

## A modeling study of the effects of size- and depth-dependent predation on larval survival

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**Abstract.** The form of the predation pressure experienced by larval stages of marine invertebrates is largely unknown. However, it is believed that the type, timing and rate of larval predation are critical in determining recruitment to adult populations. In this study, a time- and depth-dependent model of the growth and behavior of larvae of the Eastern oyster, *Crassostrea virginica*, was used to investigate the effects of different forms of size- and depth-dependent predation on larval survivorship. The simulated larval survival for a cohort experiencing size-dependent predation showed that the greatest percent of the cohort survived to competent settlement size when the predation pressure decreased with increasing larval size. Additional simulations that included different types of depth-dependent predation showed that the interaction between vertical larval migration behavior and predation determined the percent of the cohort that survived to settlement size. The simulated distributions show that a higher percent of larvae survive when the predation pressure is concentrated in the surface waters. A lower percent of larvae survive to competent settlement size when the predation pressure is concentrated near the bottom. The different forms of size- and depth-dependent predation result in variations in the number of larvae present in the water column during each larval development stage. Thus, different forms of predation impact the number of larvae available for dispersal throughout the marine environment. These results have important implications concerning the exchange of genetic material between populations.

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### Introduction

The mortality of marine planktotrophic larvae is recognized as a dominant process in structuring planktonic assemblages (e.g. Landry, 1976) and in determining recruitment to marine benthic populations (e.g. Coe, 1953; Yoshioka, 1982). Predation is a major process by which larvae are lost. Understanding larval mortality is an integral part of what has become known as recruitment limitation, in which patterns of population abundance in a given system vary as a function of the number of successful larval recruits, rather than being determined by post-settlement processes such as competition for resources (e.g. Peterson and Summerson, 1992).

Much effort has gone into the study of the density-dependent and density-independent factors that affect larval mortality. Field studies have indicated the importance of climate and prevailing ocean circulation in determining larval recruitment (e.g. Gaines *et al.*, 1985; Doherty and Fowler, 1994), whereas other studies (e.g. Yoshioka, 1982) have indicated that larval loss due to predation is important in the regulation of populations. Moreover, Verity and Smetacek (1996) argue that predation (top-down) effects are as important as resource-driven (bottom-up) factors in determining the structure and function of marine

pelagic ecosystems. As these studies show, the control of marine populations by density-independent versus density-dependent factors is to a large extent determined by the space and time scales over which the observations are made.

Numerical modeling provides an approach for investigating the competing environmental and biological effects of variable predation on the survivorship of marine larvae. However, in most models constructed for marine systems [see Hofmann and Lascara (1997) for a review], mortality is often the closure term for the model and specification of this term is difficult because of the unknown nature of predation. Moreover, the form of this term can greatly influence the time development of the simulated distributions (Landry, 1976; Steele, 1976; Peterson and Wroblewski, 1984; Steele and Henderson, 1992). Minor changes in the form of the predation term can lead to totally different model outputs, even when all other aspects of the model are held constant (Peterson and Wroblewski, 1984; Steele and Henderson, 1992). Thus, these studies show the importance of correctly specifying predation in models designed to investigate processes structuring planktonic populations.

The objectives of this study are to investigate the effect of size- and depth-dependent predation on larval survivorship using a time- and depth-dependent, size-structured model developed for the larvae of the Eastern oyster, *Crassostrea virginica*. This model includes environmental effects on larval growth and vertical migration behavior (Dekshenieks *et al.*, 1993, 1996). Although this study is focused on larvae of a specific species, the results are relevant to any species that includes a planktonic life form. The oyster larval model is described in the next section. This is followed by a series of simulations that were designed to illustrate the effects of different patterns of predation on larval survival. The final sections present a discussion of the results and conclusions of the study.

## Model

### *The governing equation*

The vertical ( $z$ ) and time ( $t$ ) dependent distribution of oyster larvae of a given size,  $L_i$ , is assumed to be governed by:

$$\frac{\partial L_i}{\partial t} + W_T \frac{\partial L_i}{\partial z} + K_z \frac{\partial^2 L_i}{\partial z^2} = \alpha_i L_{i-1} - \beta_i L_{i+1} - \gamma_i L_i \quad (1)$$

The first term on the left side of equation (1) represents the time rate of change of the number of larvae in a particular size class,  $i$ . The second term represents the effect of vertical advection on larval distribution, where  $W_T$  is a summation of the vertical advective ( $W_a$ ) and larval migration ( $W_{bi}$ ) velocities. The third term represents the effect of vertical diffusion on larval distribution, where  $K_z$  represents the rate of vertical diffusion. The first two terms on the right side of equation (1) represent larval growth. The number of larvae of a particular size changes by growth of new individuals from the previous size ( $L_{i-1}$ ) and the loss of individuals to the next largest size ( $L_{i+1}$ ). The coefficients  $\alpha_i$  and  $\beta_i$  represent the

rates at which these transfers occur. The final term on the right side of equation (1),  $\gamma_i L_i$ , represents the loss of larvae to predation.

The formulations used to describe larval growth and behavior are described briefly in the following sections. Detailed descriptions of the larval growth and migration behavior models are found in Deksheniaks *et al.* (1993) and Deksheniaks *et al.* (1996), respectively.

*Larval growth*

The larval growth model determines the rate of transfer ( $\alpha_i$  and  $\beta_i$ ) between size classes. This model was verified with observed larval growth rates (Deksheniaks *et al.*, 1993). A summary of the larval growth model is given in Table I.

*Larval migration behavior*

Swimming speeds of bivalve veliger larvae are slow relative to horizontal current velocities; thus, these larvae are usually regarded as passive particles in the horizontal plane (Mann, 1986). Vertical current velocities, however, are slow relative to the alternating swimming and sinking behavior of these larvae. Thus, these larvae can undergo directed motion in the vertical. As oyster larvae grow, their upward swimming speeds increase. However, as they increase in mass and density, their sinking velocities simultaneously increase (Galtsoff, 1964). This

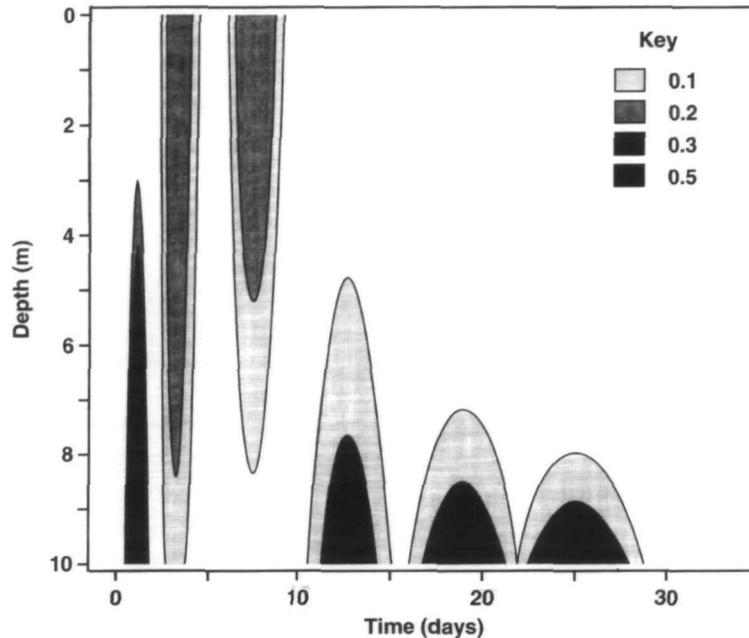
**Table I.** Summary of the oyster larval growth and development model given in Deksheniaks *et al.* (1993). The governing equation is:

$$\frac{dS}{dt} = \text{growth (food, size)} \times \text{ts factor} \times \text{turbe f}$$

The terms in the governing equations are defined and the characteristics of each are given. Data sources on which the parameterizations for the larval growth process are based are given. The figure in Deksheniaks *et al.* (1993) that shows the relationships used in the larval growth model is indicated for each term

Term	Definitions and characteristics	Data sources	Figure no.
$\frac{dS}{dt}$	Time rate of change of larval size ( <i>S</i> ) expressed in $\mu\text{m}$	Deksheniaks <i>et al.</i> (1993)	9
<i>growth (food, size)</i>	Low growth rates at low food for all sizes, maximum growth occurs at 3.0 mg AFDW $\text{l}^{-1}$ for larvae 105–135 $\mu\text{m}$	Rhodes and Landers (1973)	2
<i>ts factor</i>	Low growth at low temperatures and salinities, increased growth with increased temperature, increased growth at salinities of 17.5–25 p.p.t.	Davis (1958) Davis and Calabrese (1964)	3
<i>turbe f</i>	*Turbidity effect which is defined as: $\text{turbef} = m \text{ turb} + c$ (for turbidity < 0.1 $\text{g l}^{-1}$ ) $\text{turbef} = b e^{-\beta(\text{turb} - \text{turb}\theta)}$ (for turbidity > 0.1 $\text{g l}^{-1}$ )	Davis (1960) Huntington and Miller (1989)	4

\*Where *turb* is the ambient turbidity level ( $\text{g l}^{-1}$ ), *m* and *c* are  $(0.542)/(\text{g dry wt l}^{-1})$  and 1.0, respectively, and *b*,  $\beta$  and *turb* $\theta$  are 0.375, 0.5 ( $\text{g dry wt l}^{-1}$ ) $^{-1}$  and 2.0  $\text{g dry wt l}^{-1}$ , respectively. Two changes from Deksheniaks *et al.* (1993, 1996) should be noted: (i) the percentages in *m*, *c* and *b* are fractional forms; (ii) in the second equation for *turbe f*,  $\beta$  is negative.

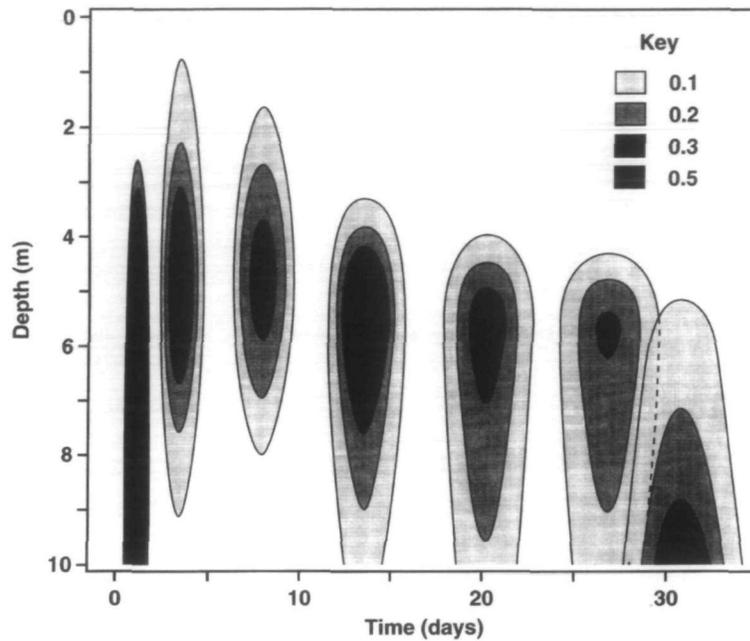


**Fig. 1. (a)** Simulated vertical- and time-dependent distribution of six larval sizes (75, 94, 150, 200, 250, 300  $\mu\text{m}$ ) obtained for a well-mixed water column. Temperature, salinity, food and turbidity are held constant throughout the water column at 24°C, 21 p.p.t., 2 mg AFDW  $\text{l}^{-1}$  and 0.0 g dry weight  $\text{l}^{-1}$ , respectively. Contours are the number of larvae per 0.5 m at time (*t*). After Figure 7 in Dekshenieks *et al.* (1996).

creates a continuously changing balance between swimming and sinking rates as the larvae grow, which results in smaller-sized larvae being distributed in the upper portion of the water column and mature larvae in the lower water column as they approach settlement size (Baker, 1991). The vertical distribution of oyster larvae as a function of time and depth shows a clear pattern of upward migration of the smaller-sized larvae and accumulation of the larger larvae near the bottom (Figure 1a). The initial larval growth rate is rapid (Dekshenieks *et al.*, 1993), only about one-third of the larval planktonic time is spent in the smaller sizes. As a result, the larval depth distribution is not symmetrical in time.

In addition to the changes in larval distribution due to larval size and swimming ability, oyster larvae undergo directed vertical migration in response to changes in salinity (Nelson, 1954; Wood and Hargis, 1971). An increase in salinity results in larvae becoming more active and swimming a greater amount of the time. Salinity decreases are associated with decreased larval activity and a downward (sinking) motion. Larval migration in response to diurnal tides introduces high-frequency variability in larval depth distribution. This variability is superimposed on the basic pattern shown in Figure 1a (Dekshenieks *et al.*, 1996).

These two types of vertical migratory behavior were included in the larval growth model in order to simulate the vertical as well as the time distribution of oyster larvae. The relationships used to formulate the larval sinking, swimming



**Fig. 1. (b)** Simulated vertical- and time-dependent distribution of seven larval sizes (75, 94, 150, 200, 250, 300, 334  $\mu\text{m}$ ) obtained for a strongly stratified water column. Stratification is imposed between 3 and 5 m in depth. Temperature and salinity values range from 24.0 to 22.9°C, and from 20.4 to 24.2 p.p.t. in the region of stratification, respectively. Food and turbidity values are held constant throughout the water column at 2 mg AFDW  $\text{l}^{-1}$  and 0.0 g dry weight  $\text{l}^{-1}$ , respectively. Contours are the number of larvae per 0.5 m at time ( $t$ ). After Figure 9 in Deksheniaks *et al.* (1996).

and behavioral responses (Table II) were derived from laboratory observations (Deksheniaks *et al.*, 1996).

#### Larval mortality

Jackson and Strathmann (1981) determined daily mortality rates for planktonic larvae of several species of marine invertebrates. Their studies resulted in a relationship between the length of the planktonic period and predation of the form:

$$MP = PT \times \lambda \quad (2)$$

where  $MP$  is the pre-competent mortality parameter,  $PT$  is the length of the pre-competent period (days) and  $\lambda$  is the larval mortality rate ( $\text{day}^{-1}$ ).

The length of the planktonic period for oyster larvae varies with environmental conditions. In temperate estuaries and bays, the planktonic period ranged from 46 days in the early spring and late fall, when temperatures are cooler, to 18 days in the summer when temperature and food supply are elevated (cf. Table III; Deksheniaks *et al.*, 1993). At a constant temperature of 24°C, salinity of 21 p.p.t.

**Table II.** Summary of the larval vertical migration and behavior model described in Deksheniaks *et al.* (1996). These equations provide an estimate for  $W_{Nt}$  which is a component of the total advective velocity,  $W_T$ , in equation (1). The migration relationships and parameters are defined. The data sources on which the parameterizations for larval behavior are based are given. Also given are the figure numbers from Deksheniaks *et al.* (1996) that illustrate the larval swimming and sinking relationships

Equation	Term	Parameter definitions	Data sources	Figure no.
$W_{Nt} = TS \times SW - (1 - TS) \times SR$	TS	Fraction of active larvae	Haskin (1964)	7-12
	SW	Larval swimming rate (mm s <sup>-1</sup> )		
	SR	Larval sinking rate (mm s <sup>-1</sup> )		
$TS = c\Delta S + d$	TS	Fraction of active larvae for increasing salinity	Kennedy and Van Heukelem (1986)	4
	$\Delta S$	Salinity change (p.p.t. time <sup>-1</sup> )		
$TS = -e\Delta S + f$	c	0.0622 $\frac{\text{fraction active}}{\text{time} \times \Delta S}$	Hidu and Haskin (1978) McCarthy (1989)	2
	d	0.3801 fraction active		
	TS	Fraction of active larvae for decreasing salinity		
	e	0.0668 $\frac{\text{fraction active}}{\text{time} \times \Delta S}$		
SW	f	0.7515 fraction active	Hidu and Haskin (1978)	2
	SW	Larval swimming rate (mm s <sup>-1</sup> )		
$SR = 2.665e^{0.0058(SZ - 220)}$	SR	Larval sinking rate (mm s <sup>-1</sup> )	Hidu and Haskin (1978)	3
	SZ	Larval size ( $\mu\text{m}$ )		

Changes from Deksheniaks *et al.* (1996) should be noted: (i) TS represents the fraction of active larvae, not percent activity.

**Table III.** Summary of simulation results showing the number and percent larval survival for the different types of size- and depth-dependent mortality. An initial cohort of 10 000 individuals was used in all simulations

Mortality type	Mortality form	Number settling	Percent larval survival
Size-dependent	Constant	104	1.04
	Increasing	51	0.51
	Decreasing	222	2.22
Depth-dependent	Constant	104	1.04
	Increasing	8	0.08
	Decreasing	1256	12.56
	Surface	8796	87.96
	Region of stratification	4465	44.65
	Benthos	1393	13.93

and food concentration of 2 mg AFDW l<sup>-1</sup>, where AFDW represents ash-free dry weight, oyster larvae develop to competent settlement size in ~32 days. These environmental conditions are favorable, but not optimal, for larval growth.

For invertebrates with a pre-competent period of several weeks, Jackson and Strathmann (1981) found that estimates of MP exceeding 3.0 are appropriate. The MP value calculated by Jackson and Strathmann (1981) for the larvae of

*Balanus balanoides* was 4.6. Assuming this value, and using a pre-competent planktonic period of 32 days, results in a daily mortality rate for oyster larvae of  $0.143 \text{ day}^{-1}$ . This mortality rate was used as the base rate in this study.

The mortality rate specified in this study is based solely on predation. It should be noted that many other factors are involved in determining larval survivorship in any year, including environmentally determined variations in larval life span (Deksheniaks *et al.*, 1993, 1996) and changes in dispersal pattern (Mann, 1988; Epifanio, 1995; Deksheniaks *et al.*, 1996). Thus, the overall mortality rate that was used in this study may have been lower than that which normally occurs for bivalve larvae in the field. Despite this fact, the relative patterns in larval survival between the simulations would not have changed if a higher daily mortality rate had been used.

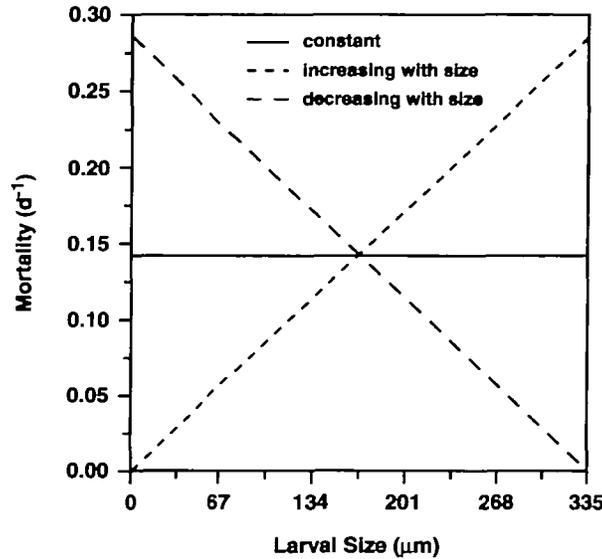
#### *Model implementation*

Larval size is given as length in  $\mu\text{m}$ , where the length is the maximum anterior–posterior distance (Carriker, 1979). Oyster larvae are  $\sim 65 \mu\text{m}$  after fertilization and grow to a competent setting size of  $\sim 335 \mu\text{m}$  (Stafford, 1913; Galtsoff, 1964). For this modeling study, the larval life history was partitioned into 271 size classes with an interval of  $1 \mu\text{m}$ .

Equation (1) was solved in a domain that was 10 m in depth, with a vertical resolution of 0.5 m, using boundary conditions of no flux of larvae through the surface or the bottom. A single cohort of 10 000 individuals, each  $65 \mu\text{m}$  in length, was introduced at the bottom of the model domain on the first day of the simulation, which corresponds to input due to spawning by adult oysters. Equation (1) was solved numerically using a Crank–Nicholson implicit finite difference scheme with a time step of 12 min.

All simulations, with the exception of the simulation in which predation was concentrated in the region of stratification, used constant environmental conditions of  $24^\circ\text{C}$ , 21 p.p.t.,  $2 \text{ mg AFDW l}^{-1}$  and  $0.0 \text{ g dry weight l}^{-1}$ . These conditions are favorable, but not necessarily optimal, for larval growth (Deksheniaks *et al.*, 1993). Under these conditions, oyster larvae reach settling size in  $\sim 32$  days (Figure 1a). For the simulation in which predation was concentrated in the region of stratification, a sharp gradient in temperature and salinity was imposed between 3 and 5 m. The larval distributions produced by this vertical profile (Figure 1b) differ from those obtained for constant conditions (Figure 1a) in that the upward migration of the larvae is reduced. The strong stratification results in the highest concentration of all larval stages being centered at or just below the salinity and temperature gradient.

The form of  $\gamma_i$  in equation (1) differed between simulations in order to investigate the effect of variations in the type of predation stress. The first series of simulations were designed to investigate size-dependent predation on oyster larval survivorship. The form of  $\gamma_i$  used in these simulations (Figure 2) distributed the predation pressure differently on different sizes of larvae. A uniform predation pressure that used the base mortality rate obtained from equation (2) provides a reference against which the effects of predation pressure that increases or



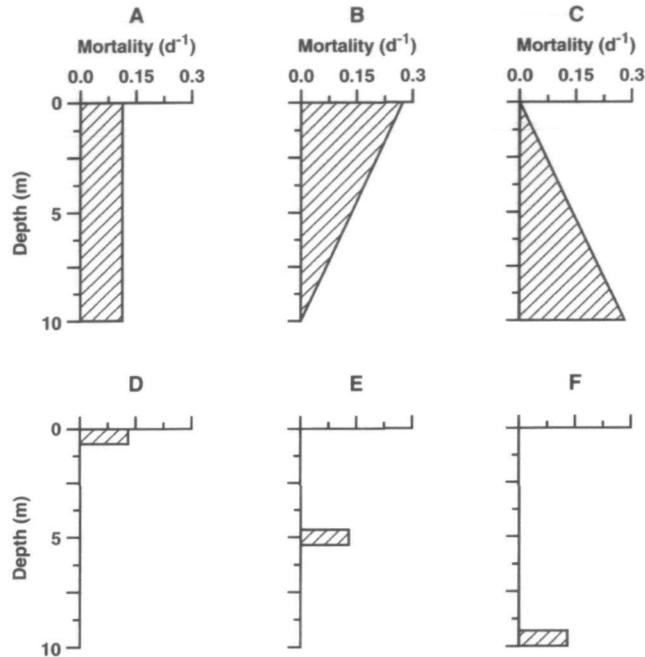
**Fig. 2.** The relationships used to specify the size-dependent predation rates ( $\text{day}^{-1}$ ) are: constant at  $0.143 \text{ day}^{-1}$  for all larval sizes, increasing with increasing larval size, and decreasing with increasing larval size. The relationship for increasing predation with increasing larval size was given by  $y = 0.0011x$ ; that for predation that decreases with increasing larval size was given by  $y = -0.0011x + 0.286$ . The predation rate and larval size are given by  $y$  and  $x$ , respectively.

decreases with size can be compared (Figure 2). The latter form of predation is based on observations that the smallest sizes experience the highest rates of mortality (Landry, 1976). The integrated value of the increasing and decreasing predation pressure is such that it does not exceed that of the uniform case.

The form of  $\gamma_i$  was next modified to consider the effect of depth-dependent predation pressure on larval survival. For these simulations, the predation pressure was distributed uniformly throughout the water column (Figure 3A), allowed to decrease (Figure 3B) or increase (Figure 3C) with depth, and focused at specific depths (Figure 3D-F). The uniform predation pressure provides a reference for comparison with the other predation profiles. Depth decreasing predation allows for grazing of oyster larvae by zooplankton, larval fish and other planktonic predators while in the water column. The effect of these organisms is assumed to decrease with depth. The predation that increases with depth simulates the effect of bottom filter feeders and benthic scavengers. The predation that is focused at specific depths is based on observations indicating that oyster larvae accumulate at specific regions, such as the surface and in regions of stratification.

The integrated value of the depth decreasing and increasing predation profiles is the same as the uniform profile (Figure 3A-C), while the integrated values of the predation pressure focused at specific depths are equivalent (Figure 3D-F). In some sense, the depth- and size-dependent predation pressures are not independent given the vertical migration of the smaller oyster larvae to the surface and the sinking of the larger larvae to the bottom (cf. Figure 1a). However, the rate at

## Modeling study of larval growth and behavior



**Fig. 3.** The relationships used to specify the depth-dependent predation rates ( $\text{day}^{-1}$ ) that are: (A) constant at  $0.143 \text{ day}^{-1}$  for all depths; (B) decreasing with depth; (C) increasing with depth; (D) limited to the surface; (E) limited to the region of stratification; (F) limited to the bottom. The relationship shown in (B) was obtained from  $y = -0.0286x + 0.286$ ; that in (C) was obtained from  $y = 0.0286x$ . The mortality rate and depth are given by  $y$  and  $x$ , respectively.

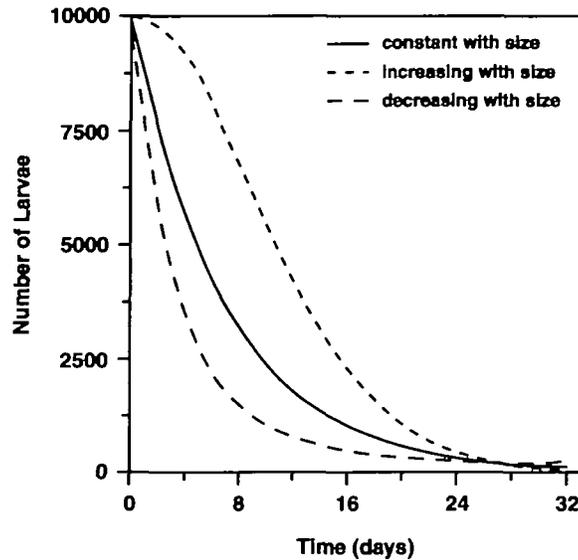
which the larvae move upwards and downwards determines the time they are exposed to the different types of predation pressure. Thus, this alters the predation relative to what would be expected from size-dependent predation alone.

## Results and discussion

### *Size-dependent predation*

Predation that is uniform on all oyster larval sizes results in a nearly exponential decrease in the number of larvae over time (Figure 4). The larval cohort is reduced by 51% after 5 days and by 76% after 10 days. After 32 days, only 1.04% of the larvae have survived to competent settlement size (Table III).

Predation that increases with larval size results in more of the larvae surviving the initial portion of the planktonic period (Figure 4). After 10 days, 54% of the original cohort are still alive. The small (75–150  $\mu\text{m}$ ) larvae are more abundant due to higher survivorship during the earlier stages of development. However, the higher predation on the larger larvae has a dramatic effect, and only 0.51% of the original cohort survive to settlement size. The overall survivorship is less than that with constant predation pressure (Table III).



**Fig. 4.** The simulated time-dependent loss of larvae exposed to the three size-dependent predation patterns shown in Figure 2.

The largest percent of larvae survive to competent settlement size when predation decreases with increasing larval size. With this predation pressure, the initial loss of small larvae is rapid and exceeds the loss that occurs with constant predation pressure (Figure 4). After 5 days, 72% of the original cohort have been lost. However, after ~10 days the rate of mortality decreases and eventually 2.2% of larvae reach a competent settlement size. This size-dependent predation loss resulted in the largest percent of the cohort reaching settlement size (Table III).

The percentages of larvae reaching competent settlement size in the simulations in which predation was varied with larval size appear similar at first glance (Table III). Although these results would seem to indicate that the type of predation makes little difference on the final survivorship of a given larval cohort, the factor of four change in survivorship among these three simulations may represent a significant difference in recruitment to the post-settlement population. For example, for a commercial species such as *C. virginica*, a factor of four increase in survivorship translates into a significant number of potential recruits to the fishery. On the other hand, yearly recruitment over many years varies much more than by a factor of four in most benthic populations including oysters (e.g. Coe, 1953; Loosanoff, 1966; Fegley *et al.*, 1994, 1997), suggesting that the variation in survivorship produced by size-selective predation is not sufficient to explain the normally observed differences in recruitment in the field.

#### *Depth-dependent predation*

*Predation throughout the water column.* The simulations that included constant predation throughout the water column and predation that increased and

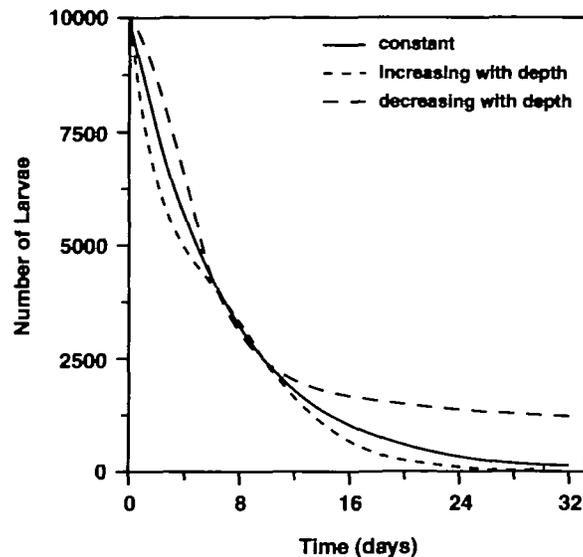


Fig. 5. The simulated time-dependent loss of larvae exposed to the three water column mortalities shown in Figure 3A–C.

decreased with depth resulted in values of larval survivorship that differed considerably. The larval survival that occurs when predation is uniform with depth (Figure 5) is identical to that obtained using size-dependent predation (cf. Figure 4). Larval loss is exponential over time and only 1.04% of the larvae survive to competent settlement size (Table III, Figure 5).

The lowest percent of larvae survive when predation increases with increasing depth. The impact of heavy predation on the mature larval sizes is to reduce the number of larvae surviving to <0.08% of the initial cohort (Table III, Figure 5). Predation that is most intense near the bottom results in loss of the majority of the mature larvae, which leaves few larvae that attain settlement size.

Predation that decreases with depth results in the highest larval survival rate; in this case, >12% of the cohort survive to settlement size (Table III, Figure 5). The initial loss of larvae is high because the majority of smaller-sized larvae are distributed in the upper water column.

*Depth-limited predation.* The simulations in which predation is focused on specific depth intervals are most variable in terms of the percent of the initial larval cohort that survive to settlement size (Table III). These simulations have the strongest coupling between larval behavior, predation effects and survival. For the same reasons that decreasing predation with depth increased larval survival, when predation is limited to just the upper region of the water column, larval survival is greatly increased (Figure 6, Table III), with >87% of the larvae surviving to competent settlement size.

Predation that is focused in the region of stratification results in >44% of the initial larval cohort surviving to competent settlement size (Table III, Figure 6).

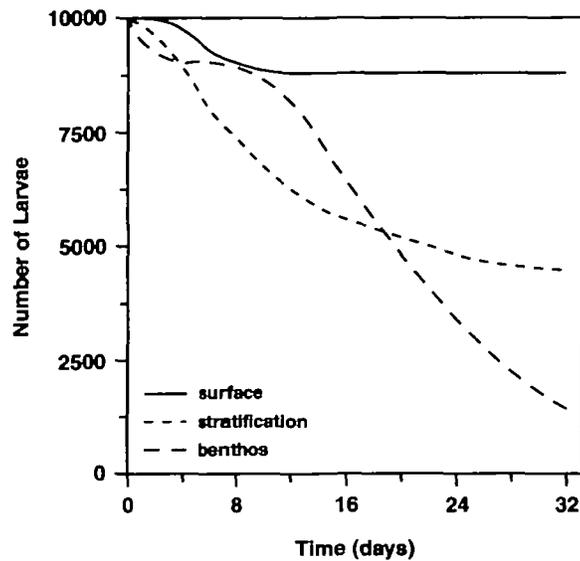


Fig. 6. The simulated time-dependent loss of larvae exposed to predation that is limited to certain regions of the water column as shown in Figure 3D-F.

Larvae have been observed to accumulate in regions of the water column that are characterized by strong temperature and salinity gradients (Harder, 1968; Tremblay and Sinclair, 1990; Mann *et al.*, 1991). Observations (Nelson, 1954; Haskin, 1964; Wood and Hargis, 1971; Kennedy and Van Heukelem, 1986) and modeling studies (Deksheniaks *et al.*, 1996) indicate that oyster larvae actively modify their swimming and sinking behavior in response to temperature and salinity gradients. Behavior that concentrates larvae may provide a rich food source for larval predators. Therefore, it might be expected that predation focused on the region of stratification would have the greatest impact on larval survivorship. This hypothesis, however, is not supported by the simulated distributions presented in this study.

In fact, the poorest larval survivorship occurs when the primary source of predation is restricted to just above the oyster bed. In this case, only 13% of the initial cohort survive to settlement size (Table III, Figure 6). These results show that the greatest impact on the percent of a cohort reaching settlement size is not from the planktonic predators. Rather, it is the benthic filter feeders and benthic scavengers that provide a greater threat to the survivability of the cohort (Table III). Thus, the simulations that compared scenarios where the relative degree of predation between water column and benthos varied, resulted in the greatest variability in terms of numbers of recruits.

*Benthic predation: A structuring element for populations*

The simulations in which larval mortality is varied over depth emphasize that survival to settlement size is highly dependent on the time spent near the bottom. In

these simulations, the benthos and demersal predators act as primary controlling factors on larval survivorship and, hence, recruitment success. Since Thorson (1966), the effect of the benthos as a predator of larvae has been considered a dominant factor structuring the ecosystem (e.g. Woodin, 1976; Elmgren *et al.*, 1986; Osman *et al.*, 1989).

Simulation results indicate that the potential for increased dispersal is not the only advantage the oyster larvae incur by migrating to the upper water column. The simulated larval distributions indicate that being in the upper water column is an advantage even in systems that have moderate levels of benthic predation. By migrating upwards for at least some part of their development, the larvae potentially increase their survivorship by partially offsetting the effects of benthic predation. This supports the suggestion of Strathmann (1990) that larval dispersal during the pre-competent period may, in fact, be a by-product of larval migration into the plankton for the purposes of avoiding predation.

#### *Implications for the population*

The percentages of larvae reaching a final competent settlement size for the nine different simulations are not necessarily indicative of the larval concentration present in the water column during larval development. Predation that increases with increasing larval size or with increasing depth in the water column results in the smaller-sized larvae having the greatest initial survivorship. These smaller-sized larvae are distributed predominantly in the upper water column (Carriker, 1951) where they can be readily dispersed by the surface currents. Predation pressure that favors the survival of the more widely dispersed smaller size classes could potentially increase gene flow and result in lower genetic variation between settlement areas (Scheltema, 1971; Strathmann, 1986). Increased gene flow allows organisms to adapt to longer-term changes in the environment, while dampening out the effects of short-term or localized disturbances (Hedgecock, 1986).

#### **Conclusions**

A time- and depth-dependent model of oyster larval growth and behavior was used to investigate the effects of size- and depth-dependent predation on larval survivorship. The simulated results showed clearly that different settlement patterns are possible for different types of predation. This reaffirms the assertion by Landry (1976), Steele (1976) and Steele and Henderson (1992) that the form of the mortality term used in models is critical in determining the accuracy of the simulated distributions. This points to the need for laboratory and field measurements that will allow the nature of predation on organisms such as oyster larvae to be quantified.

The differences in the number of larvae present in the water column, arising from the different predation pressures, could have profound effects on the dispersal of larvae and consequently on post-settlement populations. Again, this points to the need to represent predation processes accurately in numerical models, especially those designed to investigate transport patterns, residence

times and exchanges between populations. The latter point is of considerable interest for stocks of commercially important species and for studies of gene flow between populations (e.g. Mitton *et al.*, 1989). Moreover, the role of predation in determining the numbers of larvae in the water column, and hence larval dispersal, is an integral part of understanding recruitment limitation, especially for exploited species such as the oyster.

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### References

- Baker, P. (1991) Effect of neutral red stain on settlement ability of oyster pediveligers, *Crassostrea virginica*. *J. Shellfish Res.*, **10**, 455–456.
- Carriker, M.R. (1951) Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monogr.*, **21**, 19–38.
- Carriker, M.R. (1979) Ultrastructural morphogenesis of prodissoconch and early dissoconch valves of the oyster *Crassostrea virginica*. *Proc. Natl Shellfish Assoc.*, **69**, 103–128.
- Coe, W.R. (1953) Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. *Ecology*, **34**, 225–229.
- Davis, H.C. (1958) Survival and growth of clam and oyster larvae at different salinities. *Biol. Bull. (Woods Hole)*, **114**, 296–307.
- Davis, H.C. (1960) Effects of turbidity-producing materials in sea water on eggs and larvae of the clam (*Venus (Mercenaria) mercenaria*). *Biol. Bull. (Woods Hole)*, **118**, 48–54.
- Davis, H.C. and Calabrese, A. (1964) Combined effects of temperature and salinity on the development of eggs and growth of larvae of *Mercenaria mercenaria* and *Crassostrea virginica*. *US Fish. Wildl. Serv. Fish. Bull.*, **63**, 643–655.
- Dekshenieks, M.M., Hofmann, E.E. and Powell, E.N. (1993) Environmental effects on the growth and development of Eastern oyster, *Crassostrea virginica* (Gmelin, 1791), larvae: A modeling study. *J. Shellfish Res.*, **12**, 241–254.
- Dekshenieks, M.M., Hofmann, E.E., Klinck, J.M. and Powell, E.N. (1996) Modeling the vertical distribution of oyster larvae in response to environmental conditions. *Mar. Ecol. Prog. Ser.*, **136**, 97–110.
- Doherty, P. and Fowler, T. (1994) An empirical test of recruitment limitation in a coral reef fish. *Science*, **363**, 935–939.
- Elmgren, R., Ankar, S., Marteleur, B. and Ejdung, G. (1986) Adult interference with postlarvae in soft sediments: the *Pontoporeia-Macoma* example. *Ecology*, **67**, 827–836.
- Epifanio, C.E. (1995) Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. *Bull. Mar. Sci.*, **57**, 713–725.
- Fegley, S.R., Ford, S.E. and Kraeuter, J.N. (1994) Relative effects of harvest pressure and disease mortality on the population dynamics of the Eastern oyster (*Crassostrea virginica*) in Delaware Bay. Final Report, NOAA, NMFS, Northeast Regional Office, Gloucester, MA, 36 pp.
- Fegley, S.R., Ford, S.E., Kraeuter, J.N. and Haskin, H.H. (1997) The persistence of New Jersey's oyster seedbeds in the presence of MSX disease and harvest: management's role. In *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*, in press.
- Gaines, S., Brown, S. and Roughgarden, J. (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia (Berlin)*, **67**, 267–272.
- Galtsoff, P.S. (1964) The American oyster *Crassostrea virginica* (Gmelin). *US Fish. Wildl. Serv. Fish. Bull.*, **64**, 1–480.

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- Harder, W. (1968) Reactions of plankton organisms to water stratification. *Limnol. Oceanogr.*, **13**, 156–168.
- Haskin, H. (1964) The distribution of oyster larvae. In Marshall, N., Jeffries, H.P., Napara, T.A. and Siebuth, J.M. (eds), *Symposium on Experimental Marine Ecology*. Graduate School of Oceanography, University of Rhode Island, Occas. Publ. 2, pp. 76–80.
- Hedgecock, D. (1986) Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? *Bull. Mar. Sci.*, **39**, 550–564.
- Hidu, H.H. and Haskin, H. (1978) Swimming speeds of oyster larvae *Crassostrea virginica* in different salinities and temperatures. *Estuaries*, **1**, 252–255.
- Hofmann, E.E. and Lascara, C.M. (1997) An overview of interdisciplinary modeling for marine ecosystems. In Robinson, A.R. and Brink, K.H. (eds), *The Sea The Global Coastal Ocean, Part A, Processes and Methods*. John Wiley & Sons, New York, in press.
- Huntington, K.M. and Miller, D.C. (1989) Effects of suspended sediment, hypoxia and hyperoxia on larval *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.*, **8**, 37–42.
- Jackson, G.A. and Strathmann, R.R. (1981) Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.*, **118**, 16–26.
- Kennedy, V.S. and Van Heukelem, W. (1986) Responses to environmental factors by larval oysters *Crassostrea virginica*. *Am. Malac. Bull.*, **4**, 101.
- Landry, M.R. (1976) The structure of marine ecosystems: an alternative. *Mar. Biol.*, **35**, 1–7.
- Loosanoff, V.L. (1966) Time and intensity of setting of the oyster *Crassostrea virginica*, in Long Island Sound. *Biol. Bull. (Woods Hole)*, **130**, 211–227.
- Mann, R. (1986) Sampling of bivalve larvae. In Jamieson, G.S. and Bourne, N. (eds), *North Pacific Workshop on Stock Assessment and Management of Invertebrates*. *Can. Spec. Publ. Fish. Aquat. Sci.*, **92**, 107–116.
- Mann, R. (1988) Distribution of bivalve larvae at a frontal system in the James River, Virginia. *Mar. Ecol. Prog. Ser.*, **50**, 29–44.
- Mann, R., Campos, B.M. and Luckenbach, M.W. (1991) Swimming rate and responses of larvae of three mactrid bivalves to salinity discontinuities. *Mar. Ecol. Prog. Ser.*, **68**, 257–269.
- McCarthy, K.J. (1989) Influence of salinity on swimming behavior of larvae *Crassostrea virginica*. Masters Thesis, Virginia Institute of Marine Science.
- Mitton, J.B., Berg, C.J., Jr and Orr, K.S. (1989) Population structure, larval dispersal, and gene flow in the Queen Conch, *Strombus gigas*, of the Caribbean. *Biol. Bull.*, **177**, 356–362.
- Nelson, T.C. (1954) Observations of the behavior and distribution of oyster larvae. *Proc. Natl Shellfish Assoc.*, **45**, 23–28.
- Osman, R.W., Whitlatch, R.B. and Zajac, R.N. (1989) Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.*, **54**, 61–73.
- Peterson, C.H. and Summerson, H.C. (1992) Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Mar. Ecol. Prog. Ser.*, **90**, 257–272.
- Peterson, I. and Wroblewski, J.S. (1984) Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.*, **41**, 1117–1120.
- Rhodes, E.W. and Landers, W.S. (1973) Growth of oyster larvae, *Crassostrea virginica*, of various sizes in different concentrations of the chrysophyte, *Isochrysis galbana*. *Proc. Natl Shellfish Assoc.*, **63**, 53–59.
- Scheltema, R.S. (1971) Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull. (Woods Hole)*, **140**, 284–322.
- Stafford, J. (1913) *The Canadian Oyster, Its Development, Environment and Culture*. The Mortimer Co., Ottawa.
- Steele, J.H. (1976) The role of predation in ecosystem models. *Mar. Biol.*, **35**, 9–11.
- Steele, J.H. and Henderson, E.W. (1992) The role of predation in plankton models. *J. Plankton Res.*, **14**, 157–172.
- Strathmann, R.R. (1986) What controls the type of larval development? Summary statement for the evolution session. *Bull. Mar. Sci.*, **39**, 616–622.
- Strathmann, R.R. (1990) Why life histories evolve differently in the sea. *Am. Zool.*, **30**, 197–207.
- Thorson, G. (1966) Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.*, **3**, 267–293.
- Tremblay, M.J. and Sinclair, M. (1990) Sea scallop larvae *Placopecten magellanicus* on Georges Bank: vertical distribution in relation to water column stratification and food. *Mar. Ecol. Prog. Ser.*, **61**, 1–15.

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- Verity, P.G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277–293.
- Wood, L. and Hargis, W.J. (1971) Transport of bivalve larvae in a tidal estuary. In Crisp, D.J. (ed.), *Proceedings of the Fourth European Marine Biology Symposium, Bangor, 1969*. Cambridge University Press, Cambridge, pp. 29–44.
- Woodin, S. (1976) Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.*, **34**, 25–41.
- Yoshioka, P.M. (1982) Role of planktonic and benthic factors in the population dynamics of the Bryozoan *Membranipora membranacea*. *Ecology*, **63**, 457–468.

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