–34.

Fuiman, L. A., and Gamble, J. C. 1988. Predation by Atlantic herring, sprat and sand eels on herring larvae in large enclosures. Marine Ecology Progress Series 44: 1–6.

Fuiman, L. A., and Gamble, J. C. 1989. Influence of experimental manipulations on predation of herring larvae by juvenile herring in large enclosures. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 191: 359–365.

Gamble, J. C., and Fuiman, L. A. 1987. Evaluation of in situ enclosures during a study of the importance of starvation to the vulnerability of herring larvae to a piscine predator. Journal of Experimental Marine Biology and Ecology 113: 91–103.

Gamble, J. C., and Hay, S. J. 1989. Predation by the scyphomedusan *Aurelia aurita* on herring larvae enclosures: effects of predator size and prey starvation. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 191: 366–375.

Gerritsen, J., and Strickler, J. R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada 34: 77–82.

Heath, M. R. 1992. Field investigations of the early life stages of marine fish. Advances in Marine Biology 28: 1–173.

Horwitz, R. 1987. Fish. Chapt. 6 *In* Ecological Studies in the Middle Reach of the Chesapeake Bay, Calvert Cliffs, pp. 167–255. Ed. by K. Heck, Jr. Lecture Notes on Coastal and Estuarine Studies. Springer-Verlag.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2: 17–29.

Houde, E. D. 1989. Subtleties and episodes in the early life of fishes. Journal of Fish Biology (Supplement A): 29–38.

Houde, E. D., Ortner, P. B., Lubbers, L. I., and Cummings, S. R. 1989. Test of a camera-net system to determine abundance and heterogeneity in anchovy egg distributions. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 191: 112–118.

Hunter, J. R. 1984. Inferences regarding predation on the early life stages of cod and other fishes. *In* The propagation of cod *Gadus morhua*, pp. 533–562. Ed. by E. Dahl, D. D. Danielssen, E. Moksness and P. Solemdal. Institute of Marine Research, Bergen, Norway. Flodevigen Rapportser 1.

Leggett, W. C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32: 119–134.

Litvak, M. K., and Leggett, W. C. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series 81: 13–24.

Loos, J. J., and Perry, E. S. 1991. Larval migration and mortality rates of bay anchovy in the Patuxent River. NOAA Technical Report, NMFS 95.

MacKenzie, B. R., Leggett, W. C., and Peters, R. H. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? Marine Ecology Progress Series 67: 209–225.

McGurk, M. P. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine Ecology Progress Series 34: 227–242.

Miller, T. J., Crowder, L. B., Rice, J. A., and Marschall, E. A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 5: 1657–1670.

Noda, M., Gushima, K., and Kakuda, S. 1994. Local prey search based on spatial memory and expectation in the planktivorous reef fish, *Chromis chrysurus* (Pomacentridae). Animal Behaviour 47: 1413–1422.

Øiestad, V. 1985. Predation on fish larvae as a regulatory force, illustrated in mesocosm studies with large groups of larvae. NAFO Scientific Council Studies 8: 25–32.

Øiestad, V. 1988. Specific applications of meso- and macro-cosms for solving problems in fisheries research. International Council for the Exploration of the Sea C.M. 1988/ Early Life History Symposium No. 78: 1–19.

Olson, M. 1987. Zooplankton. Chapt. 2 *In* Ecological Studies in the Middle Reach of the Chesapeake Bay, Calvert Cliffs, pp. 38–81. Ed. by K. Heck, Jr. Lecture Notes on Coastal and Estuarine Studies. Springer-Verlag.

Pepin, P. 1989a. Predation and starvation of larval fish: a numerical experiment of size- and growth-dependent survival. Biological Oceanography 6: 23–44.

Pepin, P. 1989b. Using growth histories to estimate larval fish mortality rates. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 191: 324–329.

Pepin, P. 1991. The effect of temperature and size on development, mortality and survival rates of the pelagic early life stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences 48: 503–518.

Pepin, P., Shears, T. H., and de Lafontaine, Y. 1992. Significance of body size to the interaction between a larval fish

(*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). Marine Ecology Progress Series 81: 1–12.

Peterson, I. and Wroblewski, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41: 1117–1120.

Rice, J. A., Miller, T. J., Rose, K. A., Crowder, L. B., Marschall, E. A., Trebitz, A. S., and DeAngelis, D. L. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50: 133–142.

Rosenthal, H., and Hempel, G. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). *In* Marine Food Chains, pp. 344–364. Ed. by J. H. Steele. University of California Press, Berkeley.

Secor, D. H., and Dean, J. M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Canadian Journal of Fisheries and Aquatic Sciences 49: 1439–1454.

Sharp, G. D. 1987. Averaging the way to inadequacy in a varying world. American Institute of Fisheries Research Biological Briefs 16: 3–4.

Shepherd, J. G., and Cushing, D. H. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Journal du Conseil International pour l'Exploration de la Mer 39: 160–167.

Shipley, L. A., and Spalinger, D. E. 1992. Mechanisms of browsing in dense food patches: effects of plant and animal morphology on intake rate. Canadian Journal of Zoology 70: 1743–1752.

Sissenwine, M. P. 1984. Why do fish populations vary? pp. 59–94. *In* Exploitation of Marine Communities. Ed. by R. M. May. Springer-Verlag, Berlin.