

# Variability in survival of larval fish: disentangling components with a generalized individual-based model

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**Abstract:** Many factors, including intrinsic characteristics of the fish themselves and extrinsic factors of the biological environment, have the potential to regulate mortality rates during the early life of fishes. We used a detailed simulation model to rank the effects of variability in these factors on larval and early juvenile survival. Our major finding was that proportional changes in the intrinsic and extrinsic factors in the model had equal effects on cohort survival. Of the intrinsic factors, growth capacity (metabolism and assimilation efficiency), not foraging ability or starvation resistance, explained the most variance in survival. Of the extrinsic factors, predator size explained 83% of the variability in survival but proportional changes prey availability had only a minor effect. Variability in prey density required a 3-fold increase to equal the effects of predator size on survival. Despite the important effects of predation pressure on survival, it had only a minor impact on how fish died. Whether fish died from predation or starvation depended much more on the intrinsic variables related to metabolism and starvation resistance and on the density of the smallest prey type.

**Résumé :** De nombreux facteurs, dont les caractéristiques intrinsèques des poissons et les facteurs extrinsèques de l'environnement biologique, peuvent réguler les taux de mortalité au cours des premiers stades de vie des poissons. Nous avons utilisé un modèle permettant de faire des simulations détaillées pour classer les effets de la variabilité de ces facteurs sur la survie des larves et des très jeunes poissons. Le fait que des changements proportionnels dans les facteurs intrinsèques et extrinsèques du modèle aient des effets égaux sur le taux de survie de la cohorte constituait notre principale constatation. Parmi les facteurs intrinsèques, c'est la capacité de croissance (efficacité du métabolisme et de l'assimilation), et non la capacité de s'alimenter ou la résistance au manque de nourriture, qui expliquait la plus grande partie de la variance du taux de survie. Parmi les facteurs extrinsèques, la taille des prédateurs permettait de rendre compte de 83% de la variabilité dans le taux de survie, mais des changements proportionnels dans la disponibilité des proies n'avaient qu'un effet mineur. Dans le cas de la variabilité dans la densité des proies, il fallait une augmentation par un facteur de trois pour obtenir un effet égal aux effets de la taille des prédateurs sur la survie. Malgré ses effets importants sur la survie, la pression de prédation n'avait qu'un impact mineur sur la façon dont mourait le poisson. La raison de la mort du poisson, c'est-à-dire prédation ou manque de nourriture, dépendait beaucoup plus des variables intrinsèques liées au métabolisme et à la résistance au manque de nourriture, ainsi que de la densité du plus petit type de proies.

[Traduit par la Rédaction]

## Introduction

Mortality in the early life of fishes is typically very high, and small variations in these rates can result in widely varying cohort survival and subsequent recruitment (Sissenwine 1984; Houde 1987; Bailey and Houde 1989; Beyer 1989). Because of the variability in mortality rates and the large number of factors that modify them, survival to a particular age, size, or stage (i.e., recruitment) is difficult to understand and to predict. Despite an extensive search for stock-recruit relationships, simple descriptive models do not provide adequate

predictions of year-class strength. An alternative and possibly more fruitful approach to understanding mortality rates is to examine the mechanisms underlying component processes and their interactions (May 1974; Fogarty 1993).

Many previous efforts to understand the causes of mortality have focused on single processes: a critical period during which food limitation will cause massive starvation mortality (Hjort 1914), the match-mismatch of the larval period with abundant food resources (Cushing 1975), the distribution of food in the water column (Lasker 1975, 1978), oceanographic transport and retention mechanisms (Hjort 1914; Parrish et al.

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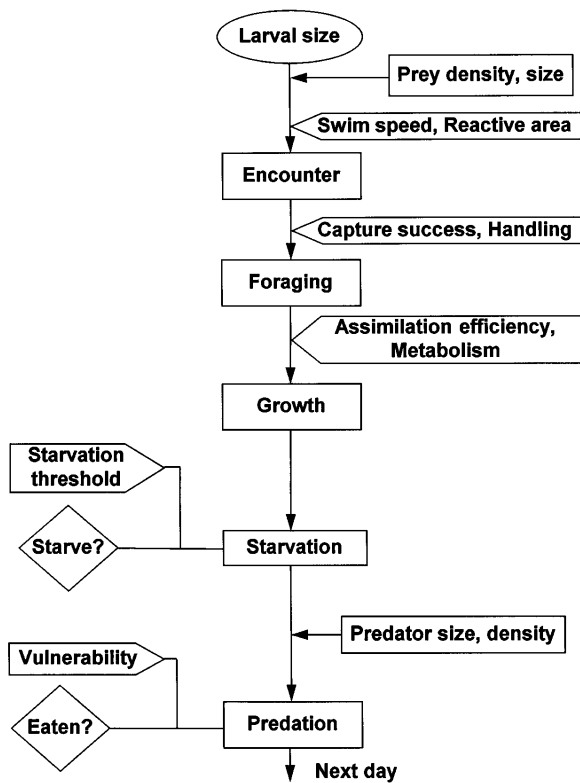
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**Fig. 1.** Flow diagram of the model. All functions in the model depend on larval size. The five submodels determine encounter, foraging, growth, starvation, and predation rates. The major processes affecting each submodel are in the pointed boxes. Characteristics of the larvae's environment (food and predators) are in the boxes with horizontal arrows. The model calculates growth rates for each larva every day of the simulation. Larvae could die from either predation or starvation. Each simulation started with 7500 larvae 3.69 mm long.



1981; Sinclair 1988), and predation (Cushing 1974; Hunter 1981, 1984; Sissenwine 1984; Bailey and Houde 1989). However, all of these processes may interact (Fritz et al. 1990), and one or several may be important at a particular time or place. Also, further complicating predictions, particular species (Houde 1987) or even individuals (Uchmanski 1985; Lomnicki 1988) may react differently to environmental conditions. Clearly, many factors including food, predators, physical processes, and differences in species or individual morphology, physiology, or behavior can influence survival of young fishes. All of these are very difficult to measure synoptically in the field and would require a massive factorial experimental design to adequately capture the dynamics in a laboratory or in mesocosms. Simulation modeling is an alternative that provides a context for evaluating the effects of many interacting factors.

We designed a detailed individual-based simulation model to compare the effects on survival of extrinsic environmental factors (food and predators) with those attributable to intrinsic characteristics of fish (foraging and bioenergetics). Individual-based models (IBMs) have become popular recently (Huston et al. 1988; DeAngelis and Gross 1992; Van Winkle et al.

1993) because they represent individuals and local interactions explicitly. Variability among individuals in foraging ability (Magurran 1986; Marschall et al. 1989) and growth (Rubenstein 1981; Uchmanski 1985; Lomnicki 1988) is common among fishes. This variability, which can result in a wide range of sizes for any age (Uchmanski 1985) and different survival probabilities for individual fish (Sharp 1987; Rice et al. 1993), can be represented easily with IBMs. IBMs can also accommodate variability in the fish's environment. In this model, we include both the prey and predators of the fish larvae, the two external factors that can directly determine survival via starvation and predation.

In addition to mortality rates, we also evaluated how variation in intrinsic and extrinsic factors affects whether fish die from predation or starvation. Much work on recruitment and larval fish has focused on sources of mortality, but the relative importance of predation and starvation mortality seems to vary greatly with species and habitat. Vulnerability to both predation and starvation generally decreases for larger fish but which is likely to be more important as a cohort of fish grows? We used the IBM to explore whether it is possible to discern any general patterns in the relative importance of starvation and predation mortality as a function of variation in intrinsic and extrinsic factors.

Because of the data limitations and because our goal was to explore general patterns in survival of young fishes, we sacrificed precision for generality (Levins 1966) and created a detailed but generalized model of larval fish; it depicts individuals in an averaged planktonic fish population and so does not necessarily describe any one species or habitat, but it should provide useful insights for larval fish in general by indicating directions, magnitudes, and relative effects. To make a general model we need a way to summarize data from various species. While each species of fish is ultimately unique, many of the processes important to survival of larval fish are size dependent (Anderson 1988; Miller et al. 1988; Beyer 1989). In the model presented here, all functions are size dependent. We drew these functions from the literature, using existing functions, or deriving our own when necessary. In our literature survey, we focused primarily on pelagic species with planktonic larvae.

Despite the large number of existing IBMs for fish, none has provided an extensive sensitivity analysis. Sensitivity analysis yields an estimate of the relative importance of model components. Most results presented in this paper are from sensitivity analyses. Ranking effects of model variables can be used to identify key processes, reduces the complexity of detailed models such as IBMs, and focuses future hypotheses, indicating which processes we may be able to ignore and which we may need to explore in more detail.

## Model description

### General

The model simulated the feeding, growth, and survival of individual fish larvae. Each fish was defined by its length, weight, and age and could die from either predation or starvation. To simulate growth and mortality of the larvae, every fish passed through a series of steps each day (Fig. 1). These steps included the major processes that affect the early life of fish

**Table 1.** Nominal length, mass, and density of the four prey types used in the model.

	Prey no.	Length (mm)	Mass ( $\mu\text{g}$ )	Density (no./mL)	$a$	$b$	Reference
Rotifer	1	0.20	0.182	0.200	1.845	1.44	Dumont et al. 1975
Nauplius	2	0.25	0.282	0.075	3.009	1.706	Culver et al. 1985
Copepodite	3	0.50	1.410	0.005	4.592	1.703	Culver et al. 1985
Copepod	4	0.83	4.988	0.0005	7.700	2.33	Dumont et al. 1975

Note: Mass was calculated from length using length–weight relations from the literature where  $\text{mass} = a \cdot \text{length}^b$ .

(Hunter 1981; Blaxter 1986; Bailey and Houde 1989) and were divided into five submodels: (i) prey encounter to estimate encounter rates of larvae with their prey, (ii) foraging to determine food consumption rates, (iii) bioenergetics–growth to convert food consumed into growth, (iv) size-dependent predation risk to calculate probabilities of mortality from predators on the larvae, and (v) starvation to define when fish would starve. Each submodel depended on a set of processes or variables (pointed boxes in Fig. 1) described in detail below. The processes in the growth and starvation submodels were functions of fish mass, while those in the prey encounter, foraging, and predation submodels were primarily functions of larval length (except capture success of feeding larvae).

We derived function parameter values in one of four ways: using functions from previous review articles (e.g., swimming speed in Miller et al. 1988), compiling and summarizing data from the literature (e.g., routine metabolic rate), using relationships directly from the literature when data were available for only one species (e.g., reactive distance as a function of fish and prey size), and estimating reasonable values when data were not available (e.g., larval capture success on non-naupliar prey). When data were compiled from different sources in which the experiments were performed at different temperatures, data were standardized to a common temperature (15°C). Although temperature will affect many of the processes in the model directly (e.g., metabolism), we did not explicitly include temperature in the model because the indirect effects of temperature on the population dynamics of larval fish prey and predators are complex and unknown and because sufficient data on how temperature influences the details of the interaction between predators and prey are not available.

In the model, the larvae's environment consisted of prey for the larvae and predators on the larvae (Fig. 1). Prey were randomly distributed in space on an intermediate scale (10s of metres) but they were aggregated into patches on a larger scale (100s of metres and 3 times more dense than nonpatches, see Letcher and Rice (1996) for more details). Thus, the prey environment of the fish consisted of patches through which the fish could swim on a daily time scale. Because the larvae were planktonic and in fairly large bodies of well-mixed water (100s of metres, well mixed within patches and outside patches), we assumed that prey densities were constant, i.e., the larvae did not affect their prey (see also Laurence 1982; Cushing 1983); this assumption is reasonable given the typically low average densities of larvae relative to their prey. We chose four prey types representing the range of typical larval fish prey (rotifer, copepod nauplius, copepodite, and copepod (Table 1)). Prey lengths and weights were estimated from the literature (Table 1). Prey densities were set at levels that decreased by about an order of magnitude with each increase in prey size-class (Hunter 1981; MacKenzie et al. 1990;

range 0.0005–0.2/mL, Table 1) and were initially set such that they yielded maximum daily consumption rates (defined below) for all fish sizes in the model. This allowed us to express prey density as a proportion of the larvae's maximum consumption.

Predators were cruising and gape limited and were defined by length and density. Starvation was mass dependent: if a larva lost a certain proportion of its previous maximum body mass, it died from starvation.

Each model simulation started with 7500 newly hatched larvae (25  $\mu\text{g}$  dry weight, 3.69 mm total length (TL), about the median hatch size of 66 species in Miller et al. (1988, their Fig. 1)). Throughout the model, we used a composite length ( $\ell$ , mm) – weight ( $W$ ,  $\mu\text{g}$  dry) relationship derived from 13 species of freshwater and marine larvae (*Archosargus rhomboidalis* (Stepien 1976), *Coregonus clupeaformis* (Taylor and Freeburg 1984), *Stenotonus chrysops* (Laurence 1979), *Pseudopleuronectes americanus* (Laurence 1979), *Melanogrammus aeglefinus* (Laurence 1979), *Menidia beryllina* (Letcher and Bengtson 1993a), *Paralichthys dentatus* (Laurence 1979), *Engraulis mordax* (Lasker et al. 1970; Theilacker 1987), *Gadus morhua* (Laurence 1979), *Theragra chalcogramma* (Yamashita and Bailey 1989), *Limanda ferruginea* (Laurence 1979), *Engraulis encrasicolus* (Regner 1983)):

$$(1) \quad W = \text{LWInt} \cdot \ell^{\text{LWExp}}$$

with parameters LWInt and LWExp. Parameter values for this and all other equations are in Table 2. During model runs, length and mass were uncoupled; fish did not lose length, but they could lose weight. Growth was added as mass, and when lengths exceeded the value defined by eq. 1 for a given mass, lengths were updated from the new mass. Larvae did not grow in length or weight until the day of first feeding (FF), defined as a function of length (Miller et al. 1988):

$$(2) \quad \text{FF} = 4.09 - \text{FFSlope} \cdot \ell$$

Larvae were vulnerable to predation before first feeding. From eq. 2, day 3 was the day of first feeding for fish in the model (3.69 mm hatch size).

### Prey encounter submodel

#### Encounter rate

Encounter rates of larvae with their prey were functions both of fish size and prey size and of prey density (Blaxter 1986). Encounter rates are the product of search volume and prey density and were computed separately for each of the four prey types. We defined encounter rate (ER, number/s) with each prey type as

$$(3) \quad \text{ER}_{\ell,i} = \text{SV}_{\ell,i} \cdot \rho_i \cdot \text{Light}$$

**Table 2.** Nominal variable and parameter values with short descriptions.

	Variable or parameter name	Nominal value	Equation no.
Initial number of fish	InitNum*	7500	—
Average initial mass ( $\mu\text{g}$ dry)	AvgStart*	25	—
CV of initial size	CVStart*	0	—
Length–weight relationship intercept	LWInt*	0.1674	1
Length–weight relationship exponent	LWExp*	3.837	1
Prey length 1–4 (mm)	PyLen(1–4)*	See Table 1	—
Prey mass 1–4 ( $\mu\text{g}$ dry)	PyMass(1–4)*	See Table 1	—
Prey density 1–4 (no./mL)	PyDen(1–4)*	See Table 1	—
Average prey density (prop. $C_{\text{max}}$ )	AvgPreyDen	0.64	—
Predator length (mm)	PredSize	50	21
Predator density (no./L)	PredDen	$1 \times 10^{-12}$	20
Prop. of day available for feeding	Light*	13/24	3,16,28
First feeding function slope	FFSlope*	0.237	2
Swimming speed intercept	SSInt*	0.776	5
Swimming speed exponent	SSExp*	1.07	5
Prop. of reactive area used for feeding	Prop*	0.5	6
Handling time slope	HTSI*	7.0151	10
Handling time intercept	HTInt*	0.264	10
Capture success numerator (prey types 1–4)	CSNum(1–4)*	0.95; 0.90; 0.70; 0.90	Fig. 2
Capture success denominator (prey types 1–4)	CSDen(1–4)*	10.0; 750.0; $5 \times 10^7$ ; $5 \times 10^8$	Fig. 2
$C_{\text{max}}$ function intercept	CmaxInt*	2.8275	13
$C_{\text{max}}$ function exponent	CmaxExp*	0.8496	13
Maximum assimilation efficiency	AssimMax*	0.8	15
Assimilation efficiency shape parameter	AssimSh*	0.002	15
Routine metabolism numerator	MetabNum*	4500	17
Routine metabolism denominator	MetabDen*	45 000	17
Specific dynamic action + egestion	SDA+E*	0.3	16,28
Activity metabolism multiplier	ActMetab*	2.5	16,28
Starvation threshold	Thresh*	0.75	18,25,26
Predator's reactive distance multiplier	PredRadM*	0.8	19
Predator's swimming speed multiplier	PredVSS*	3.0	20
Predator's capture success exponent	CaptExp*	2.28	21
Predator's capture success numerator	CaptNum*	3.37	21
Predator's capture success denominator	CaptDen*	44.76	21
Proportion of encounters that predator attacks	PropAtak*	0.5	22
Slope of the 50% mortality function	M50SI*	0.801	24

**Note:** Food for the larvae are referred to by prey numbers (1–4, Table 1). Equation numbers indicate the location of each parameter in the text. Variable names followed by an asterisk were used in the individual parameter perturbation.

where SV was search volume (mL),  $\rho_i$  was the density of prey type  $i$  (number/mL, Table 1), and Light equaled the proportion of the day (13 h/24 h) during which there was sufficient light for feeding. Light level was a constant and did not influence feeding rate. Encounter rates increased rapidly and monotonically with larger fish size but decreased with larger prey size because smaller prey had higher densities. We calculated actual encounter rates from a random distribution (Poisson) with mean and variance equal to ER.

#### Search volume

Search volume (SV,  $\text{mm}^3/\text{s}$ ) was the volume of water in which fish perceive prey and was defined as the product of the fish's swimming speed (SS) and the area of water a fish of length  $\ell$  can see (RA, see Blaxter 1986):

$$(4) \quad \text{SV}_{\ell,i} = \text{SS}_{\ell} \cdot \text{RA}_{\ell,i}$$

Swimming speeds for different species as a function of fish

length are highly variable. We used the summary relationship of Miller et al. (1988, their Fig. 6a) to provide a length-dependent estimate of average swimming speed (SS, mm/s)

$$(5) \quad \text{SS}_{\ell} = \text{SSInt} \cdot \ell^{\text{SSExp}}$$

where SSInt and SSExp were parameters. This equation yields swimming speeds of approximately 1 body length/s.

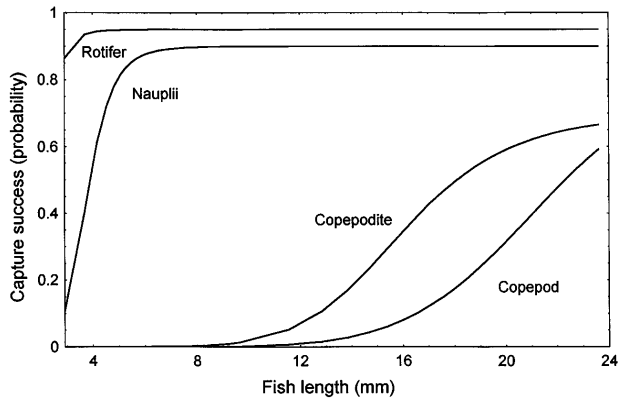
Reactive area (RA,  $\text{mm}^2$ ) was a half circle with radius equal to reactive distance and was defined for each prey type  $i$  as

$$(6) \quad \text{RA}_{\ell,i} = (\text{RD}_{\ell,i})^2 \cdot \pi \cdot \text{Prop}$$

where Prop = 0.5 and accounted for the assumption that larval fish actually perceive one half of the circle defined by reactive distance (RD) (Blaxter 1986). Search volumes increase rapidly with increases in fish size and prey size.

We defined RD (mm) as a function of both prey length ( $\text{PL}_i$ , mm, for each prey type  $i$ , Table 1) and larval length ( $\ell$ , mm) using the relationship of Breck and Gitter (1983). This

**Fig. 2.** Capture success as a function of fish length for fish feeding on the different prey in the model.



relationship has also been used in other larval fish IBMs (Rose and Cowan 1993), where

$$(7) \quad RD_{\ell,i} = \frac{PL_i}{2 \cdot \tan\left(\frac{\alpha_\ell}{2}\right)}$$

and

$$(8) \quad \alpha_\ell + 0.0167 \cdot e^{9.14 - 2.4 \cdot \ln(\ell) + 0.229 \cdot (\ln(\ell))^2}$$

**Foraging submodel**

Fish typically do not attack all prey encountered. Time spent feeding reduces search time, and fish might be expected to chose from encountered prey to maximize benefits (Charnov 1976; Stephens and Krebs 1986). To model this process, we adopted an optimal foraging approach that requires information on capture success and handling time.

Capture success (given attack, CS) was defined as a function of fish size (mass in eq. 9, but written as  $CS_{\ell,i}$  for consistency with the other length-based variables) for each of the four prey types (Fig. 2). Because most capture success studies have been conducted with larvae feeding on nauplii (*Artemia* spp. primarily), we chose a capture success function,

$$(9) \quad CS_{\ell,i} = \frac{CSNum_i \cdot mass^2}{CSDen_i + mass^2}$$

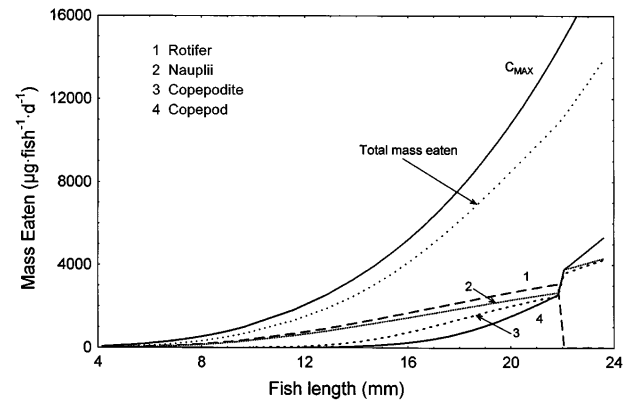
that approximated that from the literature for nauplii and generated a family of curves for the other prey for which capture was less likely for larger prey types for any given fish size (see Fig. 2). Capture success is high (95%) for most fish sizes feeding on rotifers, increases rapidly with larger fish size to a maximum for fish feeding on nauplii, and rises gradually for fish feeding on copepodites and copepods.

We defined handling time (HT, sum of pursuit, attack, and capture times) for each prey type as a function of fish length and prey length using the empirically derived equation of Walton et al. (1992):

$$(10) \quad HT_{\ell,i} = e^{HTInt} \cdot 10^{HTS(PL_i/\ell)}$$

In this form, handling time decreases rapidly with increases in fish sizes from about 3 to 10 mm in length (depending on prey

**Fig. 3.** Maximum consumption ( $C_{max}$ , equation 13), total mass eaten, and masses of the four prey types (1–4) eaten under nominal conditions (see Table 2). Masses eaten were calculated using optimal foraging methods.



size) and levels off at 1–2 s/prey for fish > 15 mm in length. Handling times were longer for larger prey types.

Using these relationships, prey types were ranked according to

$$(11) \quad \frac{Mass_i \cdot CS_{\ell,i}}{HT_{\ell,i}}$$

where  $Mass_i$  was the mass of prey type  $i$  ( $\mu\text{g}$ , Table 1),  $CS_{\ell,i}$  was the size-dependent capture success of fish feeding on prey type  $i$  (Fig. 2), and  $HT_{\ell,i}$  was the handling time for prey type  $i$ . Equation 10 indicates that prey types that provide greater mass per unit time required to successfully ingest a single prey received higher ranks.

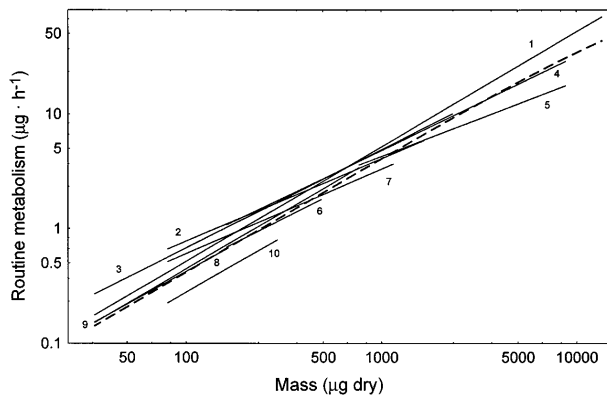
When the prey were ranked, we assigned profitabilities (benefit–cost ratios) for the ranked prey ( $j = 1, 2, 3, 4$ ) as

$$(12) \quad \frac{E_{\ell,j}}{T_{\ell,j}} = \frac{j \cdot \sum Mass_j \cdot ER_{\ell,j} \cdot CS_{\ell,j}}{1 + \sum ER_{\ell,j} \cdot HT_{\ell,j}}$$

Prey types were included in the diet sequentially on the basis of ranks until the profitability began to decrease (Charnov 1976; Stephens and Krebs 1986). In simulations under nominal conditions, fish < 22 mm in length included all prey types that they could capture in their diet (Fig. 3) and the contribution of larger prey increased as the fish grew. At sizes > 22 mm, the fish in the simulation no longer chose the prey of lowest rank (rotifers) but continued to eat the other prey. These patterns are consistent with empirical observations where prey sizes eaten by larvae increase with fish size (e.g., Hunter 1981; Blaxter 1986; Miller et al. 1990).

Once prey in the diet were determined ( $k = 1, 2, 3, \text{ or } 4$ ), the number of each prey actually eaten was calculated via the following series of steps. First, we estimated the number of successful encounters stochastically from encounter rates and capture successes with each prey type (specifically, the realized number eaten was a deviate from a binomial distribution with number of trials equal to the encounter rate per day with probability of success of  $CS_{\ell,k}$ ). This provided an estimate of the number eaten without accounting for time spent searching

**Fig. 4.** Routine metabolism from 10 studies corrected to 15°C with a  $Q_{10}$  of 3.2. The broken line represents the function used in the model (eq. 17). 1, *Scomber scombrus* (Giguere et al. 1988); 2, *Morone saxatilis* (Eldridge et al. 1982); 3, *Engraulis mordax* (Theilacker 1987); 4, *Clupea harengus* (DeSilva and Tytler 1973); 5, *Pleuronectes platessa* (DeSilva and Tytler 1973); 6, *Clupea harengus* (Almatar 1984); 7, *Pleuronectes platessa* (Almatar 1984); 8, *Achirus lineatus* (Houde and Schekter 1983); 9, *Spartus aurata* (Quartz and Tandler 1982); 10, *Anchoa mitchilli* (Houde and Schekter 1983).



or feeding on other prey. The total amount of time feeding per unit search (1 s) was

$$1 + \sum_k ER_{\ell,k} \cdot HT_{\ell,k}$$

Fish searched for and fed on all prey types during this period. Dividing the number of successful encounters with each prey type per unit search by the total time feeding gave the number of prey per second actually eaten. Multiplying the number eaten per second by the total time feeding per day ( $ER \cdot \text{Light} \cdot 60 \cdot 60 \cdot 24$ ) and by the mass of each prey yielded the daily mass of each prey type eaten (Fig. 3). Finally, summing over masses of all prey eaten gave the total mass eaten per fish per day (Fig. 3, see also Eggers 1977 for a similar derivation).

If a larva's daily projected consumption exceeded maximum consumption ( $C_{\max}$ ), the mass of food eaten for that day was set to  $C_{\max}$ , defined as

$$(13) \quad C_{\max} = C_{\text{MaxInt}} \cdot W^{C_{\text{MaxExp}}}$$

We obtained parameter values ( $C_{\text{MaxInt}}$  and  $C_{\text{MaxExp}}$ , Table 2) by assuming that a 10- $\mu\text{g}$  fish (about 3 mm TL) can eat 200% of its body weight/day and that a 30 000- $\mu\text{g}$  fish (about 23 mm TL) can eat at most 60% of its body weight/day. Larvae at high prey densities can consume from 80 to over 200% body weight/day and  $C_{\max}$  as a percentage eaten per day often decreases with fish size (Theilacker and Dorsey 1980; Letcher et al. 1996a).

#### Growth submodel

Daily growth ( $\mu\text{g}/\text{day}$ ) was the difference between net input and losses:

$$(14) \quad \text{Growth} = (I \cdot \text{AE}) - \text{TC}$$

Total input ( $I$ ,  $\mu\text{g}/\text{day}$ ) equaled consumption from the foraging

model, and net input was  $I$  times assimilation efficiency (AE). Total costs (TC,  $\mu\text{g}/\text{day}$ ) were the sum of metabolism components. Assimilation efficiency, the proportion of ingested food not egested by the fish, was a function of fish mass ( $W$ ,  $\mu\text{g}$ ),

$$(15) \quad \text{AE} = \text{AssimMax}(1 - 0.25 e^{-\text{AssimSh}(W-10)})$$

with parameters AssimMax and AssimSh (Table 2, Buckley and Dillmann 1982). AE ranged from 0.6 to 0.8 and increased rapidly with increases in fish size from 0.6 to the asymptotic maximum (0.8) at about 15 mm. AE values around 0.6–0.7 are typical for first-feeding larvae (Theilacker 1987; Houde 1989; Wieser and Medgyesy 1990). Although AE can decrease with higher ingestion rates (Boehlert and Yoklavich 1984) for juveniles, we did not make AE a function of ingestion rates because little is known about how AE changes with ingestion for larvae and because AE varies with ingestion on an hourly time scale while our feeding time scale was daily.

Total costs (TC) included routine metabolism (RM,  $\mu\text{g}/\text{day}$ ), activity metabolism (ActMetab,  $\mu\text{g}/\text{day}$ ), specific dynamic action (SDA), and egestion ( $E$ ):

$$(16) \quad \text{TC} = \text{RM} + \text{ActMetab} \cdot \text{Light} + I(\text{SDA} + E)$$

Routine metabolism was defined as a function of fish mass ( $W$ ):

$$(17) \quad \text{RM} = \frac{\text{MetabNum} \cdot W}{\text{MetabDen} + W}$$

where MetabNum and MetabDen were parameters (Table 2). We derived this relationship by plotting the function through the center of temperature-corrected routine metabolism estimates from 10 studies (Fig. 4). Routine metabolism varies by less than one-half order of magnitude among species. We assumed activity metabolism was 2.5 times routine (range of 1.9 to 2.7 across many species of larvae; Rombough 1988). Activity metabolism was set to zero when the fish were not feeding (nondaylight hours). Both SDA and  $E$  were defined as a constant proportion of ingestion ( $\text{SDA} + E = 0.30$ , see Kiorboe et al. 1987; Wieser and Medgyesy 1990).

#### Starvation submodel

Two observations motivate the formulation of the starvation submodel. First, Letcher et al. (1996b) determined that fish of different sizes die from starvation after losing a constant proportion of their previous maximum body mass (termed the starvation threshold). Second, Kiorboe et al. (1987) and Wieser et al. (1992) showed that the metabolic rates of starving larvae are less than one half (48–71%) those of feeding larvae. To model starvation, we combined a starvation threshold (Thresh) with reduced metabolic rates for fish feeding below maintenance levels. In the model,

$$(18) \quad W_{\text{fin}} = \text{Thresh} \cdot W_{\text{max}}$$

where Thresh was the proportion of previous maximum body mass ( $W_{\text{max}}$ ) at which a fish starved to death and determined the mass at death from starvation ( $W_{\text{fin}}$ ). Fish reaching  $W_{\text{fin}}$  for any value of  $W_{\text{max}}$  died from starvation.  $W_{\text{max}}$  was reset when the current value was surpassed. Thresholds calculated from the literature range from 0.58 to 0.87 (Table 3); in the model, Thresh was set at 0.75.

**Table 3.** Proportional weight loss from the onset of starvation to death by starvation for various species.

Reference	Species	Starvation threshold	Temperature (°C)
Letcher and Bengtson 1993b	<i>Menidia beryllina</i>	0.87	21
		0.63	25
		0.69	28
McGurk 1984	<i>Clupea harengus</i>	0.76	6
		0.79	8
		0.79	10
May 1971	<i>Leuresthes tenuis</i>	0.74	18
Rodgers and Westin 1981	<i>Morone saxatilis</i>	0.63	21
Toetz 1966	<i>Lepomis macrochirus</i>	0.60	24
Werner and Blaxter 1980	<i>Clupea harengus</i>	0.59	9
Rice et al. 1987	<i>Coregonus hoyi</i>	0.58	12

**Note:** Starvation threshold is the parameter Thresh in the model and equals mass at starvation divided by the fish's previous maximum mass.

We reduced the total metabolic rate for fish feeding below maintenance such that they would reach  $W_{fin}$  after the number of days defined by a size-dependent estimate of the time to starvation for nonfeeding fish (Miller et al. 1988, solid circles in their Fig. 5). The adjusted rate provided intercepts for the size-dependent metabolism-feeding rate relationships (Fig. 5, details in Appendix), which defined metabolic rate between feeding rate = 0 and feeding rate = maintenance. Equation 27 of the Appendix defines submaintenance metabolic rates for all sizes of fish in the model. Metabolic rate increased asymptotically below maintenance and was unaltered above maintenance (Fig. 5).

**Predation submodel**

We modeled predation on larvae as a series of three independent steps: probability of encounter, attack, and capture. The predator was mobile and gape limited (e.g., many piscivorous fish). To estimate encounter rate, we used the approach of Gerritsen and Strickler (1977), with the modification of Bailey and Batty (1983), which makes the encounter radius of the predator (PredRad, mm) a function of both predator and larval sizes. The encounter radius, combined with swimming speeds of both the predator ( $v$ , mm/s) and the larvae ( $SS$ , mm/s), and the density of the predators (PredDen, number/mm<sup>3</sup>), determined the larvae's encounter rate with predators (ERwPred, number/s). The encounter radius of the predator (PredRad) was a linear function of the predator's swim speed ( $v$ , where  $v = (\text{predator length})\text{PredVSS}$ , see Table 2) and the length of the larvae was

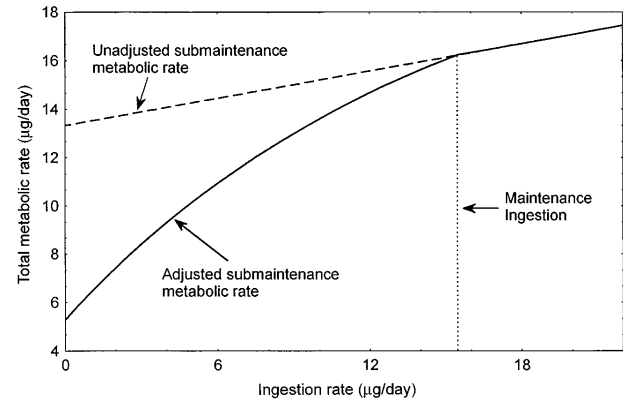
$$(19) \text{PredRad} = \text{PredRadM} + R_L$$

where PredRadM was  $0.8v$  (Cowan et al. 1996) and  $R_L$  was  $2(\text{larval length})/\pi^2$  (Bailey and Batty 1983). The encounter rate was estimated as

$$(20) \text{ERwPred} = \pi \cdot \text{PredRad}^2 \cdot \frac{SS^2 \cdot 3 \cdot v^2}{3 \cdot v} \cdot \text{PredDen}$$

Given an encounter, larvae were eaten if they were also at-

**Fig. 5.** Metabolic rate as a function of ingestion rate (solid line) for a 4-mm fish. Below maintenance, metabolic rate was adjusted so that the intercept of the metabolic rate – ingestion rate function caused starving fish to die after the appropriate number of days from a size-dependent time to 50% mortality relation (Miller et al. 1988). Between starving and maintenance, metabolic rate increased nonlinearly, after which it increased as a result of SDA costs only. Both the intercept of the adjusted submaintenance metabolic rate and maintenance ingestion rate will vary with fish size. The unadjusted metabolic rate (broken line) is shown for comparison. Details of the derivation are in Appendix 1.



tacked and captured. The proportion attacked (PropAtak) nominally equaled 0.5 (arbitrarily chosen to yield mortality rates of about 99%) and we used the summary predator – prey capture success (PPCS) function of Miller et al. (1988, their Fig. 8):

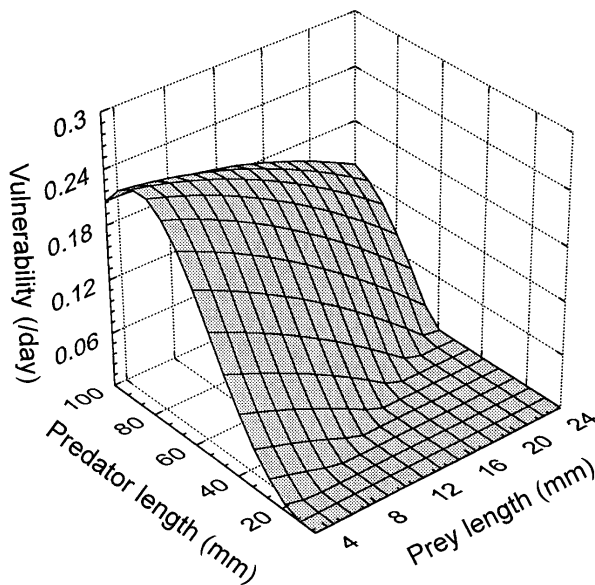
$$(21) \text{PPCS} = 100 - \left( \frac{\left( \frac{\text{PredLen}}{\ell} + \text{CaptNum} \right)^{\text{CaptExp}}}{\text{CaptDen}} \right)$$

where CaptNum, CaptDen, and CaptExp were parameters (Table 2), PredLen was the predator's length (mm), and  $\ell$  was the larva's length (mm). Because larvae could encounter more than one predator per day, we calculated the daily probability of capture as a set of conditional probabilities. For example, for a larva to be captured on the second encounter, it had first to be encountered twice and avoid capture on the first encounter. Written as conditional probabilities, larval vulnerability (Vuln, day<sup>-1</sup>) summed over  $n$  separate encounters equaled  $P(\text{encounter} = n) \cdot P(\text{not eaten on attempt } n-1 | \text{encounter on attempt } n) \cdot P(\text{eaten on attempt } n)$ , where  $P(x)$  stood for the probability of event  $x$ , and  $p(x|y)$  was the probability of  $x$  given the occurrence of  $y$ , i.e.,

$$(22) \text{Vuln} = \sum_n \frac{\lambda_n \cdot e^{-\lambda}}{n!} \cdot (1 - z)^{n-1} \cdot z$$

where  $n$  indexed encounters, and  $z$  was the probability of being eaten once encountered (PropAtak-PPCS). The first term in eq. 22 calculated the random (Poisson) probability of  $n$  encounters given an expected number of  $\lambda$  encounters, where  $\lambda$  equaled the mean number of encounters per day (ERwPred multiplied by the number of seconds per day that larvae were vulnerable to predators (Light:24-60-60)). In model runs,  $n$  equaled 5

**Fig. 6.** The larvae's daily probability of being eaten as a function of predator and larval lengths. Vulnerability represents the combined probabilities of encounter, attack, and capture (eq. 22).



because vulnerability always converged to a single value with  $n < 5$  (the probability of more than 5 encounters without a successful capture was very unlikely). Larvae that were attacked were eaten if a random number drawn from a uniform distribution (0,1) was less than the probability of being eaten (Vuln).

When larvae were small (4–12 mm), vulnerability increased to a maximum then decreased slightly with increases in predator size (Fig. 6). Vulnerability for larger larvae was lower and increased monotonically with predator size (see Bailey and Houde 1989). The minimum predator size to which larvae were vulnerable also increased with larval size.

## Model testing and application

### Model evaluation

We used two criteria to evaluate the performance of the model qualitatively. In both cases, we compared model output from a single run under nominal conditions with data reported in the literature. First, we assessed the feeding and growth models by comparing growth efficiency with a published summary (Houde 1989). Second, we compared the time course of starvation and predation mortality with available field estimates (Hewitt et al. 1985). Gross growth efficiency (growth/ingestion) is a useful measure for comparison because it standardizes growth per unit consumption and, except at very low ingestion rates ( $< 10\%$  body weight/day), declines only slightly with higher ingestion (Checkley 1984; Letcher and Bengtson 1993b).

### Individual parameter perturbation

To test proportional sensitivity of key model outputs (number of survivors, number eaten, and number starved) to 56 model parameter values (Table 2), we adjusted the parameter values  $\pm 10\%$ . Sensitivities were calculated as  $(|y_+ - y_-|)/(y_0 \cdot 0.2)$ ,

where  $y_+$  and  $y_-$  were the output values with parameters adjusted  $\pm 10\%$ , respectively (three replicates) and  $y_0$  was the mean output value (from 10 runs with different random number seeds) using unadjusted parameters. Sensitivities  $< 1$  indicate that the change in the parameter value had a less than proportional effect on the output value, and values  $> 1$  suggest that the parameter had a disproportionately large effect on the response variable. This analysis indicates which parameters have the greatest effect on model results and which functions must therefore be measured with the greatest care during parameter estimation.

### Relative effects of intrinsic and extrinsic factors

We conducted a Monte Carlo error analysis (Bartell et al. 1986) to partition the variance in survival into components resulting from variance in intrinsic and extrinsic factors. In a Monte Carlo error analysis, variable values are drawn from a random distribution for each run. Conducting a multiple regression on the output gives partial  $r^2$  values that indicate how much of the variance in the dependent variables can be explained by each independent variable. Partitioning the variance in survival suggests which variables have the largest effects on survival. Error analysis differs from individual parameter perturbation because all variables are modified simultaneously during each run instead of adjusting single parameter values a fixed amount. While this requires many more runs, it provides a more realistic measure of the effects of changing variables because many variable value combinations are possible in a single run. Error analysis also differs from individual parameter perturbation in this case because we adjusted variables (e.g., predator size) and results of calculations (e.g., search volume, total metabolism) instead of parameters (e.g., the slope of a relationship). Adjusting variables indicates the effect of changes in the process itself.

In the error analysis, we adjusted the values of the major variables in each submodel (see Fig. 1) by drawing values from normal distributions with a 10% coefficient of variation (CV, standard deviation (SD)/mean) for each variable. We varied food densities and the predation, starvation, growth, encounter, and foraging submodels (Table 4). We determined actual variable values used in each run by drawing a deviate from a truncated normal distribution (mean = 0, SD = 1, range of  $-2$  to  $2$ ) and multiplying nominal variable values (Table 2) by the deviate divided by two times the CV and adding this number to the nominal value. Extending the range of the normal distribution from  $-2$  to  $2$  and subsequently dividing the deviate by 2 excluded extreme values while expressing most of the normal distribution. For variables with a single value throughout each simulation (predator size, prey density, etc.), the value used was determined at the beginning of each simulation and was maintained throughout the simulation. For variables that were the result of a calculation (total metabolism, search volume, etc.), a single value was also determined for each run but calculations for each fish each day were adjusted with the single deviate. We used a single CV range for all variables because confidence interval estimates were not available for all intrinsic variables. We conducted 1000 runs of the model and used forward stepwise linear regression (SAS Institute Inc. 1989) to partition the variance in survival among the independent variables.



**Table 4.** Results from the Monte Carlo error analysis.

Submodel	Variable	Variable type	Survival		Proportion eaten	
			Partial $r^2$	Predicted change (+10%)	Partial $r^2$	Predicted change (+10%)
Predation	Predator size	Extrinsic	0.35	-66.96	0.12	0.08
	Predator density	Extrinsic	0.02	-15.69	0.01	0.02
Starvation	Starvation threshold	Intrinsic	0.01	-9.39	0.25	-0.10
Food	Prey density	Extrinsic	0.05	25.80	0.00	0.00
Growth	Total metabolism	Intrinsic	0.15	-40.60	0.26	-0.12
	Assimilation efficiency	Intrinsic	0.15	40.59	0.12	0.07
	Maximum consumption	Intrinsic	0.00	4.28	0.00	0.00
Encounter	Search volume	Intrinsic	0.06	24.94	0.09	0.07
Foraging	Capture success	Intrinsic	0.06	25.21	0.08	0.07
	Handling time	Intrinsic	0.00	-1.20	0.00	0.00

**Note:** For each run (1000 total), variable values were drawn from a normal distribution using a nominal distribution and a 10% coefficient of variation. The linear effects of key variables from the five submodels were included in the analysis. Partial  $r^2$  values represent the proportion of the variance in survival or the proportion of mortality resulting from predation explained by each variable, and predicted changes indicate the change in number surviving as a result of a +10% change in the actual variable (intercepts; survival, 75.02; proportion eaten, 0.72).

**Results**

**Model evaluation**

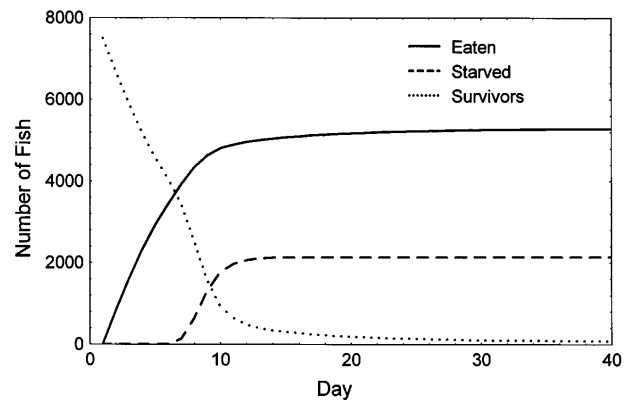
Gross growth efficiency near maximum consumption (70–90%  $C_{max}$ ) ranged from 0.21 to 0.29 under nominal conditions in the model. This compares well with Houde’s (1989) estimate of 0.29 for 10 species of marine fish larvae. Also, mortality rates in the model were high (> 99%) under nominal conditions, with predation mortality dominating during the first 9 days and a spike of starvation mortality during days 9 and 10 (Fig. 7). After day 11, almost no fish starved, while the predation mortality continued, but at a much lower rate (about 10/day vs. 700/day before day 10). This is similar to the pattern found for larvae of *Trachurus symmetricus*, jack mackerel (Hewitt et al. 1985), where predation dominated mortality but starvation was important briefly during about 5 days after first feeding.

**Individual parameter perturbation**

Many parameters had proportional sensitivities greater than 1. Of the 56 parameters tested, 27 had sensitivities > 1 when survival was the response variable, as did 18 and 7 parameters when the output variables were number starved and eaten, respectively. Survival was highly sensitive to changes in many parameters partially because survival under nominal conditions was low (70 individuals or < 1% of starting number). In this case, a change in survival of only 7 fish (0.09% of starting number) in response to a ±10% change in parameter value resulted in a proportional sensitivity > 1. This is a small change, especially when the SD in survival under nominal conditions was 11.3 fish after 10 replicate runs (Table 5) and sensitivities were calculated from three replicate runs. It is remarkable, in fact, that so few parameters (about half of those tested) had proportional sensitivities for survival < 1.

Changes in the length–weight exponent (LWExp) had by far the greatest effect (proportional sensitivity = 63.4) on survival (Table 5). This was due, in part, to the fact that LWExp was an exponent where a 10% change will have a larger effect than if the parameter were a linear part of the function. The intercept of the length–weight relation also had a relatively high proportional sensitivity (4.5, Table 5). Increasing the

**Fig. 7.** Cumulative survivorship and mortality as a result of predation or starvation from a single nominal model run.



value of either parameter resulted in lower survival because length was calculated from mass in the model and higher parameter values gave shorter lengths for any given mass.

Changes in the components of predation and growth had particularly large effects on survival. Parameters involved with both encounter (PredVSS, PredRadM) and capture (CaptExp, CaptDen) of larvae by predators had relatively high proportional sensitivities (all > 4.5, Table 5), as did changes in growth (CmaxExp, AssimMax) of the larvae themselves and larval encounter rates with their prey (SSExp). Characteristics of the prey for the larvae (size, density) had relatively small effects, except for the length of rotifers (PyLen1).

While the effects of prey on larval survival were not dominant, they were more important in determining how the larvae died (starvation or predation). The length of rotifers had the second or third highest proportional sensitivity when number of larvae eaten or starved was the response variable (Table 5). This difference in proportional sensitivity between survival and mortality reflects the interaction between predation and starvation mortality. When rotifers were small, 634 more larvae starved and 608 fewer were eaten on average than when they were at the nominal size. The net result was a decrease in survival of 34 fish. Many of the larvae that would have been

**Table 5.** Proportional sensitivities (number after parameter name) of the top 10 parameters (out of 56 total) for 3 response variables.

Rank	Survivors		No. eaten		No. starved	
1	LWExp <sup>a</sup>	63.4	LWExp <sup>a</sup>	2.4	LWExp <sup>a</sup>	7.9
2	PredVSS <sup>b</sup>	7.5	Thresh <sup>a</sup>	1.6	PyLen1 <sup>c</sup>	3.9
3	CmaxExp <sup>a</sup>	6.7	PyLen1 <sup>c</sup>	1.5	Thresh <sup>a</sup>	3.8
4	CaptExp <sup>b</sup>	6.7	MetabNum <sup>a</sup>	1.4	SSExp <sup>a</sup>	3.6
5	AssimMax <sup>a</sup>	5.7	SSExp <sup>a</sup>	1.4	MetabNum <sup>a</sup>	3.5
6	SSExp <sup>a</sup>	5.2	MetabDen <sup>a</sup>	1.3	MetabDen <sup>a</sup>	3.2
7	PredRadM <sup>b</sup>	4.6	LWInt <sup>a</sup>	1.2	LWInt <sup>a</sup>	3.1
8	CaptDen <sup>b</sup>	4.5	PredVSS <sup>b</sup>	1.1	SSInt <sup>a</sup>	2.6
9	LWInt <sup>a</sup>	4.5	SSInt <sup>a</sup>	1.0	AssimMax <sup>a</sup>	2.6
10	PyLen1 <sup>c</sup>	4.3	ActMetab <sup>a</sup>	1.0	PredVSS <sup>b</sup>	2.5

**Note:** Unadjusted (10 runs with nominal parameter values) mean  $\pm$  SD are as follows: survivors,  $70.3 \pm 11.3$ ; no. eaten,  $5271.8 \pm 23.8$ ; no. starved,  $2157.9 \pm 25.7$ . See Table 2 for parameter descriptions.

<sup>a</sup>Encounter, foraging, and growth parameters.

<sup>b</sup>Predator-related parameters.

<sup>c</sup>Food-related parameters.

eaten starved because encounter rates with rotifers were lower because of their small size. Like changes in the length of rotifers, changes in the starvation threshold (Thresh) had essentially no effect on survival (proportional sensitivity = 0.36) but also had the second or third highest proportional sensitivity when number of larvae eaten or starved was the response variable (Table 5). While rotifer length and starvation threshold had relatively large impacts on how fish die (predation or starvation), the net result on survival was dampened by the interaction between predation and starvation.

Whether fish were eaten or starved seemed to be influenced mainly by parameters that affected starvation, while overall survival was determined chiefly by those that affected predation. While 4 of the highest 10 sensitivities for survival were predation-related parameters, only one (PredVSS) was in the top 10 for number eaten or starved (Table 5). Besides rotifer length and starvation threshold, number of larvae eaten or starved was most sensitive to changes in parameters related to a larva's encounter rate with food (SSExp, SSInt) and larval growth (MetabNum, MetabDen, AssimMax). Changes in growth were important for both survival and number of larvae starving or eaten because both starvation and predation were functions of size: starvation was the extreme result of slow growth and faster growth reduced vulnerability to predators. Starvation was the dominant source of mortality only under cases of extreme food limitation (and very limited predation pressure).

### Error analysis

Overall, the linear (main effects) factors explained 85% of the variance in survival (Table 4); the remaining 15% was due to interactions among the variables. Like the individual parameter perturbation, changes in variables of two of the submodels explained large portions of the variance in survival: the predation submodel (37%) and the growth submodel (30%). The encounter, foraging, and food availability submodels each accounted for only about one sixth as much variance as the predation or growth submodels (each around 5% of the total variance, Table 4). Among particular submodel variables, predator size had the biggest effect on survival, explaining 35% of the variance in survival, while only two other variables could account for >10% of the variance (total metabolism,

15%; assimilation efficiency, 15%). Overall, changes in the extrinsic and intrinsic variables had about equal effects on survival: the extrinsic variables explained 42% of the variance and the intrinsic variables explained 43% of the variance in survival. This result suggests a research focus on characteristics of both the environment (extrinsic factors) and the fish themselves (intrinsic factors) to predict survival.

Regression models from the stepwise analysis (Table 4) indicated magnitudes and directions of effects on survival. Predicted changes gave the effect on number surviving as a result of a  $\pm 10\%$  change in each variable. For example, a 10% increase in predator size (50 to 55 mm) would cause a decrease in survival of 67 fish. The magnitudes of the predicted changes mirrored those of the partial  $r^2$  values but the directions were variable. Increasing any of the predation variables or the variables total metabolism, handling time, and starvation threshold had negative effects on survival, while changes in the remaining variables had positive effects.

The results of the Monte Carlo error analyses indicate that the most important processes affecting survival were predation and growth. These results may be somewhat misleading, however, if the natural range of variation in individual variables is very different from 10% CV. For example, if the range of a particular variable is  $\ll 10\%$  CV, then the error analysis would likely overestimate its effect. Overestimation was probably not a problem for the dominant extrinsic variable, predator size, which can vary widely depending on year, season, and location (Bailey and Houde 1989).

Effects may have been underestimated if the natural range of a variable is >10% of the mean. This may have been the case for food availability. Prey densities can vary widely spatially and temporally. To assess what level of variability in food availability would be required to cause food availability to have an effect on survival similar to that of variation in the dominant variables (e.g., predator size), we increased the CV in prey densities 2-, 5-, and 10-fold in three separate sets of 1000 runs. CVs for all other variables were nominal (10%), and from these runs, we calculated partial  $r^2$  values as above. Results of this analysis indicated that variation in prey densities about 3 times greater than nominal (i.e., CV = 30%) resulted in an effect on survival equal to that of predator size

(CVs in prey densities with corresponding partial  $r^2$ s: 10%, 0.05; 20%, 0.19; 50%, 0.47; 100%, 0.56). Widely varying prey densities, reflecting differences among years, seasons, or locations, can have a dominant effect on larval fish survival but only when prey density CVs are about 3 times greater than those of the other variables.

While extrinsic and intrinsic factors had equal effects on survival, extrinsic factors had only a small effect on whether fish died from either predation or starvation. Intrinsic factors explained 6 times more of the variation (80 vs. 13%, Table 4) in the proportion of fish that died as a result of predation versus starvation than did extrinsic factors. Total metabolism (26%) and starvation threshold (25%) each accounted for 2 times more of the variance than any other variable, indicating that variation in metabolic rate and sensitivity to starvation is likely to have the largest effect on whether fish die from predation or starvation. Combined with the variance in survival, these results suggest that susceptibility to starvation will generally influence whether fish get eaten or starve but will only have a limited effect on total numbers dying and that predation will have a major impact on survival but only a limited one on whether fish get eaten or starve (explained 12% of the variance, Table 4). Increasing starvation susceptibility reduces the proportion of mortality as a result of predation but has only a limited effect on survival because many of the fish that are starving would otherwise have been eaten. Changes in predation can have a major impact on survival because increased predation pressure through changes in predator size will affect all fish in the cohort, both healthy and unhealthy, and not just the starving fish. This observation highlights the dominant importance of predation as a factor regulating survival.

## Discussion

With the model presented in this paper, we asked whether survival in young fish was dominated by a few key processes and whether these processes represented characteristics of the fish (intrinsic factors) or characteristics of the fish's environment (extrinsic factors). The primary result of this exercise was that the extrinsic and intrinsic factors explained similar amounts of variance in survival and that they cannot be viewed in isolation. Predator length and larval growth had the largest effects on survival. Analyzing mortality patterns, Houde (1987) also identified predation and growth rate as important regulators of survival of young fish. In our model, changes in variables relating to these two factors alone explained 67% of the variance in survival, suggesting a focus on predation and growth capacity in future studies.

Growth was the intrinsic variable with by far the largest effect on survival, accounting for 70% of the variance resulting from the intrinsic factors. This result suggests that growth differences among fish, which could be viewed as differences among species (Houde 1987, 1989) or as differences among populations within species (Conover 1990; Present and Conover 1992), can have a significant impact on survival, equaling the effects of the extrinsic variables. On an even finer scale, growth differences among individuals within cohorts can also influence individual survival (Rose and Cowan 1993) as well as cohort survival (Rice et al. 1993). The strong influence of growth on survival suggests that isolating sources of growth variability among individuals, cohorts, populations,

and species will contribute to our understanding of survival in young fish and the level of aggregation at which it is determined.

While the genetic basis of growth differences among species is clear, the extent of differences among individuals within a species is less well understood. In our model, we assumed that variability in intrinsic factors has a genetic basis and we identified, by allowing proportional variation in all variables, which factors had the largest effects on survival. In real populations, these critical factors may not all vary proportionately and selection may actually act to reduce variance in the most important variables. If this is true, there may not be sufficient variability in intrinsic factors within a population for individual differences to affect survival and variability in the extrinsic factors could dominate survival. This observation points to a clear need to assess individual variability in intrinsic factors. Once established, the variability could be easily incorporated into an IBM. Care should be taken, however, to assess the covariance structure among variables to avoid unrealistic combinations.

Many of the previous approaches to understanding survival of larval fish have centered on the effects of food density (e.g., Hjort 1914; Cushing 1975; Lasker 1978). In contrast, results from our model showed that changes in food density had only a small effect on survival (explained only 5% of the variance) compared with proportional changes in the other variables. The potential effect of food density may have been underestimated, though, because the range of food densities in the field is probably much greater than simulated here. At very low food densities, survival can be severely limited as most fish starve, but this may be an extreme effect of food density reflecting poor years or unfavorable oceanographic conditions. However, small variations in food density will have relatively little effect on survival. In fact, simulations indicated that proportional variation in food availability would need to be about 3 times greater than variation in predator length for the effects of food availability to equal those of predator length. When prey densities are highly variable (i.e., patchy seasonally or over large spatial scales), differences in prey availability could have a substantial impact on survival.

A criticism of the way in which we varied food densities in the error analysis may be that we adjusted all prey together. In a separate set of 1000 runs, in which we allowed the four prey types to vary independently, the summed effects of the prey explained even less of the total variance in survival (2%). Another possible criticism is that the effects of food density may have been obscured by variability in the intrinsic factors. If the foraging and bioenergetics parameters of a species are sufficiently understood, we could remove this level of variability and test just for the effects of the extrinsic factors. Assuming that this was so, we also varied only the extrinsic factors in an additional set of 1000 runs. The combined effects of the four prey still accounted for only 5% of the variance in survival whereas the changes in predator size and density explained 83%.

The importance of variability in prey densities could also be masked by large predator sizes. To address the question of how small predators would have to be for food availability to have an important effect on survival, we varied predator size and prey densities over a wide range of values ( $\pm 75\%$  of nominal). Variation in food availability had a negligible effect on

survival above predator sizes of about 30 mm, but below 30 mm, survival ranged from 0% at low prey densities ( $< 20\% C_{\max}$ ) to 20–40% (depending on predator size) when prey densities were high ( $80\% C_{\max}$ ). Thus, there was a strong interaction between predator size and food availability such that variation in food availability only had an important effect on survival when predators were smaller than 30 mm.

The effect of the extrinsic factors on survival was dominated by a single variable: variability in predator size alone accounted for 83% of the variance in survival as a result of extrinsic factors. A 10% increase in predator size reduced survival by almost 100% and had a 4-fold greater effect than a 10% increase in predator density and a 2.5-fold larger effect than a 10% increase in prey density. The importance of predation as a factor capable of regulating year-class strength has gained acceptance in the last 20 years (Cushing 1974; Hunter 1981; Sissenwine 1984; Bailey and Houde 1989). The analysis presented here reinforces that notion and suggests that changes in predator size will have a much larger effect than proportional changes in predator density. As with prey density, substantial changes in predator density (e.g., when predators are patchily distributed in space) could have significant impacts on larval fish survival, but relatively small changes in density will not. Predator size may have a larger effect on larval fish survival than predator density because size affects both encounter rates and predator capture success whereas density influences encounter rates only. Research on growth rates and the size structure of predators may yield particularly useful information.

Very high mortality rates are common for fish with pelagic larvae (Sissenwine 1984; Beyer 1989). Disease (Sissenwine 1984) and the indirect effects of physical transport processes (Sinclair 1988; Hare and Cowen 1993) may occasionally influence mortality rates, but most mortality results from predation or starvation (Hunter 1981; Houde 1987). One approach to understanding recruitment has been to divide mortality into components resulting from predation or starvation (Hewitt et al. 1985; Theilacker 1986). However, a focus on whether fish are eaten or starve may yield less information than evaluating characteristics of the survivors (Fritz et al. 1990). This is because predation and starvation interact through compensatory size-dependent processes: starving fish are often more likely to get eaten, thus many fish get eaten that would have starved otherwise. For example, under nominal conditions in model simulations, 82% of the cohort starved without predators compared with 28% with predators, indicating that predators ate 54% of the cohort that would have starved in the absence of predators. Simulations also revealed that the way in which fish died depended predominately on intrinsic factors (characteristics of the fish). Within a species, defined by a particular set of variable values, the relative importance of starvation and predation mortality may be fairly fixed; larvae are either relatively susceptible or unsusceptible to starvation (McGurk 1984; Rice et al. 1987, Table 3). This suggests that examining the relative importance of predation and starvation mortality may be useful mainly for comparisons across species or possibly when predators and food are scarce. Otherwise, results from the simulations suggest that to understand recruitment better we should focus on growth rates of larvae and on the size structure of the predators.

Under most circumstances, predation was the most impor-

tant source of mortality. This was due in part to the inescapable timing of predation and starvation mortality; larvae can be eaten while feeding endogenously, but they can only starve after they have depleted their yolk reserves. In model runs, about half of the cohort was eaten before any starved. Very high levels of starvation seem likely only under a restricted set of circumstances: minimal predation pressure combined with low food levels. Starvation's minor impact on survival is reinforced by the observation that changes in the starvation threshold, the variable that defined how quickly fish starved, had almost no effect on survival in the individual parameter perturbation or in the error analysis.

While the model presented here was developed to represent a generalized, "typical" planktonic fish larvae, it could be applied to any particular species with planktonic larvae given species-specific parameter estimates. An accurate model of the early life survival for a particular species will be difficult to achieve, however, because the parameters of many functions in the model had a disproportionately large effect on survival. Even if species-specific estimates of all the necessary parameters could be made, the model would still have limited predictive power because model predictions are highly sensitive to variations in many of the parameters. While quantitative predictions may be elusive, predicted qualitative patterns of survival should be robust. To make the best possible model, the following intrinsic parameters should be estimated with the greatest care: the larval length–weight exponent and intercept, maximum consumption exponent, asymptotic assimilation efficiency, the swimming speed exponent, the proportion of the reactive area in which a larva can perceive prey, and parameters in the routine metabolism equation (Table 5).

In a fairly simple model of a young fish's life, we have tried to determine which pieces of a very complicated puzzle might have the biggest impacts on survival. We included components of the fish's biological environment (extrinsic factors) and a detailed description of the fish (intrinsic factors). Within this context, we found that predator size and the fish's capacity for growth had about equally large effects on survival. Both food level and the fish's foraging ability had surprisingly small effects on survival, reflecting the idea that starvation is generally relatively unimportant as a major source of mortality. Our results suggest that small, but proportional, changes in food density will have a relatively small effect on survival compared with those of predator size and larval potential for growth. More extreme variations in food availability, seasonal and large-scale patchiness, or very small predators can increase the importance of food level as a factor controlling larval survival. Further, our results suggest that within a species, good descriptions of metabolic rates and assimilation efficiency will be more important than estimates of foraging ability.

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## Appendix

To calculate submaintenance metabolic rates for all fish sizes and feeding rates, we began by defining  $W_{fin}$  (the mass at

starvation) as a function of the proportion of mass remaining after 1 day of starving ( $\beta$ ) and the number of days that fish of size  $W_{\max}$  took to starve (M50):

$$(23) \quad W_{\text{fin}} = W_{\max} \cdot \beta^{M50}$$

From Miller et al. (1988, their Fig. 5, solid circles), we estimated

$$(24) \quad M50 = M50S1 \cdot \ell$$

where M50S1 was the slope of the relationship between fish length ( $\ell$ ) and days to 50% mortality (M50). Because

$$(25) \quad W_{\text{fin}} = W_{\max} \cdot \text{Thresh} = W_{\text{init}} \cdot \beta^{M50}$$

where Thresh was the starvation threshold, we could solve for  $\beta$  in terms of Thresh and M50:

$$(26) \quad \beta = \text{Thresh}^{\frac{1}{M50}}$$

Percentage weight loss per day for starving fish was represented by  $1 - \beta$  and weight loss (metabolic rate) in units of mass for starving fish was represented by  $(1 - \beta)W$ . This esti-

mate is very similar to the relationship in Kiorboe et al. (1987) when their data are adjusted to 15°C with a  $Q_{10}$  of 3.2.

We assumed that the metabolic rate below maintenance was a decelerating exponential curve with intercept  $(1 - \beta)W$ , which rose slowly to maintenance metabolic rate (Fig. 5). We described metabolism below maintenance as a function of ingestion rate ( $I$ ,  $\mu\text{g}/\text{day}$ ) as follows:

$$(27) \quad \text{SubMaint}(I) = (1 - \beta) \cdot W \cdot \text{Maint} \cdot \left(1 - e^{-\frac{cI}{\text{Maint}}}\right)$$

where Maint equaled maintenance ration and  $c$  was a variable that scaled the slope of SubMaint( $I$ ) for the different levels of Maint for fish of different mass. Maint was derived from eq. 14 with growth set equal to 0:

$$(28) \quad \text{Maint} = \frac{\text{RM} + (\text{ActMetab} - 1) \cdot \text{RM} \cdot \text{Light}}{1 - \text{SDA} \cdot \text{AE}}$$

and  $c$  was derived by setting  $y(I) = \text{Maint} = I$  and solving eq. 27 for  $c$ :

$$(29) \quad c = -\ln\left(\frac{\text{Maint} - (1 - \beta) \cdot W}{\text{Maint}} - 1\right)$$