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ENVIRONMENTAL EFFECTS ON THE GROWTH AND DEVELOPMENT OF EASTERN OYSTER, *CRASSOSTREA VIRGINICA* (GMELIN, 1791), LARVAE: A MODELING STUDY

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ABSTRACT The effects of temperature, food concentration, salinity and turbidity on the growth and development of *Crassostrea virginica* larvae were investigated with a time-dependent mathematical model. Formulations used in the model for larval growth are based upon laboratory data. Simulations were done using temperature conditions characteristic of Laguna Madre, Galveston Bay, Apalachicola Bay, North Inlet and Chesapeake Bay. These simulations show that the duration of the planktonic larval phase, which is determined by larval growth rate, decreases at lower latitudes in response to warmer water temperatures. Also, oysters in the more southern locations have a longer spawning season during which the oyster population can produce more larvae. Simulations were done for Galveston Bay and Chesapeake Bay using idealized time series of food supply that included higher concentrations in the spring, summer or fall. Additional simulations considered the effects of increased food supply in both spring and fall seasons. The results show that shifting the period of enhanced food supply from March-April to April-May, when temperatures are warmer, reduces the minimum larval planktonic period from 44 to 34 days. Shifting the fall bloom from August-September to September-October, however, does not appreciably change the minimum larval planktonic period. The final set of simulations considered the effect of low salinity events and turbidity on the planktonic period of the larvae of *Crassostrea virginica*. By imposing a simulated low salinity (5 ppt) event of one month duration in August, the larval planktonic time is increased by about 39% over normal August salinities. Turbidity concentrations less than 0.1 g l^{-1} result in slightly decreased planktonic times. These model results show clearly the importance of ambient environmental conditions in determining the planktonic time of larvae of *Crassostrea virginica*, and hence their ultimate recruitment to the adult oyster population.

INTRODUCTION

The failure to obtain a significant correlation between broodstock size and yearly spatfall success in many species, including the eastern oyster *Crassostrea virginica*, indicates that adult fecundity and/or larval survival are as important as adult abundance in determining the viability of the population (Prytherch 1929, Loosanoff and Engle 1940, Olson and Olson 1989). Understanding the basic causes of the large year-to-year variation in spatfall success at any site (Loosanoff 1966, Kenny et al. 1990) and the apparent latitudinal gradient in adult population stability (persistence and resilience) (Powell et al., in press), requires that the interaction of environmental factors on oyster reproduction and larval survival be examined over a wide range of environmental conditions.

The timing and intensity of spawning of *Crassostrea virginica*, is influenced by a variety of factors, some of which are temperature, salinity and food supply. A recent modeling study (Hofmann et al. 1992) showed that, for conditions representative of mid-latitude bays, the timing of the spring increase and fall decrease in water temperature relative to the spring and fall phytoplankton blooms can significantly alter the pattern, frequency and intensity of spawning in an oyster population. Depending upon the juxtaposition of the spring temperature and food supply increase, the first spawning may occur any time from April to June. The timing of the final fall spawn is equally as variable. The key spawning pulses, which account for the majority of the reproductive effort, may also occur at widely different times during the spawning season in response to variations in environmental conditions. As a consequence, the environment experienced by larvae of *Crassostrea virginica* may encompass a wide range of temperature, salinity and food conditions.

Once the larvae are spawned, recruitment to the adult population is determined by the survivability of the larvae in the plankton. Survivorship can be expected to be inversely correlated with larval life span because most factors controlling mortality, like predation, should be functions of the time of exposure, namely larval life span. The time spent in the plankton is determined by the larval growth and developmental rates which are significantly affected by environmental conditions.

Loosanoff and Davis (1963) and Loosanoff (1965) showed that temperature and food concentration were the two primary environmental variables affecting the development of *Crassostrea virginica* larvae. Additional studies demonstrated that salinity (Butler 1949, Davis 1958, Davis and Calabrese 1964, Ulanowicz et al. 1980), turbidity (Davis 1960, Carriker 1986, Huntington and Miller 1989), and oxygen content (Widdows et al. 1989) also affect larval growth and survival. These studies, while providing insight into the factors controlling larval growth, typically considered only one or two environmental factors. However, in the environment it is the combined effect of all environmental factors that determines the growth, development and ultimate survivorship of the larvae.

To investigate the interaction of environmental factors on the growth and development of oyster larvae, we developed a time-dependent numerical model that combines the effects of food concentration, temperature, salinity and turbidity on the growth and development of oyster larvae. Formulations for larval growth and development are taken from laboratory experiments and are combined with time series of monthly-averaged food, temperature,

salinity and turbidity measurements from several bays along the east coast of the U.S. and the Gulf of Mexico, ranging from Chesapeake Bay to the Laguna Madre.

The model was used to simulate oyster larval growth and development over a range of latitudes in response to varying environmental conditions. Simulations are presented that illustrate the importance of the timing of events, such as the occurrence of the spring bloom in relation to increasing water temperature, to the survival and potential recruitment success of the larvae. The results of this study, while specific to the larvae of *Crassostrea virginica*, have relevance to any organism whose life history contains a planktonic larval stage. The conclusions from this study relate to the more general questions concerning the processes that determine larval survivability and ultimately recruitment success.

The following section presents the formulations that were used to model the growth and development of the oyster larvae. The simulations presented in the results section are designed to illustrate the isolated effect of temperature as well as the combined effects of temperature, food, salinity and turbidity on larval growth and development. These results are followed by a discussion and summary.

MODEL

Larval Development

Before describing the larval growth and development model, it is first useful to discuss the characteristics of the larval life history that are important to the model. Stafford (1913) and Galtsoff (1964) present measurements of larval development (measured in μm) at 24°C as a function of time. These data sets, when normalized by total developmental time at 24°C, allow construction of a growth curve that expresses larval development as a fraction of total developmental time (Fig. 1). The representation of larval growth as a fraction of total developmental time standardizes the growth curve. In this way, the variability in total developmental time, resulting from development at different temperatures is eliminated. This approach assumes that larval oyster development is equi-proportional, which means that a given stage persists for the same fraction of total development independent of temperature. However, the duration of a given stage will vary with temperature.

For the first 8% of its development the oyster larva is non-feeding. Larval growth during this time is supported by a small energy reserve which is sufficient for the larva to increase in its

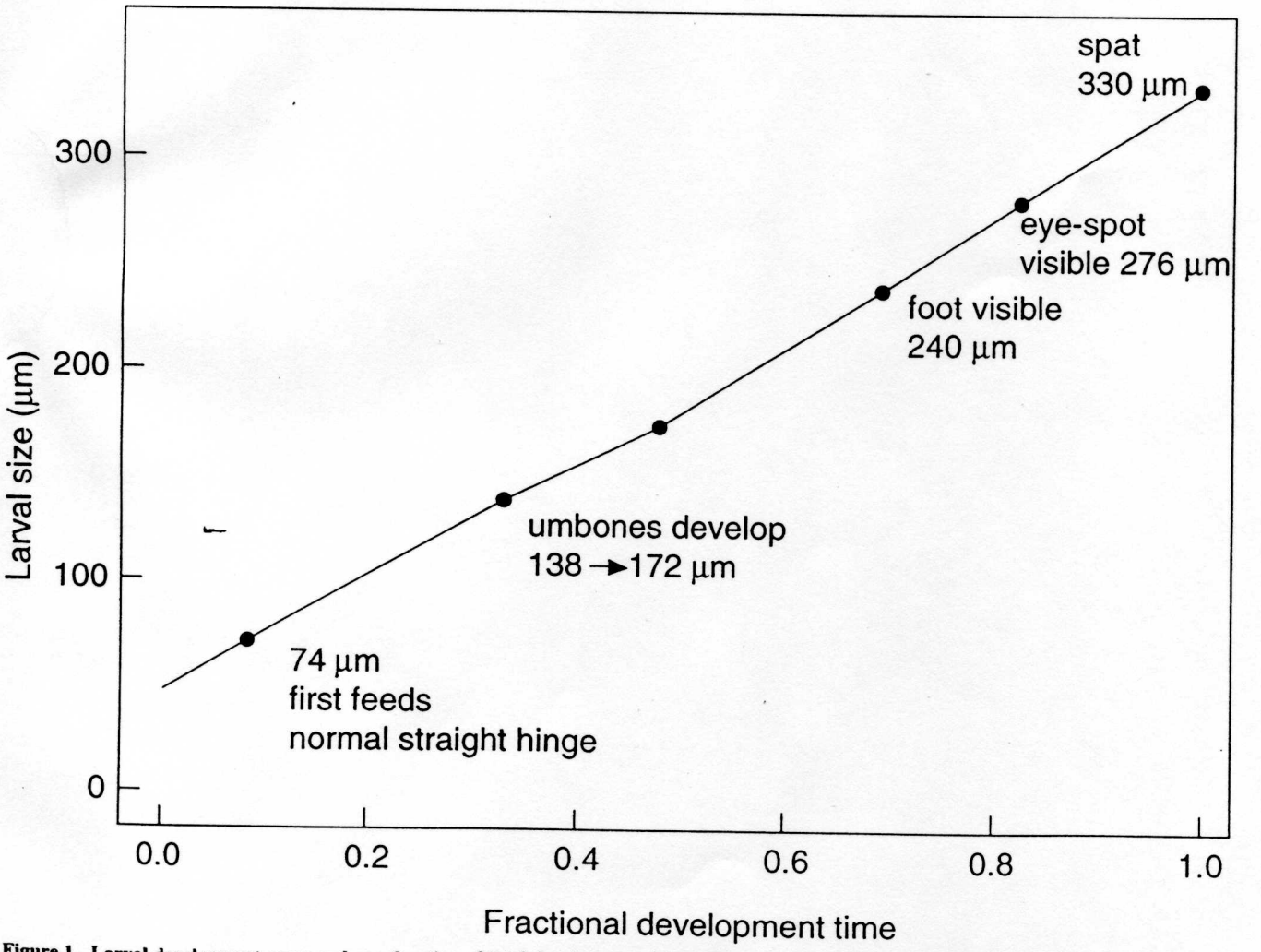

Figure 1. Larval development expressed as a fraction of total developmental time. The sizes given for the larval developmental stages represent average population values. Data used to construct the figure are from Galtsoff (1964) and Stafford (1913). Developmental times were measured at 24°C and 26.5 ppt. Major changes in larval development are indicated.

length dimension about 20 μm (Galtsoff 1964, Stafford 1913). The larva first feeds when it measures 74 μm (Yonge 1960, Galtsoff 1964). After it begins feeding, larval growth rate is determined by *in situ* environmental conditions. Settlement occurs when the larva measures 300 to 350 μm (Galtsoff 1964).

Governing Equation

The larval model includes the effects of temperature, salinity, food concentration and turbidity on larval growth and development. Stated mathematically:

$$\frac{dS}{dt} = growth(food, size) * \text{tsfactor} * \text{turbef} \qquad (1)$$

where S is larval size [a *length* measurement; anteroposterior distance in μm (Carriker 1979)]. The increase in larval size over time is determined from measurements that relate ambient food concentration and larval size to growth rate. This growth rate is then modified by the ambient temperature and salinity (*tsfactor*) and turbidity effects (*turbef*). The effect of hypoxia on larval development (Widdows et al. 1989) is not included in the model because observations to adequately describe this effect on larval growth and development are lacking for the environments considered in this study. Also, in most of the bays used in this study, prolonged periods of low oxygen do not occur. The measurements and relationships used to formulate the terms on the right side of equation (1) are described below. Equation (1) was solved numerically using an Euler method with a time step of one day.

Growth Rate

Food availability has a major effect on the growth rate of the larvae of *Crassostrea virginica* (Loosanoff and Davis 1963, Loosanoff 1965). In many growth models constructed for planktonic organisms (e.g., Steele and Frost 1977, Hofmann and Ambler 1988) the effect of available food is obtained from relationships between ingestion rate and ambient food concentration. The ingested food is then apportioned with an energetics-based approach to satisfy requirements for growth, development, reproduction and other metabolic responses. For the larvae of *Crassostrea virginica,* some feeding rates and energetics measurements are available (Baldwin and Newell 1991, Chrétiennot-Dinet et al. 1991). However, these measurements are not sufficient to allow derivations of relationships that include a range of environmental conditions, e.g., temperature effects on ingestion rate. Therefore, an approach that does not depend explicitly on relationships for individual metabolic processes was used to obtain larval growth and developmental rates.

Rhodes and Landers (1973) measured larval growth rates at 28°C and 26 ppt, for several food concentrations and for larval sizes that ranged from 74.2 to 255 μm. These laboratory measurements were linearly interpolated to obtain larval growth rates at intermediate sizes and food concentrations (Fig. 2). The food concentrations shown in Figure 2, encompass the full range of values that larvae experience in the environment. The growth rate at 255 μm was assumed to apply for larval sizes from 255 to 330 μm (settlement size), for all food concentrations.

The larval growth rates given in Figure 2, show low growth rates at low food concentrations at all sizes. Maximum growth rates occur at larval sizes of 105 to 135 μm, at food concentrations

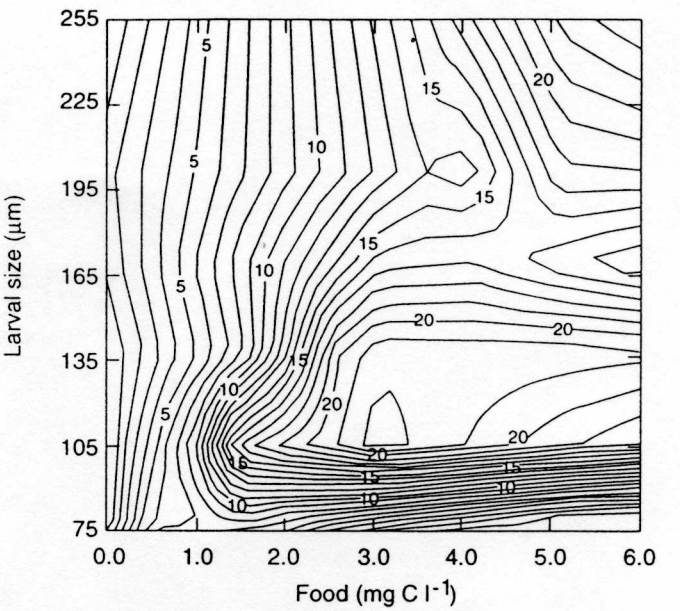

Figure 2. Effect of varying food concentration (at 28°C and 26 ppt) on larval growth rate, as a function of larval size. The contours represent larval growth rate in μm d^{-1}. Contour interval is 1.0 μm d^{-1}.

of 3.0 mg C l^{-1}. The growth rates are used to specify the growth term on the right hand side of equation (1) for a given larval size and ambient food concentration.

Temperature-Salinity Effects

Davis (1958) and Davis and Calabrese (1964) present measurements of oyster larval growth rate in μm d^{-1} for a range of temperatures (17.5 to 32.5°C) and salinities (7.5 to 27.5 ppt). These data were linearly interpolated to obtain larval growth rates at intermediate temperature and salinity values.

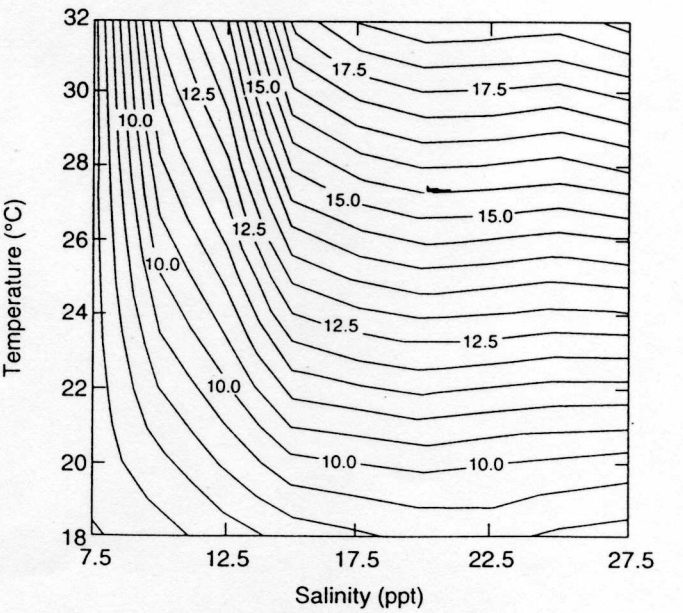

Figure 3. Temperature and salinity effects (at optimal food concentration) on larval growth rate. The contours represent larval growth rate in μm d^{-1}. Contour interval is 0.5 μm d^{-1}.

TABLE 1.

Fractional change in larval growth rate at specific salinities and temperatures. See text for details.

Temperature °C	Salinity (ppt)						
	5.0	7.5	12.5	17.5	22.5	27.5	32.0
15	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	0.0	0.47	0.52	0.56	0.58	0.55	0.55
20	0.0	0.48	0.57	0.63	0.63	0.62	0.62
22	0.0	0.49	0.63	0.72	0.73	0.72	0.72
24	0.0	0.49	0.68	0.81	0.82	0.82	0.82
26	0.0	0.49	0.73	0.90	0.92	0.92	0.92
28	0.0	0.49	0.78	0.99	1.01	1.02	1.20
30	0.0	0.49	0.83	1.08	1.10	1.11	1.11
32	0.0	0.49	0.88	1.18	1.20	1.21	1.21
35	0.0	0.49	0.88	1.18	1.20	1.21	1.21

The general features of the temperature and salinity effects on larval growth rate are as expected (Fig. 3). At low salinities and temperatures the larval growth rate is low. As temperature increases, larval growth rate increases at all salinity values. At all temperatures, salinities of 17.5 to 25 ppt, result in slightly increased larval growth rates. This suggests that salinities in this range are optimal for the growth of larvae of *Crassostrea virginica*.

The upper and lower bounds of the temperature and salinity effects on growth rate (Fig. 3) were extended to 15°C, 0 ppt and 35°C, 32 ppt respectively, to encompass the range of possible values to which the larvae might be exposed. Larvae kept at or below 15°C show no growth, while larvae maintained at temperatures of 17.5°C show minimal growth (Davis and Calabrese 1964). By assuming zero growth at 15°C and using the measured growth rate at 17.5°C, the larval growth rates between 15 and 17.5°C were obtained by linear interpolation. Below 15°C, larval growth rate is assumed to be zero. A drastic reduction in larval growth occurs at temperatures greater than 35°C, but not before (Davis and Calabrese 1964). Therefore, the upper limit for temperature was set at 35°C. The larval growth rates were extended to 35°C by using the measured value at 32°C, across all salinities. This assumes that larval growth rate is constant between 32 and 35°C.

Larvae of *Crassostrea virginica* show no growth at salinities below 5 ppt, and minimal growth at 7.5 ppt (Davis 1958). Therefore, larval growth rate is assumed to be zero between 0 and 5 ppt, and growth rates between 5 and 7.5 ppt were obtained by linear interpolation using the measured value at 7.5 and zero growth at 5

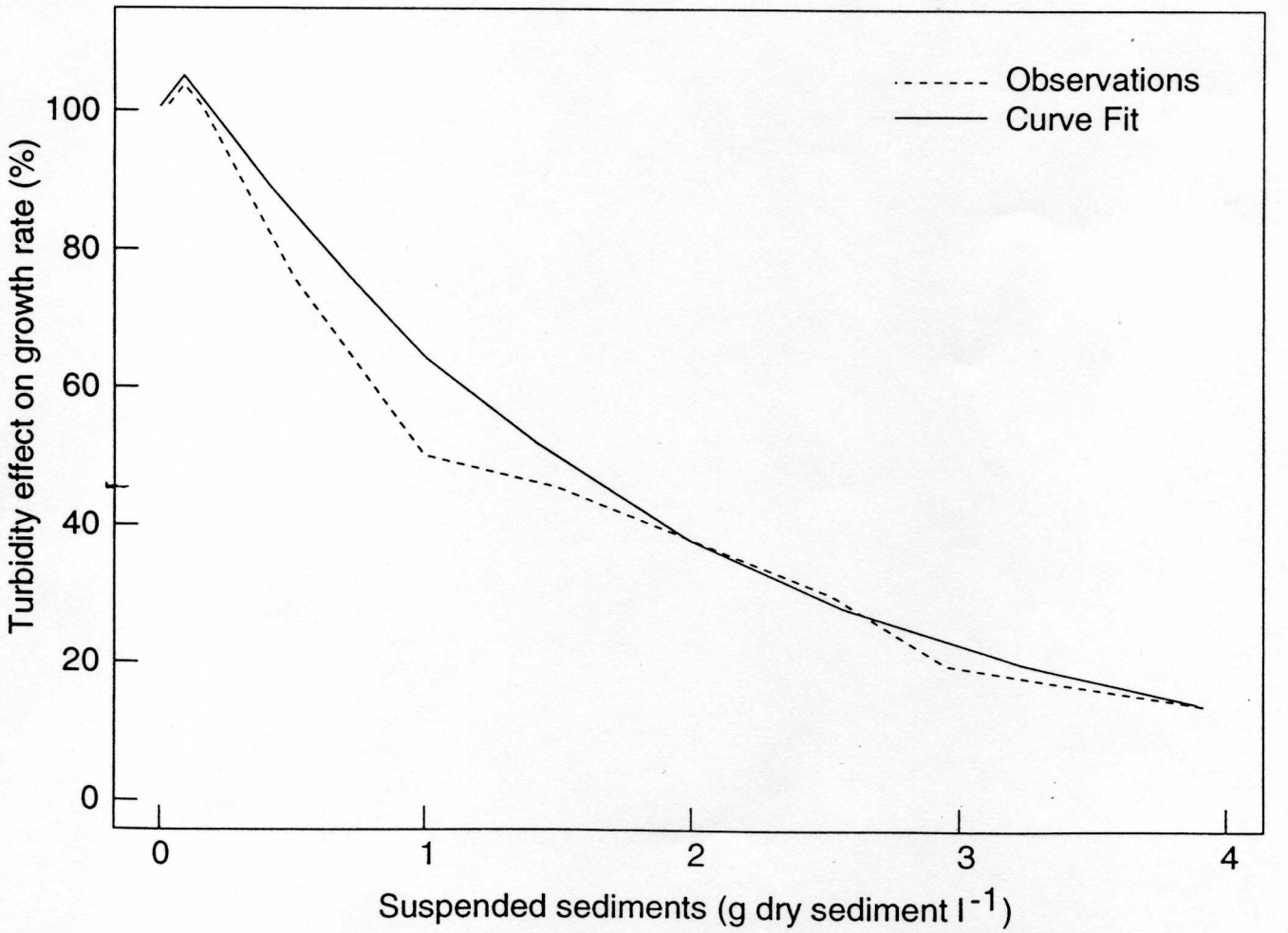

Figure 4. The effect of turbidity on growth rate of *Mercenaria mercenaria* larvae. Dashed line is constructed from measurements given in Davis (1960) and Huntington and Miller (1989). Solid line represents the curve fit to these data.

TABLE 2.

Characteristics of the monthly-averaged temperature time series used in the model. All temperatures expressed in °C. Spring warming and fall cooling were assumed to occur when temperature increased and decreased to 20°C, respectively.

Bay	Minimum Temperature	Maximum Temperature	Average Temperature	Spring Warming	Fall Cooling
Chesapeake Bay[1]	1.0	26.0	14.9	May 1	Sept 15
North Inlet[2]	9.8	28.2	19.2	May 1	Oct 3
Apalachicola Bay[3]	8.9	26.7	20.4	April 20	Nov 15
Galveston Bay[4]	10.0	27.0	19.8	April 20	Nov 11
Laguna Madre[3]	12.2	29.2	22.9	March 4	Nov 24

[1] Berg and Newell 1986, [2]Crosby and Roberts 1990, [3]Powell et al. 1992, [4]Soniat and Ray 1985

ppt. Above 27.5 ppt larval growth rate was held constant at the rate for 27.5 ppt for all temperatures. This assumes a constant salinity effect on larval growth rate at salinities between 27.5 and 32 ppt.

In order to modify the larval growth rates shown in Figure 2 by temperature and salinity effects, the growth rates shown in Figure 3 were normalized by the temperature (28°C) and salinity (26 ppt) value at which the food dependent growth rates were obtained. The resultant values (Table 1) scale the larva growth at any temperature or salinity relative to that at 28°C and 26 ppt. This normalization assumes that temperature and salinity effects are equivalent across all size classes and at all food concentrations, as is true for juvenile and adult oysters (Powell et al. 1992).

Turbidity

Laboratory studies have shown that suspended sediment concentrations greater than 0.1 g dry sediment l^{-1} produce a reduction in growth rate of *Mercenaria mercenaria* larvae (Huntington and Miller 1989). However, sediment concentrations below this value result in an enhancement of larval growth rate (Davis 1960, Huntington and Miller 1989). Assuming that the measurements given for *Mercenaria mercenaria* in Davis (1960) are representative of the growth response of *Crassostrea virginica* larvae to turbidity, a relationship relating turbidity effects to larval growth rate was obtained as:

for turbidity values <0.1 g l^{-1}

$$turbef = m * turb + c \quad (2)$$

for turbidity values >0.1 g l^{-1}

$$turbef = be^{\beta(turb - turb\theta)} \quad (3)$$

where *turb* is the suspended sediment concentration in g dry wt l^{-1}. The first relationship gives the fractional enhancement of larval growth rate, with m and c equal to 0.542% (g dry wt $\cdot l^{-1})^{-1}$ and 1.0%, respectively. The second relationship gives the frac-

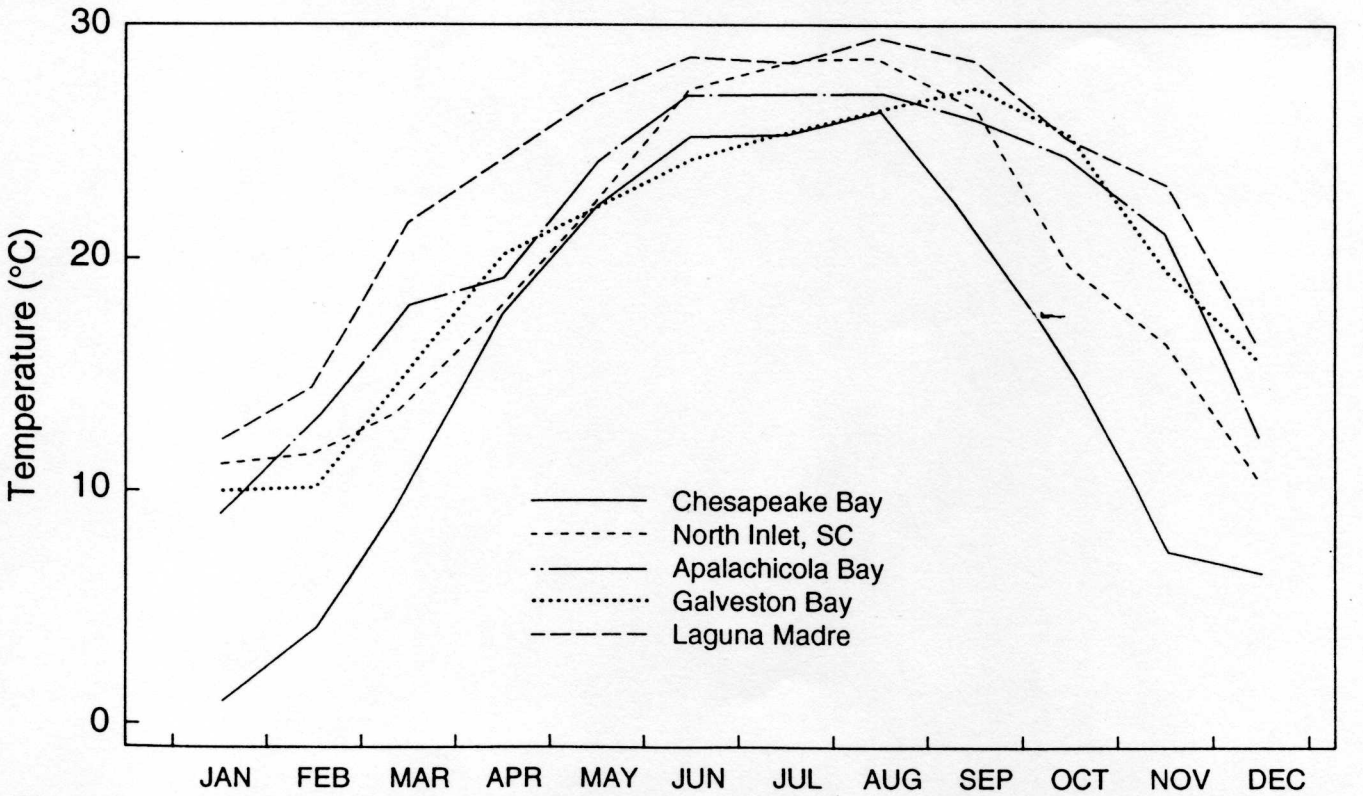

Figure 5. Monthly-averaged temperature time series for five different bays. Temperature values are plotted at the middle of each month. See Table 2 for literature citations for the source of these data.

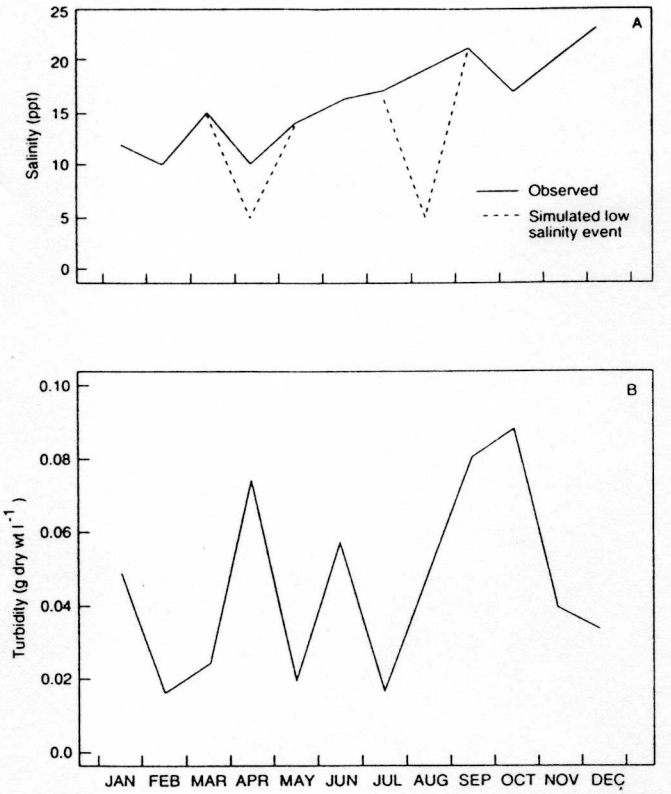

Figure 6. A: Monthly-averaged salinity values from Galveston Bay, Texas measured by Soniat et al. (1984). Salinity values are plotted at the middle of each month. The dashed lines represent simulated low salinity events imposed in mid-April and mid-August. B: Monthly-averaged turbidity values from Galveston Bay, Texas measured by Soniat (1982). Turbidity values are plotted at the middle of each month.

tional decrease in larval growth at higher turbidity concentrations, where the values of b, β and $turb\theta$ are 0.375%, 0.5 (g dry wt $l^{-1})^{-1}$, 2.0 g dry wt l^{-1}, respectively. These relationships are used to specify the fractional change in larval growth rate in equation (1). The correspondence between equations (2) and (3) and the observations is shown in Figure 4.

Environmental Forcing

Temperature

The temperature distributions used as input to the model consisted of monthly-averaged time series from five bays along the east coast of the United States and the Gulf of Mexico (Table 2, Fig. 5). All of the temperature time series extend for one year. In general, all time series show the temperature variations that are expected for temperate mid-latitude bays. The spring increase in temperature and the fall decrease in temperature occurs later in the spring and earlier in the fall respectively, in the more northerly bays (Table 2).

Salinity and Turbidity

The salinity time series used in the model is from Galveston Bay, Texas (Fig. 6a), which has been chosen to be representative of a temperate latitude bay in a majority of the simulations presented in this paper. Salinity in Galveston Bay tends to be low (less than 15 ppt) during spring months as a result of increased freshwater discharge. During summer and fall months, salinity increases. Maximum salinities of about 20 to 25 ppt usually occur in August and persist throughout the fall. These trends are typical of most estuarine systems.

On occasion, estuarine systems are influenced by short-term periods of freshwater discharge. This may occur in the spring, for example, in response to spring storms. To simulate the effects of this type of event, the Galveston Bay salinities were modified by imposing a low salinity event, which decreases to 5 ppt and then increases back to the normal salinity level over a one month period, on April 15th and on August 15th. These modifications were imposed, so that the effects of low salinity events on larval growth could be investigated.

The monthly-averaged turbidity values (Fig. 6b) used in the model are also from Galveston Bay, Texas (Soniat 1982). These values range from 0.005 to 0.088 g dry sediment l^{-1}, with maximum values occurring in the spring and fall. These measured turbidity values are below the concentration at which larval growth is inhibited (cf. Fig. 4).

Food Concentration

Phytoplankton biomass (and production) in estuarine systems exhibits considerable seasonal variability in terms of when maxima may occur. For example, in Chesapeake Bay, chlorophyll maxima have been observed to occur as distinct spring or fall blooms (Harding et al. 1986), as a spring or fall bloom (Malone et al. 1986, Malone et al. 1988), or as a summer maxima (Malone et al. 1988). Similar variability in the seasonal distribution of phytoplankton biomass maxima have been observed in Galveston Bay (Wilson, unpub. obs.).

The wide temporal range over which maxima in phytoplankton biomass occur could have considerable impact on survival of oyster larvae, which depend on this for food supply. To test this effect, idealized time series, in which the timing of the maximum in food supply was varied, were used to specify environmental food concentrations. These time series include a single maximum in food supply in spring (Fig. 7a), summer (Fig. 7b), and fall (Fig. 7c) as well as maxima in the spring and fall (Fig. 7d). The range chosen for the food values in these time series is based upon that observed for Galveston Bay (Soniat and Ray 1984). The yearly-integrated food supply is the same for all the time series that include a single maximum. The double maxima time series gives a slightly higher (14%) yearly food availability.

As a comparison, a food supply time series was constructed from observations reported in Soniat and Ray (1984) from the western central portion of Galveston Bay (Fig. 7e). This time series shows a maximum in food supply during summer months (May to September). More recent observations (Wilson, unpub. obs.) also show a summer maximum in food supply for this region of Galveston Bay. Malone et al. (1988) suggested that a summer maximum in phytoplankton productivity may be a general characteristic of mid-latitude, partially-stratified estuaries.

RESULTS

Model Verification

Observations on the effect of temperature on total oyster larval developmental time given in Davis and Calabrese (1964) provide an independent check on the simulated larval developmental times. These observations (Fig. 8) are in agreement with developmental times obtained at a specific temperature from laboratory culture experiments for Chesapeake Bay oyster larvae (Dupuy

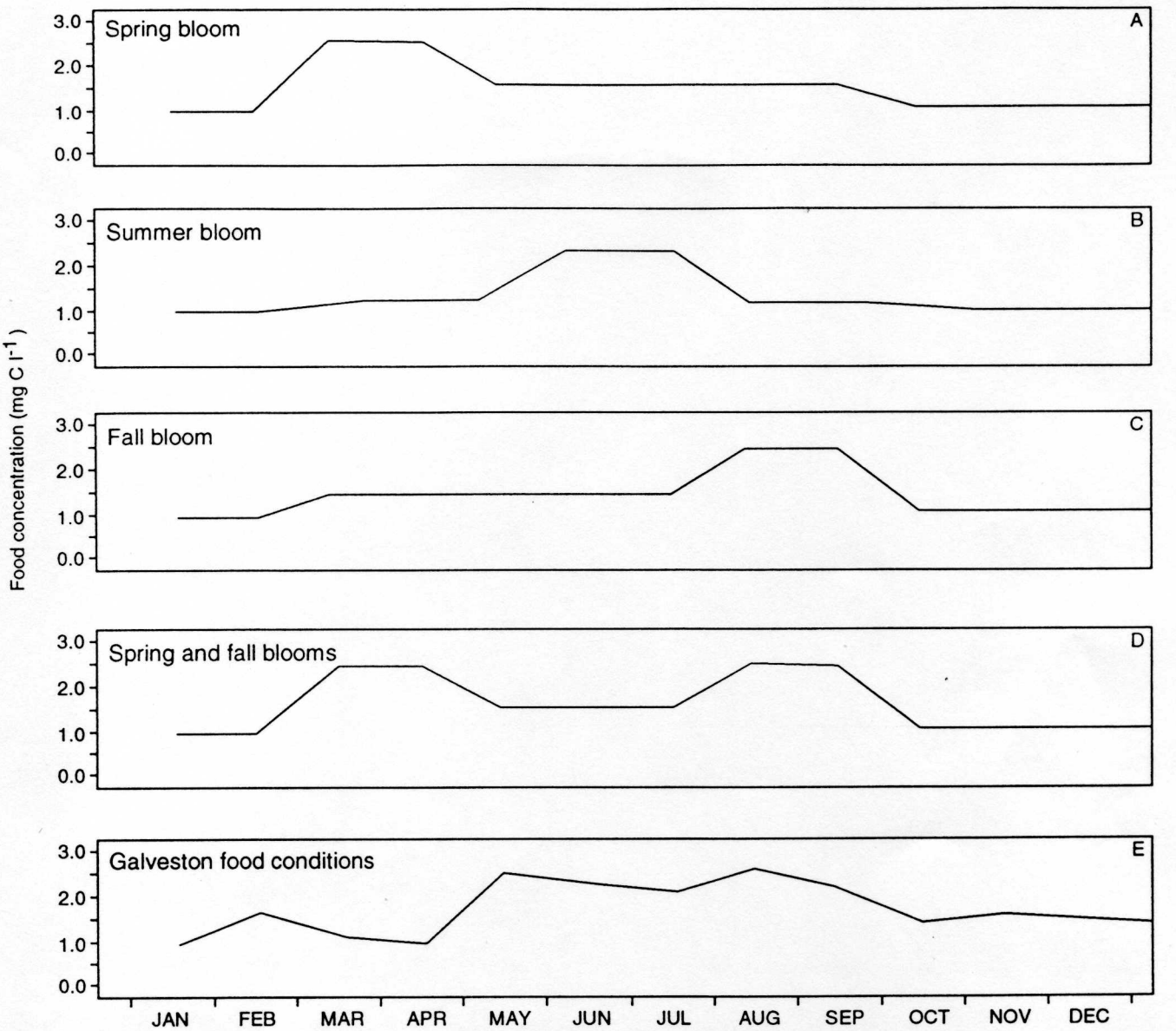

Figure 7. Idealized and measured time series used to specify the ambient food concentration for the larval model in mg C l^{-1}. A: Spring bloom in March-April. B: Summer bloom in June-July. C: Fall bloom in August-September. D: Spring bloom in March-April and fall bloom in August-September. E: Monthly-averaged food concentrations measured for Galveston Bay by Soniat and Ray (1984).

1977). The observed developmental times shown in Figure 8 can be used to obtain a relationship from which total developmental time in days, D, at a specific temperature, T, can be estimated:

$$D = ae^{-\alpha(T-T_i)} \quad (4)$$

The base temperature, T_i, was chosen to be 24°C. The values of the coefficients a and α are 25 days and 0.1099°C^{-1}, respectively. This relationship assumes optimal salinity and food conditions. A comparison of the developmental times estimated from equation (4) and the observed developmental times is given in Figure 8.

Numerous simulations were run with constant and idealized environmental time series to ensure that the larval developmental response was correct. One such simulation used the temperature and salinity (24°C and 26.5 ppt) conditions that correspond to those used in the laboratory experiments from which Figure 1 was generated. Galtsoff (1964) did not report the food concentration used in these experiments; however, given the developmental times, it is unlikely that the larvae were food limited. Therefore, the food concentration in the simulation was held constant at an optimal value of 3 mg C l^{-1} (Fig. 2). For these environmental conditions, the total simulated developmental time was 25 days. The total time obtained from equation (4) is 25 days.

The importance of food supply for the growth and development of oyster larvae is emphasized when comparing simulations using the previous temperature and salinity conditions (24°C and 26.5 ppt) for a range of food concentrations. The larval developmental time extends to 37 days for food concentrations of 2 mg C l^{-1}. Doubling the food concentration to 4 mg C l^{-1}, gives a larval period of 23 days, which is a 38% reduction over the previous.

The larval developmental curve obtained from the simulation using a food concentration of 2 mg C l^{-1} (Fig. 9a) is similar to the measured developmental curve (Fig. 1). Larval growth rate is rapid through the first 20% of development (after first feeding), which corresponds to a time of rapid increase in length. Larval

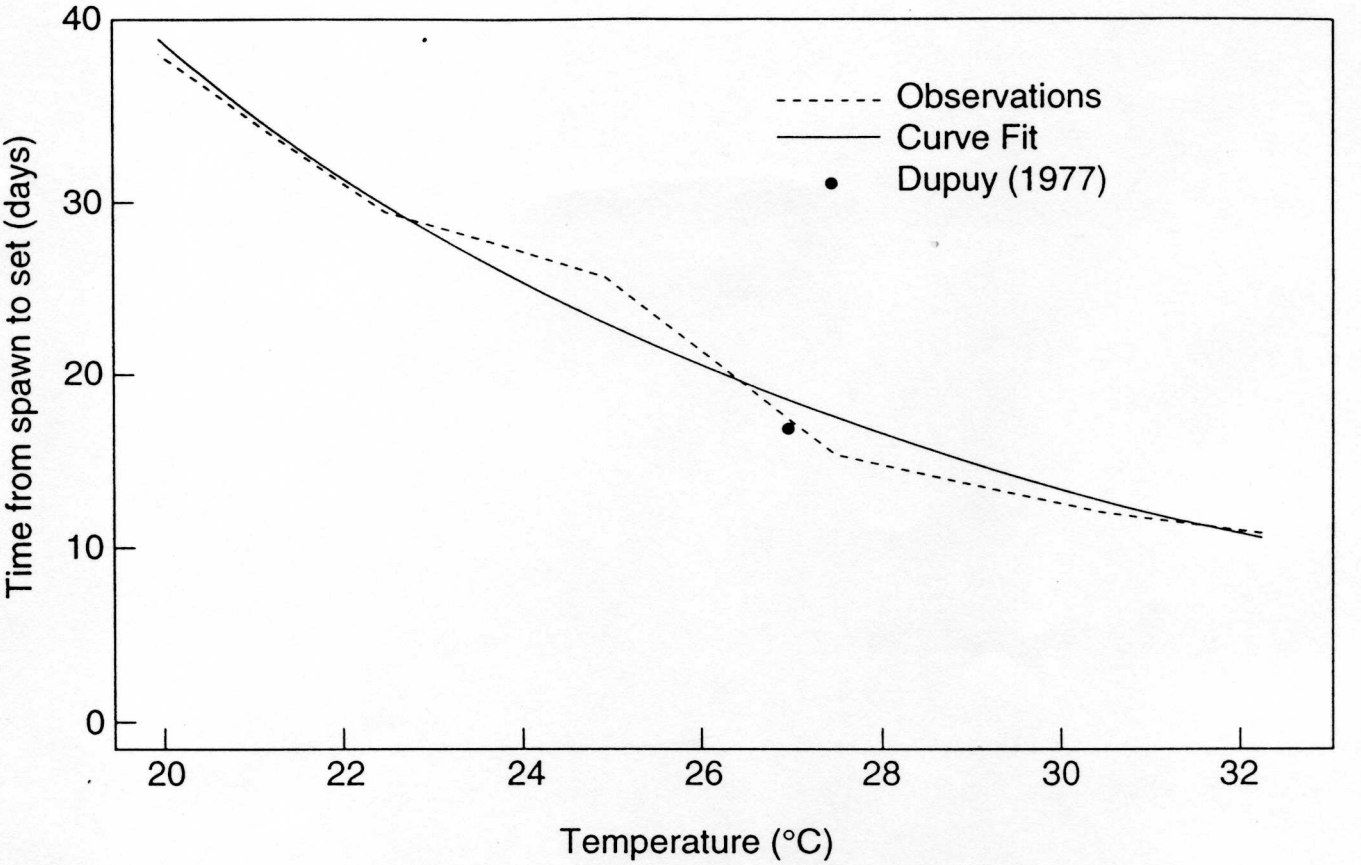

Figure 8. The effect of temperature on total development time of oyster larvae. The dashed line represents data from Davis and Calabrese (1964). The solid line represents the curve fit to these data using equation (4). The filled circle represents larval development time measured by Dupuy (1977).

growth rate decreased markedly between 138 and 172 μm and continued to decrease until the larvae metamorphosed at 330 μm.

The pattern of larval growth rate and increase in size is similar when temperature, salinity and food concentrations (26°C, 19 ppt, 2.5 mg C l^{-1}) measured in Galveston Bay, Texas in August are input into the model (Fig. 9b). Overall, the characteristics of the simulated larval development correspond to developmental curves derived from laboratory measurements. The primary difference is that larval growth rate is higher, which results from higher temperatures in Galveston Bay. These comparisons show that the model given by equation (1) adequately describes oyster larval growth and development. Therefore, the model was used to test hypotheses concerning the effects of temperature, food availability, low salinity events and turbidity on oyster larval development. The results of these simulations are given in the following sections.

Temperature

The first series of simulations considered temperature effects on oyster larval development. The other environmental conditions were assumed to be optimal; a constant salinity of 24 ppt, food concentrations that include a spring bloom (Fig. 7a) and zero turbidity. The monthly-averaged temperature time series from the five bays (Fig. 5) were used to specify ambient temperature conditions, which allows the comparison of temperature effects on larval development across a latitudinal gradient as well as seasonal effects within specific bays. The simulations were initialized by introducing larvae on the last day in March and every 10 days thereafter. Simulations were ended when the larvae either attained, or failed to attain, the size of 330 μm at which metamorphosis occurs.

The time from spawn to metamorphosis (Fig. 10) shows differences within individual bays as well as between bays. The largest range in total planktonic time occurs in Chesapeake Bay. Larval planktonic time decreases with decreasing latitude (Table 3). In the summer months, the larval planktonic times in different bays are similar, varying only from 14 to 20 days. The three southernmost bays show similar trends in planktonic life span even into the fall, with Laguna Madre consistently having larvae with the shortest planktonic life span. However, the fall planktonic life spans increase dramatically from Laguna Madre to Chesapeake Bay. The practical result of this trend is that the last settlement occurs progressively later in the fall from north to south. The simulated spawning seasons for each bay are in agreement with spawning seasons defined from field studies (Table 3).

Food Availability

In Galveston Bay, Texas, water temperatures begin to increase in March and reach 20°C in April (Fig. 5; Table 2). A spring bloom in March-April may coincide with this warming. The larval development, occurring in response to these temperature and food conditions and a constant salinity of 24 ppt, results in the planktonic times shown in Figure 11a. The minimum time from spawn to set is 44 days in early April, when increased food is available

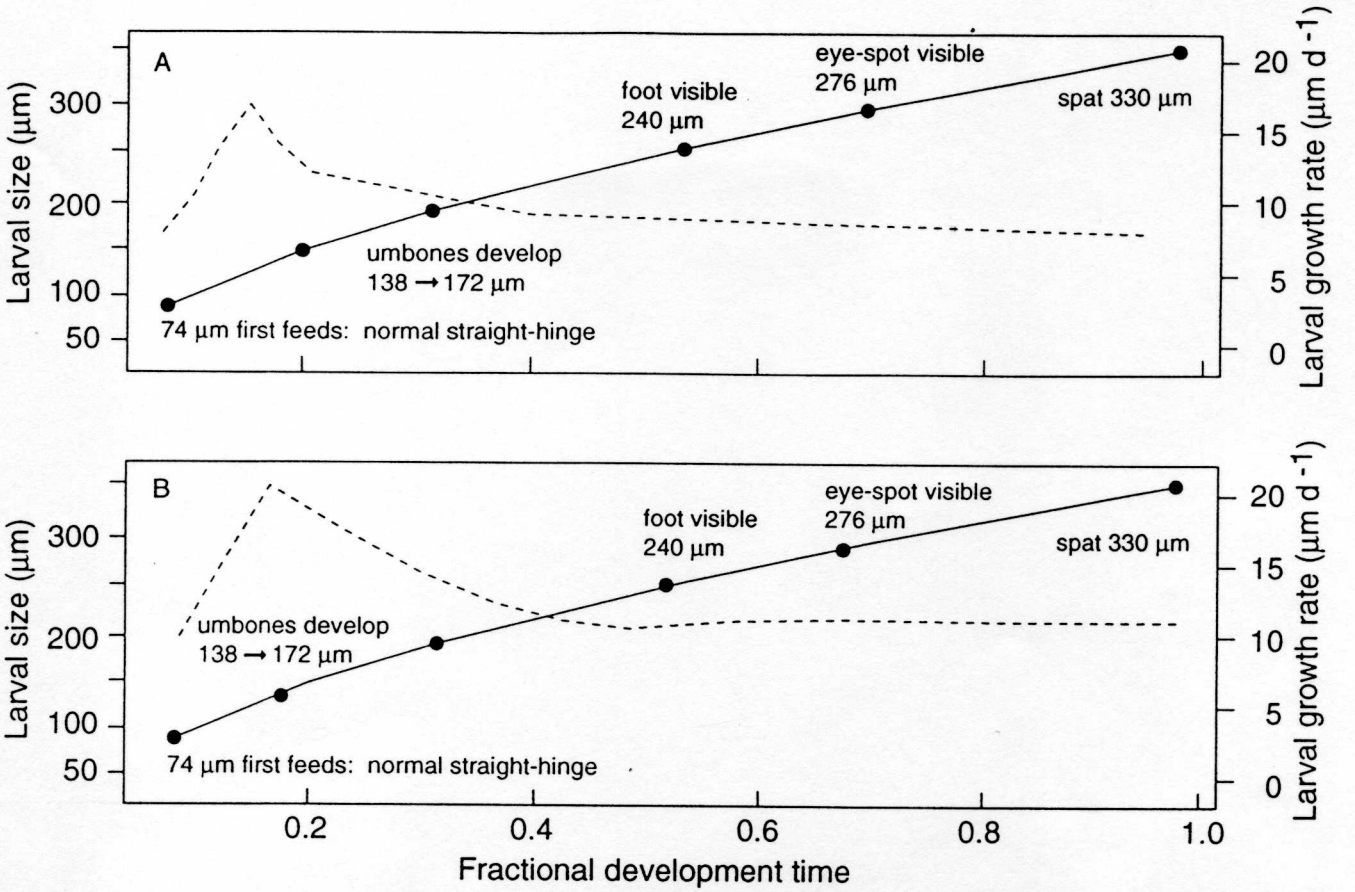

Figure 9. A: Simulated development (solid line) and growth rate (dashed line) for larvae exposed to environmental conditions of; 24°C, 26.5 ppt, 2 mg C l^{-1} food, and zero turbidity. B: Simulated development (solid line) and growth rate (dashed line) for larvae exposed to temperature, salinity and food conditions typical of Galveston Bay, Texas, and zero turbidity.

(Table 4). Later in April and May, planktonic time increases, then decreases into the summer months, and increases again in the fall. The shorter times initially are the result of increased food, which enhances larval growth rate. Throughout the remainder of the year developmental time is controlled primarily by temperature in this simulation.

Moving the spring bloom to April and May, so that it occurs after the spring increase in temperature, results in significantly decreased planktonic times relative to the earlier bloom. Once the increased food is no longer available, larval development and planktonic time are once again primarily temperature controlled.

Imposing a bloom, in June and July, when temperatures average 24 to 25°C, results in planktonic times of 28 days (Table 4). An early to mid-summer maximum in food supply results in long planktonic times in the spring and fall and reduced times in the mid to late summer (Fig. 11b). Similar patterns in larval planktonic time are obtained with the Soniat and Ray (1984) food time series.

A planktonic bloom in August-September coincides with the time when temperatures in Galveston Bay are still elevated. The combination of warm temperatures and enhanced food availability result in 25 day planktonic periods (Table 4). As the food availability decreases and the waters cool into the fall months, larval development slows and planktonic times are longer (Fig. 11c). The occurrence of a bloom in September-October extends the period of minimum planktonic time further into the fall, offsetting the decrease in temperature (Fig. 11c). The enhanced food concentrations produce increased larval growth rates into the fall similar to the introduction of a bloom in August-September.

A year in which spring and fall blooms coincide with the spring and fall temperature increases results in planktonic times shown in Figure 11d. In this case, the impact of the spring bloom is minimal because of cooler water temperatures. Increased food availability coupled with higher fall temperatures results in a dramatically shorter planktonic period of 25 days in August and September as compared to the 44 day planktonic period in the spring (Table 4).

As a comparison, the monthly-averaged Chesapeake Bay temperatures (Fig. 5) were used with the six idealized food time series to obtain larval planktonic times for a more northern bay. Salinity was held constant at 24 ppt and turbidity was zero. The results of these simulations (Table 4) show that shifting the spring bloom has little effect on reducing planktonic times in Chesapeake Bay because of the cooler spring temperatures that characterize this bay. A bloom in June and July in Chesapeake Bay results in the shortest planktonic period of 27 days. While a bloom during the same time frame in Galveston Bay does result in an abbreviated planktonic period, the shortest larval planktonic periods occur in Galveston Bay in August when the bay temperatures exceed the June and July values.

Blooms that occur early in the fall, after warming occurs, have more of an effect on reducing larval planktonic times than the

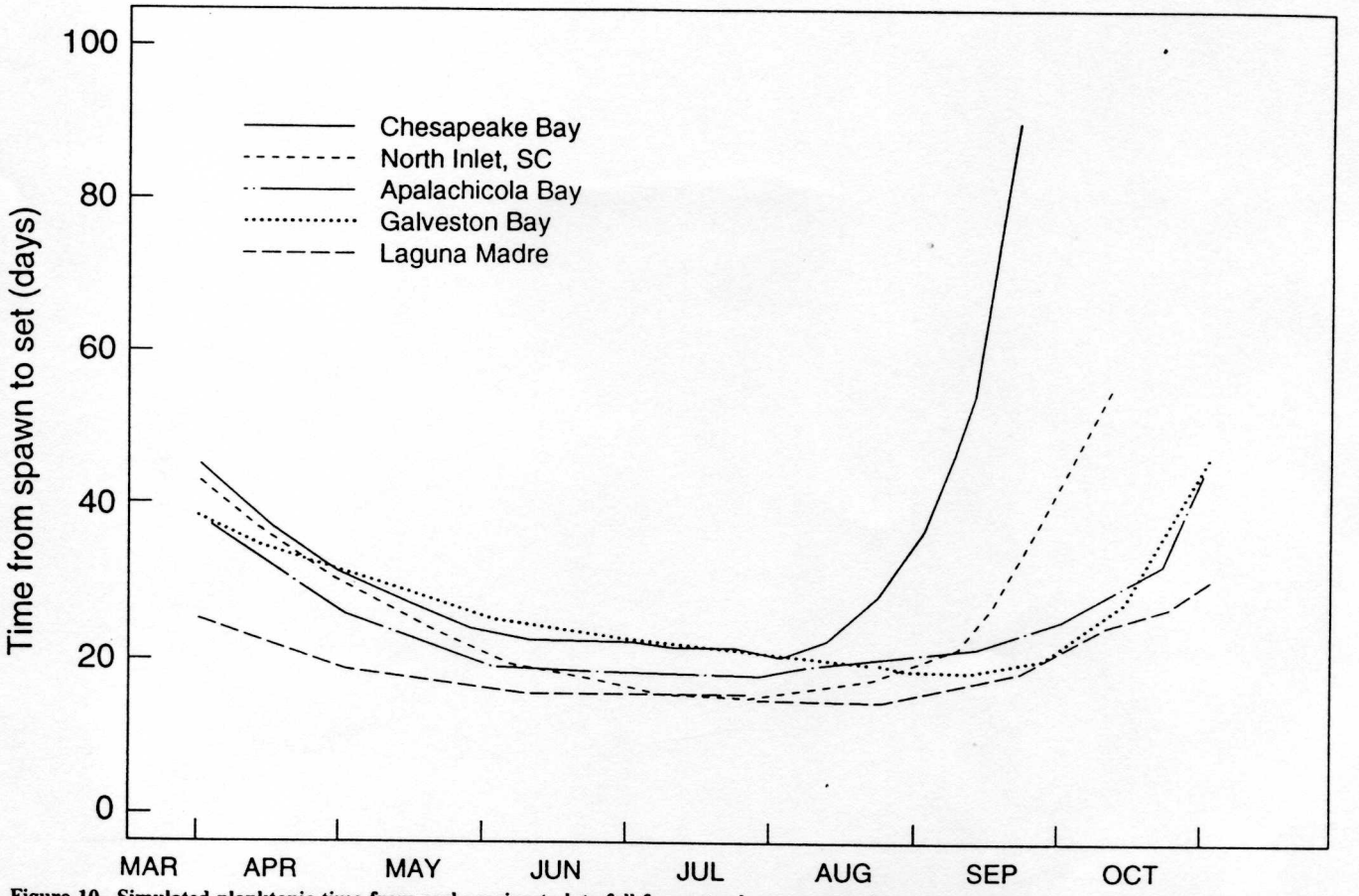

Figure 10. Simulated planktonic time from early spring to late fall for oyster larvae exposed to temperature time series for the five indicated bays.

spring blooms. Consistently, the maximum larval period in the Chesapeake Bay is April to May, irrespective of the timing of the maximum food availability. Galveston Bay by contrast tends to have maximum larval planktonic times in the fall. This difference arises from the delay in spring warming in Chesapeake Bay relative to Galveston Bay. However, the average larval planktonic time in Chesapeake Bay is somewhat shorter than that for Galveston Bay. The earlier fall cooling in Chesapeake Bay (Fig. 5) shortens the period during which fall settlement can occur. Hence, the longer planktonic times that can occur in Galveston Bay in the fall are not possible in Chesapeake Bay. Therefore, the planktonic time in Chesapeake Bay averaged over a spawning season tends to be slightly shorter.

Galveston Bay Food, Salinity and Turbidity Conditions

The simulated larval planktonic times obtained using temperature, food and salinity conditions from Galveston Bay, Texas (Fig. 12a), show extended larval planktonic periods in the spring and fall, with abbreviated larval periods during the summer months (Table 5). More rapid growth, resulting in a shorter planktonic period, is observed in the summer months when temperatures are higher and food availability is greatest.

TABLE 3.

Summary of temperature effects on larval developmental times from five bays. The duration (days) and month during which minimum and maximum larval planktonic times occur in each bay are shown. Also shown are the average larval planktonic times (days) and the time span (months) from first set to the last viable fall set.

Bay	Minimum Larval Period (days: month)	Maximum Larval Period (days: month)	Average Larval Period (days)	First to Last Set (months)
Chesapeake Bay	20: Aug	89: Sept	32.2	July to early October[1]
North Inlet	15: July	55: Oct	25.7	May to October[2]
Apalachicola Bay	18: June–Aug	46: Nov	24.2	April to November[3]
Galveston Bay	18: Sept	46: Nov	25.9	April to November[3]
Laguna Madre	14: Aug	30: Nov	18.5	April to November[3]

[1] Andrews 1954, [2]Lunz 1954, [3]Hopkins 1955

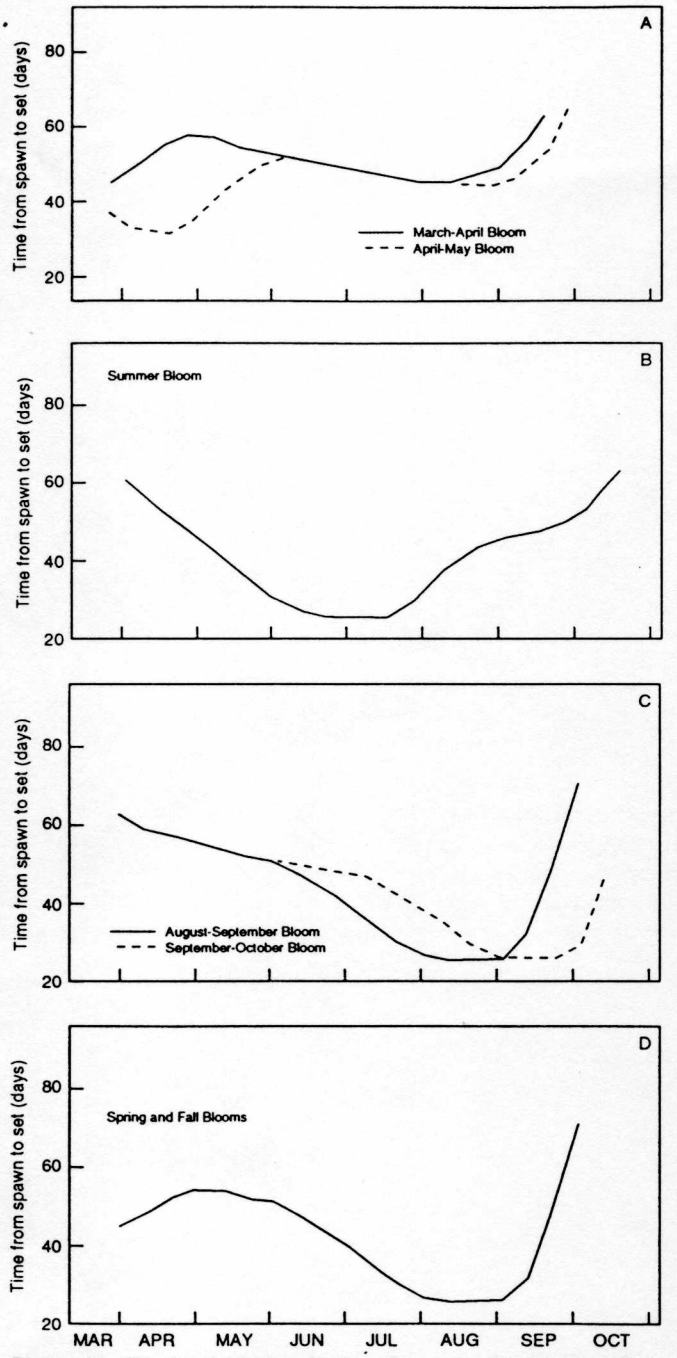

Figure 11. Simulated planktonic time for oyster larvae exposed to food conditions in which the maximum food supply occurred in; A: March-April and April-May blooms. B: June-July. C: August-September and September-October blooms. D: March-April and August-September blooms.

Imposing a simulated low salinity event (Fig. 6a), in August (Fig. 12a) significantly alters the amount of time the larvae are in the water column. Reducing the salinity in August from 19 ppt to 5 ppt, and back to normal levels, decreases the larval growth rate and correspondingly increases planktonic time from 25 days (at 19 ppt) to a maximum of 38 days during the low salinity event.

Imposing a simulated low salinity event in April (Fig. 12a) also extends the time the larvae are in the water column. However, normal April salinities are 12 ppt, and planktonic times produced by this salinity are on the order of 52 days. A spring low salinity event only increases the April planktonic period by about 4 days, as compared to the extension of the larval period by 13 days that occurs during the low salinity event in August.

Similarly, a small change in simulated larval planktonic period is observed when turbidity values characteristic of Galveston Bay are included (Fig. 12b; Table 5). However, the effect of turbidity in this case *increases* the larval growth rate, thereby decreasing the amount of time the larvae are in the water column. The turbidity levels from Galveston Bay (Soniat and Ray 1984) are all below 0.1 g dry wt l^{-1} and these low sediment concentrations enhance larval growth rates by a small factor (Fig. 4). While the larval planktonic period is abbreviated by the Galveston turbidity levels, it is only decreased by a maximum of 4 days in the late fall. The turbidity values used in these simulations are relatively low. With increases in turbidity levels an extension of the larval planktonic period can be expected.

DISCUSSION

Temperature Effect

Oyster larvae can tolerate a wide range of temperatures. However, variability within this range can have a major effect on larval physiology. The major trend observed in the temperature simulations, the warmer the temperatures (below lethal temperature) the shorter the larval time span, is a trend already well documented for oyster larvae (Davis and Calabrese 1964, Dupuy et al. 1977).

However, the simulations of planktonic time span show that the implication of this is that the average larval life span, the minimum, and particularly the maximum larval time periods decline in length with decreasing latitude. The major difference in larval planktonic time between the bays used in this study occurs in the fall. Of the five simulated bays Chesapeake Bay cools earliest in the fall, therefore this bay has the shortest time window within which a viable fall set can occur each season. In a bay like Laguna Madre, where temperatures are elevated late into the fall, a potential remains for a viable set as late as the first week of November.

This effect of the temperature on larval life span across a latitudinal gradient has been documented in field studies. The first spawning of oysters in Long Island Sound and Milford Harbor, Connecticut was observed to occur in the first week of July (Loosanoff and Engle 1940). By the middle of July, oysters in these areas in shallow and moderately deep sites were half or more than half spawned. The majority of the oysters completed spawning early in August; however, oysters at deep-water sites continued to spawn until early September. In contrast, *Crassostrea virginica* populations in the southern regions of the Gulf Coast have been observed to spawn in April or earlier, with setting occurring from April through November (Hopkins 1955). Thus, for Milford Harbor oyster larvae, a three month time window exists within which a viable set may occur; whereas, this time frame is extended to eight months along the Gulf Coast. This provides oysters five additional months within which successful recruitment to the adult population is possible.

Timing of Food Availability

The Galveston Bay and Chesapeake Bay simulations that include the effects of food concentration show that this environmental variable can have an important effect on oyster larval growth

TABLE 4.

Summary of the effect of food availability on larval periods in Galveston Bay (GB) and Chesapeake Bay (CB). The duration (days) and month of the minimum and maximum larval planktonic times are shown for each bay. Also shown are the average larval planktonic times (days) for each bay. The Galveston Bay simulation results that were obtained using the food supply time series given in Soniat and Ray (1984) are denoted by S&R.

Bloom Condition	Min. Larval Period		Max. Larval Period		Av. Larval Period	
	GB	CB	GB	CB	GB	CB
March–April	44: April	39: July	60: Sept	59: April–May	48.6	43.9
April–May	34: April	34: May	63: Oct	49: May	44.6	39.9
June–July	28: June–July	27: June	60: April	66: April	42.3	39.8
S&R	25: August	—	54: Oct	—	34.2	—
Aug–Sept	25: Aug–Sept	27: Aug	69: Oct	64: April–May	43.4	40.1
Sept–Oct	25: Sept–Oct	34: Aug	62: April	64: May	43.1	42.5
Spring and Fall Bloom	25: Aug–Sept	27: July	69: Oct	59: April	41.5	39.3

rate and hence planktonic time span. Increased food concentrations in spring months before water temperatures increase have little effect on larval planktonic time. However, if increased food occurs with or following the spring warming, planktonic time is reduced. The effect of both summer and fall blooms in both bays is to increase growth rates and thus decrease planktonic time. This effect occurs independent of the timing of the bloom because of the warmer temperatures that are found at these times of the year.

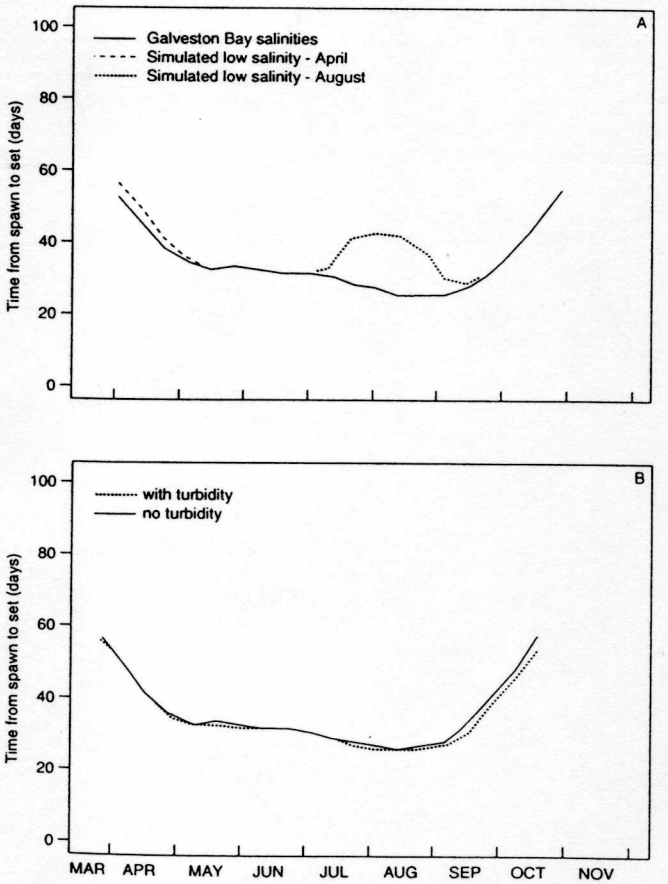

Figure 12. A: Simulated planktonic times produced by Galveston Bay conditions and idealized low salinity events imposed in April and August. B: Simulated planktonic times for Galveston Bay conditions with (dashed line) and without (solid line) the effects of turbidity.

Moreover, unlike the spring bloom case, the positive effect of a late fall bloom on shortening larval life span overrides the lengthening effect of the initial decrease in fall temperature. Dramatically shorter larval time spans are the result.

Overall then, increased food concentration in the fall has a larger effect on larval growth rate than does increased concentrations in the spring or summer in Galveston Bay. The effect of increased food in the spring, summer or fall is to reduce larval planktonic times for the period surrounding the bloom. This latter point is of particular importance because increased spawning by the adult oyster populations occurs in response to increased food concentrations (Hofmann et al. 1992). Preparation for spawning by the adult oysters takes several weeks to two months depending on temperature and food supply (Hofmann et al. 1992, Choi et al. 1989). Thus, larvae will likely appear in the water column in the later stages of a bloom. Hence, the period of co-occurrence of adequate food and optimal temperatures could be shorter for the oyster larvae than for the adult population. Certain spawns may be doomed to failure by dropping temperatures that dramatically extend larval time spans and, consequently, decrease larval survivorship. Spawns later in the spring, in the summer months, or early in the fall that coincide with increased food conditions will result in the shortest planktonic time, thereby increasing survivorship to settlement by limiting loses to predation or advection from the system.

Other Environmental Factors

Salinity concentration and distribution in estuarine environments arises from the combination of tidal effects, freshwater run-

TABLE 5.

Summary of minimum and maximum larval planktonic times (days) and month of occurrence for the simulations that used Galveston Bay environmental conditions.

	Minimum Larval Period (days: month)	Maximum Larval Period (days: month)	Average Larval Period (days)
Galv temp, salin, food	25: Aug	54: Oct	35.9
Low salinity, April	25: Aug	56: April	36.5
Low salinity, August	28: Sept	54: Oct	37.4
Turbidity	25: Aug	55: April	34.1

off and river inputs. As a result, the salinity environment encountered by oyster larvae can vary considerably over short (e.g., tidal) or long (e.g., seasonal) time scales. One feature of estuarine environments is that they experience extended periods of low salinity water that result from increased freshwater inputs. Episodes of low salinity are considered to be beneficial to adult oyster populations because they result in lower disease prevalence and decreased predator densities (Ray 1987). On the basis of simulation results, Hofmann et al. (1992) observed that a decrease in salinity (as long as salinities remain above 5 ppt) has considerably less effect on adult oyster populations than does a small change in temperature or food concentration. However, the larval simulations indicate that extended periods of low salinity have a pronounced effect on larval growth rate. Larval growth is slowed, under prolonged conditions of low salinity, thus extending the time required for development to settlement size.

These modeling results are indirectly supported by field observations. Abbe (1988) observed that higher oyster larval recruitment in the central Chesapeake Bay was related to periods of sustained salinity higher than 16 ppt. In general, the fair recruitment events observed between 1976 and 1979 coincided with high salinity conditions; whereas, poor recruitment years were characterized by low salinity. Above average recruitment in the central Chesapeake Bay in 1980–1982 and 1985 also coincided with periods of high salinity.

Furthermore, Ulanowicz et al. (1980) used forty years of observations of fishing effort, spat production, salinity, water and air temperatures and precipitation to construct a multivariate model for production of annual harvest of oysters in the central Chesapeake Bay. This analysis showed that sustained high salinity was a dominant factor affecting spat production, with spat production increasing with increasing salinity. Hence, the frequency and spatial distribution of low salinity water may be a factor in determining settlement patterns of oyster larvae.

The final environmental variable considered in this modeling study was turbidity. Larvae of *Crassostrea virginica* are exposed to the varying turbidity levels that characterize estuarine environments. For the Galveston Bay conditions used in this study, turbidity concentrations were below those that adversely effect larval growth rate. In fact, the low levels provide an enhancement of growth rate which shortens larval planktonic time. However, sustained periods of high turbidity can reduce larval growth rates. In contrast to salinity, where larvae were more sensitive than the adults, turbidity exerts a lesser impact on larvae than it does on the adult populations where filtration efficiency is adversely affected (Hofmann et al. 1992). However, if increased turbidity levels were to coincide with other environmental conditions that slow larval growth rate (e.g., reduced food, cold temperatures, low salinity) then turbidity could be a factor determining the survivorship of oyster larvae.

SUMMARY

The simulations that consider only temperature effects on the growth and development of larvae of *Crassostrea virginica* provide a range of minimum and maximum planktonic times for specific bays across a latitudinal gradient. The implication of these results is that the period during which bivalve larvae are available for recruitment to adult populations decreases with increasing latitude. The addition of food concentration shows the importance of this environmental variable in regulating larval growth and development. As was found for adult oyster populations (Hofmann et al. 1992) the timing of food availability relative to water temperature is important in determining larval planktonic time and hence the survivability of larvae. The addition of the effects of salinity and turbidity also modify the time required for oyster larvae to reach settlement size.

Throughout development and over a spawning season larvae of *Crassostrea virginica* are exposed to varying conditions of temperature, food concentration, salinity and turbidity. It is the cumulative effect of all these environmental variables that determines larval survivorship. Therefore, management strategies for an oyster fishery must be broad enough to include habitat effects on larval survivorship, which ultimately determines recruitment to the adult population.

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