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MODELING OYSTER POPULATIONS II. ADULT SIZE AND REPRODUCTIVE EFFORT

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ABSTRACT A time-dependent model of energy flow in post-settlement oyster populations is used to examine the factors that influence adult size and reproductive effort in a particular habitat, Galveston Bay, Texas, and in habitats that extend from Laguna Madre, Texas to Chesapeake Bay. The simulated populations show that adult size and reproductive effort are determined by the allocation of net production to somatic or reproductive tissue development and the rate of food acquisition, both of which are temperature dependent. For similar food conditions, increased temperature reduces the allocation of net production to somatic tissue and increases the rate of food acquisition. This temperature effect, however, is mediated by changes in food supply. Within the Gulf of Mexico, oyster size declines from north to south because increased temperature decreases the allocation of net production to somatic growth. An increase in food supply generally results in increased size as more energy is used in somatic growth; however, at low latitudes, as food supply increases, adult size decreases because the allocation of more net production to reproduction outweighs the effect of increased rates of food acquisition. Variations in temperature and food supply affect reproductive effort more than adult size because the rate of energy flow through the oyster is higher in warmer months when most net production is allocated to reproduction and small changes in temperature substantially change the spawning season. The wide range of reproductive effort expected from small changes in temperature and food supply suggest that comparisons of adult size and reproductive effort between oyster populations can only be made within the context of a complete environmental analysis of food supply and associated physical parameters and an energy flow model.

INTRODUCTION

Populations of any species tend to have a characteristic mean adult size, which is defined as the size reached by the average surviving adult individual in the dominant cohort. When the characteristic adult size is considerably below that characteristic of the population, the population is described as stunted (Hallam 1965). Stunting is generally considered to result from suboptimal conditions such as extreme environments or low food resources.

In the Gulf of Mexico, populations of the American oyster (*Crassostrea virginica*) exhibit a latitudinal gradient in characteristic adult size (Fig. 1, Table 1). Mean adult size decreases with decreasing latitude on the eastern and western coasts of the Gulf. At the extremes of this distribution, most oysters fail to reach the standard size limit of 7.6 cm that is required for commerical exploitation (e.g. Hofstetter 1977, Berrigan 1990). The nearly complete restriction of the Gulf of Mexico oyster fishery to the northern Gulf is the practical result of this trend. Additionally, year-to-year variations in mean adult oyster size show similar variations throughout the Gulf of Mexico (Wilson et al. 1992). That is, the characteristic adult oyster size increases or decreases uniformly among the many populations in the Gulf. Variation in age cannot be completely excluded as a contributor to these trends; however, the annual mortality in oyster populations from predators and disease exceeds 75% throughout the Gulf of Mexico (e.g. Butler 1953a, Moore and Trent 1971, Powell et al. 1992a) and fished and unfished populations were included in the analysis. Accordingly, the oyster populations sampled in the Gulf of Mexico were composed primarily of individuals that were one to two years in age (Wilson et al. 1992). Hence, size rather than age accounts for the trends seen in these populations.

The similar trends on both sides of the Gulf of Mexico in oyster size with latitude and the year-to-year variability in mean adult size suggest that one or more climatic variables limit oyster size. The correlation with latitude suggests temperature as a likely variable. From a physiological perspective, temperature may affect adult size by regulating the division of net production into somatic and reproductive tissue growth and by regulating the relative rates of filtration and respiration. As temperature increases, more net production is allocated to reproduction. Filtration and respiration rates also increase, but the rate of increase in filtration rate is greater (Powell et al. 1992b). Therefore, a complex interaction of temperature with oyster physiology may place an upper limit on adult size.

Related to adult size is the concept of reproductive senility (Peterson 1983) in which fecundity per unit biomass declines at large size or old age. The existence of reproductive senility in oysters remains to be determined. However, respiration rate rises faster than filtration rate with increasing body size (Klinck et al. 1992, Powell et al. 1992b). The different scaling of respiration and filtration with body size suggests that the scope for growth in oysters must eventually be curtailed at large size which will result in declining fecundity per unit biomass (Powell et al. 1992b). Consequently, populations of lower characteristic size may spawn more per unit biomass.

The objectives of this study are to investigate processes that contribute to variation in the characteristic adult size of oyster populations within a particular habitat and over a latitudinal gradient in temperature and to address the possible influence of reproductive senility in oyster populatious. These objectives are addressed using an energy flow model (Fig. 2) developed for post-settlement oyster populations. A series of simulations are presented for Galveston Bay, Texas that consider the effect of variations in temperature, food supply and salinity on adult oyster

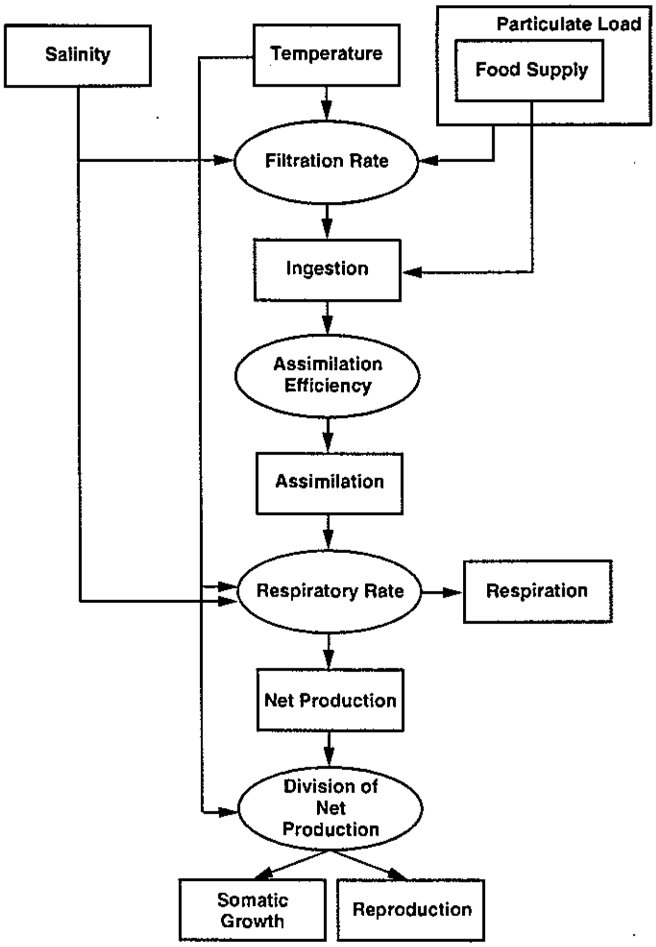

Figure 2. Schematic of the oyster population model.

size. Aside from reductions in oyster growth rate from diseases (Ray and Chandler 1955, Matthiessen et al. 1990) and perhaps genetic differences (Grady et al. 1989, Reeb and Avise 1990) these are likely to be the most important factors controlling size in oyster populations. The effect of latitudinal temperature effects is investigated with simulations that use environmental conditions appropriate for the Laguna Madre, Apalachicola Bay and Chesapeake Bay, as well as Galveston Bay.

THE MODEL

Basic Characteristics

The oyster population model (Fig. 2) is designed to simulate the dynamics of the post-settlement phase of the oyster's life from newly-settled juvenile through adult. Therefore, the oyster's size spectrum was partitioned into 10 size classes (Table 2), that are not equally apportioned across biomass. The lower size limit represents the size at settlement (Dupuy et al. 1977); the upper size limit represents an oyster larger than those normally found in the Gulf of Mexico. In Galveston Bay, for example, the largest oysters routinely collected are 7 to 8 g dry wt (Fig. 3), which corresponds to model size class 9. Thus, the largest size class, 10, is large enough to prevent boundary effects in the model solutions at the upper end of the size-frequency distribution. 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:

TABLE 2.

Biomass and length dimensions of the oyster size classes used in the model. Biomass is converted to size using the relationship given in White et al. (1988), denoted by WPR, and Paynter and DiMichele (1990), denoted by PD. The market-size/submarket-size boundary is about one size class smaller using the conversion from Paynter and DiMichele (1990). The upper size class length conversions obtained from the Paynter and DiMichele (1990) relationship are extrapolations and are, therefore, less accurate, as are the final two conversions obtained from the White et al. (1988) relationship. The range of length to biomass relationships in Galveston Bay, Texas is shown in Figure 3.

Model Size Class	Biomass (g ash free dry wt)	Length (WPR) (mm)	Length (PD) (mm)
1	1.3×10^{-7}–0.028	0.3–25	0.15–21.4
2	0.028–0.10	25–35	21.4–35.7
3	0.10–0.39	35–50	35.7–61.7
4	0.39–0.98	50–63	61.7–89.4
5	0.98–1.94	63–76	89.4–117.6
6	1.95–3.53	76–88	117.6–149.5
7	3.53–5.52	88–100	149.5–178.9
8	5.52–7.95	100–110	178.9–207.1
9	7.95–12.93	110–125	
10	12.93–25.91	125–150	

2.5 in, 3.0 in and 3.5 in, respectively. Adult oysters, those individuals capable of spawning, are defined as individuals weighing more than 0.65 g ash-free dry weight, about 50 mm in length (Hayes and Menzel 1981), although gonadal development has been observed at somewhat smaller sizes (Coe 1936, Burkenroad 1931). Hence, size classes 1 to 3 are juveniles.

The following conversions and scaling factors were used in the oyster model. For simplicity, these are not explicitly shown in the governing equations that are described in the following section. First, all calculations were done in terms of energy (cal m^{-2}). Oyster caloric content was obtained by applying a caloric conversion of 6100 cal g dry wt^{-1} (Cummins and Wuycheck 1971), and the food available to the oysters was converted to caloric equivalents by using 5168 cal g dry wt^{-1}. The model calculations use biomass exclusively (and calories) and so are independent of oyster growth form and length-to-biomass relationships. To relate the biomass size classes, defined in Table 2, to lengths for comparison to the available measurements and the standard measures of fishery management, the length-to-biomass conversion given in White et al. (1988) was used. This conversion is only an approximation, however, given the variation in growth forms found in oysters within bays and throughout their latitudinal range. The model results are presented in terms of biomass, which can be converted to any local specific lengths by using an alternative length-to-biomass relation and the size class boundaries given in Table 2. One example, from Paynter and DiMichele (1990) is shown in Table 2 for comparison.

Second, gains, losses or transfers of energy (or biomass) between oyster size classes were expressed as specific rates (day^{-1}) which were then applied to the caloric content in a size class. For example, ingestion (cal day^{-1}) divided by a caloric value in cal gives a specific rate (cal day^{-1}/cal = day^{-1}), which is then used to calculate incremental changes in a size class. Because the size classes in the model are not of equal size, transfers between size classes were scaled by the ratio of the average weight of the

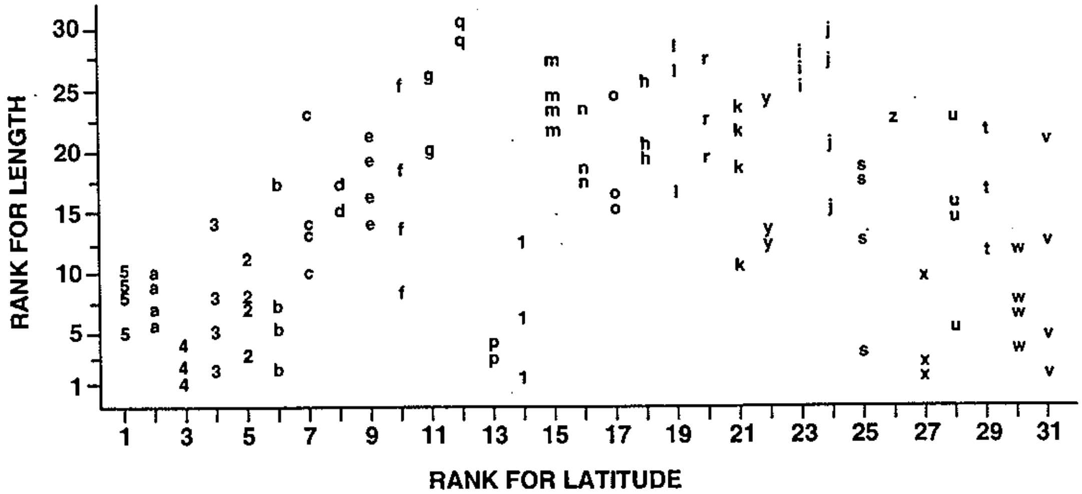

Figure 1. Mean adult oyster size (length) versus latitude plotted as the rank-order of latitude versus the rank-order of size [see Wilson et al. (1992) for details]. The four values for each size and latitude, referenced by letter (a–z) or number (1–5), are those given in Table 1 for 1986 to 1989. Bays with the characteristically smaller sizes are the more southerly bays on either side of the Gulf of Mexico (on the left), the bays in the Florida Panhandle (right), and Tiger Pass and the Mississippi Delta.

TABLE 1.

Oyster population mean length (cm) and fraction of the population in advanced reproductive state (spawning or ready to spawn) for thirty-one bay systems around the Gulf of Mexico that were sampled from 1986 to 1989 as part of the NOAA Status and Trends program. Details of the sampling sites are given in Wilson et al. (1992). Bays are listed beginning with the southern most bay in Texas and proceding clockwise around the Gulf of Mexico. The high fraction ready to spawn in the northern Gulf of Mexico in 1986 (bays l to s) resulted from sampling late in the year. Year and Julian Day were used in the statistical analysis of these data to control for this effect.

	Length				Fraction in Advanced Reproductive State			
Bay Systems	1986	1987	1988	1989	1986	1987	1988	1989
a Laguna Madre	8.16	6.95	6.04	6.03	0.14	0.86	0.27	0.15
b Corpus Christi Bay	7.41	5.67	5.52	7.04	0.13	0.00	0.14	0.23
c Aransas Bay	8.47	8.20	8.19	6.38	0.05	0.02	0.04	0.05
d San Antonio Bay	8.68	8.36	–	–	0.09	0.70	–	–
e Matagorda Bay	9.38	8.30	6.92	7.07	0.20	0.05	0.05	0.21
f East Matagorda Bay	10.13	8.37	6.72	6.29	0.10	0.00	0.14	0.23
g Brazos River	–	–	8.57	7.14	–	–	–	0.33
h Galveston Bay	9.03	8.56	8.55	8.33	0.14	0.09	0.04	0.10
i Sabine Lake	10.44	9.65	9.66	8.40	0.00	0.15	0.00	0.00
j Lake Calcasieu	11.48	8.27	7.99	9.32	0.00	0.00	–	0.00
k Joseph Harbor	8.36	8.79	8.19	7.06	0.67	0.00	–	0.14
l Vermillion Bay	8.72	9.66	9.91	9.06	0.93	0.00	0.25	0.00
m Caillou Lake	9.73	10.36	8.18	8.20	0.83	0.14	0.00	0.13
n Lake Barre/Felicity	8.96	9.22	7.17	7.49	0.97	0.04	0.00	0.21
o Barataria Bay	10.08	9.57	7.04	6.86	0.89	0.00	0.15	0.35
p Tiger Pass	–	–	5.80	5.72	–	–	–	0.27
q Pass a Loutre	–	–	11.23	10.57	–	–	0.00	0.00
r Breton Sound	9.66	8.50	7.71	8.47	0.93	0.07	0.04	0.04
s Lake Borgne	8.94	7.27	7.52	5.68	1.00	0.00	0.07	0.00
t Mississippi Sound	8.40	7.15	7.10	7.20	0.00	0.00	0.00	0.13
u Mobile Bay	8.62	9.03	6.03	6.66	0.13	0.00	0.00	0.13
v Pensacola Bay	9.09	4.55	6.02	6.46	0.08	0.00	0.05	0.09
w Choctawatchee Bay	7.74	4.95	6.67	5.97	0.09	0.00	0.00	0.03
x St. Andrew Bay	6.01	4.81	6.53	6.35	0.64	0.00	0.10	0.06
y Apalachicola Bay	8.43	7.35	8.29	6.64	0.13	0.07	–	0.04
z Apalachee Bay	–	–	–	7.29	–	–	–	0.00
1 Cedar Key	7.44	5.16	6.71	5.39	0.07	0.00	0.08	0.00
2 Tampa Bay	6.58	5.90	6.37	6.44	0.25	0.41	0.23	0.57
3 Charlotte Harbor	6.52	5.30	6.47	6.64	0.00	0.00	0.48	0.27
4 Rookery Bay	6.70	5.26	4.67	5.47	0.00	0.13	0.11	0.13
5 Everglades	8.06	6.56	6.56	5.84	0.08	0.20	0.10	0.00

Therefore, a governing equation for each oyster size class can be written as

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

for $j = 1, 10$, with $P_{rj} = 0$ 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 this 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 a negative scope for growth, equation (1) is modified as

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

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. Implementation of the model given by equation (3) requires that the processes that result in production and/or loss of somatic and reproductive tissue be described in mathematical terms. The functional relationships used in the model and the rationale for particular choices are given in the following sections.

Filtration Rate, Ingestion and Assimilation

For this model, the filtration rate relationship given by Doering and Oviatt (1986) was adapted to oysters using Hilbert's (1977) biomass-length relationship to obtain filtration rate for each size class as a function of temperature (T) and biomass:

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

and

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

where filtration rate, FR_j, is given as ml filtered ind^{-1} min^{-1} and W_j is the ash-free dry weight in g for each size class. Powell et al. (1992b) show that equations (4) and (5) yield results comparable to a more general equation derived for all bivalves, including oysters, over the size range appropriate for this model. In addition, equation (4) has the advantage of containing the temperature-dependency described in more detail by Loosanoff (1958), an attribute not present in most other filtration rate equations (Doering and Oviatt 1986). Measurements (Loosanoff 1958) suggest that the rate of increase of filtration rate moderates at temperatures above 25°C, in accordance with a general trend for bivalves described by Winter (1978), and declines above 32°C. However, equation (4) yields realistic values throughout the normal temperature range, so it is used in the model without modification for lower filtration rates at even higher temperatures.

Equation (4) was modified to allow for salinity effects on filtration rate as described by Loosanoff (1953). Filtration rate decreases as salinity drops below 7.5 ppt and ceases at 3.5 ppt. In mathematical terms:

$$\begin{array}{ll} S \geqslant 7.5 \text{ ppt} & FR_{aj} = FR_j \\ 3.5 < S < 7.5 \text{ ppt} & FR_{aj} = FR_j(S - 3.5)/4.0 \\ S \leqslant 3.5 \text{ ppt} & FR_{aj} = 0 \end{array}$$

where S is the ambient salinity and FR_j is the rate obtained from equation (4). [Note that the second salinity relationship was misprinted in Powell et al. (1992b) and Hofmann et al. (1992).]

The reduction in feeding efficiency at high particulate loads, characterized by pseudofeces production, was included as a depression in filtration rate rather than as a separate function as used by Soniat (1982). From data presented in Loosanoff and Tommers (1948), total particulate content can be related to a reduction in filtration rate as

$$\tau = (4.17 \times 10^{-4})10^{0.418x} \qquad (7)$$

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 an expression for filtration rate modified by total particulate content, $FR_{\tau j}$, of the form:

$$FR_{\tau j} = FR_{aj}\left[1 - .01\left(\frac{\log_{10} \tau + 3.38}{0.0418}\right)\right]. \qquad (8)$$

Equation (8), if applied to total particulate content (inorganic + organic), approximates the results of Haven and Morales-Alamo (1966) and 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. We assume all particles are removed by filtration, a slight overestimate (Palmer and Williams 1980), that oysters feed more or less continuously (Higgins 1980a), and that filtration rate does not vary with food availability (Higgins 1980b, Valenti and Epifanio 1981).

Filtration rate times the ambient food concentration gives oyster ingestion. To the extent that oysters can select nitrogen-rich particles from the filtered material for ingestion, equation (8) yields an underestimate of ingestion (Newell and Jordan 1983). Assimilation is obtained from ingestion using an assimilation efficiency of 0.75, an average value obtained from Tenore and Dunstan (1973), Langefoss and Maurer (1975), and Valenti and Epifanio (1981).

Respiration

Oyster respiration, R_j, as a function of temperature and oyster weight in each size class was obtained from Dame (1972) as

$$R_j = (69.7 + 12.6T)W_j^{b-1} \qquad (9)$$

where b has the value 0.26. Equation (9) conforms to the more general relationship for all bivalves obtained by Powell and Stanton (1985).

Salinity effects on oyster respiration over a range of temperatures were parameterized using data given in Shumway and Koehn (1982) as follows:

$$T < 20°\text{C} \qquad R_r = 0.007T + 2.099$$

and

$$T \geqslant 20°\text{C} \qquad R_r = 0.0915T + 1.324;$$

where R_r is the ratio of respiration at 10 ppt to respiration at 20 ppt:

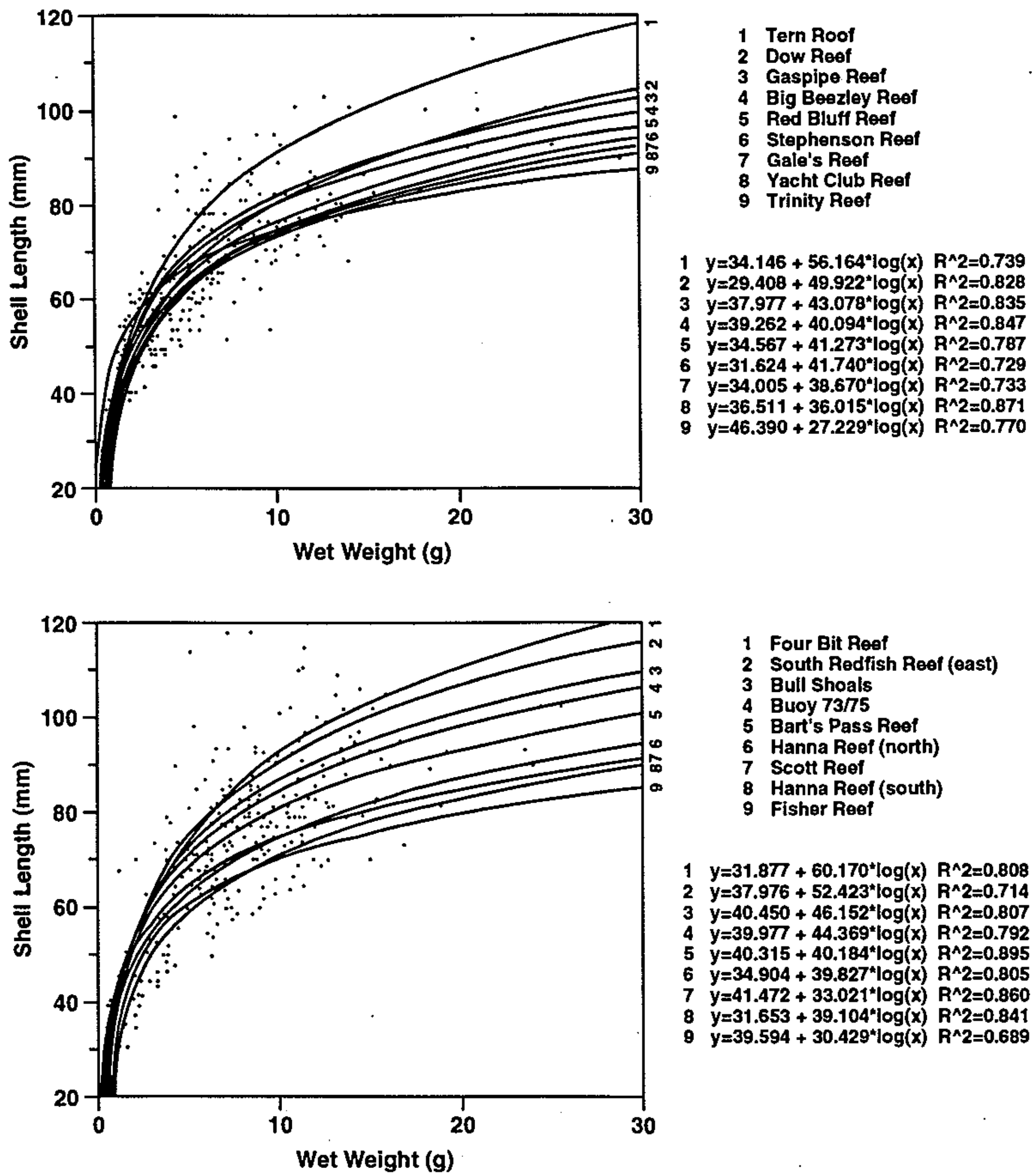

Figure 3. Shell length versus wet weight for oysters collected at eighteen locations in Galveston Bay, Texas. The curves indicate the empirical relationships obtained nsing the data from the different locations. The numbers on the curves correspond to those for the empirical relationships from each site.

current size class (in g dry wt or cal) to that of the size class from which energy was being gained or to which energy was being lost:

$$\frac{W_j}{W_{j-1}} \text{ or } \frac{W_j}{W_{j+1}}$$

where W is the median value for biomass (in g dry wt) in size class j. This ensured that the total number of individuals in the simulated population was conserved in the absence of recruitment and mortality. Finally, each specific rate for each transfer between size classes was scaled to the relative size of the respective classes:

for transfers up: $W_j/(W_{j+1} - W_j)$
for transfers down: $W_j/(W_j - W_{j-1})$.

Governing Equation

The change in oyster standing stock with time in each size class (O_j) is the result of changes in net production and the addition of individuals from the previous size class or loss to the next largest size class by growth. Excretion was not included since it is a minor component of the oyster's energy budget (Boucher and Boucher-Rodoni 1988). Following White et al. (1988), net production in any size class, NP_j, is the sum of somatic (P_{gj}) and reproductive tissue (P_{rj}) production which is assumed to be the difference between assimilation (A_j) and respiration (R_j):

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

TABLE 3.

Summary of the environmental conditions used for the oyster population simulations. Inclusion of a time varying monthly-averaged temperature, salinity, food concentration or turbidity time series is indicated by V. For simulations that used constant salinity or food conditions the values are given in ppt or mg l^{-1}, respectively. Some simulations used an idealized (I) food time series that included increased concentrations in the spring and fall to simulate blooms. Exclusion of an environmental variable is denoted by N.

Area	Temperature	Salinity	Food	Turbidity	Figure
Galveston Bay	V	24	0.5	N	4a, b
Galveston Bay	V	24	1.0	N	5a
Galveston Bay	V	24	1.5	N	5b
Galveston Bay	V	V	V	N	6a
Galveston Bay	V	V	V	V	6b
Galveston Bay	V	7	0.5	N	7a
Galveston Bay	V	7	1.0	N	7b
Galveston Bay	V	7	1.5	N	7c
Chesapeake Bay	V	V	V	N	9a
Laguna Madre	V	24	V	N	9b
Laguna Madre	V	24	0.5	N	10a
Apalachicola Bay	V	24	0.5	N	10b
Chesapeake Bay	V	24	0.5	N	10c
Laguna Madre	V	24	1.0	N	11a
Apalachicola Bay	V	24	1.0	N	11b
Chesapeake Bay	V	24	1.0	N	11c
Laguna Madre	V	24	I	N	13a
Galveston Bay	V	24	I	N	13b
Chesapeake Bay	V	24	I	N	13c

tion and gonadal tissue development is nearly identical. Consequently, a spring settlement is used to initialize the simulations described in the following sections.

Overall, the growth rates, gonadal tissue production and adult size of the simulated oyster populations shown in Figure 4 are in agreement with measurements from Galveston Bay. Some oysters reach size class 5 (63 mm) in about 45 days and size class 6 (76 mm) in about 72 days after settlement. These growth rates are similar to those found for oysters in Galveston Bay and around the Gulf coast in general (Powell et al. 1992a, Ingle and Dawson 1952, Hayes and Menzel 1981). Gonadal tissue production and spawning in oyster populations in the northern Gulf of Mexico is normally restricted to the summer months (Wilson et al. 1990). Consequently, reproductively-advanced oysters make up the majority of the population only from April to October. This same pattern is seen in the simulated population. In Galveston Bay the upper limit on oyster size is 80 to 100 mm and the mean oyster length is about 85 mm (Table 1; Wilson et al. 1992). Adult oyster size at the end of the simulation approaches this value.

Local Controls on Adult Size

Food Supply

Food supply is an important factor governing the growth and development of post-settlement oyster populations. Within any one bay, local conditions can result in large variations in the food concentrations experienced by these populations. To investigate this effect on oyster adult size, constant food supplies that bracketed the range of typical food variations measured in Galveston Bay (Soniat et al. 1984) were tested. The pattern of development for an oyster population exposed to a food supply double that used in the basic simulation (Fig. 5a) is not substantially different. A stable size-frequency distribution develops in about 1.5 years. However, the details of the population do differ. The final size-frequency distribution shows that most of the individuals are in size classes 8 and 9, 100–125 mm. Gonadal tissue development occurs throughout the year, but reaches maximum development in the larger animals in the fall. A further increase in food supply by 50% results in a simulated population that rapidly increases in size (Fig. 5b) and has the majority of the individuals in size class 8 and larger. Development of gonadal tissue occurs in the larger individuals throughout the year. Overall, these simulations demonstrate that oyster size increases with increasing food concentration.

Food supply does not remain constant throughout the year in Galveston Bay at the levels used in the previous simulations. Rather, in many years, food supply shows maximum values in the spring and fall that are associated with the spring and fall plankton blooms and reduced food values in the winter. Hence, a monthly-averaged food time series from Galveston Bay (Soniat et al. 1984) was used with the model. This simulation also used observed salinity values for Galveston Bay. The time varying food supply results in the simulated oyster population shown in Figure 6a. The final adult size for this population is intermediate between that obtained for the constant low and medium food simulations. The majority of the adults are found in size classes 7 and 8 (88–110 mm). Maximum gonadal tissue production is also associated with these size classes and occurs in the late summer and fall. A constant salinity of 24 ppt results in a simulated population (not shown) that is almost identical to that shown in Figure 6a.

Turbidity

In estuarine systems, like Galveston Bay, total seston includes inorganic particles that can interfer with filtration and reduce ingestion rates at high enough concentrations. Hence, the overall food supply is effectively reduced. When monthly-averaged turbidity values (Soniat et al. 1984) from Galveston Bay are included as part of the food supply, the effect is to reduce the overall size of the oyster population and gonadal tissue development (Fig. 6b). The final adult size is reduced to 63 to 88 mm (size classes 5 and 6) and is similar to that obtained at the low constant food supply of 0.5 mg l^{-1}. Gonadal tissue development is confined to a smaller portion of the year.

Salinity

Estuarine systems are frequently characterized by extended periods of low salinity. As many laboratory and field studies have shown, the filtration and respiration rates of oysters are adversely affected at salinities below 7.5 ppt and 15 ppt, respectively. Consequently, episodes of low salinity could result in reduced size and reduced gonadal tissue development. To test the effect of this environmental variable, the development of oyster populations during extended periods of low salinity (7 ppt) over a range of food concentrations was simulated (Fig. 7).

The effect of low salinity is to reduce the overall size of the adult population and to hinder the development of gonadal tissue at a given food concentration. The effect of low salinity is most pronounced at low food concentration (Fig. 7a) where the scope for growth is most reduced. The final adult size is reduced relative to the equivalent high salinity case (cf. Fig. 4a) and gonadal tissue

$R_r = R_{10\ ppt}/R_{20\ ppt}$. Equations (9) and (10) were combined to obtain respiration over a range of salinities as:

$$S \geq 15 \text{ ppt} \qquad R_j = R_j,$$
$$10 \text{ ppt} < S < 15 \text{ ppt} \qquad R_j = R_j(1 + [(R_r - 1)/5((15 - S))])$$
$$S \leq 10 \text{ ppt} \qquad R_j = R_j R_r.$$

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

$$R_{effj} = 0.054T - 0.729 \tag{12}$$

for January to June and

$$R_{effj} = 0.047T - 0.809 \tag{13}$$

for July to December. Equations (12) and (13) were derived empirically from the field observations of Soniat and Ray (1985). Disagreement exists in the literature concerning the extent to which oyster reproduction is temperature acclimatized (Loosanoff and Davis 1953, Stauber 1950, Loosanoff 1969). However, from the studies of Butler (1955), Kaufman (1979) and Quick and Mackin (1971), acclimatization appears unimportant over the latitudinal range of Chesapeake Bay to the southern Gulf of Mexico. Equations (12) and (13) may not hold north of Delaware Bay.

The portion of new production that goes to reproduction is given by

$$P_{rj} = R_{effj} NP_j, \text{ for } j = 4, 10, \tag{14}$$

Somatic growth is the remaining fraction. In cases where $NP_j < 0$, we assume preferential resorption of gonadal tissue to cover the debt, although some data suggest the contrary (Pipe 1985). Gonadal resorption is commonly observed in stressed oysters (e.g. Gennette and Morey 1971) and in the fall and winter when food is reduced (Kennedy and Battle 1964). For juveniles and adults with no gonadal tissue, resorption of somatic tissue occurs. We assume 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.

Although a considerable literature exists on factors controlling the initiation of spawning (e.g. Stauber 1950, Loosanoff 1965, Dupuy et al. 1977), including empirical temperature-dependent relationships (Loosanoff and Davis 1953, Kaufman 1979), little is understood about factors controlling the frequency of spawning over the entire spawning season (e.g. Davis and Chanley 1956). In our model, spawning occurs when the cumulative reproductive biomass of a size class exceeds 20% of the standing stock; an estimate based on data presented in Gallager and Mann (1986) and Choi et al. (1993).

Model Implementation and Environmental Forcing

The model described by equation (3) was solved numerically using an implicit (Crank-Nicolson) tridiagonal solution technique with a one day time step. The external forcing for the model is from time series that specify ambient temperature, salinity, food concentration and turbidity conditions. Each simulation was run for 6 years which is sufficient time for transient adjustments to disappear and for the oyster population to reach an equilibrium in response to a given set of environmental conditions.

Numerous simulations (not shown) were performed initially using real and idealized time series for the environmental variables. These simulations, some of which are reported by Powell et al. (1992b) and Hofmann et al. (1992), were used to calibrate and verify the transfers between size classes and the overall population characteristics and to provide guidance as to model sensitivity to various parameters. These simulations demonstrated that temperature and food concentration had more of an effect on the structure and character of the simulated oyster populations than variations (i.e. ±10%) in individual model parameters. It should be noted that all of the parameters in the model are specified from either field or laboratory measurements; no free parameters need to be empirically determined. Therefore, the focus of this modeling study is on the effect of variations in environmental conditions on characteristic adult oyster size and fecundity.

The simulations described in the following sections used observed monthly-averaged time series of temperature of two years length from Galveston Bay (Soniat and Ray 1985), the Laguna Madre (Powell et al. 1992b) and Chesapeake Bay (Galtsoff et al. 1947). The temperature values were linearly interpolated to obtain values at one day intervals to be consistent with the time step used in the model. For a six year simulation, the two-year temperature time series was repeated three times.

For most of the simulations described in the following section, salinity values were held constant at 24 ppt to remove the effect of low salinity on oyster respiration and filtration rates and to emphasize temperature effects. For some Galveston Bay simulations, a low salinity (7 ppt) event was imposed and one Chesapeake Bay simulation used the salinity time series given in Galtsoff et al. (1947). Food and turbidity values were specified as described for each simulation. A summary of the environmental conditions used for the simulations is given in Table 3.

RESULTS

Basic Simulation

The time evolution of an oyster population that resulted from the settlement of a cohort of ten individuals in mid-May (day 140) that were subsequently exposed to the monthly-averaged temperatures from Galveston Bay, a constant salinity (24 ppt) and a constant food supply of 0.5 mg l^{-1} was simulated. No recruitment or mortality was allowed so that the same individuals were tracked from settlement onwards, about 5.5 years. This simulation provided a basic case to which other simulations could be compared. Following settlement, the oyster population increases in biomass during the first 1.5 years of the simulation (Fig. 4a) after which it reaches a steady population distribution that is in equilibrium with the imposed environmental conditions. The majority of the population at the end of the simulation is in size classes 5 and 6 (63 to 88 mm). In the first two years of the simulation, gonadal tissue is present in size classes 4 to 6. However, as the population stabilizes, gonadal tissue is confined to size classes five and larger. Gonadal tissue development occurs in the adult size classes throughout the summer and into the fall, with the maximum development as a fraction of body weight occurring in late July of each year.

A fall larval set, exposed to the same environmental conditions, results in a similar population distribution (Fig. 4b). The oyster population stabilizes with the same size-frequency distribu-

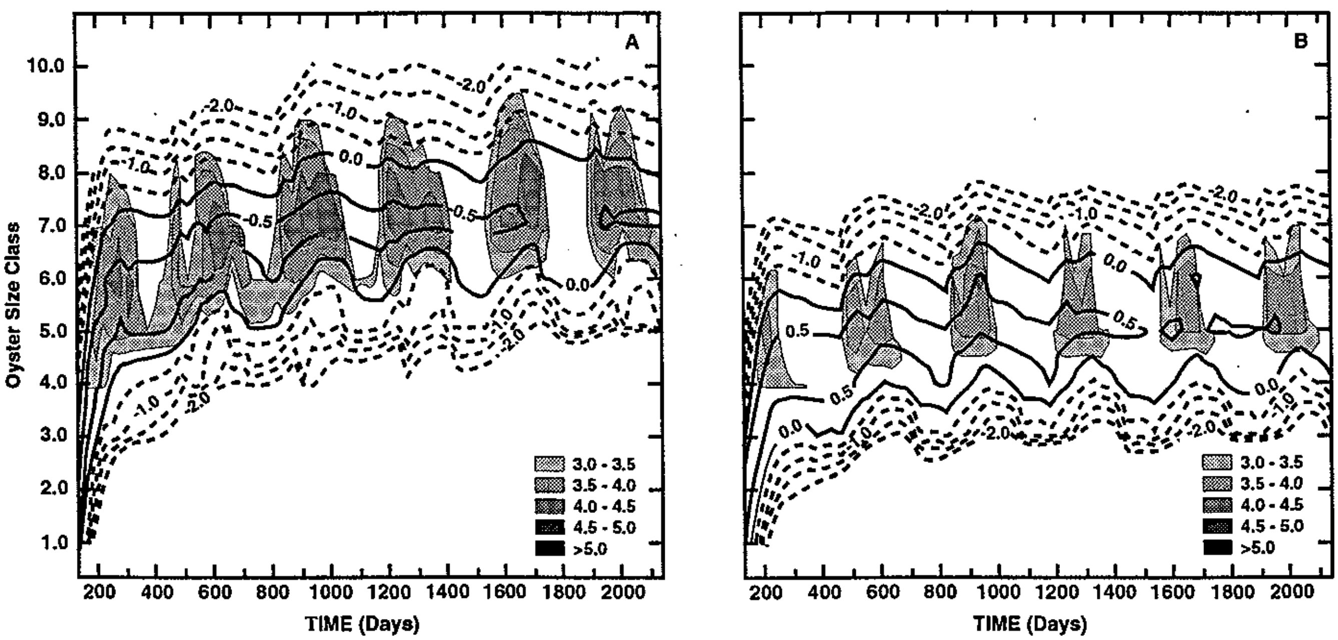

Figure 6. Simulated oyster population distribution and gonadal tissue development that results from Galveston Bay environmental conditions and food conditions A) without, and B) with turbidity. Otherwise same as Figure 4.

Latitudinal Controls on Adult Size

Temperature

The monthly temperature distributions that are characteristic of Laguna Madre, Texas (26°N), Galveston Bay, Texas (29°N), Apalachicola Bay, Florida (30°N) and Chesapeake Bay, Virginia (38°N) show that all three bays reach about the same temperature (28°C) in the summer (Dekshenieks et al. 1993). The primary difference over this latitudinal range is in the winter temperatures and duration of cold conditions. To test the effect of temperature on oyster size and gonadal tissue development over such a latitudinal range, a series of simulations that used idealized temperature time series were done. All simulations used six months of warm (28°C) temperature. The remaining six months were set at 25°C, 20°C, 15°C and 10°C to represent winter conditions in the four bays, respectively.

For all the temperature conditions, the mode of the oyster population, after 5.5 years of simulation, was found in size class 7, 88–100 mm (Fig. 8). However, the population distribution about this mode varied considerably from bay to bay. The small temperature difference between winter and summer conditions in Laguna Madre, resulted in the oyster population being dominated by essentially a single size class. Adult size increased between Laguna Madre and Galveston Bay, with about 40% of the population found in size class 8. This model result agrees with observations of increased adult oyster size in Galveston Bay relative to Laguna Madre. However, the simulated size distributions suggest that adult size decreases between Galveston Bay and Chesapeake Bay, which is opposite of the trend seen in the measurements. This difference in simulated and observed adult size arises from the similar time periods used for the warm and cool temperatures.

As a check on the above results, realistic temperature distributions for Chesapeake Bay and Laguna Madre were used with the model (Fig. 9). The simulated population size-frequency distribution for Chesapeake Bay shows that oysters of size classes 6 and 7 (70–100 mm) are produced by the summer of the second year. The juvenile growth rates and adult size obtained from the model agree with those reported for Chesapeake Bay oyster populations by Butler (1953b) and Beaven (1952). Yearly fluctuations in biomass are higher in Chesapeake Bay because scope for growth is negative for longer periods during the winter.

Adult size in Chesapeake Bay (size class 8) is larger relative to that in the Laguna Madre (size class 7). This difference arises despite the shorter growing season in Chesapeake Bay (Butler 1953b). The Chesapeake Bay simulation (Fig. 9a) allows more time at intermediate temperatures where somatic, but not reproductive, tissue is developed. The practical result is a larger adult population. Thus, the temperature range as well as the length of time exposed to a temperature are important determinants of adult size.

Food Supply

A low (0.5 mg l^{-1}) constant supply of food alters the size distribution of adult oysters from Laguna Madre to Chesapeake Bay (Fig. 10). The simulated adult size is essentially the same throughout the Gulf of Mexico. Adult oysters in Laguna Madre (Fig. 10a), Galveston Bay (Fig. 4a) and Apalachicola Bay (Fig. 10b) are found in size class 6. Gonadal tissue production is about the same in the three bays, with that in Laguna Madre being somewhat higher and extending over more of the year. Chesapeake Bay oysters (Fig. 10c) are slightly smaller (size class 5) which results from decreased filtration rate and hence reduced net production in response to the colder winter temperatures in this bay. Winter temperatures in Laguna Madre allow a higher rate of filtration which results in this bay having the largest oysters at the low food levels.

Doubling the available food supply to 1.0 mg l^{-1}, results in the largest oysters being produced at the mid-latitude sites, Galveston Bay (Fig. 5a) and Apalachicola Bay (Fig. 11b). The smaller adult size occurs in Laguna Madre (Fig. 11a) because more of the available food supply is used to produce reproductive rather than somatic tissue. Adult size in Chesapeake Bay (Fig. 11c) is also smaller than that in the mid-latitude bays. However, this arises

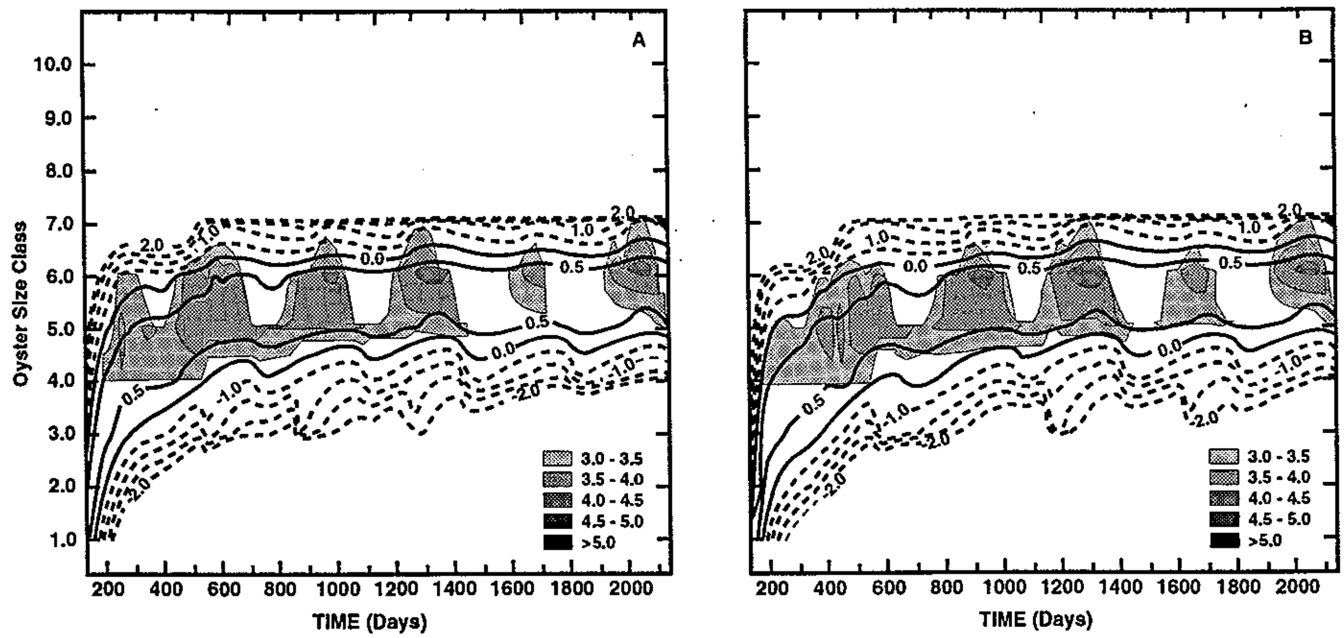

Figure 4. Comparison of the time evolution of oyster populations and gonadal tissue development produced by recruitment of a cohort of ten individuals into size class 1 on A) Julian Day 140 (mid-May) and B) Julian Day 240 (early August). Isolines represent the number of individuals which are given in terms of the logarithm of the number of oysters ($\log_{10} N$). Size class boundaries are defined in terms of biomass (ash free dry weight) as shown in Table 2. Hence, the zero contour corresponds to one individual. Population values less than this are indicated by the dashed lines; solid lines are population values greater than one individual. Shading for the amount of gonadal tissue development represents the logarithm of calories ($\log_{10}$ cal) with the darkest shades corresponding to the highest values. Contour interval is 0.5 for the number of individuals m^{-2} and 1.0 for gonadal tissue production. Numbers of individuals or calories are plotted opposite the size class designations, not halfway between; hence, on day 140 all individuals are in size class 1 opposite the grid mark labeled 1. The caloric values can be expressed as Joules by using a conversion of 4.18 Joules cal^{-1}.

production is less. Similar trends are observed for low salinity conditions at the higher food concentrations (Fig. 7b, c). However, higher food concentrations offset the deleterious effects of low salinity somewhat by providing more energy for growth. Comparison of the simulated populations at low (Fig. 7) and high salinity conditions (Figs. 4 and 5) shows that the effect of reduced salinity is minor relative to that of reduced food. Therefore, the detrimental effects of low salinity on oyster populations can be reduced by high, but not unusually high food supplies.

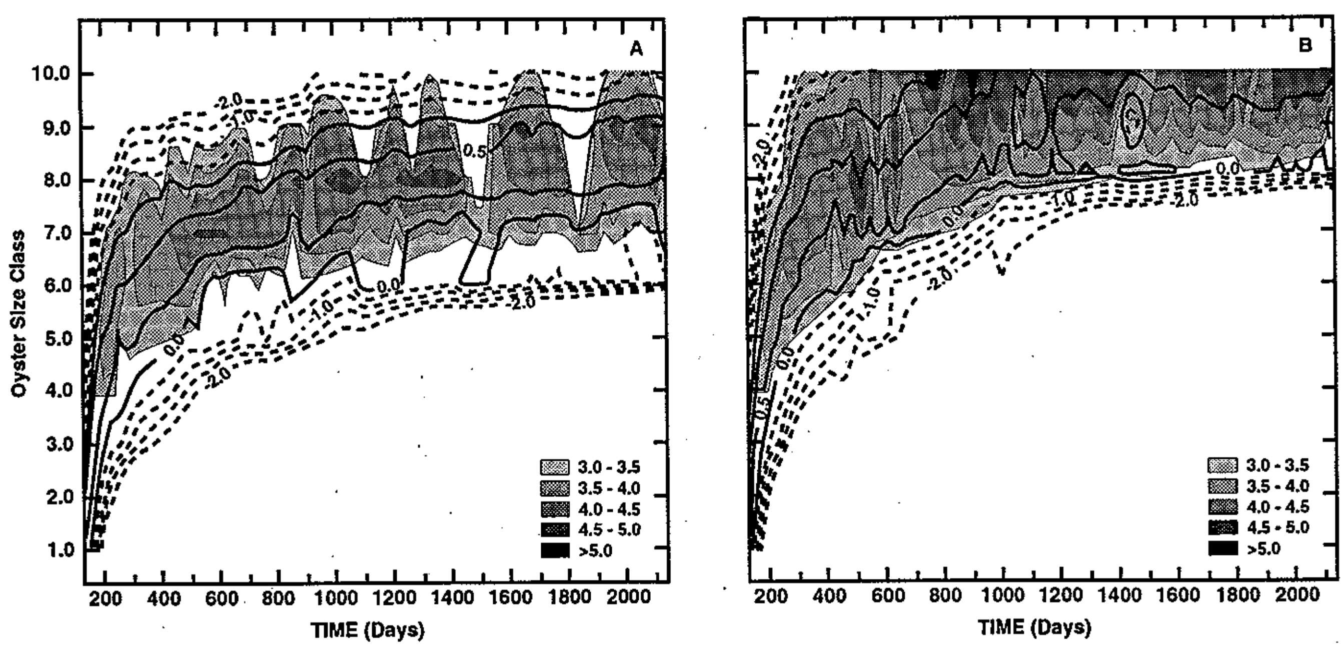

Figure 5. Simulated oyster population distribution and gonadal tissue development that results from Galveston Bay environmental conditions and constant food concentrations of A) 1.0 mg l^{-1} and B) 1.5 mg l^{-1}. Otherwise same as Figure 4.

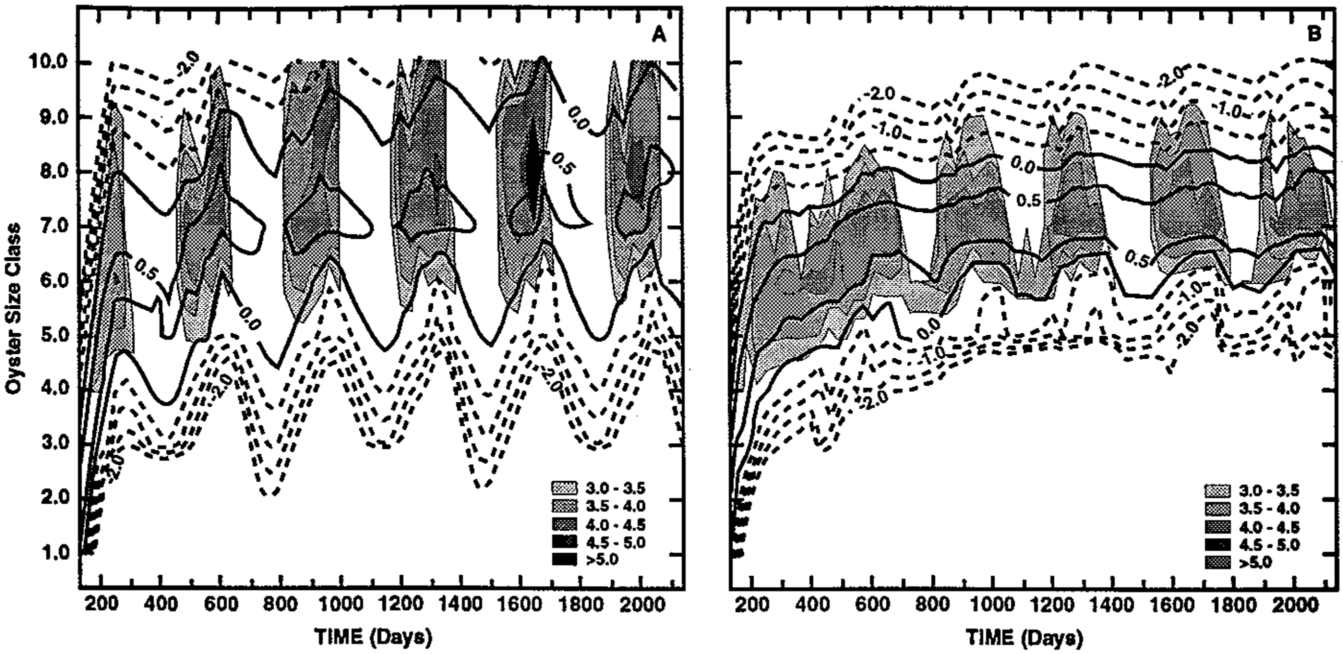

Figure 9. Simulated oyster population distribution and gonadal tissue development that results from temperature, salinity and food conditions characteristic of A) Chesapeake Bay and B) Laguna Madre. Observations on food distributions are lacking for Laguna Madre. Hence, the Galveston Bay food time series was used in this simulation. Otherwise same as Figure 4.

The spawning frequency and pattern associated with the simulated populations from Laguna Madre, Galveston Bay and Chesapeake Bay is shown in Figure 12. In general spawning is associated with the larger size classes and the spawning season tends to be longer at lower latitudes. Also, the most southerly bays tend to have continuous spawning; whereas, that in Chesapeake Bay tends to be confined to discrete pulses. This same trend is observed in the observations from the NOAA Status and Trends program (Table 2). More oysters were found in late reproductive phase, ready to spawn or spawning at lower latitudes.

Spawning season is usually defined by the period of time during which mature eggs are present or by the period of actual spawning. The simulated spawning season, as defined by significant spawning events, is about 100 days in Laguna Madre (Fig. 12a), somewhat shorter in Galveston Bay (Fig. 12b) and even shorter in Chesapeake Bay (Fig. 12c). A tendency towards a spring and fall spawning peak occurs in Galveston Bay (last two years of simulation) and an even stronger tendency towards this occurs in Chesapeake Bay. Significant gonadal material is present for about 200 days (7 months) in Galveston Bay, 160 days (5 months) in Chesapeake Bay, and nearly all year in Laguna Madre. These features of the stimulated spawning season are within the range of values reported for oyster populations and fit the trend toward shorter spawning seasons at higher latitudes (e.g. Hopkins 1935, Stauber 1950, Ingle 1951, Heffernan et al. 1989, and previous references). The development of reproductive material in the simulated oyster populations, from initiation to first spawning, takes about 40 days in Galveston Bay and 60 days in Chesapeake Bay. This is somewhat slower than the 20 to 40 days suggested by Kaufman (1979) and Loosanoff and Davis (1953). However, these time intervals were based on results from constant temperature incubations, which will result in shorter times. Hayes and Menzel (1981) recorded mature gametes in oysters that were 40 to 50 days old, which is similar to what is observed in the simulated populations from Galveston Bay. Egg production, over a two month period, recorded for Delaware Bay oysters held in the laboratory was 3×10^7 to 4×10^7 eggs per female (Davis and Chanley 1955). This study did not report food levels. Egg number, estimated from the simulation results for Chesapeake Bay and Galveston Bay, using the approach described in Klinck et al. (1992), is 1.7×10^8 and 3×10^8 eggs per female, respectively, for a spawning period of about 100 days.

The extent to which these differences and similarities in spawning frequency and pattern result from variations in environmental conditions is discussed in Hofmann et al. (1992). For this study, the interest is in the extent to which these differences and similarities result from variations in adult size. Oyster populations in Laguna Madre (Fig. 13a), Galveston Bay (Fig. 13b) and Chesapeake Bay (Fig. 13c) show a restriction in the period of reproductive effort, as measured by spawn production, over the course of the six-year simulation. This is a consequence of the increased size of the population rather than of increased age. Smaller oysters are more likely to have a positive energy balance and cal allocate a larger fraction of their total assimilated energy to reproduction. As a result, they can spawn more frequently. This trend is independent of the pattern or frequency of spawning and is observed for all ranges of environmental conditions.

A summary of reproductive effort, derived from the simulations, as it relates to average adult size, food supply and latitude is given in Table 4. These results show the strong relationship that exists between reproductive effort, temperature and food supply. Overall reproductive effort is more variable than adult size. For example, in Galveston Bay a reduction in food supply, produced by increased turbidity, gives a 67% reduction in average adult size, but an 85% decrease in reproductive effort (Fig. 6a vs. Fig. 6b). Similarly, the change in temperature that occurs between Galveston Bay and Laguna Madre reduces adult size by 6%, but increases reproductive effort by 23%. Higher temperatures produce higher filtration rates which give increased net production.

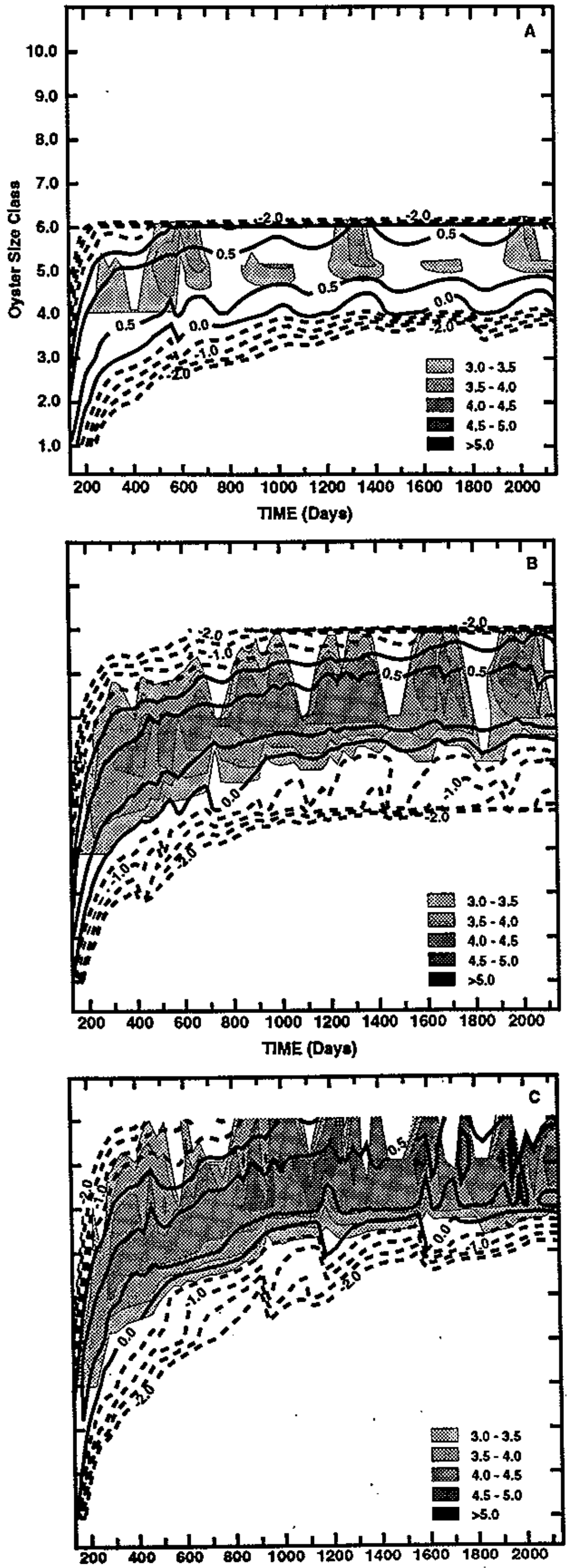

Figure 7. Simulated oyster population distribution and gonadal tissue development that results from Galveston Bay temperatures, low salinity (7 ppt) conditions and food concentrations of A) 0.5 mg l^{-1}, B) 1.0 mg l^{-1}, and C) 1.5 mg l^{-1}. Otherwise same as Figure 4.

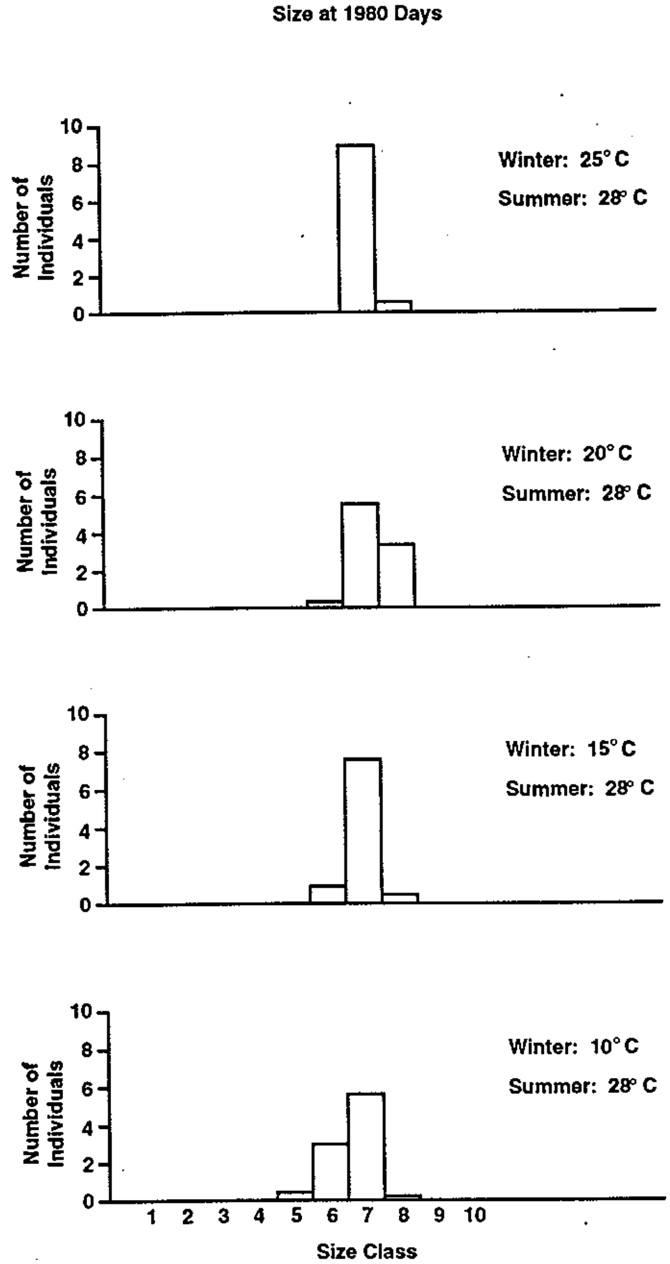

Figure 8. Simulated size frequency distribution from year six for four idealized temperature time series. Other environmental conditions were constant salinity (24 ppt), Galveston Bay food conditions and no turbidity.

due to the colder temperatures which limit winter net production rather than the production of reproductive tissue.

Environmental Controls on Reproductive Potential

The simulations presented in Figures 4–11 show that gonadal tissue development changes for a given set of environmental conditions. This in turn determines the reproductive potential (spawning) of an oyster population. The ability to check the accuracy of the reproductive portion of the population model is limited due to the paucity of observations that provide measurements of oyster reproductive state, oyster size, and environmental conditions concurrently. However, there are some general trends that should appear in the simulated populations.

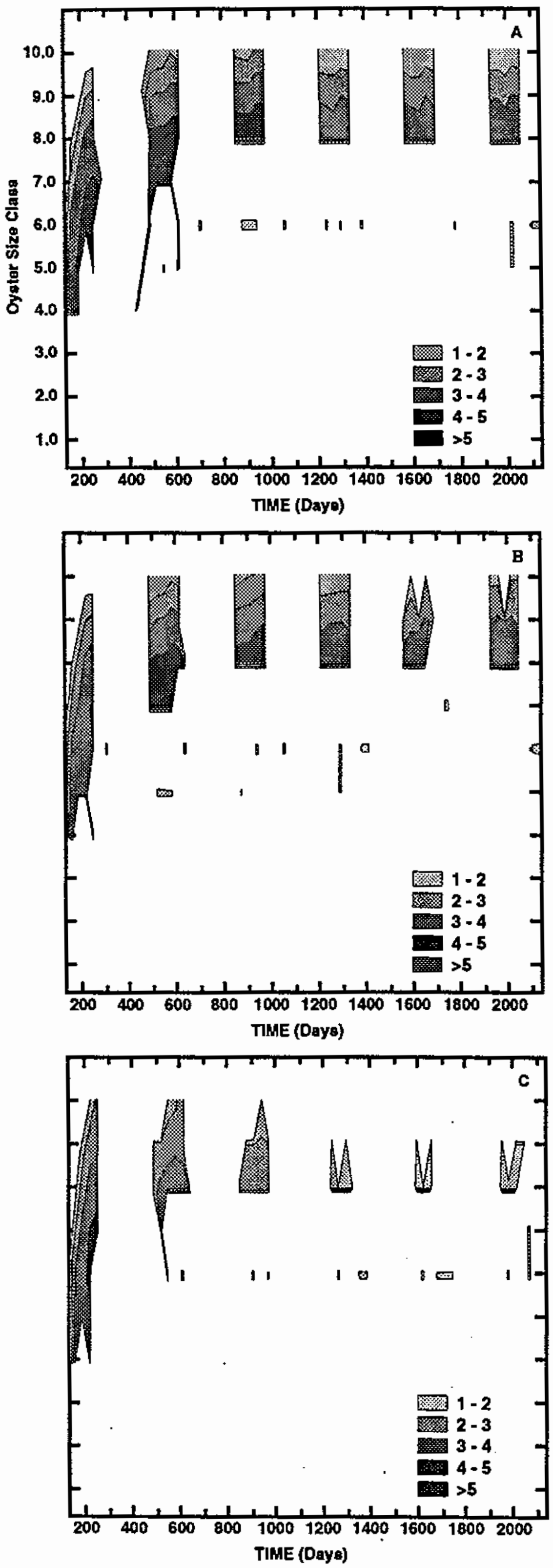

Figure 12. Comparison of spawning intensity versus oyster population size in A) Laguna Madre, B) Galveston Bay and C) Chesapeake Bay. Spawning intensity is shown as $\log_{10}$ calories spawned with a contour interval of 1. Spawning intensity for Laguna Madre and Chesapeake Bay was obtained from the simulated oyster populations shown in Figures 9b and 9a, respectively. The Galveston Bay spawning intensity was obtained from the constant salinity simulation that was essentially identical to the simulation results shown in Figure 6a.

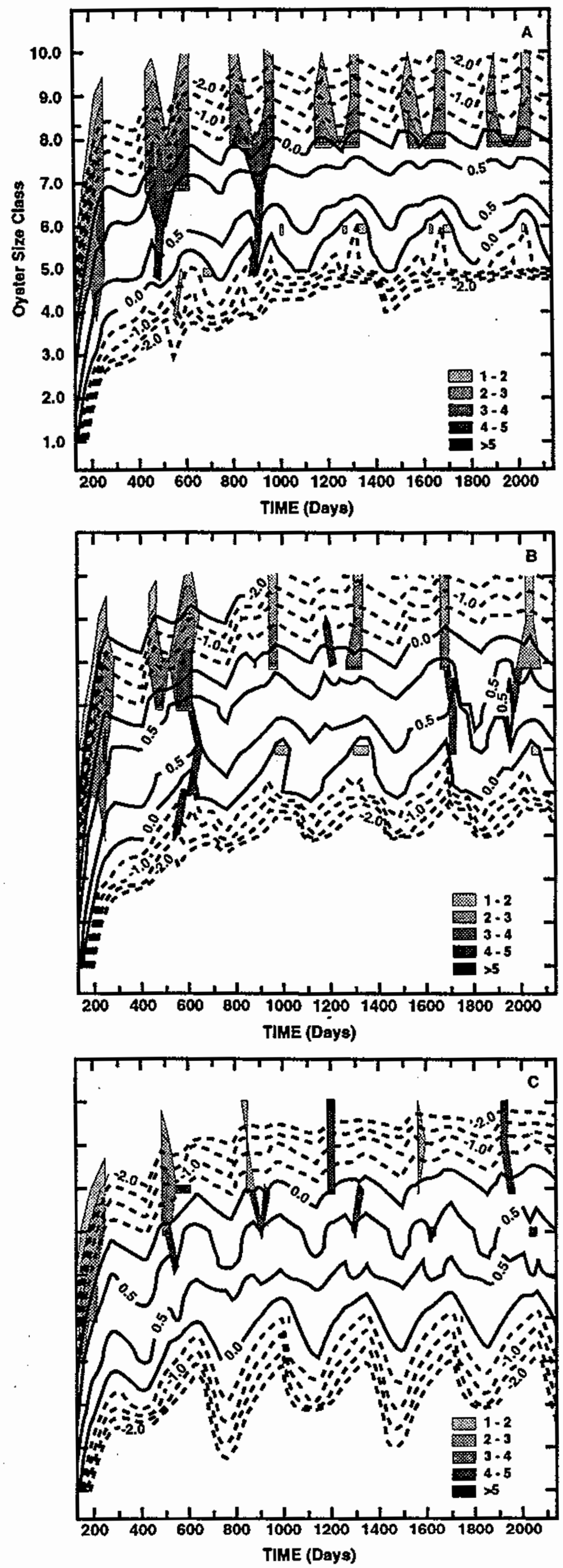

Figure 13. Simulated oyster population distribution and spawn production for A) Laguna Madre, B) Galveston Bay and C) Chesapeake Bay obtained using an idealized food time series. Spawning intensity is shown as $\log_{10}$ calories spawned with a contour interval of 1. Otherwise same as Figure 4.

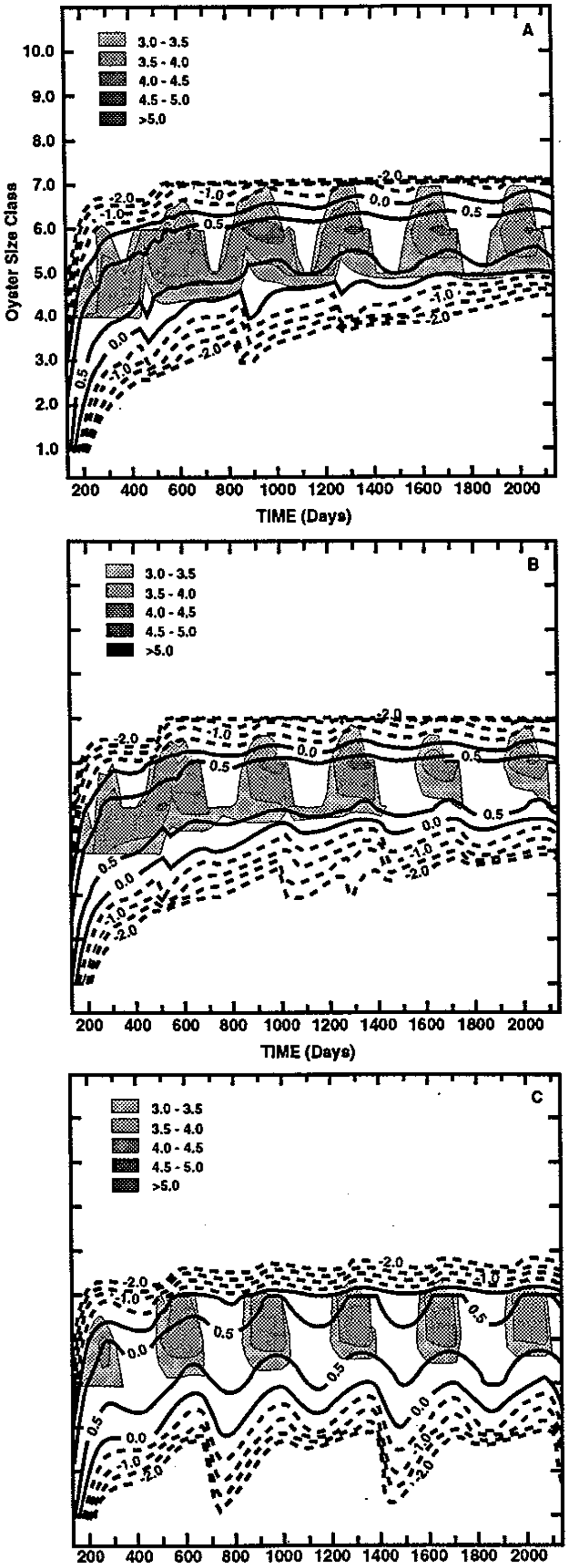

Figure 10. Simulated oyster population distribution and gonadal tissue development that results from constant low food (0.5 mg l^{-1}) supply and environmental conditions characteristic of A) Laguna Madre, B) Apalachicola Bay and C) Chesapeake Bay. Otherwise same as Figure 4.

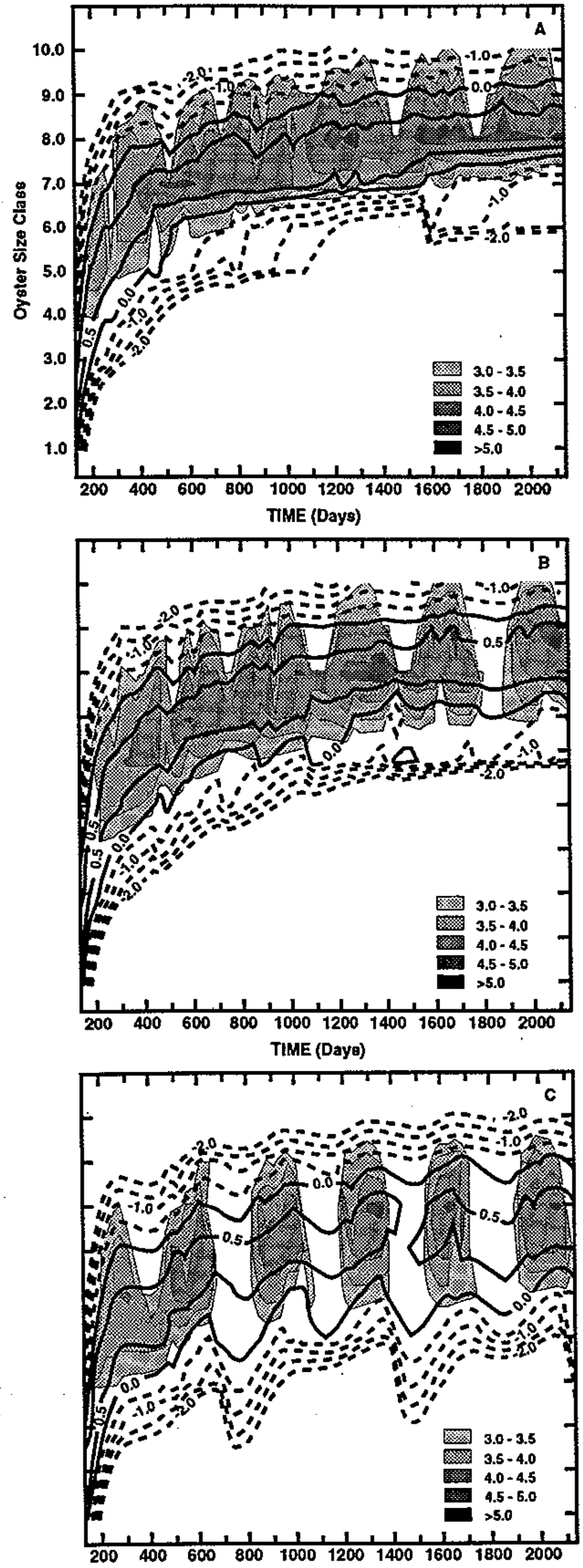

Figure 11. Simulated oyster population distribution and gonadal tissue development that results from medium food (1.0 mg l^{-1}) supply and environmental conditions characteristic of A) Laguna Madre, B) Apalachicola Bay and C) Chesapeake Bay. Otherwise same as Figure 4.

many individuals reach adult size typical of the lower latitude sites despite the cooler temperatures and more restricted growing season (e.g. Butler 1953b).

Adult Size (Biomass)

The shape of the growth curve for bivalves—whether size continuously increases at some declining rate or asymptotes to some maximum size (e.g. Levinton and Bambach 1970)—is probably more a function of environment than genetics. It is significant that the simulated oyster populations reached sizes characteristic of populations throughout the latitudinal range from Laguna Madre to Chesapeake Bay solely on the basis of physiology and environment. No upper limit for oyster growth or adult size was included in any of the formulations used to describe oyster physiology. Limitations on size in the simulated populations come from the balance between winter and summer somatic production less the energy expended in reproduction:

$$P_{gj_{summer}} - P_{gj_{winter}} = A_j - P_{rj}. \qquad (15)$$

In adult oysters, net production is normally negative in the winter and for the most part is balanced by somatic growth in the spring and fall. Cessation or slowing of growth in the summer (e.g. Beaven 1950) in disease-free oyster populations is normally due to reproduction and spawning which accounts for most of the net production in older animals. Hence, the relationship given above should result in a stable, but seasonally-oscillating, variation in adult oyster size. In the simulated population distributions, the balance between winter loss in net production and spring-summer-fall gain begins in the second or third year depending on the ambient temperature and food supply. Exceptions to this occur only when food supply is very high.

Growth rate in the hard clam, *Mercenaria mercenaria,* has a concave parabolic relationship with temperature (Ansell 1968). Growth rates are lowest at low and high seasonal temperatures and maximum at intermediate temperatures. Multiplying equations 4 and 12, and assuming a food supply adequate to minimize the effect of respiration on the energy budget and ignoring the dependence of filtration rate on length, yields a parabolic dependence for oyster growth rate on temperature of the same form

$$G \propto bT - aT^2 \qquad (16)$$

where a and b are the constants in equation 12 and T is temperature. If equation (16) is applied over the latitudinal range from Laguna Madre to Chesapeake Bay, then oyster growth rate and hence size should decrease at the southern and northern ends of the distribution. Maximum growth rate and largest adult size would be found near the center of this range. However, both the oyster and the hard clam (Ansell 1968) deviate from this expected distribution in that adult size remains constant over a wide latitudinal range that includes habitats from the northern Gulf of Mexico to north of Delaware Bay.

The observed rather than expected [as suggested by equation (16)] latitudinal distribution in size is also reproduced in the simulated oyster population distributions. This relationship between size and latitude arises through temperature effects on the allocation of net production to somatic and reproductive tissue growth and on filtration rate which determines the rate of food acquisition. The longer periods of low temperature in the spring and fall found at higher latitudes result in more time in which food is plentiful occurring at temperatures that favor somatic growth. As a result, decreased filtration rates at lower temperatures are balanced by an increase in food apportioned to somatic growth and size remains stable. Reproductive potential, however, declines in these populations.

Reduced size at lower latitudes is common in bivalves (e.g. Bauer 1992). Such a gradient in animal size can result from variations in temperature in one of two ways. First, an environment characterized by low food supplies and warm temperatures can produce large adult oysters despite increased reproduction because the total gain in energy from higher winter filtration rates results in a net accumulation of somatic tissue. The decline in size at low latitudes in the Gulf of Mexico suggests that this is not the normal condition. Alternatively, an environment characterized by moderate-to-high food supply and warm temperatures can produce smaller adult oysters because the greater allocation of net production to reproduction balances the positive effect of temperature on the rate of food acquisition. This is the more usual case.

Stunting, the presence of a relatively small adult size in a population, is generally considered to result from restricted food supply. The results of this modeling study suggest that, at least for oysters, temperature and reproductive effort are also important in restricting animal size. Hence, stunted populations can occur at the edge of the species' range where physiology directly limits size as well as in populations that fail to reach the size expected for their position within the latitudinal range.

The observed oyster sizes from around the Gulf of Mexico (Fig. 1) show two exceptions to the general trend of decreasing size at lower latitudes. It should be noted that the data presented in Figure 1 are in terms of length, rather than biomass, and so are subject to the aforementioned caveats concerning the plasticity of oyster growth form. First, the adult length observed at lower latitudes on both sides of the Gulf of Mexico is about 1 to 2 cm less than the average length observed in the northern Gulf. Such a length decrease is not easily produced in the simulated populations with a simple reduction in temperature and one biomass-length relationship. A 0.5 to 1 cm reduction in length is typical of the simulated populations. A temperature-dependent change in growth form modifying the size-to-biomass relationship may also be involved. Second, oysters from Moblie Bay through the Florida Panhandle area and in Tiger Pass on the Mississippi Delta are unusually small. This region characteristically has the coldest winter temperatures in the Gulf of Mexico (Collier 1954). However, the possibility that the colder temperatures reduce the growing season and thus limit adult size is not supported by the simulated populations. Even colder temperatures in Chesapeake Bay fail to reduce adult biomass. Either food supply is unusually meager in these two areas or mortality rates are unusually high. Thus, stunting may be of local (Tiger Pass) or regional (Florida Panhandle) extent. The effect of a change in growth form can be discounted in this case because the length-biomass relationship given in White et al. (1988) is adequate for at least some of these populations.

Butler (1953b) showed that oysters in Chesapeake Bay and the northern Gulf of Mexico reached about the same size in terms of length. The simulations summarized in Figure 14 generally show that Gulf of Mexico oysters slightly exceed Chesapeake Bay oysters in length when biomass is converted using a single length-biomass relationship. A latitudinal difference in growth form would explain this differential. Kent (1988) describes a wide range in growth forms from Chesapeake Bay, so that within-bay variations cannot be discounted. However, the relationship given in Paynter and DiMichele (1990) for a Chesapeake Bay population from Tolley Point Bar predicts oysters much longer for a given

TABLE 4.

Reproductive effort, average adult size and the ratio of the two calculated from year six of the simulated populations shown in the indicated figures. One simulation used is not shown (NS). This simulation used monthly-averaged temperature and food conditions from Galveston Bay, Texas, a constant salinity of 24 ppt and no turbidity. The results of this simulation were similar to those shown in Figure 6a. Size and reproductive effort are based on simulations tbat used the environmental time series defined in Table 3. Lower food supply, higher turbidity, or the inclusion of disease (e.g. *Perkinsus marinus*) could be expcected to reduce thses values.

Location	Reproductive Effort (kcal)	Average Size (g dry wt)	Ratio (kcal:g dry wt^{-1})	Figure Number
Laguna Madre vs.	266.71	4.87	54.77	11a
Galveston Bay	260.92	5.12	50.96	NS
Laguna Madre vs.	218.79	4.62	47.36	13a
Galveston Bay	179.03	4.89	36.61	13b
Galveston Bay vs.	129.77	4.73	27.44	13a
Chesapeake Bay	47.47	4.24	11.19	13c
Galveston Bay vs.	156.49	5.18	30.21	6a
Galveston Bay	24.21	1.81	13.36	6b

However, most of the net production is allocated to reproductive rather that somatic tissue development.

DISCUSSION AND SUMMARY

General Characteristics

Adult size and reproductive effort in oyster populations are determined by the temperature- and season-dependent allocation of net production to somatic and reproductive tissue development which in turn depends upon the temperature regulation of filtration rate. Salinity and turbidity affect oyster physiology through a reduction in the rate of food acquisition and cannot be distinguished from a simple reduction in food supply. Although respiration rate varies non-linearly with body mass and is affected by salinity, the overall effect of environmental conditions on respiration rate is small and can be ignored, in most situations.

A summary of simulated adult oyster size that results from variations in local and latitudinal controls on growth is given in Figure 14. These simulations considered only environmental control on oyster biomass. Oyster growth form is extremely plastic, although Kent (1988) argues for some predictable influences of local habitat. Nevertheless, the shell length achieved in the various simulated populations may vary over a wide range (Table 2). Unfortunately, much of the available oyster measurements are in terms of shell length or condition index rather than biomass. In this discussion, except where noted, oyster size is considered strictly in terms of biomass, and where needed, conversions to length are done as shown in Table 2.

The simulations indicate that adult oysters in Chesapeake Bay tend to be about the same size in terms of biomass as those in Galveston Bay (Fig. 14a), when presented with equivalent food supplies, salinities and levels of turbidity, despite the difference in temperature regimes. Water temperatures in Chesapeake Bay tend to be colder for longer periods than in Galveston Bay. Thus, the temperature-dependent control on the allocation of net production results in more going to somatic rather than reproductive tissue development.

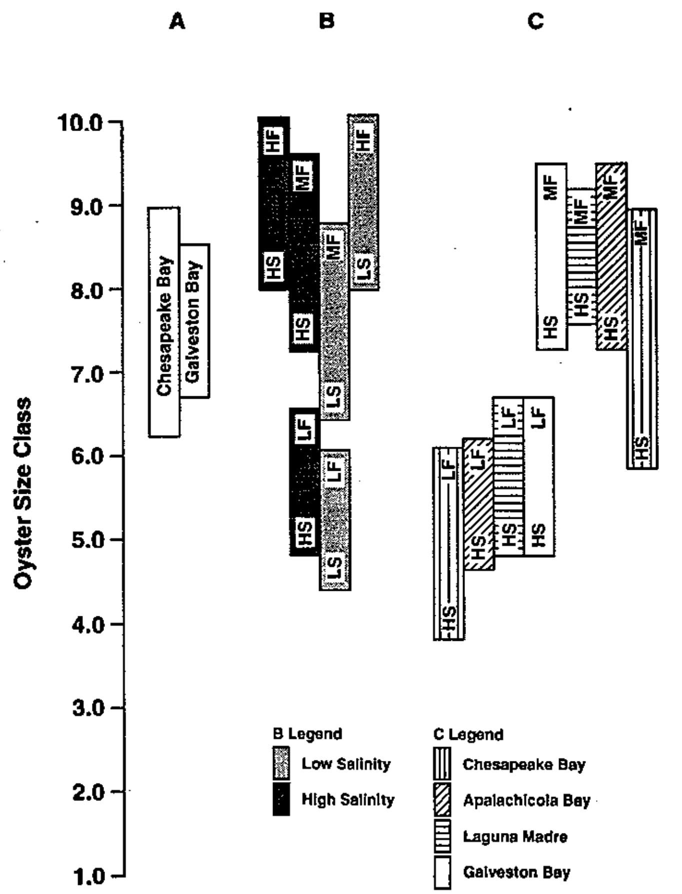

Figure 14. Comparison of adult size from year six of the simulations from A) Galveston and Chesapeake Bays (Figs. 6a and 9a), B) Galveston Bay for high and low salinity at a range of food concentrations (Figs. 4a, 5 and 7) and C) four bays and a range of food concentrations. High and low salinity values are 24 ppt and 7 ppt and are designated by HS and LS, respectively. Designations for high (1.5 mg l^{-1}), medium (1.0 mg l^{-1}), and low (0.5 mg l^{-1}) food concentrations are HF, MF and LF, respectively.

Variations in local environmental conditions also affect adult oyster biomass. Low salinity conditions in an environment such as Galveston Bay can result in reduced adult size (Fig. 14b). However, the effect of low salinity can be compensated for by increases in food supply. Low salinity conditions combined with high food conditions can result in adult biomass that is similar to that obtained during high salinity conditions. The largest reduction in adult oyster size occurs when low salinity is combined with a restricted food supply.

The importance of food in determining adult biomass over a latitudinal range is illustrated in Figure 14c. For all bays, low food conditions produced adult oysters that were about the same size, size classes 5 to 6. The only exception is Chesapeake Bay where somewhat smaller, size class 4, adult oysters are produced by low food conditions. Medium food conditions result in larger adult oysters for all bays with minimal overlap with the size produced by low food conditions. Galveston and Apalachicola Bays have similar sized adult oyster populations. Individuals in Laguna Madre tend to be a bit smaller. The warmer temperatures in Laguna Madre result in more of net production going to form reproductive tissue, thereby producing more spawn and smaller individuals. Chesapeake Bay populations show a wider range of adult size, but weight and this prediction agrees with a biomass-length relationship obtained by Newell (University of Maryland, pers. comm.) from the Choptank River subestuary of the Chesapeake Bay. Lunz (1938) suggested that a primary influence of anthropogenic activities on oyster growth form was to decrease width and length, but with more of an effect on width. If true, this would explain a perceived variation between oyster size reported by Butler (1953b) and the more recent measurements reported by Paynter and DiMichele (1990) and Newell (University of Maryland, pers. comm.). Unfortunately, the observations reported in Butler (1953b) are not in terms of biomass. The same trend might explain the tendency in the simulated oyster populations from Chesapeake Bay to be slightly lower in weight and, therefore, length, than the northern Gulf of Mexico oysters (e.g. Fig. 11). The weight obtained from the simulated populations would result in a longer oyster in Chesapeake Bay using the conversions of Paynter and DiMichele (1990) and Newell (University of Maryland, pers. comm.).

The simulated oyster populations suggest an explanation for the concordance in year-to-year oscillations in oyster size throughout the Gulf of Mexico (Wilson et al. 1992). Climatic cycles, such as El Niño, change the Gulf-wide temperature and rainfall regime (Powell et al. 1992a). Size, through the direct effect of temperature on the allocation of net production to somatic and reproductive tissue or indirectly through variations in food supply, could be affected by climatic variations in temperature and rainfall. Furthermore, such climatic effects are likely introduced through variations in temperature during the colder part of the year. For example, the difference between a warm and cold winter could be sufficient to significantly alter adult size.

Reproduction

The reproductive processes included in the oyster population model are based upon simple empirical relationships; however, the simulated population distributions show trends typical of oyster populations throughout the east coast of the U.S. and the Gulf of Mexico. This suggests that reproductive effort in oysters is primarily a function of a genetically-determined temperature-dependent allocation of net production into somatic and reproductive tissue development and an environmentally determined scope for growth. This temperature dependency may be described by simple linear relationships such as those given by equations (12) and (13) which may reflect temperature-dependent reaction rates in protein synthesis or hormonal control. The mechanism underlying the temperature-dependent allocation of net production would appear to be an important unknown in the reproductive physiology of oysters.

Reproductive potential is the result of the same physiological and environmental conditions that govern adult size, i.e. the temperature- and season-dependent rate of food acquisition and the temperature-dependent allocation of net production into somatic growth and reproduction. However, small changes in either result in more pronounced changes in reproductive effort than in adult size. For example, the rate of food acquisition is higher in warmer months when most net production is allocated to reproduction. Hence, small changes in available food are magnified during this period. The effect of small variations in environmental conditions on oyster reproduction and spawning is discussed in detail by Hofmann et al. (1992).

The wide range of reproductive efforts produced from small changes in temperature or food supply suggests that comparisons of reproductive effort between oyster populations can only be made within the context of a complete environmental analysis of food supply, environmental conditions and a total energy budget for the animal. The wide range of reproductive efforts reported for bivalves in general (see Powell and Stanton 1985 for a review) probably results from these interactions. Thus, correlations between size and reproductive effort will be location and time specific, and general conclusions based upon such correlations may not be valid. For example, the relationship between temperature and reproduction given by Kaufman (1979) requires similar rates of food acquisition among populations to provide valid comparisons.

The assumption that populations of larger individuals should reproduce more is not always correct. For many situations, populations of smaller individuals may have a greater reproductive effort per unit of biomass. The simulated population distributions suggest that decreases in reproductive effort are related to increased size rather than to age. The apparent reproductive senility in these populations results from the differential scaling of filtration and respiration rate with body size, which reduces scope for growth at a given food supply in larger animals.

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LITERATURE CITED

Ansell, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographical range. *J. Cons. Perm. Int. Explor. Mer.* 31:364–409.

Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. *J. Anim. Ecol.* 61:425–436.

Beaven, G. F. 1950. Growth observations of oysters held on trays at Solomons Island, Maryland. *Proc. Natl. Shellfish. Assoc. for 1949* 43–49.

Beaven, G. F. 1952. Some observations on rate of growth of oysters in the Maryland area. *Conv. Add. Natl. Shellfish. Assoc.* 90–98.

Berg, J. A. & R. I. E. Newell. 1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuar. Coastal Shelf Sci.* 23:375–386.

Berrigan, M. E. 1990. Biological and economical assessment of an oyster resource development project in Apalachicola Bay, Florida. *J. Shellfish Res.* 9:149–158.

Boucher, G. & R. Boucher-Rodoni. 1988. In situ measurement of respiratory metabolism and nitrogen fluxes at the interface of oyster beds. *Mar. Ecol. Prog. Ser.* 44:229–238.
Burkenroad, M. D. 1931. Sex in the Louisiana oyster, *Ostrea virginica*. *Science* 74:71–72.
Butler, P. A. 1949. Gametogenesis in the oyster under conditions of depressed salinity. *Biol. Bull. (Woods Hole)* 96:263–269.
Butler, P. A. 1953a. Importance of local environment in oyster growth. *Proc. Gulf Caribb. Fish. Inst.* 5:99–106.
Butler, P. A. 1953b. Oyster growth as affected by latitudinal temperature gradients. *Commer. Fish. Rev.* 15(6):7–12.
Butler, P. A. 1955. Reproductive cycle in native and transplanted oysters. *Proc. Natl. Shellfish. Assoc.* 46:75–81.
Chanley, P. E. 1958. Survival of some juvenile bivalves in water of low salinity. *Proc. Natl. Shellfish. Assoc.* 48:52–65.
Choi, K. S., D. H., Lewis, E. N. Powell & S. M. Ray. 1993. Quantitative measurement of reproductive output in the American oyster, *Crassostrea virginica* (Gmelin), using an enzyme-linked immunosorbent assay (ELISA). *Aquaculture and Fisheries Management* 24:299–322.
Coe, W. R. 1936. Environment and sex in the oviparous oyster *Ostrea virginica*. *Biol. Bull. (Woods Hole)* 71:353–359.
Collier, A. 1954. A study of the response of oysters to temperature, and some long range ecological interpretations. *Natl. Shellfish. Assoc. Conv. Pap. for 1953* 13–38.
Conover, W. J. 1972. A Kolmogorov goodness-of-fit test for discontinuous distributions. *J. Am. Stat. Assoc.* 67:591–596.
Craig, M. A., E. N. Powell, R. R. Fay & J. M. Brooks. 1989. Distribution of *Perkinsus marinus* in Gulf coast oyster populations. *Estuaries* 12:82–91.
Cummins, K. W. & J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Int. Ver. Theor. Angea. Limnol. Verh.* 18:1–158.
Dame, R. F. 1972. The ecological energies of growth, respiration and assimilation in the intertidal American oyster *Crassostrea virginica*. *Mar. Biol. Berl.* 17:243–250.
Davis, H. C. & P. E. Chanley. 1956. Spawning and egg production of oysters and clams. *Proc. Natl. Shellfish. Assoc.* 46:40–58.
Dekshenieks, M., E. E. Hofmann & E. N. Powell. 1993. Environmental effects on the growth and development of the larvae of *Crassostrea virginica:* a modeling study. *J. Shellfish Res.* 12:241–254.
Doering, P. H. & C. A. Oviatt. 1986. Application of filtration rate models to field populations of bivalves: An assessment using experimental mesocosms. *Mar. Ecol. Prog. Ser.* 31:265–275.
Dupuy, J. L., N. T. Windsor & C. E. Sutton. 1977. Manual for design and operation of an oyster seed hatchery. Virginia Institute of Marine Science, Gloucester Point, Virginia. 104 pp.
Engle, J. B. 1947. Commercial aspects of the upper Chesapeake Bay oyster bars in light of the recent oyster mortalities. *Proc. Natl. Shellfish. Assoc. for 1946* 42–46.
Epifanio, C. E. & J. Ewart. 1977. Maximum ration of four algal diets for the oyster *Crassostrea virginica* (Gmelin). *Aquaculture* 11:13–29.
Ford, S. E. & A. J. Figueras. 1988. Effects of sublethal infection by the parasite *Halosporidium nelsoni* (MSX) on gametogenesis, spawning, and sex ratios of oysters in Delaware Bay, USA. *Dis. Aquat. Org.* 4:121–133.
Gallager, S. M. & R. Mann. 1986. Growth and survival of *Mercenaria mercenaria* (L.) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. *Aquaculture* 56:105–121.
Galtsoff, P. S., W. A. Chipman, Jr., J. B. Engle & H. N. Calderwood. 1947. Ecological and physiological studies of the effect of sulphate pulp mill wastes on oysters in the York River, Virginia. *U.S. Fish Wildl. Serv. Fish. Bull.* 51:58–186.
Garton, D. W. 1986. Effect of prey size on the energy budget of a predatory gastropod, *Thais haemastoma canaliculata* (Gray). *J. Exp. Mar. Biol. Ecol.* 98:21–33.
Gennette, A. F. & S. W. Morey. 1971. The effects of heated water on the gonadal development of the oyster *Crassostrea virginica* (Gmelin). *Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser.* 13:98–104.
Grady, J. M., T. M. Soniat & J. S. Rogers. 1989. Genetic variability and gene flow in populations of *Crassostrea virginica* (Gmelin) from the northern Gulf of Mexico. *J. Shellfish Res.* 8:227–232.
Hallam, A. 1965. Environmental causes of stunting in living and fossil marine bethonic invertebrates. *Palaeontology (Lond.)* 8:132–155.
Haven, D. S. & R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol. Oceanogr.* 11: 487–498.
Hayes, P. F. & R. W. Menzel. 1981. The reproductive cycle of early setting *Crassostrea virginica* (Gmelin) in the northern Gulf of Mexico, and its implications for population recruitment. *Biol. Bull. (Woods Hole)* 160:80–88.
Heffernan, P. B., R. L. Walker & J. L. Carr. 1989. Gametogenic cycles of three marine bivalves in Wassaw Sound Georgia II *Crassostrea virginica* (Gmelin, 1791). *J. Shellfish Res.* 8:61–70.
Hibbert, C. J. 1977. Growth and survivorship in a tidal-flat population of the bivalve *Mercenaria mercenaria* from Southampton Water. *Mar. Biol., Berl.* 44:71–76.
Higgins, P. J. 1980a. Effects of food availability on the valve movements and feeding behavior of juvenile *Crassostrea virginica* (Gmelin). I. Valve movements and periodic activity. *J. Exp. Mar. Biol. Ecol.* 45: 229–244.
Higgins, P. J. 1980b. Effects of food availability on the valve movements and feeding behavior of juvenile *Crassostrea virginica* (Gmelin). II. Feeding rates and behavior. *J. Exp. Mar. Biol. Ecol.* 46:17–27.
Hofmann, E. E., E. N. Powell, J. M. Klinck & E. A. Wilson. 1992. Modeling oyster populations III. Critical feeding periods, growth and reproduction. *J. Shellfish Res.* 11(2):399–416.
Hofstetter, R. P. 1977. Trends in population levels of the American oyster *Crassostrea virginica* (Gmelin) on public reefs in Galveston Bay, Texas. *Tex. Parks Wildl. Dept. Tech. Rept.* 24:1–90.
Hopkins, A. E. 1935. Factors influencing the spawning and setting of oysters in Galveston Bay, Tex. *Bull. U.S. Bur. Fish.* 47:57–83.
Ingle, R. M. 1951. Spawning and setting of oysters in relation to seasonal environmental changes. *Bull. Mar. Sci. Gulf Caribb.* 1:111–135.
Kaufman, Z. F. 1979. Dependence of the time of gamete maturations and spawning on environmental temperature in the Virginia oyster *Crassostrea virginica*. *Hydrobiol. J. (Engl. Transl. Gidrobiol. Zh.)* 14:29–30.
Kennedy, A. V. & H. I. Battle, 1964. Cyclic changes in the gonad of the American oyster, *Crassostrea virginica* (Gmelin). *Can. J. Zool.* 42: 305–321.
Kennedy, V. S. & L. B. Krantz. 1982. Comparative gametogenic and spawning patterns of the oyster *Crassostrea virginica* (Gmelin) in central Chesapeake Bay. *J. Shellfish Res.* 2:133–140.
Kent, B. 1988. Making Dead Oysters Talk. Techniques for Analyzing Oysters from Archaeological Sites. Maryland Historical Trust, Jefferson Patterson Park and Museum, Maryland. 105 pp.
Klinck, J. M., E. N. Powell, E. E. Hofmann, E. A. Wilson & S. M. Ray. 1992. Modeling oyster populations: The effect of density and food supply on production. *Proc. Adv. Mar. Tech. Conf.* 5:85–105.
Langefoss, C. M. & D. Maurer. 1975. Energy partitioning in the American oyster, *Crassostrea virginica* (Gmelin). *Proc. Natl. Shellfish. Assoc.* 65:20–25.
Levinton, J. S. & R. K. Bambach. 1970. Some ecological aspects of bivalve mortality patterns. *Am. J. Sci.* 268:97–112.
Loosanoff, V. L. 1953. Behavior of oysters in water of low salinities. *Proc. Natl. Shellfish. Assoc.* 43:135–151.
Loosanoff, V. L. 1958. Some aspects of behavior of oysters of different temperatures. *Biol. Bull. (Woods Hole)* 114:57–70.
Loosanoff, V. L. 1965. Gonad development and discharge of spawn in oysters of Long Island Sound. *Biol. Bull. (Woods Hole)* 114:546–561.
Loosanoff, V. L. 1969. Maturation of gonads of oysters, *Crassostrea virginica*, of different geographical areas subjected to relatively low temperatures. *Veliger* 11:153–163.

Loosanoff, V. L. & H. C. Davis. 1953. Temperature requirements for maturation of gonads of northern oysters. *Biol. Bull.* (*Woods Hole*) 103:80–96.

Loosanoff, V. L. & F. D. Tommers. 1948. Effect of suspended silt and other substances on rate of feeding of oysters. *Science* 107:69–70.

Lunz, G. R. 1938. Comparison between pre-colonial and present-day oysters. *Science* (*Wash. D.C.*) 87:367.

Matthiessen, G. C., S. Y. Feng & L. Leibovitz. 1990. Patterns of MSX (*Haplosporidium nelsoni*) infection and subsequent mortality in resistance and susceptible strains of Eastern oyster, *Crassostrea virginica* (Gmelin, 1791), in New England. *J. Shellfish Res.* 9:359–365.

Moore, D. & L. Trent. 1971. Setting, growth and mortality of *Crassostrea virginica* in a natural marsh and a marsh altered by a housing development. *Proc. Natl. Shellfish. Assoc.* 61:51–58.

Newell, R. I. E. 1985. Physiological effects of the MSX parasite *Haplosporidium nelsoni* (Haskin, Stauber & Mackin) on the American oyster *Crassostrea virginica* (Gmelin). *J. Shellfish Res.* 5:91–95.

Newell, R. I. E. & S. J. Jordan. 1983. Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 13:47–53.

Palmer, R. E. & L. G. Williams. 1980. Effect of particle concentration on filtration efficiency of the bay scallop *Argopecten irradians* and the oyster *Crassostrea virginica*. *Ophelia* 19:163–174.

Paynter, K. T. & L. DiMichele. 1990. Growth of tray-cultured oysters (*Crassostrea virginica*) in Chesapeake Bay. *Aquaculture* 87:289–297.

Peterson, C. H. 1983. A concept of quantitative reproductive senility: application to the hard clam, *Mercenaria mercenaria*. *Oecologia* (*Berl.*) 58:164–168.

Pipe, R. K. 1985. Seasonal cycles in and effects of starvation on egg development in *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 24:121–128.

Powell, E. N., J. D. Gauthier, E. A. Wilson, A. Nelson, R. R. Fay & J. M. Brooks. 1992a. Oyster disease and climate change. Are yearly changes in *Perkinsus marinus* parasitism in oysters (*Crassostrea virginica*) controlled by climatic cycles in the Gulf of Mexico? *P. S. Z. N. I.: Mar. Ecol.* 13:243–270.

Powell, E. N., E. E. Hofmann, J. M. Klinck & S. M. Ray. 1992b. Modeling oyster populations I. A commentary on filtration rate. Is faster always better? *J. Shellfish Res.* 11(2):387–398.

Powell, E. N. & R. J. Stanton, Jr. 1985. Estimating biomass and energy flow of molluscs in palaeo-communities. *Paleontology* (*Lond.*) 28:1–34.

Quick, J. A., Jr. & J. G. Mackin. 1971. Oyster parasitism by *Labyrinthomyxa marina* in Florida. *Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser.* 13:1–55.

Ray, S. M. & A. C. Chandler. 1955. *Dermocystidium marinum*, a parasite of oysters. *Exp. Parasitol.* 4:172–200.

Reeb, C. A. & J. C. Avise. 1990. A genetic discontinuity in a continuously distributed species: mitochondrial DNA in the American oyster, *Crassostrea virginica*. *Genetics* 124:397–406.

Shumway, S. E. & R. K. Koehn. 1982. Oxygen consumption in the American oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 9:59–68.

Soniat, T. M. 1982. Studies on the nutritional ecology and ecological energetics of oysters from Galveston Bay. Ph.D. dissertation, Texas A&M University. 162 pp.

Soniat, T. M. & S. M. Ray. 1985. Relationships between possible available food and the composition, condition and reproductive state of oysters from Galveston Bay, Texas. *Contrib. Mar. Sci.* 28:109–121.

Soniat, T. M., S. M. Ray & L. M. Jeffrey. 1984. Components of the seston and possible available food for oysters in Galveston Bay, Texas. *Contrib. Mar. Sci.* 27:127–141.

Stauber, L. A. 1950. The problem of physiological species with special reference to oysters and oyster drills. *Ecology* 31:109–118.

Tenore, K. R. & W. M. Dunstan. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Mar. Biol.* 21:190–195.

Valenti, C. C. & C. E. Epifanio. 1981. The use of a biodeposition collector for estimation of assimilation efficiency in oysters. *Aquaculture* 25:89–94.

White, M. E., E. N. Powell & S. M. Ray. 1988. Effects of parasitism by the pyramidellid gastropod *Boonea impressa* on the net productivity of oysters (*Crassostrea virginica*). *Estuar. Coastal Shelf Sci.* 26:359–377.

Wilson, E. A., E. N. Powell, M. A. Craig, T. L. Wade & J. M. Brooks. 1990. The distribution of *Perkinsus marinus* in Gulf coast oysters: Its relationship with temperature, reproduction, and pollutant body burdens. *Int. Rev. Gesamten Hydrobiol.* 75:533–550.

Wilson, E. A., E. N. Powell, T. L. Wade, R. J. Taylor, R. J. Presley & J. M. Brooks. 1992. Spatial and temporal distributions of contaminant body burden and disease in Gulf of Mexico oyster populations: the role of local and large-scale climatic controls. *Helgol. Meeresun.* 46:201–235.

Winter, J. E. 1978. A review on the knowledge of suspension-feeding in lamelli-branchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13:1–33.

Wright, D. A. & E. W. Hetzel. 1985. Use of RNA:DNA ratios as an indicator of nutritional stress in the American oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 25:199–206.