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Modeling Oyster Populations. IV. Rates of Mortality, Population Crashes, and Management

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Modeling oyster populations. IV: Rates of mortality, population crashes, and management*

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Abstract.—A time-dependent energy-flow model was used to examine how mortality affects oyster populations over the latitudinal gradient from Galveston Bay, Texas, to Chesapeake Bay, Virginia. Simulations using different mortality rates showed that mortality is required for market-site oysters to be a component of the population's size-frequency distribution; otherwise a population of stunted individuals results. As mortality extends into the juvenile sizes, the population's size frequency shifts toward the larger sizes. In many cases adults increase despite a decrease in overall population abundance. Simulations, in which the timing of mortality varied, showed that oyster populations are more susceptible to population declines when mortality is restricted to the summer months. Much higher rates of winter mortality can be sustained. Comparison of simulations of Galveston Bay and Chesapeake Bay showed that oyster populations are more susceptible to intense population declines at higher latitudes. The association of population declines with disease agents causing summer mortality and the increased frequency of long-term declines at high latitudes result from the basic physiology of the oyster and its population dynamics cycle. Accordingly, management decisions on size limits, seasons and densities triggering early closure must differ across the latitudinal gradient and in populations experiencing different degrees of summer and winter mortality relative to their recruitment rate. More flexible size limits might be an important management tool. When fishing is the primary cause of mortality, populations should be managed more conservatively in the summer. The latitudinal gradient in resistance to mortality requires more conservative management at higher latitudes and different management philosophies from those used in the Gulf of Mexico.

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One of the unfortunate characteristics of oyster *Crassostrea virginica* populations is their susceptibility to periods of heavy mortality, which can extend from a few months to a few years in duration. Oyster population abundances drop precipitously during these times and may remain low for extended periods (Schlesselman, 1955; Engle, 1956; Laird, 1961; Engle and Rosenfield, 1962). Why populations decline over several years or crash over shorter periods of time can usually be explained by killing floods (Andrews et al., 1959; Soniat and Brody, 1988; Soniat et al., 1989) or disease epizootics (Needler and Logie, 1947; Andrews and Hewatt, 1957; Mackin and Hopkins, 1962) although predators and overfishing have occasionally received some credit (Moore and Pope, 1910; Menzel et al., 1957; Quast et al., 1988).

A review of the literature shows that declines and crashes in oyster populations have some interesting characteristics (Mackin and Wray, 1950; Mackin et al., 1950; Menzel, 1950, a and b; Menzel and Hopkins, 1953; Owen, 1953; Gunter, 1955; Mackin and Sparks, 1962; Hofstetter et al., 1965; Copeland and Hoese, 1966; Hofstetter, 1966; Gilmore et al., 1975; and previously cited references):

1 With the exception of killing floods, the times of the year with the most intense mortality are usually restricted to the summer and early fall and to areas of higher salinity. Warm temperatures and high salinities promote the growth of the disease-producing organisms *Perkinsus marinus* and *Haplosporidium nelsoni* (Ray and Chandler, 1955; Andrews and Hewatt, 1957) and predation by such pests as the oyster drill, *Thais haemastoma* (Garton and Stickle, 1980; Stickle, 1985).
2 Population crashes or significant declines have been documented throughout the oyster's latitudinal range. However, except for permanent changes in salinity,

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owing to levee building for instance (Mackin and Hopkins, 1962), population recovery rates appear to be more rapid at lower latitudes (compare Owen, 1953; Hofstetter, 1983; Stanley and Sellers, 1986; Mackenzie, 1989).

3 Major population crashes resulting in long-term loss or decline of the *C. virginica* fishery have occurred almost exclusively along the northeast coast of North America. Moreover, significant population declines occurred earlier in the century at higher latitudes (viz. Canada, 1910s, Mid-Atlantic area, 1950s; Delaware and Chesapeake Bays, 1980s) (Stanley and Sellers, 1986; Mountford and Reynolds, 1988; Mackenzie, 1989; and others referenced previously), although more than one significant population has declined in some areas.

These trends in oyster population dynamics gleaned from the literature are not well documented. Much literature is anecdotal and significant exceptions do exist. Nevertheless, taken as a whole, these trends suggest two hypotheses: 1) a latitudinal gradient in susceptibility to population crashes exists in oyster populations; and 2) as temperature varies both latitudinally and seasonally, temperature, through its effect on oyster physiology (e.g. Koehn and Bayne, 1989), may determine the susceptibility of oyster populations to potentially destabilizing episodes of mortality.

In this study, we tested these hypotheses using a population dynamics model. The results of the modeling exercise were then used to examine some basic decisions required for fishery management; viz. the timing and length of the fishing seasons and the size limits set for the fishery to obtain a maximum sustainable yield (e.g. Glude, 1966; Hofstetter and Ray, 1988; Young and Martin, 1989).

The model

Perspective and basic characteristics

The oyster population model shown in Figure 1 is designed to investigate the dynamics of the post-settlement phase of the American eastern oyster's, *Crassostrea virginica*, life from newly settled juvenile through adulthood. The model consists of a system of ten coupled ordinary differential equations, with each equation representing a size class of oyster; however, the ten size classes are not evenly divided across the length or biomass spectrum (Table 1). Size class 1 includes newly settled juveniles (Dupuy et al., 1977). Size class 10 corresponds to oysters that are larger than those normally found in natural populations. The boundaries between size classes 4 and 5, 5 and 6, and 6 and 7 represent size limits that have been used or considered for market-size oysters: 2.5 in; 3.0 in and 3.5 in, respectively. We define adults, individuals capable of spawning, as individuals weighing more than 0.65 g ash-free dry weight, about 50 mm in length (Hayes and Menzel, 1981). Therefore, size classes 1 to 3 are juveniles.

Table 1

Biomass and length dimensions of the oyster *Crassostrea virginica* size classes used in the model. Biomass is converted to size using the relationship given in White et al. (1988).

Model Size class	Biomass (g ash-free dry wt)	Length (mm)
1	1.3×10^{-7} – 0.028	0.3 – 25.0
2	0.028 – 0.10	25.0 – 35.0
3	0.10 – 0.39	35.0 – 50.0
4	0.39 – 0.98	50.0 – 63.5
5	0.98 – 1.94	63.5 – 76.0
6	1.95 – 3.53	76.0 – 88.9
7	3.53 – 5.52	88.9 – 100.0
8	5.52 – 7.95	100.0 – 110.0
9	7.95 – 12.93	110.0 – 125.0
10	12.93 – 25.91	125.0 – 150.0

All calculations were done in terms of energy in $cal \cdot m^{-2}$. When necessary, oyster energy is converted to oyster biomass by using a caloric conversion of 6100 $cal \cdot g\ dry\ wt^{-1}$ for oysters (Cummins and Wuycheck, 1971) and biomass to an approximate length by using White et al.'s (1988) biomass-length conversion. To calculate any gain, loss, or transfer of energy (or biomass) between size classes, an additional conversion was made to express the gain, loss or transfer in terms of a specific rate (day^{-1}) which was then multiplied by the caloric quantity in a size class. Transfers between size classes were scaled by the ratio of the average weight of the current size class (in g dry wt or cal) to that of the size class from which energy was gained or to which energy was lost. This ensured that the total number of individuals in the model was conserved, in the absence of recruitment and mortality. Because, the size classes in the model are not equivalent in dimension, each specific rate for each transfer between size classes was scaled by the ratio between the two size classes:

$$\text{for transfers up:} \quad W_j/(W_{j+1}-W_j)$$
$$\text{for transfers down:} \quad W_j/(W_j-W_{j-1}),$$

where W is the median biomass (in g dry wt) in size class j. For simplicity, we will not include any of these conversions and scaling factors in the equations given subsequently.

Governing equation

The change in oyster standing stock with time in each size class (O_j) is the result of changes in net production (NP_j), taken to be the sum of the production of somatic (P_{gj}) and reproductive (P_{rj}) tissue, and the addition of individuals from the previous size class or loss to the next largest size class by growth. Following White et al. (1988), net productivity is assumed to be the difference between assimilation (A_j) and respiration (R_j),

$$NP_j = P_{gj} + P_{rj} = A_j - R_j. \quad (1)$$

Accordingly,

$$\frac{dO_j}{dt} = P_{gj} + P_{rj} + (\text{gain from } j-1) - (\text{loss to } j+1) \quad (2)$$

for j = 1,10 recognizing P_{rj} = 0 for j = 1,3.

Resorption of either gonadal or somatic tissue results in loss of biomass. When NP_j<0, oysters lose biomass and transfer into the next lower size class. This is an important difference between our size class model and a size class model based on linear dimensions; shell size does not change, however biomass does during periods of negative scope for growth. This is the basis for the use of condition index as a measure of health in oysters (e.g. Newell, 1985; Wright and Hetzel, 1985). To allow for this, equation 2 must be modified as

$$\frac{dO_j}{dt} = P_{gj} + P_{rj} + (\text{gain from } j-1) - (\text{loss to } j+1) + (\text{gain from } j+1) - (\text{loss to } j-1) \quad (3)$$

for j = 1,10. The last two terms on the right side of Equation 3 represent the individuals losing biomass and, thus, translating down to the next lower size class.

The relationships used to parameterize the processes in Equation 3 are described in the following sections. More details and a discussion of the assumptions and supporting data for the model were presented by Klinck et al. (1992), Powell et al. (1992) and Hofmann et al. (1992). Accordingly, the basic oyster size class model is outlined only briefly. However, calculations of spawning size and recruitment, mortality, and the effect of oyster density on feeding are specific to this study and are described in more detail.

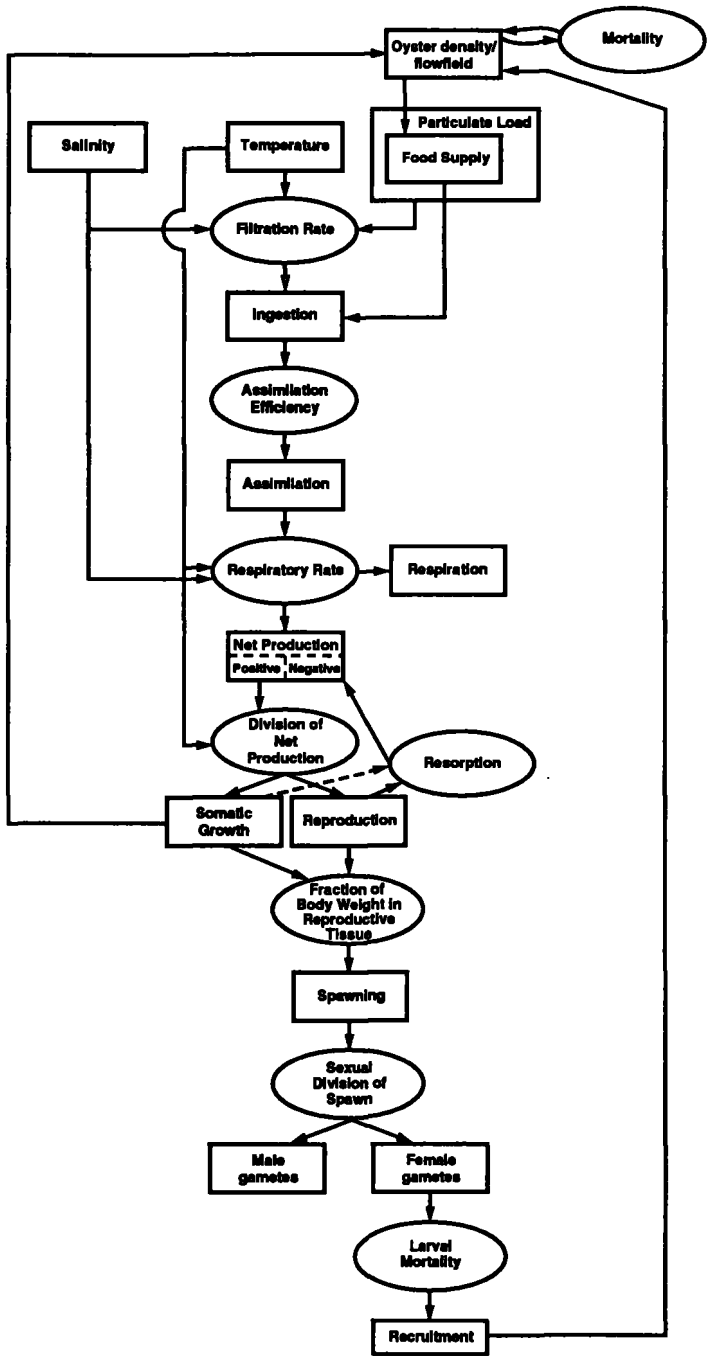


Figure 1
Schematic diagram of the energy flow model.

Feeding and assimilation

Ingestion rate depends upon the filtration rate and the ambient food concentration. We adapted Doering and Oviatt's (1986) equa-

tion for filtration rate to oysters (Powell et al., 1992) to obtain filtration rate as a function of biomass and temperature (T):

$$FR_j = \frac{K_j^{0.96} T^{0.95}}{2.95}, \quad (4)$$

and

$$K_j = W_j^{0.317} 10^{0.669}, \quad (5)$$

where filtration rate (FR_j) is in mL filtered ind^{-1} min^{-1} and W_j is the ash-free dry weight in g for each size class. Equation 4 contains the temperature-dependency described by Loosanoff (1958).

Filtration rate was further modified by salinity as described by Loosanoff (1958). Filtration rate decreases as salinity drops below 7.5‰ and ceases at 3.5‰. In mathematical terms:

$$\begin{array}{ll} \text{at } S \geq 7.5‰ & FR_{sj} = FR_j \\ \text{at } 3.5 < S < 7.5‰ & FR_{sj} = FR_j (S - 3.5)/4.0 \\ \text{at } S \leq 3.5‰ & FR_{sj} = 0. \end{array} \quad (6)$$

where S is ambient salinity and FR_j is the filtration rate obtained from Equation 4.

The reduction in feeding efficiency at high particulate loads was included as a reduction in filtration rate according to Loosanoff and Tommers (1948)

$$\tau = (4.17 \times 10^{-4})\,(10^{0.0418x}), \quad (7)$$

where τ is the total particulate content (inorganic + organic) in g·L^{-1} and x is the percent reduction in filtration rate.

Solving Equation 7 for the percent reduction in filtration rate gives a modified expression for filtration rate of the form:

$$FR_{tj} = FR_{sj}\left[1 - 0.01\left(\frac{\log_{10}\tau + 3.38}{0.0418}\right)\right]. \quad (8)$$

Equation 8, if applied to total particulate content (inorganic + organic), limits ingestion rate to approximately the maximum value found by Epifanio and Ewart (1977). Therefore, an additional term to lower ingestion efficiency at high food concentrations was not used.

The effect of oyster density on food availability was parameterized from measurements given in Lund (1957) as

$$f = \frac{k}{[k/f_o - 1]\,e^{-rd} + 1}, \quad (9)$$

where f is the fractional reduction in food, d is oyster density expressed as L filtered hr^{-1}·m^{-2}, and f_0=0.001, an arbitrarily low number conforming to the expectation that food supply is not affected by low oyster density. For the high flow (59 L hr^{-1}) conditions given in Lund (1957), k = 0.31 and r = 1.36×10^{-6}. For low flow (12 L hr^{-1}) conditions, k = 0.57 and r = 9.746×10^{-7}. Food availability at a given oyster density is estimated as $(1-f)$ times the ambient food concentration. Filtration rate times the ambient available food concentration then gives oyster ingestion. Assimilation is obtained from ingestion using an assimilation efficiency of 0.75 (Powell et al., 1992).

Respiration

Oyster respiration as a function of temperature and oyster weight was obtained from Dame (1972) as

$$R_j = (69.7 + 12.6T) W_j^{b-1}, \quad (10)$$

where R_j is in µL O_2 consumed hr^{-1}·g dry wt^{-1} and b = 0.75.

Salinity effects on oyster respiration were parameterized from data given in Shumway and Koehn (1982) by obtaining a ratio (R_r) of respiration at 10‰ to respiration at 20‰, $R_r = \frac{R_{10‰}}{R_{20‰}}$, and regressing this ratio against temperature. This yielded two equations:

$$\begin{array}{ll} \text{at } T < 20°C & R_r = 0.007T + 2.099; \\ \text{at } T \geq 20°C & R_r = 0.0915T + 1.324; \end{array} \quad (11)$$

which were then used to obtain respiration rate as follows:

$$\begin{array}{ll} S \geq 15‰ & R_{Tj} = R_j; \\ 10‰ < S < 15‰ & R_{Tj} = R_j\left(1 + [(15 - S)(R_r - 1)/5]\right); \\ S \leq 10‰ & R_{Tj} = R_j R_r. \end{array} \quad (12)$$

Shumway and Koehn (1982) identified effects of salinity on respiration at 20‰; however, we used a 15‰ cutoff to conform to Chanley's (1958) observations on oyster growth.

Reproduction

For adult oysters (j=4,10), net production was apportioned into growth and reproduction by using a temperature-dependent reproduction efficiency of the form

$$R_{effj} = 0.054T - 0.729 \quad (13)$$

for January to June and

$$R_{effj} = 0.047T - 0.809 \quad (14)$$

for July to December. Equations 13 and 14 were derived empirically from the field observations of Soniat and Ray (1985) and may not hold north of Delaware Bay (Hofmann et al., in press).

The portion of net productivity going into reproduction is given by

$$P_{rj} = R_{effj} NP_j, \text{ for } j = 4,10. \quad (15)$$

Somatic growth is the remaining fraction. In cases where $NP_j < 0$, we assume preferential resorption of gonadal tissue to cover the debt. For juveniles and adults with no gonadal tissue, resorption of somatic tissue occurs. We assume that reduced reproduction at low salinity (Engle, 1947; Butler, 1949) results from decreased filtration rate and increased respiratory rate and so include no specific relationship for this effect.

Spawning of the oyster population occurs when the total cumulative reproductive biomass of the population exceeds 20% of the total oyster biomass (Choi et al., 1993). This value is lower than the estimates of Galtsoff (1964) and Deslous-Paoli and Heral (1988), but comes from direct measurements of egg content. Once spawning occurs, the total reproductive biomass is apportioned into male and female biomass according to Kennedy (1982)

$$f_{ratio} = 0.021 L_b - 0.62. \quad (16)$$

where f_{ratio} is the ratio of females to males and L_b is shell length in mm obtained from biomass (White et al., 1988). Oysters can change their sex, and Kennedy (1982) suggested that the ratio of males to females is affected by oyster density, salinity, and stress. While perhaps important in some situations, no data exist to parameterize these relationships adequately. They are not included in the model.

The female portion of reproductive biomass (R_f) is converted into eggs spawned by

$$\text{Number of eggs spawned} = R_f \; 1/6133 \; 1/W_{egg} \quad (17)$$

where 6133 is the egg's caloric content (cal g dry wt^{-1}) (Klinck et al., 1992) and W_{egg} is egg weight obtained from

$$W_{egg} = 2.14 \times 10^{-14} V_{egg}, \quad 18$$

where oyster egg volume (V_{egg}) is from Gallager and Mann (1986). The factor 2.14×10^{-14} represents conversions for density, dry wt to wet wt, and μm^3 to cm^3. The egg weight, 13 ng dry wt, calculated from Equation 18 is close to experimentally determined egg weights (Lee and Heffernan, 1991; Choi et al., 1993).

Larval recruitment and mortality

Larval growth rate, which determines the time spent in the plankton, is controlled by ambient food concentration, temperature, salinity, and turbidity. Therefore, larval life span can range from twenty to sixty days (Dekshenieks et al., in press). For the purposes of this modeling study, larval life span was assumed to be twenty days, which may be an underestimate for some environmental conditions, but is in general agreement with observations (Prytherch, 1929; Dupuy et al., 1977; Bahr and Lanier, 1981). We allow an additional 10 days for the larvae to grow to the mean biomass represented by size class one in the post-settlement model. Thus, thirty days after spawning, larvae appear in the simulated post-settlement oyster population as new recruits to the first size class (j=1).

While in the plankton, oyster larvae undergo considerable mortality from a variety of sources. Larval mortality is included in the model by using a simple linear relationship of the form

$$\text{Number of larvae recruited spawn}^{-1} = s(\text{Number of eggs spawned}) \quad (20)$$

where s determines the rate at which individuals are lost per spawn (in spawn^{-1}). No attempt is made to differentiate among sources of oyster larval mortality.

Post-settlement population mortality

Post-settlement oyster populations undergo natural mortality from diseases and predators and man-induced mortality through fishing. Both natural and man-induced mortality vary with season and size of individual. Adult mortality was modeled by using a linear mortality relationship of the form

$$\text{Number dying time}^{-1} = k_d \, (\text{Number living}), \text{ for } j = k,l \quad (21)$$

where k_d determines the daily mortality rate (in day^{-1}) and k and l are the inclusive size classes being affected by mortality. As with larval mortality, this approach does not differentiate among the many sources of oyster mortality. However, the ef-

fect of these mortality sources is implicit in the value chosen for k_d and the size class range used (k,l).

Environmental forcing

Monthly-averaged time series of temperature measured in Galveston Bay (Soniat and Ray, 1985) and Chesapeake Bay (Galtsoff et al., 1947) were used as input to the model (Fig. 2). Each time series is two years in length and each shows temperature trends expected for mid-latitude temperate bays: cool in fall and spring and warm in summer. For a 6-year simulation, the 2-year time series shown in Figure 2 was repeated three times. Salinity values were held constant throughout the year at 24‰ to simplify the discrimination between salinity and temperature effects.

Monthly-averaged values of food concentration were also input into the model (Fig. 2). However, unlike the temperature time series, idealized time series, constructed to illustrate particular types of food availability, were used. This approach was used so that the occurrence and magnitude of features such as the spring and fall phytoplankton blooms could be manipulated (Fig. 2, A and C) or eliminated (Fig. 2B). However, the general characteristics of the idealized food time series are representative of measured values (Soniat et al., 1984; Berg and Newell, 1986). The basic idealized food time series consisted of low winter levels (0.5 mg·L^{-1}), higher summer levels (0.75 mg·L^{-1}) and still higher values for two months in the spring and fall to simulate spring and fall bloom levels (1.25 mg·L^{-1}). A summary of the environmental conditions used for each simulation is given in Table 2.

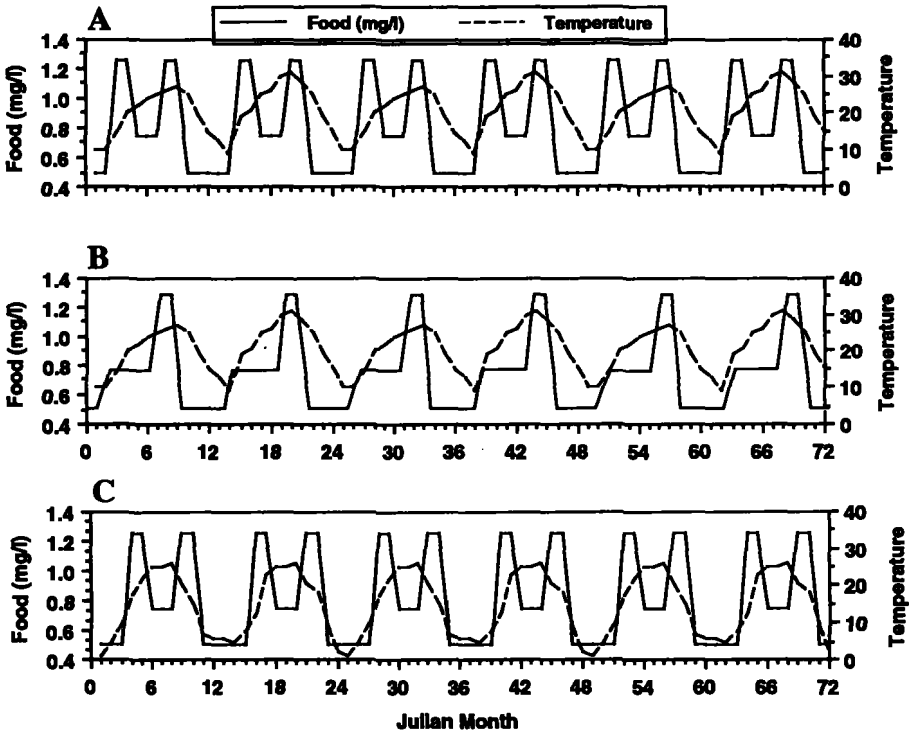


Figure 2

Monthly-averaged time series of temperature and food concentration used as environmental forcing for the oyster population model. (A) Temperatures from Galveston Bay (Soniat and Ray, 1985) and plankton biomass for years having blooms in March–April and August–September. (B) Temperatures from Galveston Bay and plankton biomass for years having one bloom in August-September. (C) Temperatures from Chesapeake Bay with plankton biomass for years having blooms in April-May and September-October. See Table 2 for a description of the food time series used.

Table 2

Summary of environmental and biological conditions used for the oyster *Crassostrea virginica* population simulations. The figure (F) or table (T) displaying the results of each simulation is indicated. All simulations were run using a constant salinity of 24‰, no turbidity, and low flow conditions characteristic of sheltered reefs. An appropriate seasonal time series for temperature was used for Galveston Bay (GB) or Chesapeake Bay (CB) as required (Fig. 2). Three initial densities were used. The numbers per size class for the 10 size classes at these densities are:

low (L):	0	0	0	0	0	0	10	0	0	0
medium (M):	0.1	1.5	5.1	9.2	13.3	5.6	1.4	0.1	0	0
high (H):	490	2240	3637	3217	2502	289	6	0	0	0

A series of standardized food time series was used as depicted in Figure 2. These consisted of 5 winter months at 0.5 $mg \cdot L^{-1}$, 3 or 5 summer months at 0.75 $mg \cdot L^{-1}$ and 2 or 4 bloom months in the spring and/or fall of 1.25 $mg \cdot L^{-1}$. Blooms were of 2-month duration. When two blooms occurred, the two 2-month blooms were separated by 3 summer months. When one 2-month bloom occurred, the bloom was preceded or succeeded by 5 summer months. Table designations are: A/S, August–September bloom; M/A-A/S, March–April and August–September blooms; A/M-S/O, April–May and September–October blooms. Mortality was expressed as a yearly rate: a rate of 99% for instance would have removed 99% of the biomass in one year if no recruitment or growth occurred. For yearly (Y) mortality, this rate was applied for the entire year. For summer (S) mortality, this yearly rate was applied only to the months of April through September. For winter (W) mortality, the yearly rate was applied only to the months of October through March. Recruitment was the fraction of eggs spawned that successfully recruited to the population. In each case, the lowest size class suffering mortality is given (e.g. 5). In every case, all larger size classes also suffered mortality at the same yearly rate: all smaller size classes were unaffected. All simulations began on Julian day 1 (January 1) and were run for 6 years.

Case	Table or figure	Bay	Food time series	Fraction of spawn recruited	Yearly mortality rate	Season of mortality	Size class suffering mortality	Beginning density (day 1)
1	F-3	GB	M/A-A/S	10^{-7}	NA	NA	NA	L
2	F-4,T-2	GB	M/A-A/S	10^{-7}	50%	Y	≥5	H
3	T-2	GB	M/A-A/S	10^{-7}	75%	Y	≥5	H
4	T-2,3,4	GB	M/A-A/S	10^{-7}	90%	Y	≥5	H
5	T-2	GB	M/A-A/S	10^{-7}	99%	Y	≥5	H
6	F-5,T-2,3,4	GB	M/A-A/S	10^{-7}	99.9%	Y	≥5	H
7	T-3	GB	M/A-A/S	10^{-7}	90%	Y	≥3	H
8	F-6	GB	M/A-A/S	10^{-7}	99%	Y	≥3	H
9	F-7,T-3	GB	M/A-A/S	10^{-7}	99.9%	Y	≥3	H
10	F-8	GB	M/A-A/S	10^{-7}	99%	Y	≥1	H
11	F-10e,T-3,4	GB	A/S	10^{-7}	90%	Y	≥5	H
12	F-10f,T-3,4	GB	A/S	10^{-7}	99.9%	Y	≥5	H
13	T-3,4	GB	A/S	10^{-7}	90%	Y	≥3	H
14	F-9,T-3	GB	A/S	10^{-7}	99.9%	Y	≥3	H
15	T-4	GB	A/S	10^{-8}	90%	Y	≥3	H
16	F-10g	GB	A/S	10^{-8}	75%	Y	≥3	H
17	F-10h	GB	A/S	10^{-8}	50%	Y	≥3	H
18	F-10a	GB	A/S	10^{-8}	75%	Y	≥5	H
19	F-10b,T-4	GB	A/S	10^{-8}	90%	Y	≥5	H
20	F-10c	GB	A/S	10^{-8}	99%	Y	≥5	H
21	F-10d,T-4	GB	A/S	10^{-8}	99.9%	Y	≥5	H
22	T-4	GB	M/A-A/S	10^{-8}	99.9%	Y	≥5	H
23	T-4	GB	M/A-A/S	10^{-8}	90%	Y	≥5	H
24	F-11,13,T-5	GB	M/A-A/S	10^{-8}	99.9%	W	≥5	H
25	T-5,6	GB	M/A-A/S	10^{-8}	99%	W	≥5	H
26	T-5	GB	M/A-A/S	10^{-8}	90%	W	≥5	H
27	T-5	GB	M/A-A/S	10^{-8}	90%	S	≥5	H
28	T-5,6	GB	M/A-A/S	10^{-8}	99%	S	≥5	H
29	F-12,13,T-5	GB	M/A-A/S	10^{-8}	99.9%	S	≥5	H
30	T-5,6	GB	M/A-A/S	10^{-8}	90%	S	≥3	H
31	F-14,T-5	GB	M/A-A/S	10^{-8}	99%	S	≥3	H

Table 2 (Continued)

Case	Table or figure	Bay	Food time series	Fraction of spawn recruited	Yearly mortality rate	Season of mortality	Size class suffering mortality	Beginning density (day 1)
32	F-14,T-5	GB	M/A-A/S	10^{-8}	99%	W	≥3	H
33	T-5,6	GB	M/A-A/S	10^{-8}	90%	W	≥3	H
34	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥5	M
35	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥5	M
36	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥6	M
37	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥6	M
38	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥7	M
39	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥7	M
40	T-5	GB	A/M-S/O	10^{-8}	99.9%	W	≥5	H
41	F-15,16,T-5	GB	A/M-S/O	10^{-8}	99.9%	S	≥5	H
42	T-5	GB	A/M-S/O	10^{-8}	90%	W	≥3	H
43	T-5,6	GB	A/M-S/O	10^{-8}	90%	S	≥3	H
44	F-19,20	CB	A/M-S/O	10^{-8}	99%	S	≥5	H
45	T-6	CB	A/M-S/O	10^{-8}	90%	S	≥3	H
46	T-6	CB	M/A-A/S	10^{-8}	90%	S	≥3	H
47	T-6	CB	M/A-A/S	10^{-8}	99%	S	≥5	H
48	F-21,T-6	CB	M/A-A/S	10^{-8}	99%	W	≥5	H
49	T-6	CB	M/A-A/S	10^{-8}	90%	W	≥3	H
50	T-6	CB	A/M-S/O	10^{-8}	90%	W	≥3	H
51	F-20	CB	A/M-S/O	10^{-8}	99%	W	≥5	H

Model solution

The model described by Equation 3 was solved numerically by using an implicit (Crank-Nicolson) tridiagonal solution technique. The time step for model integration was one day. Simulations were run for six years which is sufficient time for the model solutions to adjust so that trends in population levels could be identified in the simulations.

Results

Model initialization

The system of equations given by Equation 3 requires that an initial oyster population size-frequency distribution be specified. The simulations described in the following sections are designed to investigate seasonal and latitudinal mortality effects on oyster population size frequency and stability. Therefore, it proved useful to begin the simulations with a size-frequency distribution representative of a crowded population; that is, one suffering little mortality. In this way, changes in the simulated oyster populations will be the result of mortality only. Also, using the same initial population distribution allows for comparison between simulations throughout the entire 6-year simulated time period.

The initial oyster size-frequency distribution was obtained from a simulation that was started with 10 individuals·m^{-2} in size-class 7 on 1 January. The food time series for this simulation contained two phytoplankton blooms of two months duration (March/April, August/September) with intervening summer months and winter months as detailed in Figure 2. Dense bivalve populations can deplete the surrounding water column of food (Fréchette et al., 1991). We used Lund's (1957) low flow conditions to simulate the effect of oyster density on food supply. Such conditions might be typical of an enclosed or sheltered reef (Powell et al., 1987). No mortality was allowed in any size class.

The time development of the simulated population (Fig. 3A) shows that the mean size of the population slowly declines from size class 7 to size class 3, as population density increases about 3 orders of magnitude. These trends are characteristic of a crowded population: high population density and reduced adult size. Reproduction continues throughout the simulation (Fig. 3, A and C) with a strong fall spawning pulse (Fig. 3B) occurring in response to the fall phytoplankton bloom (Hofmann et al., 1992). Therefore, food limitation is not sufficient to cap population growth; however, the rate of population increase has dramatically declined over the 6-year simulation. It is the population size-frequency distribution at the end of the 6-year simulation (Fig. 3D) that is used to initialize the mortality simulations described in the following sections.

Effect of continuous mortality

The first set of simulations considered the oyster population that would be produced in Galveston Bay, Texas, when continuous mortality (mortality throughout the year) is imposed on size classes 5 and larger. Oyster size class 5 approximates the 2.5 in size limit often desired by the oyster fishery as opposed to the standard size limit of 3 now enforced in most areas. Over this series of simulations, the rate of yearly mortality was varied from 50% to 99.9%, the two extremes being depicted in Figures 4 and 5. For an oyster population with no recruitment, these rates would result in a reduction of the population by 0.5 and 0.999, respectively, in one year. In our simulations, where recruitment and mortality constantly change population abundance, a 50% mortality rate does not necessarily result in the loss of one-half of the individuals in the population in one year.

Over this series of simulations (Table 3, Figs. 4 and 5), as mortality rate increases from 50% to 99.9%, density declines by about 80% and the size-frequency distribution shifts slightly to lower size classes. Population reproductive effort declines as the number of adults declines, but individual reproductive effort increases. At the lower mortality rate, spawning is primarily confined to a single strong pulse in the fall. At the higher mortality rate, spawning effort is distributed between a spring and fall spawning peak; the fall peak is stronger and extends over a longer time (Fig. 4A vs. Fig. 5A).

Moreover, spawning is higher in every other year (Figs. 4C and 5C). In the temperature time series for Galveston Bay (Fig.

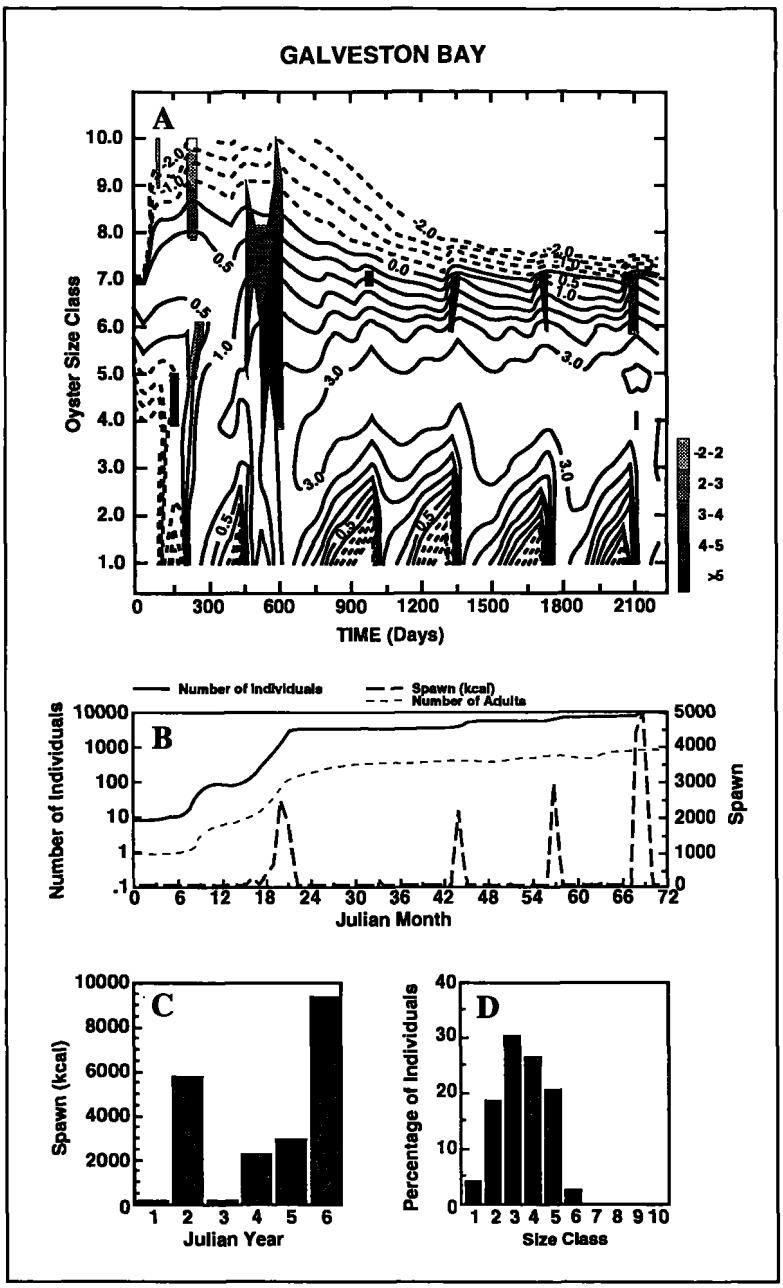


Figure 3

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population with no mortality, allowing the population to approach the carrying capacity of the environment. (**A**) The number of individuals per size class and reproductive effort per size class. Values are plotted opposite the size class designation, not halfway between; hence all individuals in size class 7 are opposite the grid mark labeled 7 on day 1 of this simulation. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Hence, the zero contour corresponds to one individual. Population concentrations less than this are indicated by dashed lines; population concentrations greater than this by solid lines. Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal) with the darkest shades corresponding to highest values. Contour interval is 0.5 for the number of individuals and 1.0 for reproductive effort. (**B**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. Values can be converted into joules by multiplying by 4.16 j·cal^{-1}; into biomass by using 6100 cal·g dry wt^{-1}; and into the equivalent number of fully developed eggs by 13 ng·egg^{-1} ×6.133×10^{-6} cal·ng^{-1}. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Additional data and explanation in Table 2, case 1.

2A), one winter is colder and one summer warmer than the other. As a result, the first year in each pair is characterized by lower reproductive effort as decreased temperatures reduce filtration and ingestion rate and switch net production towards somatic growth. Warmer temperatures the second year result in a larger reproductive effort.

Within these simulated oyster populations, a complex interaction exists between population density, size frequency, and mortality rate. Increasing mortality removes individuals, thereby increasing the available food supply for the remaining individuals. Increased food supply results in increased spawning effort, which then increases population density. This in turn then gives reduced spawning effort. This feedback results in potential population equilibria of different densities and size frequencies for each level of mortality (Table 3). Even at 99.9% yearly mortality, however, the population sustains itself at a fairly dense level. Of more significance, each population approaches an equilibrium or nearly so, such that recruitment balances mortality over this range of mortality rates. Year-to-year shifts in population size over the 6-year simulation show neither continually strong declines nor increases in population density for any of the mortality rates.

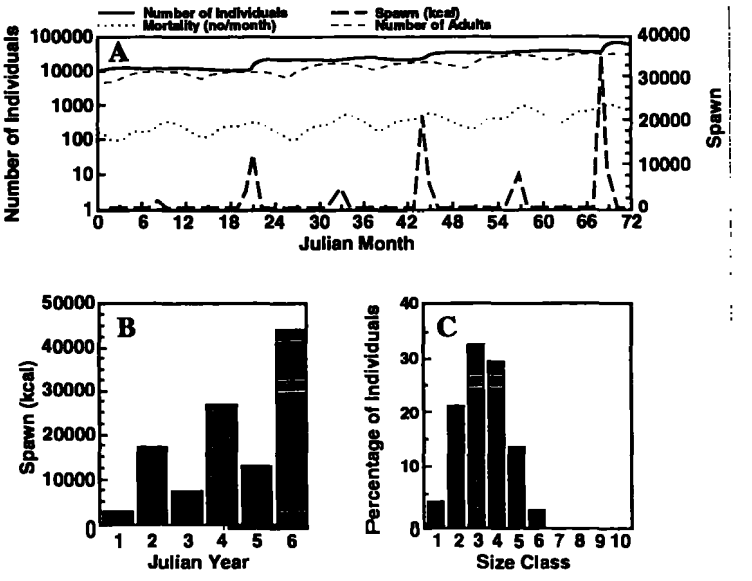


Figure 4

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 50% per year on size classes 5 and larger. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further explanation in Figure 3 and Table 2, case 2.

In Figures 6–8, we compare the time-development of oyster populations exposed to similar overall mortality levels, but in which mortality extends into lower size classes than in Figures 4 and 5. In these simulations, mortality was imposed either on all adult sizes and the larger juveniles (Figs. 6 and 7) or on all size classes (Fig. 8). Figures 7 and 5 differ only in the size classes exposed to mortality (5 and larger vs. 3 and larger) as do Figures 6 and 8 (3 and larger vs. 1 and larger). As high (90–99.9%) yearly mortality rates are imposed on smaller oyster size classes (Figs. 6–8), the population becomes more susceptible to significant population declines. For example, a 99.9% yearly mortality rate had little effect when mortality was restricted to size classes 5 and larger (Fig. 5), but results in a population crash if size classes 3 and larger are similarly exposed (Fig. 7). Many more individuals die before reproducing in the latter case than in the former. A mortality rate of 99.9% is required for a population crash at size classes 3 and larger (Fig. 7), but only 99% at size class 1 and larger (Fig. 8). As mortality extends into the smaller size classes, the mortality rate that the population can sustain decreases. We note that, although these mortality rates seem high, they are well within the typical range for juvenile survivorship in bivalve communities (e.g. Powell et al., 1984; Cummins et al., 1986).

Table 3

A comparison of final density in simulated *Crassostrea virginica* populations after 6 years and total reproductive effort in year 6 at various rates of yearly mortality. Additional details in Table 2.

Case	Mortality rate (%)	Ending density (day 2160) (ind·m^{-2})	Total reproductive effort in year 6 (kcal·m^{-2})
2	50	50,748	43,158
3	75	16,966	15,093
4	90	33,112	46,426
5	99	12,295	14,211
6	99.9	16,565	19,896

Furthermore, as mortality extends into lower size classes, the size-frequency distribution shifts to larger sizes (Figs. 6C, 7C, 8C). The effect is significant because only in cases where mortality is high do oysters grow large enough to reach marketable size for the oyster fishery (size class 6 and larger). Removal of smaller individuals increases the available food supply for the survivors, thereby allowing some to attain market-size.

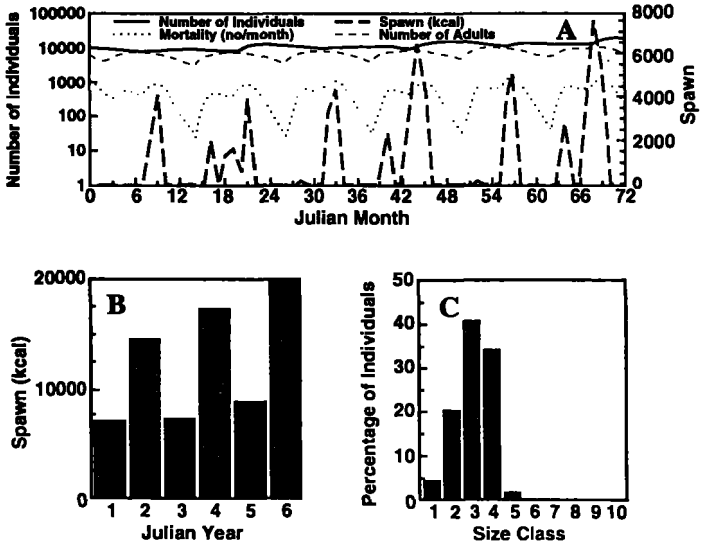
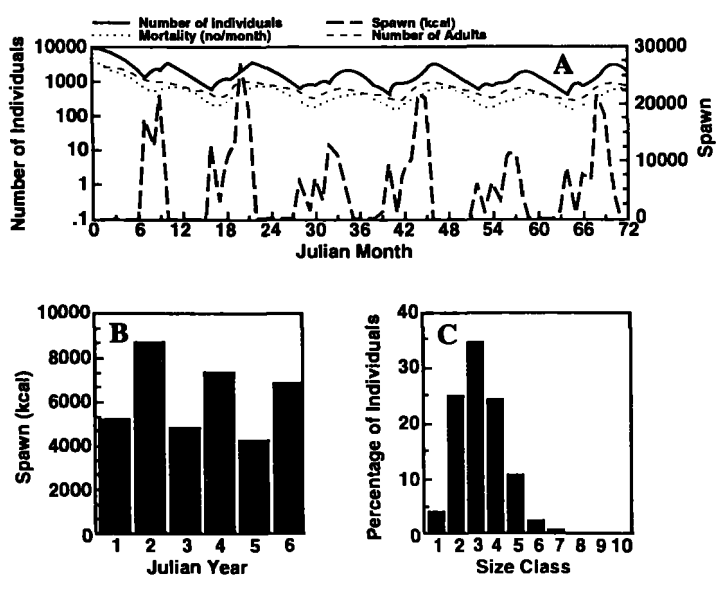


Figure 5

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% per year on size classes 5 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further explanation in Figure 2 and Table 2, case 6.



Effect of food supply

Interactions between food supply and mortality rate are potentially important in determining population density and size-frequency distribution. In years in which a spring bloom is reduced or fails to occur (Fig. 2B), the available food spectrum is shifted in time and total food supply for the year is reduced. In Figure 9, we examine the effect of the failure of the spring bloom. Figure 9 can be compared directly with Figure 7, the two differing only in food supply. A failed spring bloom shifts the food spectrum as well as decreasing the total food available over the year.

Hofmann et al. (1992) showed that the food supply time series used for Figure 9 results in a strong fall spawning pulse. With an imposed yearly mortality of 99.9% in size classes 3 and larger and no spring bloom, the simulated oyster populations (Fig. 9) are not substantially different from those shown in Figures 6–8. However the simulated oyster population shown in Figure 9 is characterized by a stronger fall spawning pulse, as expected, whereas the previous simulations generally had spawning more evenly distributed over the spawning season. The population still reaches a stable distribution and the size-frequency distribution includes individuals in the larger size classes (Fig. 9C). Thus, continuous yearly mortality overrides the effects of variations in the timing of food supply.

Figure 6

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99% per year restricted to size classes 3 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 8.

However, in this and other simulations, the population density is consistently higher after six years with the lower, more restricted food supply associated with the missing spring bloom (e.g. Fig. 7 vs. 9; Table 4). The effect occurs regardless of the size-class distribution of mortality or the mortality rate. The initial surmise that more food should result in higher densities is not confirmed. Reproductive effort is higher at the higher food supply only in the first year (Fig. 7 vs. 9) and declines more rapidly thereafter as population density declines. Initially this would appear to be counterintuitive; more food should result in higher population densities and greater reproductive effort. However, increased food in the spring increases growth rate so that more oysters grow more rapidly into size classes suffering mortality. As a result, the number of adults and population reproductive potential declines. This results in a lower population density. The model simulations indicate that oyster population abundance is the result of a complicated interplay between the timing of food supply, reproductive effort, and mortality.

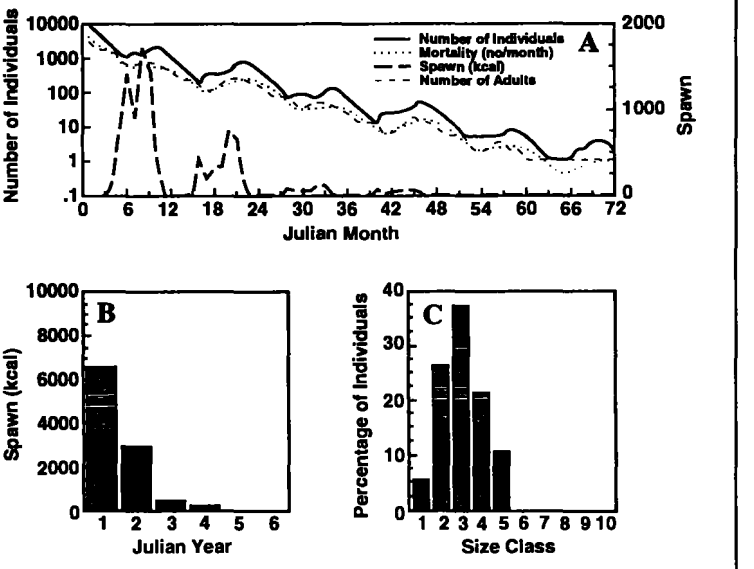


Figure 7

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 3 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 9.

Lowered recruitment success

An additional source of mortality for oyster populations is through decreased survivorship of the planktonic larvae (Table 5, Fig. 10). Lower larval survivorship results in decreased recruitment success and lower population densities, as expected. However, loss of the spring bloom enhances oyster population density as before (Table 5). Nevertheless, a reduction in recruitment success, when combined with mortality on the post-settlement population, results in populations that are less resistant to population crashes. For example, a tenfold reduction in recruitment success in a population exposed to a 75% mortality rate in size classes 3 and larger produces the effect observed for a mortality rate of 99.9% with an order of magnitude higher recruitment success.

One additional important concept arises from this series of simulations. Simulations that included high recruitment success and various mortality rates produced final size-frequency distributions similar to those shown in Fig. 10, E and F. Few individuals are found in size classes 5 and larger. The legal size for the oyster fishery is typically size classes 6 and larger. No fishery could exist under these conditions. High population density produces stunted individuals. A reduction in recruitment success over a range of mortality rates (Fig. 10, A–D) gives size-frequency distributions shifted towards the larger size classes. In fact, more market-sized animals exist in these populations than in the ones shown in Figure 10, E and F. Shifting mortality to lower size classes results in even more market-size individuals (Fig. 10, G–H). A successful fishery requires some degree of mortality, including juvenile mortality.

Effect of seasonal mortality

The commercial oyster fishery is typically confined to a winter season. In some cases, a restricted summer season is also allowed. Agents of natural mortality, like *Perkinsus marinus* and *Thais haemastoma*, typically extract a greater toll during the summer. The effect of mortality restricted to the summer and to the winter is illustrated in Figures 11 and 12, respectively, and in Table 6. For this series of simulations, we define winter as the months of October through March and summer as the months of April through September. Thus each simulated oyster population has the same number

of days (180) with and without mortality. Regardless of the mortality rate, when mortality is restricted to size classes 5 and larger, populations suffer a greater reduction in density when mortality is restricted to the summer (compare Fig. 11B and 12B; Table 6). Summer mortality depresses reproductive effort and depressed reproductive effort, continued over time, results in lower population density.

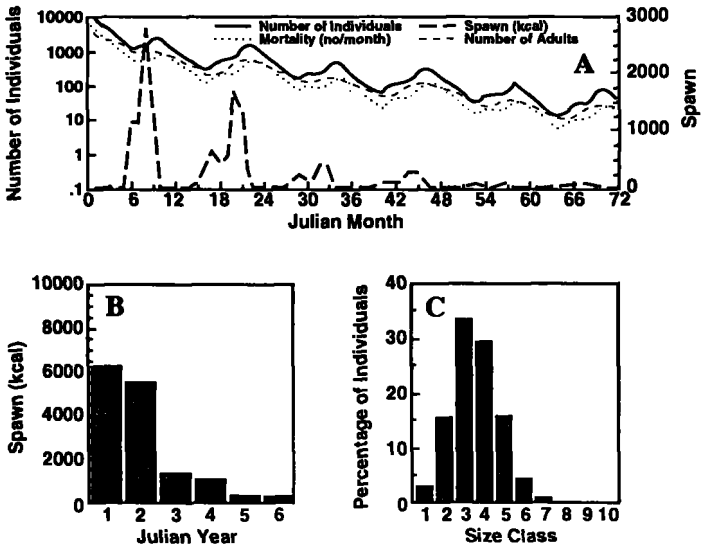


Figure 8

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99% imposed on all size classes. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 10.

Examining the population size-frequency distribution over the year for simulated oyster populations suffering winter (Fig. 13, A and B) and summer (Fig. 13, C and D) mortality suggests an explanation for the more detrimental effect of summer mortality on population density. Figure 13 shows snapshots of the population's size-frequency distribution at various times during the year. When mortality is imposed only during the winter, the population size-frequency distribution shifts to larger size classes in the summer in response to increased growth rate produced by warmer temperatures. Therefore, during the fall spawning season the population is dominated by the larger size classes that account for much of the reproductive effort. Winter mortality then shifts the population size-frequency distribution back to smaller individuals (Fig. 13B) and the cycle begins again. Hence, winter mortality allows the population to replace, during the next summer and fall, the individuals that are lost.

In contrast, restricting mortality to summer months produces a population size-frequency distribution that varies little over a year (Fig. 13, C and D). The variation that does occur is a shift towards smaller individuals in the summer. For example, more individuals are found in size classes 6 and 7 in September in populations that experi-

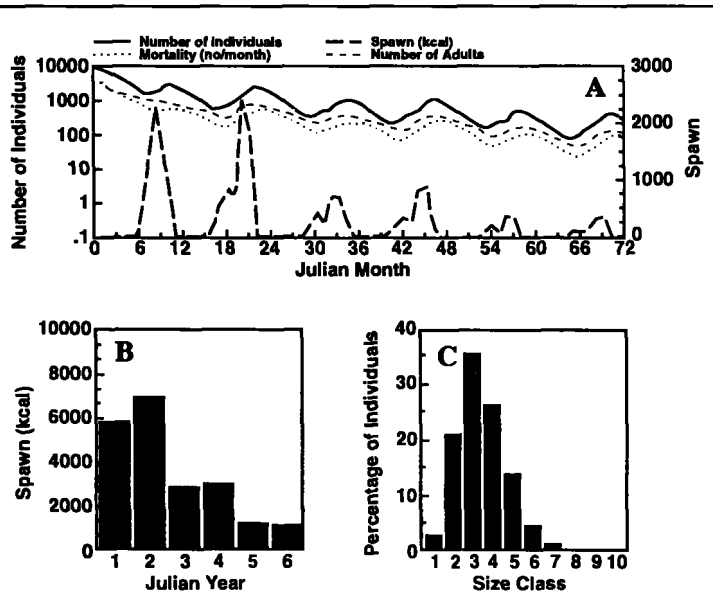


Figure 9

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 3 and larger and in which the food time series contained only the fall bloom. The case is comparable to Figure 7 in which two blooms occurred. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 14.

ence winter (Fig. 13B) rather than summer (Fig. 13D) mortality. The shift to smaller individuals in populations with summer mortality results in lowered reproductive effort. Hence, lost individuals are not replaced in the fall and winter and the population declines.

As mortality extends into the juvenile size classes, the difference in winter and summer mortality should decrease and the seasonal shift in size-frequency as a function of mortality should disappear because a greater fraction of the total mortality occurs in individuals contributing relatively little to the population's spawning potential. This is confirmed by the model (Fig. 14, Table 6). Interestingly, although the seasonal variations in size-frequency distributions are muted, changes in size-frequency distribution over the year are still greater for populations that experience winter mortality. These populations show a slight shift to smaller size classes in the winter.

To examine the effect of varying food supply, we placed the spring and fall blooms one month later in the year (April/May and August/September) and then compared the time development of oyster populations suffering winter or summer mortality with those previously described when the blooms occurred one month earlier (Tables 6 and 7). For populations experiencing winter mortality, delaying the spring and fall blooms by one month (Fig. 2C) does not significantly change the simulated populations from those obtained for the earlier blooms, even when mortality extends to the juvenile size classes (3 and larger). However, for summer mortality, delaying the blooms by one month dramatically improves the population's ability to sustain itself (Fig. 12 vs. Fig. 15; Table 5). Moving the spring and fall blooms one month later in the year produces 1) a strong spring spawning pulse as well as the fall pulse and 2) a shift in the population size-frequency distribution toward the larger size classes, although yearly changes in the size-frequency distribution are still characteristic of summer mortality (Fig. 16 vs. 13). As a result, spawning effort increases under the delayed-bloom condition as fall spawning extends beyond the summer season of mortality. Accordingly, variation in the timing of food supply, under certain circumstances, can be important in the success of an oyster population, particularly in cases where adult mortality is restricted to the summer months.

Table 4

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with and without a spring phytoplankton bloom. Additional details in Table 2.

Case	Spring bloom?	Ending density (day 2,160) (ind·m^{-2})	Total reproductive effort in year 6 (kcal·m^{-2})
9	Yes	2	12
14	No	248	1,003
7	Yes	2,602	7,787
13	No	2,788	7,398
6	Yes	16,565	19,896
12	No	32,513	36,569
4	Yes	33,112	46,426
11	No	42,758	39,217

Table 5

A comparison of final density in simulated *Crassostrea virginica* populations after 6 years and total reproductive effort in year 6 at various rates of recruitment, with and without a spring phytoplankton bloom. Additional details in Table 2.

Case	Mortality rate	Recruitment	Ending density (day 2,160) (ind·m^{-2})	Total reproductive effort in year 6 (kcal·m^{-2})
		No spring bloom		
13	90%	10^{-7}	2,788	7,398
15		10^{-8}	2	26
11	90%	10^{-7}	42,758	39,217
19		10^{-8}	1,067	12,480
12	99.9%	10^{-7}	32,513	36,569
21		10^{-8}	11	236
		Spring bloom		
6	99.9%	10^{-7}	16,565	19,896
22		10^{-8}	1	40
4	90%	10^{-7}	33,112	46,426
23		10^{-8}	328	4,935

Size limits for the fishery

Three size limits have been used or considered as the legal limit for market-size oysters: 2.5 in, 3.0 in,

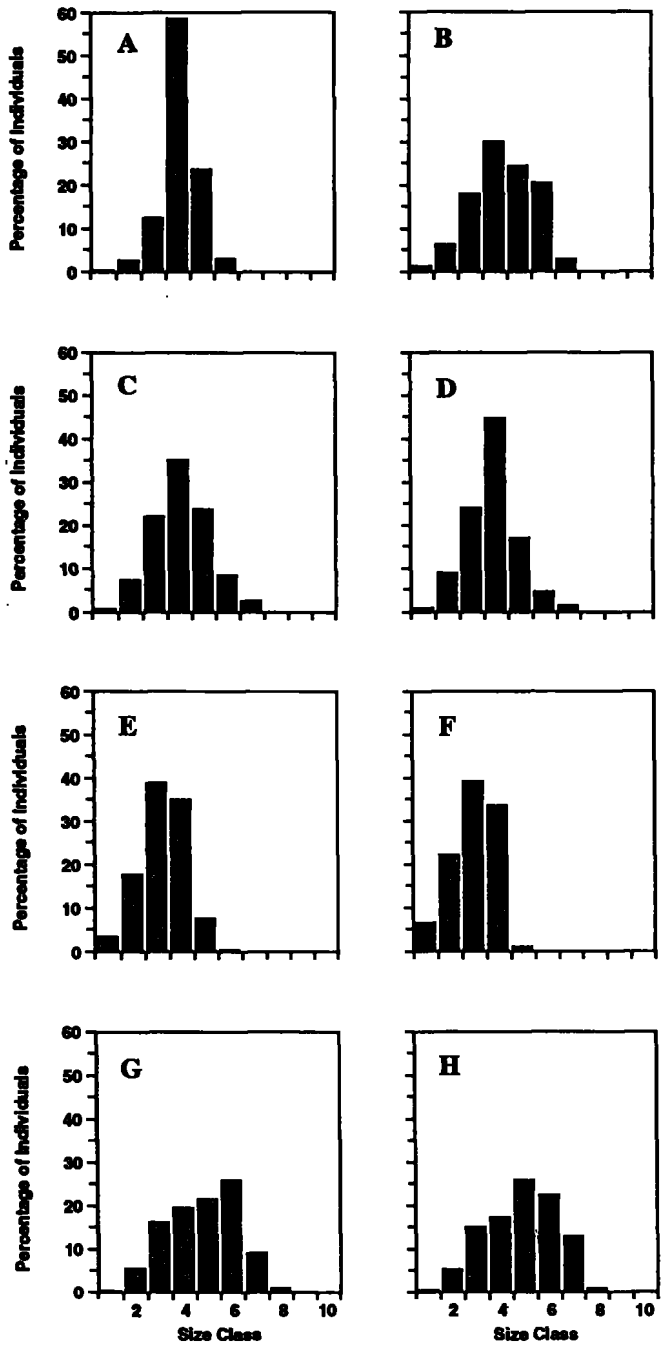


Figure 10

A comparison of the final size-frequency distributions (day 2,160) in simulated *Crassostrea virginica* populations exposed to a Galveston Bay temperature time series following 6 years of recruitment, growth, and mortality under varying degrees of recruitment and mortality. In each case, size classes 5 and larger were exposed to continuous mortality at a yearly rate of (H) 50%, (A and G) 75%, (B) 90%, (C and E) 99%, (D and F) 99.9%. Recruitment was tenfold higher (or larval mortality tenfold less severe) in E and F. Mortality rates extend down into size classes 3 and 4 in G and H. Further information in Figure 3 and Table 2, cases 11, 12, 16–21.

and 3.5 in. These correspond to size classes 5, 6, and 7 in the model. The simulations used to test the effect of these size limits were initialized with a population size-frequency distribution having a component in the larger size classes (Fig. 12). With a yearly mortality rate of 99%, oyster populations increase when mortality is restricted to size class 7 and larger (3.5 in) but decline rapidly if mortality includes size classes 5 and 6 (2.5 in) (Fig. 17). Hence, a change in the legal size limit may have a substantial effect on the fishery and on the oyster population as a whole. Of course, the specific results would vary according to the biomass-to-length conversion used.

As the fishing season typically is confined to the winter, we examined the effect of changing size limits when mortality was restricted to the winter or to the summer months (Fig. 17). Overall, the same pattern persisted in both seasons. Populations declined more under the smaller size limits. However, several significant differences are also observed:

1 Populations in which mortality was restricted to the summer had a stronger spring spawning pulse; most spawning occurred in the midsummer and early fall in populations suffering only winter mortality.
2 Reproductive effort and population density was consistently higher in populations suffering winter mortality (Fig. 18, C, D, and E), density by a factor of 2 to 4, reproduction by a factor of 2 to 8; increased reproductive effort occurred both because the number of adults increased and because those adults spawned more with the result that reproduction was more than proportionately higher.
3 The size-frequency distribution was shifted toward the smaller size classes in populations having winter mortality (Fig. 18, A and B) but had little impact on the size-frequency distribution with summer mortality.

Overall, the number of market-size oysters available at the end of the simulation was higher at the larger size limits (Fig. 18F). As a result, a greater potential yield was available to the fishery at the larger size limits. One reason for the higher yield available to the fishery at the larger size limit (≥3.5 in) is the shift in size-frequency distribution toward larger size classes with adult mortality. A second reason is the protection of a larger portion of the reproductive population. However, if unchecked, the continually growing population in the last set of simulations, where

Table 6

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with mortality restricted to the winter or the summer season and with the spring and fall phytoplankton blooms early in the year or one month later. Additional details in Table 2.

Case	Season	Ending density (day 2,160) (ind·m^{-2})		Total reproductive effort in year 6 (kcal·m^{-2})	
	Mortality: ≥5	Bloom: Early	Late	Bloom: Early	Late
24, 40	Winter	287	220	5,168	4,344
29, 41	Summer	36	500	606	6,904
25	Winter	467		7,365	
28	Summer	253		3,586	
26	Winter	1,400		4,529	
27	Summer	1,333		13,107	
	Mortality: ≥3				
33, 42	Winter	403	595	5,890	8,664
30, 43	Summer	623	692	7,766	8,829
32	Winter	5		111	
31	Summer	5		91	

Table 7

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with mortality restricted to the winter or the summer season and with the spring and fall phytoplankton blooms early in the year or one month later, in Chesapeake Bay and Galveston Bay. Additional details in Table 2.

Case	Bay	Ending density (day 2,160) (ind·m^{-2})		Total reproductive effort in year 6 (kcal·m^{-2})	
	Mortality: ≥5	Bloom: Early	Late	Bloom: Early	Late
	Winter				
48	Chesapeake	394		3,924	
25	Galveston	467		7,365	
	Summer				
47	Chesapeake	102		644	
28	Galveston	253		3,586	
	Mortality: ≥3				
	Summer				
46, 45	Chesapeake	72	85	328	542
30, 43	Galveston	623	692	7,766	8,829
	Winter				
49, 50	Chesapeake	122	84	832	606
33, 42	Galveston	403	595	5,890	8,664

mortality was restricted to size class 7 and larger (≥3.5 in), would eventually negate both effects as population density increased.

Effect of latitude on population stability

In Figure 19 and Table 7, we compare the time-development of oyster populations under the temperature conditions of Chesapeake Bay with those under the temperature conditions of Galveston Bay (Fig. 15). In comparison with the Galveston Bay populations, those in Chesapeake Bay are characterized by densities 2 to 5 times lower, reproductive efforts as much as a factor of 10 lower, size-frequency distributions considerably shifted toward the large size classes (Figs. 20 and 21), and discrete spo-

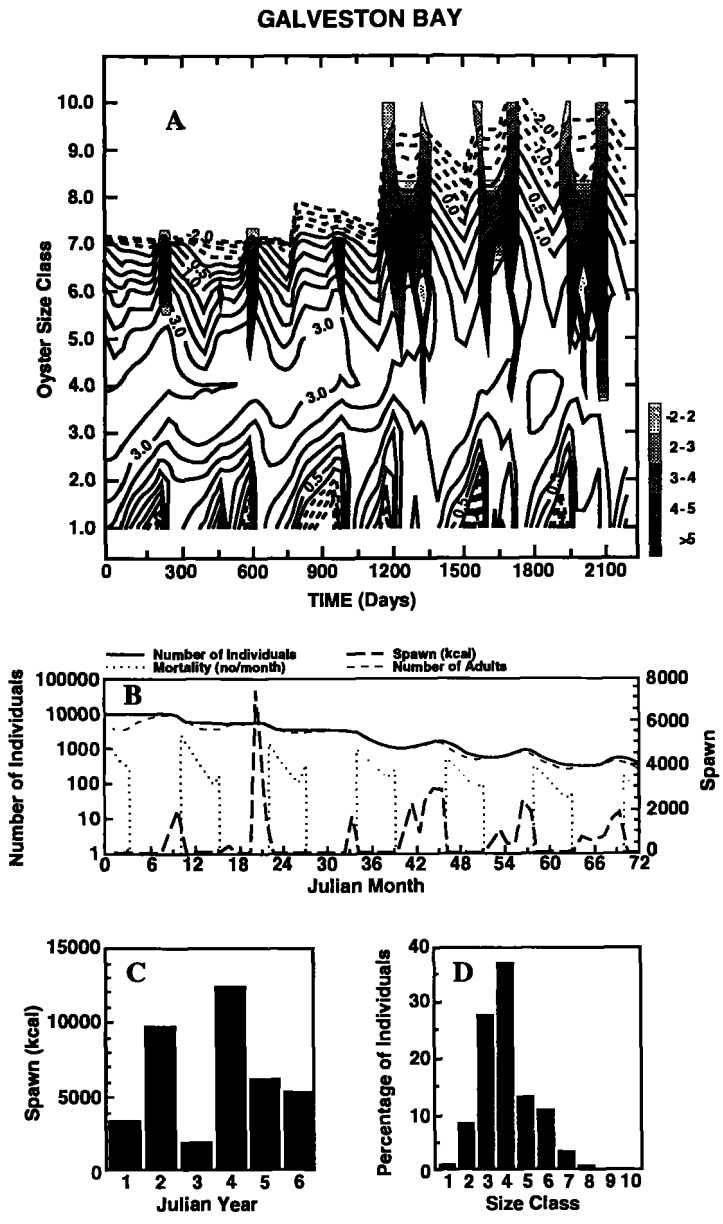


Figure 11

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 5 and larger and in which mortality occurred only during the winter. Compare Figure 12. (**A**) The number of individuals per size class and reproductive effort per size class. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal). (**B**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 24.

radic spawning pulses typically strongest in midsummer. Like Galveston Bay populations, a shift in the timing of the spring and fall blooms has little effect on the seasonal changes in size-frequency distribution (Fig. 21) but considerable effect on the resulting population density in some cases. Populations experiencing winter mortality are more affected by variations in the timing of the food supply than populations experiencing summer mortality. Unlike Galveston Bay populations, populations experiencing summer mortality have lower population densities than populations experiencing winter mortality only when the blooms occur in March/April and August/September. Delaying the blooms by one month results in little variation between populations experiencing summer and winter mortality. The most significant factor producing differences between the Galveston Bay and Chesapeake Bay populations is the cooler temperatures that characterize Chesapeake Bay. This results in reduced reproductive effort with more net production going to support somatic tissue growth (Table 7).

Discussion

The importance of mortality

Unlike an oyster population, an oyster fishery cannot persist without large adult individuals. One of the consistent messages of this modeling exercise is the requirement of mortality for the population to produce larger, market-size individuals. Either adult or juvenile mortality will suffice, as both juveniles and adults compete for food (Powell et al., 1987). Low rates of mortality result in crowding, food limitation, and a stunted population. As mortality extends into the juvenile size classes, and finally into the larval stages (modeled as a reduction in recruitment, reduced reproductive effort, or produced by the colder temperatures of Chesapeake Bay) the population on the average becomes skewed more and more towards the larger adult size classes. Frequently, this proportional shift was sufficient to result in an increase in adult density despite an overall lower population density. An even higher rate of mortality reversed this trend; the popula-

tion size-frequency shifted again towards smaller size classes as adult individuals were rapidly removed from the population. Clearly, for a successful fishery, a delicate balance exists between sufficient mortality to permit the fishery to exist and too much mortality which will reduce the harvestable yield.

Food supply is a complicating factor. Increased food supply will not always result in increased population density or increased harvestable yield. The timing of the food supply interacts in subtle ways with the timing and intensity of mortality, sometimes producing higher densities and sometimes lower ones. The simulations show that the effect of variations in food supply is complex; no simple rules apply and a number of feedback mechanisms exist. In one case, for example, lower population density resulted from increased food supply because increased growth permitted more oysters to enter the size classes that were exposed to mortality, thereby resulting in a population that declined. In another case, a one-month change in the timing of the spring and fall blooms changed population density by a factor of 2 at the same mortality rate. In other cases, little impact occurred in the population despite, for example, the complete failure of the spring bloom.

Population stability and population crashes

The stability of oyster populations is sensitive to several factors, including the timing and intensity of mortality, latitude, and food supply. (We use the term stable in the sense of Underwood [1989] for populations able to recover quickly from perturbation. The terms elasticity and resiliency might also be used.) Increased mortality reduced population density in every comparison. Oftentimes, a relatively stable equilibrium occurred as recruitment balanced mortality over the long term. In all cases, however, mortality rates sufficient to destabilize this equilibrium could be found and a population decline resulted. When mortality extended over a wider range of size classes or affected larval survivorship, population destabilization occurred more easily. In the former case, more oysters

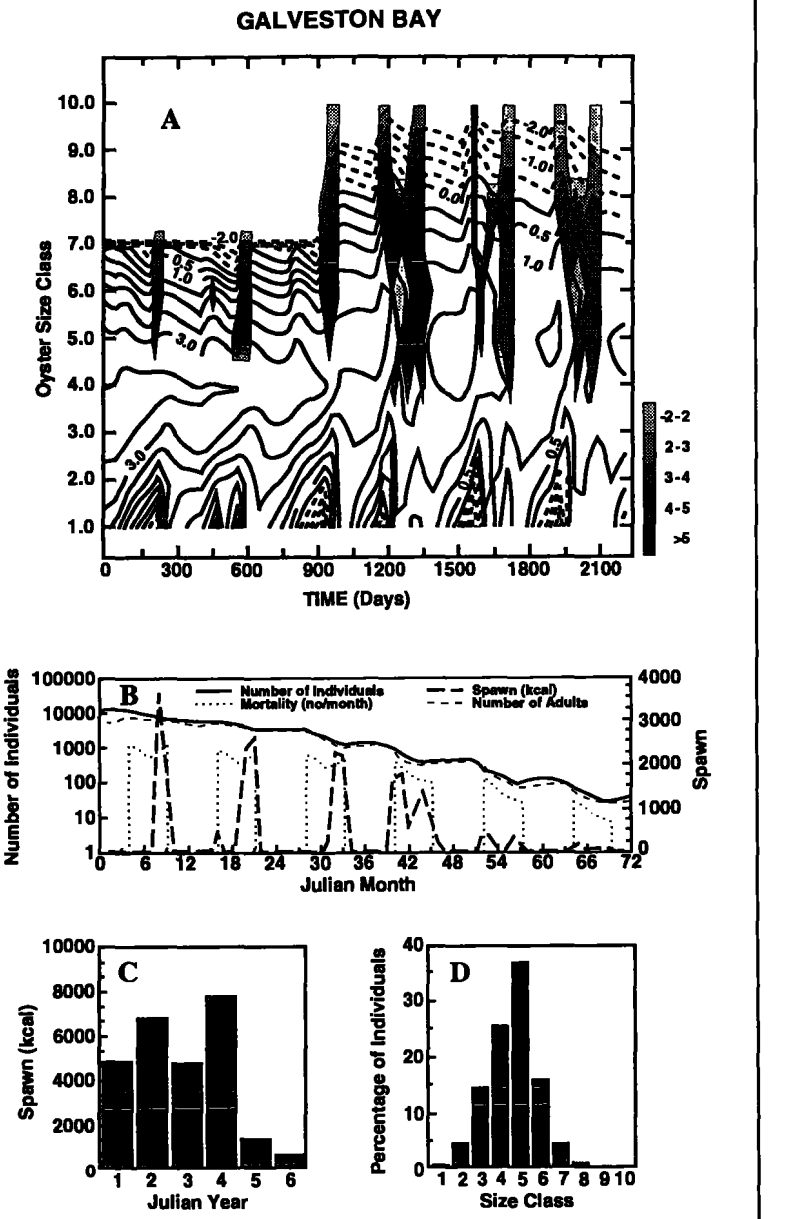


Figure 12

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 5 and larger and in which mortality occurred only during the summer. Compare Figure 11. (**A**) The number of individuals per size class and reproductive effort per size class. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal). (**B**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Further information in Figure 2 and Table 2, case 29.

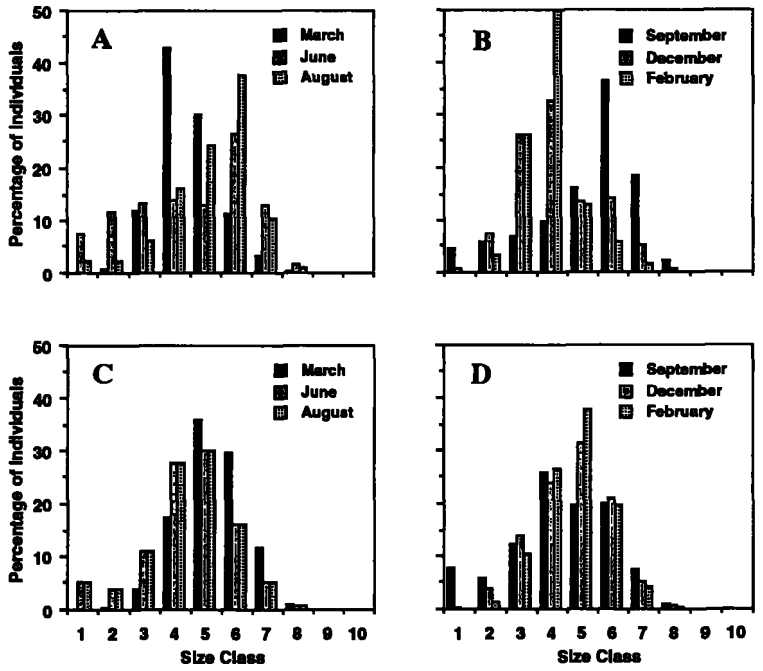
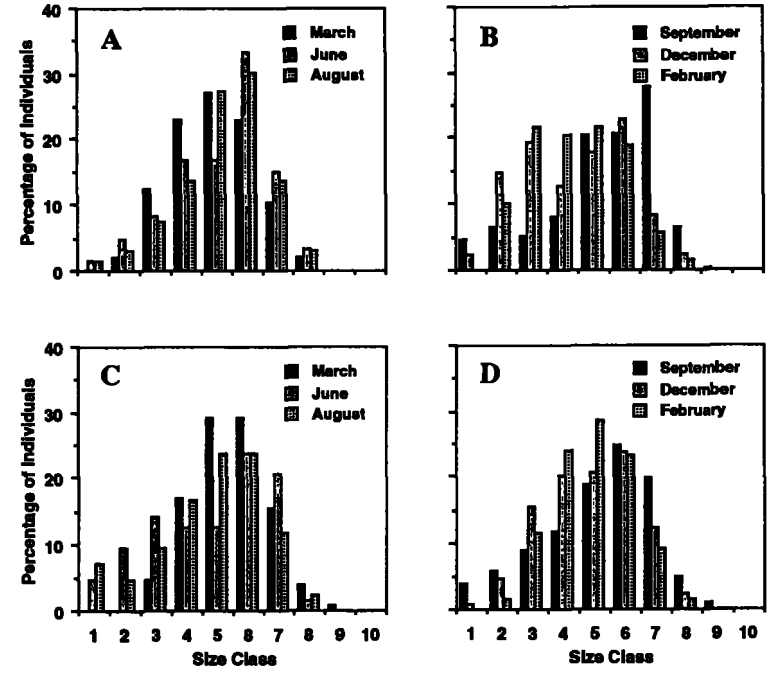


Figure 13

A comparison of the changes in size-frequency distribution through the year in the two *Crassostrea virginica* populations depicted in Figures 11 and 12. (**A** and **B**) a population suffering winter mortality; (**C** and **D**) a population suffering summer mortality. Mortality in both cases was restricted to size classes 5 and larger.



were exposed to mortality. In the latter case, lowered recruitment no longer balanced the higher rates of mortality.

In cases where mortality was imposed for time periods of less than one year, mortality restricted to the six summer months (April–September) nearly always resulted in decreased population density compared to mortality restricted to the winter months. Rarely did the two yield similar results. Never did summer mortality have a lesser impact. The effect was noted at different latitudes, in populations having mortality restricted to a variety of differing size classes, and in populations varying in larval survivorship. However, adult mortality was required. Extending mortality into the juvenile size classes minimized the effect.

Nearly all reports of population crashes in oyster populations result from adult summer mortality, recruitment failure, or floods. Most predators and parasites are most effective in the summer. The series of simulations presented here suggests that the explanation for the importance of adult summer mortality does not necessarily reside in the fact that the most significant agents of adult mortality (except the fishery) operate most effectively in the summer. Although this may well be true, the oyster itself would appear to be more susceptible to mortality in the summer. That is, a greater chance of population crashes in the summer may be physiologically preordained. One potentially important mechanism causing this increased susceptibility is the temperature control on the partitioning of somatic tissue and reproductive tissue in the winter, spring, and summer. Fewer individuals are present in the adult size

Figure 14

A comparison of the changes in size-frequency distribution through the year in simulated *Crassostrea virginica* populations having size classes 3 and larger exposed to mortality. Compare to Figure 13 where mortality was restricted to size classes 5 and larger. (**A** and **B**) mortality restricted to the winter; (**C** and **D**) mortality restricted to the summer. More information in Figure 3 and Table 2, cases 31 and 32.

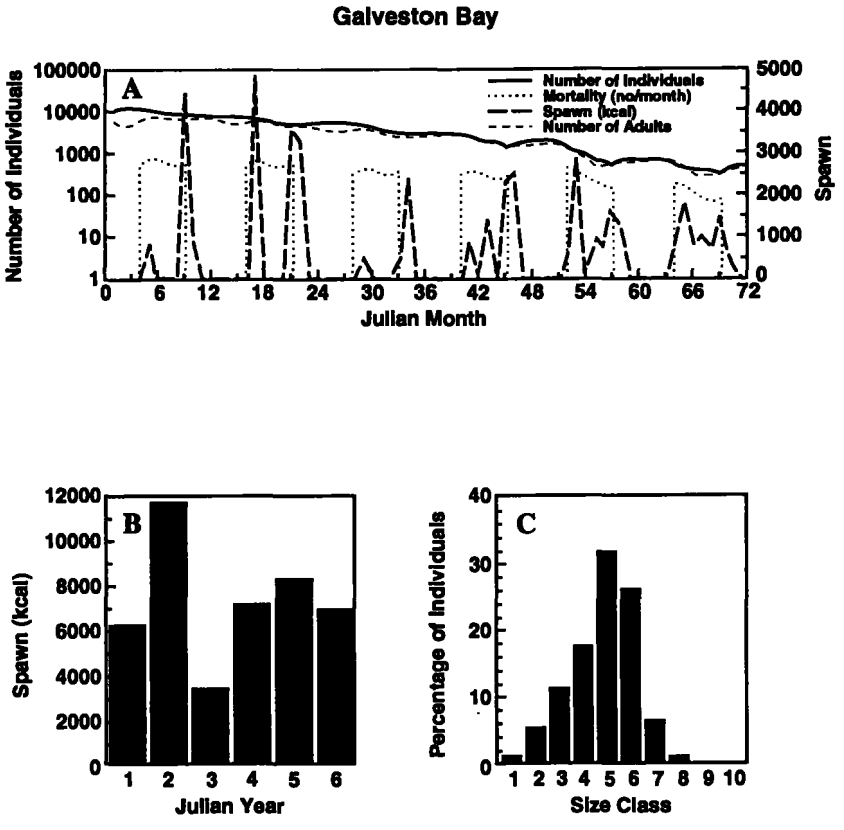


Figure 15

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to summer mortality at a yearly rate of 99.9% restricted to size classes 5 and larger and in which the food time series contained blooms in April/May and September/October. Figure 12 contains comparable results in which the food time series contained two blooms one month earlier. For additional information, see Figure 3 and Table 2, case 41.

classes in the winter, hence losses are minimized. Juveniles grow rapidly to adulthood in the spring and spawn in the summer. As a result, reproductive effort is higher and population stability is enhanced when mortality is restricted to the winter.

One of the interesting observations from the simulations is the consistent difference in the seasonal shifts in size-frequency distribution exhibited by populations suffering adult summer or winter mortality. Populations impacted most significantly by summer mortality had relatively stable size-frequency distributions over the year. Winter mortality produced strong seasonal shifts in the size-frequency distribution. The results suggest that seasonal shifts in size-frequency distributions might provide a useful measure of the relative importance of summer and winter mortality and of adult mortality in oyster populations. For example, the seasonal cycle in market-sized individuals on some Galveston Bay reefs (e.g. Figure 2.1 in Quast et al., 1988) is similar to the seasonal shifts observed in simulated populations in which mortality was restricted to the winter months, suggesting that the fishery might be an important source of mortality in these populations.

Latitudinal gradient in stability

Although not conclusive, the literature reviewed earlier suggests a latitudinal gradient may exist in oyster population stability. Populations at higher latitudes may be more susceptible to population crashes. The Galveston Bay and Chesapeake Bay simulations support this possibility. Simulated popu-

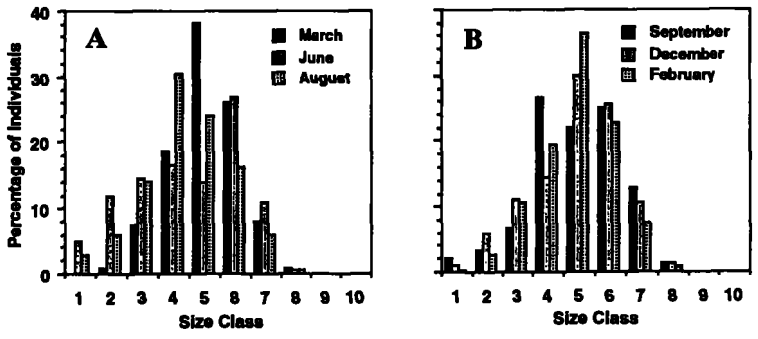


Figure 16

The seasonal changes in size-frequency distribution of the *Crassostrea virginica* population depicted in Figure 15. Figure 13 gives comparable results for the comparable simulation depicted in Figure 12.

lations in Chesapeake Bay were more susceptible to population crashes than those in Galveston Bay. Simulated populations in Galveston Bay consistently had higher population densities after 6 years. Reproductive effort was higher because more of the year occurred within the temperature range conducive to spawning. Higher reproductive effort balanced a larger rate of mortality; hence mortality rates had to be substantially higher in Galveston Bay to effect a population crash. Although not simulated, recovery rates should have been faster as well. Like the distinction between winter and summer mortality, this latitudinal gradient in population stability would appear to result from the basic physiology of the oyster. The fundamental physiological mechanisms associated with reproduction and the division of net production into somatic and reproductive growth would appear to be responsible.

Implications for fisheries management

The methods for managing the *C. virginica* fishery are generally limited to three somewhat interconnected decisions: 1) what size limit should be set; 2) what season should be allowed; and 3) what population density should trigger season closure? The setting of size limits may depend on biological and economic issues. Only biological issues will be considered here. Two aspects of oyster physiology are most important in determining size limits.

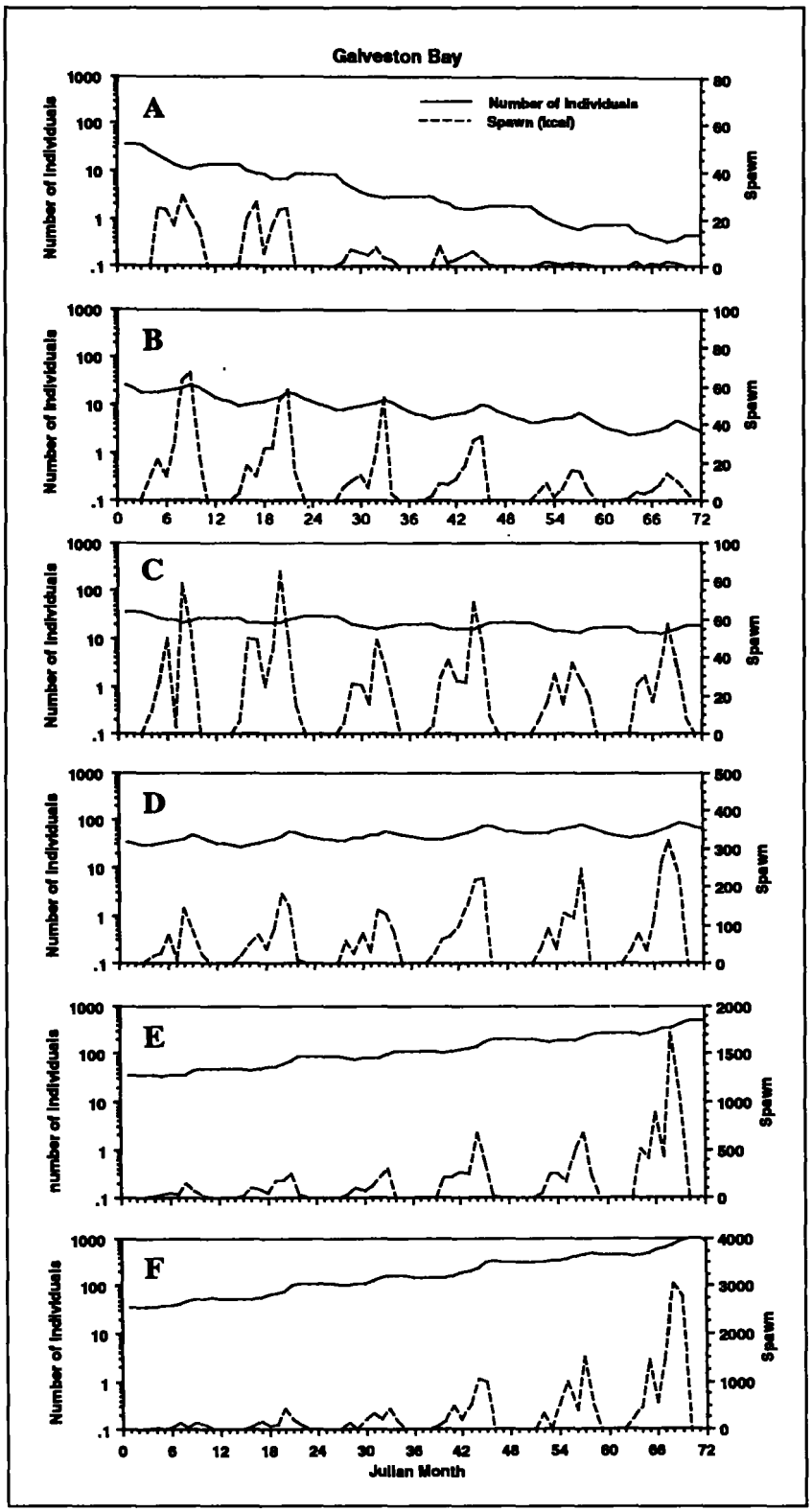
First, under conditions of crowding and at lower latitudes, oysters fail to grow to large size. The former is due to food-limiting conditions. The latter is due to warmer temperatures resulting in the shunting of net production into reproductive growth (Hofmann et al., in press). A considerable body of data supports food limitation in oyster populations, from aspects of spatial distribution (Powell et al., 1987), to reduced growth in crowded locations (Osman et al., 1989), and the observation of increased growth coincident with high mortality (Crosby et al., 1991). A latitudinal gradient in size bespeaks of the importance of temperature in determining the degree to which net production is allocated to somatic growth (Hofmann et al., in press). Both phenomena are reproduced by the model. Clearly, in either case, the setting of size limits as currently done has the effect of artificially reducing yield. If economic considerations warrant it, lower size limits should be set in these populations. In crowded conditions, adult mortality might even increase adult size and yield.

Second, raising size limits increases population density and, under certain conditions, the resulting increase in reproductive effort can eventually result in an increased number of market-size oysters at the larger size limit. Such conditions are met in populations of relatively low density where oysters of legal size are already abundant. Of importance is the recognition that this condition occurs only in populations suffering a relatively high degree of mortality relative to the recruitment rate. Many other agents of mortality, besides the fishery, are important in oyster populations and these agents generally do not respect legal size limits. The model suggests that raising size limits will only be effective if the fishery is the predominant cause of mortality in the population or if other agents of mortality are generally restricted to these same size classes. If all adults are affected, then raising size limits will be ineffective.

Besides the setting of size limits, management policy normally includes a restriction of the fishing season. Fishing seasons on public grounds are generally restricted to the winter months. In some cases, certain areas are set aside for a summer season as well. Natural mortality rates are high in oyster populations, generally greater that 70% per year (Mackin, 1959). Oyster populations in the Gulf of Mexico withstand this degree of mortality without long-term population declines. In this sense, the populations are stable (other species are stable at much higher mortality rates, e.g. Zonneveld [1991]). Rates of recruitment are sufficient to balance mortality over the long term. Nevertheless, population declines do occur (Sindermann, 1968; and others referenced previously) and these have, on occasion,

Figure 17

Comparison of the time development of simulated *Crassostrea virginica* populations exposed to mortality in three differing size classes: (A and B), sizes 5 and larger; (C and D) sizes 6 and larger; (E and F) sizes 7 and larger. Cases A, C, and E show the time development under conditions where mortality was restricted to the summer. Cases B, D, and F show the time development under conditions where mortality was restricted to the winter. Further information in Figure 3 and Table 2, cases 34–39.



been blamed on overfishing. Although no adequate data are available, one suspects that the fishery may be a principle source of mortality in the winter, but not in the summer when the various other agents of mortality, such as diseases and predators, are active.

Oyster populations are more resistant to winter mortality than to summer mortality. The increased likelihood of an intense population decline during the summer observed throughout the oyster's latitudinal range is a product of the basic physiology of the oyster. Simulated oyster populations were most resistant to population declines when mortality was restricted to the winter months under nearly all conditions of recruitment, size-class specific mortality and food supply; they were never less resistant. The simulations suggest that oyster populations can withstand substantially higher rates of mortality in the winter than in the summer and, under conditions where fishing is the primary cause of mortality, populations should be managed more conservatively during the summer season.

A latitudinal gradient in stability exists in oyster populations. Population declines without short-term recovery are more likely at higher latitudes. The simulations suggest that populations should be more and more sensitive to natural agents of mortality and to management decisions at ever increasing latitudes. In effect, populations in the Gulf of Mexico, by their physiology, can withstand the vagaries of nature and the mistakes of man much easier than populations on the Mid-Atlantic and northeast coasts of the United States. The evidence suggests the need for more conservative oyster management at higher latitudes. In effect, the Gulf of Mexico populations and the northeastern

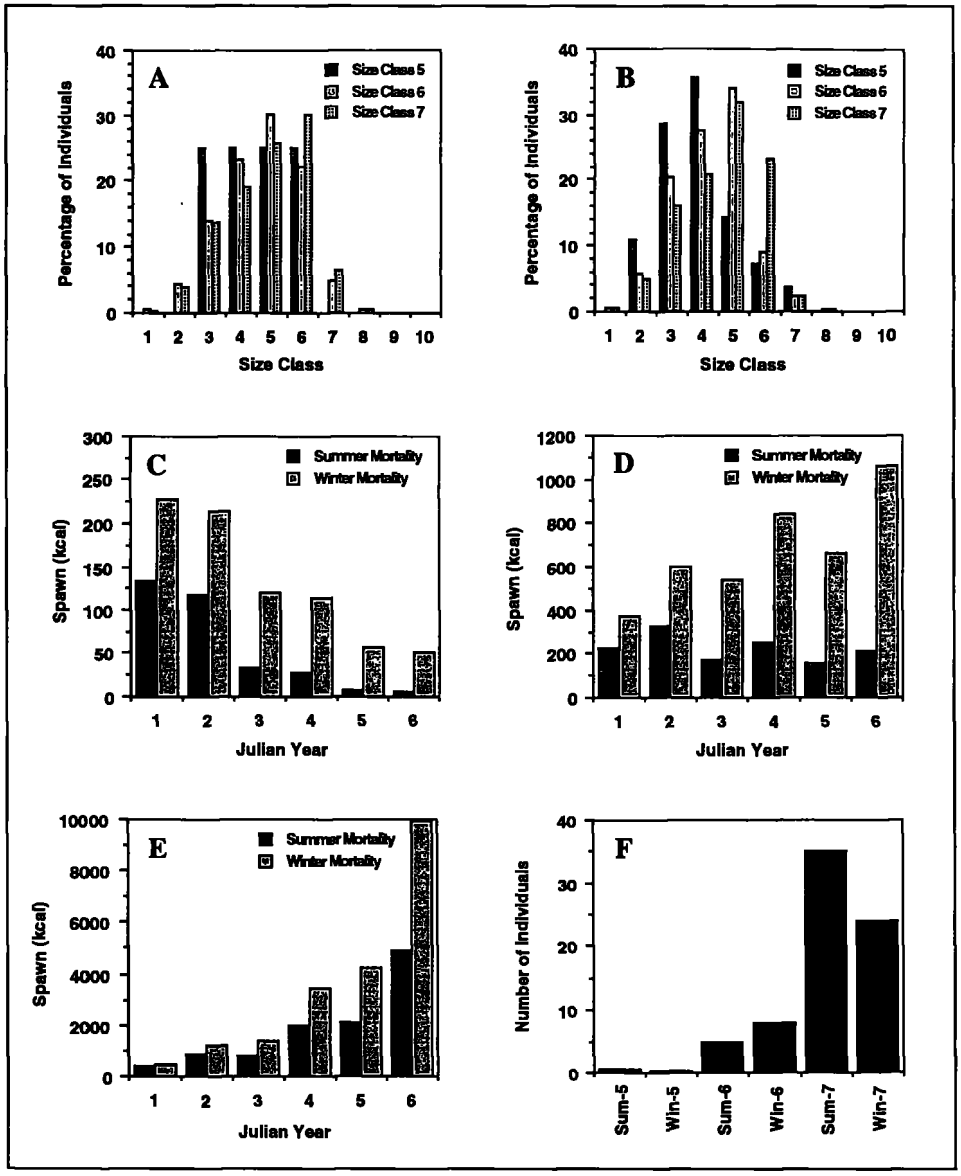


Figure 18

A comparison of the final size-frequency distributions (day 2,160) (**A** and **B**), the yearly reproductive efforts (**C, D,** and **E**) and the number of market-size individuals in the *Crassostrea virginica* population after 6 years (**F**) for the simulations depicted in Figure 17. (A) mortality restricted to the summer (Fig. 17, A, C, and E). (B) mortality restricted to the winter (Fig. 17, B, D, and F). (C) Yearly reproductive effort for populations exposed to mortality in sizes 5 and larger (Fig. 17, A and B). (D) Yearly reproductive effort for populations exposed to mortality in sizes 6 and larger (Fig. 17, C and D). (E) Yearly reproductive effort for populations exposed to mortality in sizes 7 and larger (Fig. 17, E and F). (F) The number of market-size individuals in the population after 6 years, restricting the calculation of market-size individuals to the same classes suffering mortality, 5 and larger (sum-5, Fig. 17A; win-5, Fig. 17B), 6 and larger (sum-6, Fig. 17C; win-6, Fig. 17D) and 7 and larger (sum-7, Fig. 17E; win-7, Fig. 17F).

populations exist under different physiological constraints and these constraints demand different management philosophies and decisions.

Acknowledgments

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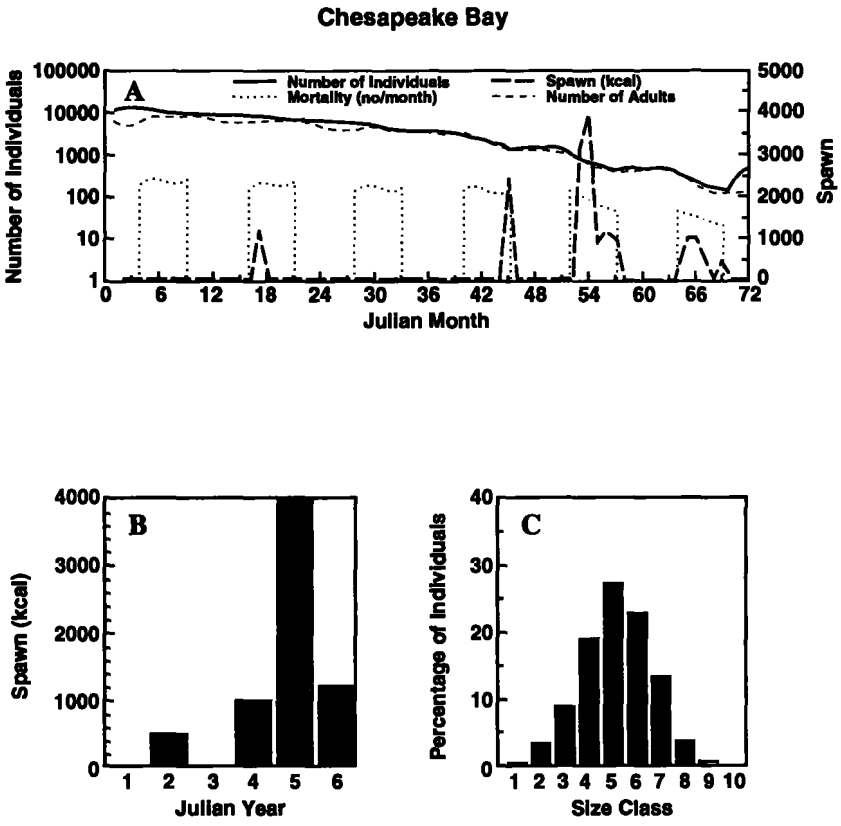

Figure 19
The time development of a simulated *Crassostrea virginica* population exposed to a seasonal temperature regime for Chesapeake Bay and summer mortality. Additional information in Figure 3 and Table 2, case 44.

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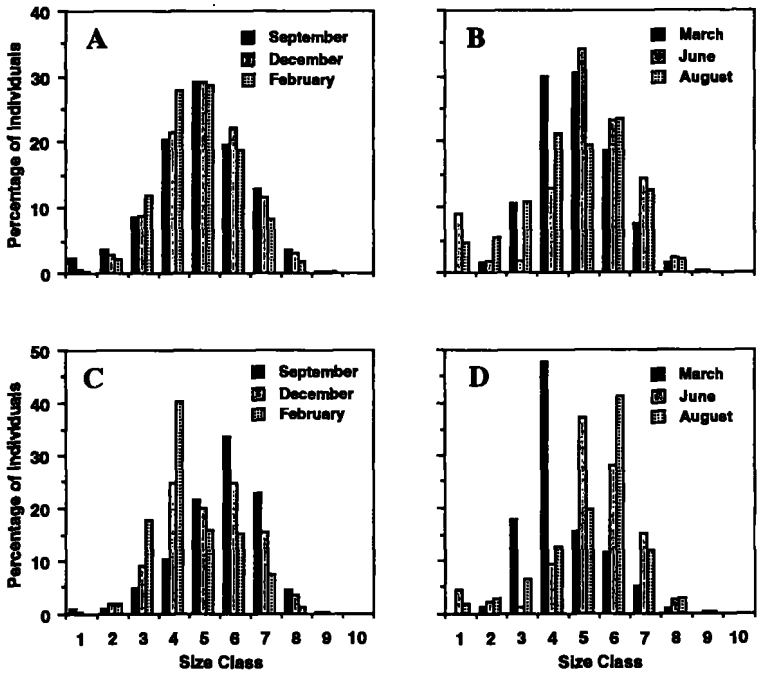

Figure 20

The seasonal shift in size-frequency distribution for two *Crassostrea virginica* populations in Chesapeake Bay. (**A** and **B**) exposed to summer mortality; (**C** and **D**) exposed to winter mortality. (A and B) coincide with the simulation depicted in Figure 19. (C and D) coincide with Table 2, case 51.

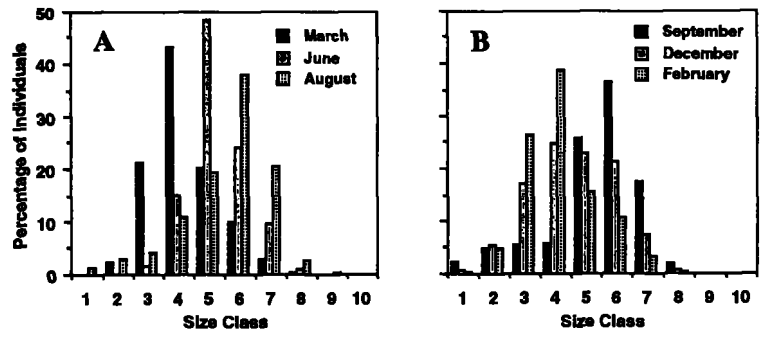

Figure 21

The seasonal shift in size-frequency distribution of a *Crassostrea virginica* population in Chesapeake Bay exposed to an (**A**) early spring (March/April) and (**B**) early fall (August/September) bloom. The complementary case of two later blooms is depicted in Figure 20, C and D. More information can be found in Table 2, case 48.

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