1998

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Thomas M. Soniat

Eric N. Powell

Eileen E. Hofmann
Old Dominion University, ehofmann@odu.edu

John M. Klinck
Old Dominion University, jklinck@odu.edu

Original Publication Citation

Soniat, T.M., Powell, E.N., Hofmann, E.E., & Klinck, J.M. (1998). Understanding the success and failure of oyster populations: The importance of sampled variables and sample timing. *Journal of Shellfish Research, 17*(4), 1149-1165.

Journal of Shellfish Research, Vol. 17, No. 4, 1149–1165, 1998.

UNDERSTANDING THE SUCCESS AND FAILURE OF OYSTER POPULATIONS: THE IMPORTANCE OF SAMPLED VARIABLES AND SAMPLE TIMING

THOMAS M. SONIAT,[1] ERIC N. POWELL,[2]
EILEEN E. HOFMANN,[3] AND JOHN M. KLINCK[3]
[1]*Department of Biological Sciences*
Nicholls State University
Thibodaux, Louisiana 70310
[2]*Haskin Shellfish Research Laboratory*
Institute of Marine and Coastal Sciences
Rutgers, The State University of New Jersey
Port Norris, NJ 08349-9736
[3]*Center for Coastal Physical Oceanography*
Old Dominion University
Norfolk, Virginia 23529

ABSTRACT One of the primary obstacles to understanding why some oyster populations are successful and others are not is the complex interaction of environmental variables with oyster physiology and with such population variables as the rates of recruitment and juvenile mortality. A numerical model is useful in investigating how population structure originates out of this complexity. We have monitored a suite of environmental conditions over an environmental gradient to document the importance of short time-scale variations in such variables as food supply, turbidity, and salinity. Then, using a coupled oyster disease population dynamics model, we examine the need for short time-scale monitoring. We evaluate the usefulness of several measures of food supply by comparing field observations and model simulations. Finally, we evaluate the ability of a model to reproduce field observations that derive from a complex interplay of environmental variables and address the problem of the time-history of populations. Our results stress the need to evaluate the complex interactions of environmental variables with a numerical model and, conversely, the need to evaluate the success of modeling against field observations of the results of complex processes. Model simulations of oyster populations only approached field observations when the environmental variables were measured weekly, rather than monthly. Oyster food supply was estimated from measures of total particulate organic matter, phytoplankton biomass estimated from chlorophyll a, and total labile organic matter estimated from a regression between chlorophyll a and total labile carbohydrate, lipid, and protein. Only the third measure provided simulations comparable to field observations. Model simulations also only approached field observations when a multiyear time series was used. The simulations show that the most recent year exerts the strongest influence on oyster population attributes, but that the longer time-history modulates the effect. The results emphasize that year-to-year changes in environment contribute substantially to observed population attributes and that multiyear environmental time series are important in describing the time-history of relatively long-lived species.

KEY WORDS: *Crassostrea virginica,* modeling, *Perkinsus marinus,* population dynamics, seston

INTRODUCTION

The American oyster, *Crassostrea virginica,* is notable for its ability to maintain commercial populations over a wide latitudinal range and over a wide range of local environmental gradients, chief of which are gradients in salinity, turbidity, and food supply. Although the American oyster is a well-studied species, the interaction of salinity, temperature, and food supply on commercially productive populations is still poorly understood and the degree to which other variables, such as current flow, are important under certain conditions remains largely unknown. Nevertheless, the interaction of salinity, turbidity, and food supply with the annual temperature cycle and their joint influence on the susceptibility of the American oyster to disease may explain much of the yearly variability observed in oyster populations.

The interaction of these variables, however, produces complex and sometimes counterintuitive results. Some high-salinity populations are productive, despite high disease intensities and heavy adult mortality, conditions that produce local extinctions elsewhere. Some low-salinity populations exhibit poor growth and low-productivity, despite the absence of disease, conditions that produce commercially important populations elsewhere. Modeling of oyster population dynamics has indicated that variations in food supply and turbidity, independent of salinity, may explain these diverse observations (Hofmann et al. 1992, Powell et al. 1994b). Food supply and turbidity are contrapuntal variables in their influence on oyster ingestion. Increased food supply normally results in increased ingestion, until ingestion is restricted by gut passage time (Hughes 1980). Increased turbidity reduces ingestion rate by reducing food quality and reducing filtration rate (Powell et al. 1992b, Loosanoff and Tommers 1948). Thus, food supply and turbidity are important mediators of population success over a wide range of environmental conditions.

The persistence and productivity of oyster populations is determined by a complex interaction of such environmental variables as temperature and food supply with oyster physiology and with such population variables as rates of recruitment and juvenile mortality. Modeling studies have emphasized this complexity (Powell et al. 1992b, Powell 1994b, Buxton et al. 1981, Soniat and Brody 1988). The complexity is also apparent in experimental studies evaluating the importance of many variables in population success (e.g., Buxton et al. 1981, Bayne et al. 1988, Ólafsson et al. 1994).

Combining field observation and numerical modeling to investigate the complex basis for population structure rests first on the collection of data necessary to describe the environmental and

biological milieu. Typically, data collection faces sampling limitations imposed by time and resources. Four aspects of this problem are pertinent. First, in many cases, only a limited suite of environmental and biological variables can be measured; however, the choice of which variables to measure may not be easily determined. Some may be more important in some places than in others, and the simplest to measure may not be the most important. Second, in some cases, as in the case of food supply, uncertainty exists in what should be measured. Various estimators of food supply, for example, include total organic carbon, total organic nitrogen, chlorophyll a, and lipid/carbohydrate/protein (Soniat et al. 1984, Soniat and Ray 1985, Wilson-Ormond et al. 1997). The assimilation efficiency of oysters varies profoundly across a variety of food resources differentially targeted by these measures (Langdon and Newell 1990, Powell et al. 1992b, Tshikhon-Lukanina 1982). Third, the frequency of sampling is an issue. Studies normally target sampling on once per month intervals. Fegley et al. (1992) and Wilson-Ormond et al. (1997) have shown the importance of short time-scale changes in environmental variables for oyster populations. Hofmann et al. (1992) emphasized the importance of the timing of phytoplankton blooms relative to the seasonal temperature cycle. Thus, events on less than month time-scales may be crucial in understanding population success. Fourth, on the other hand, Ulanowicz et al. (1980) and Powell et al. (1996), among others, discussed the importance of the time-history of the population in shaping population structure. Thus, the length of the time series may be crucial in interpreting differences in population structure. Any population represents the time-history of environmental events over at least the last few generations. The degree to which any one year's events control future population structure is not well understood, but certainly disease epizootics seem to have a multiyear history of development and decay (Powell et al. 1996). This generational effect will restrict the information gained from comparisons of simultaneously run biological and environmental sampling programs, while lengthening the necessary sampling period to encompass a longer time series.

The purpose of our investigation is threefold. First, we monitored a suite of environmental conditions over an environmental gradient to document the importance of short time-scale variations in such variables as food supply, turbidity, and salinity. Then, using a model, we examined the need for short time scale monitoring. Second, we evaluated the usefulness of several measures of food supply by comparing field observations and model simulations obtained using them. Finally, we evaluated the ability of a model to reproduce field observations that derive from a complex interplay of environmental variables, and we sought to determine the adequacy of our choice of monitoring variables. Along the way, we addressed the problem of generational memory or the time history of populations. Our results stress the need to evaluate the complex interactions of environmental variables with a numerical model and, conversely, the need to evaluate the success of modeling against field observations of the results of complex processes.

MATERIALS AND METHODS

Sample Sites and Protocol

Environmental variables, seston composition, and oyster population parameters were sampled from April 1992 to March 1993 at three sites in the Terrebonne Basin of southcentral Louisiana. Sample reefs along a salinity gradient were chosen to provide accessible, unharvested, unplanted, subtidal, and persistent populations of oysters. All sites were adjacent to Bayou Petit Caillou, a local source of fresh water. Site 1 (Savin Canal) is a low-salinity, protected (bayou-like) habitat, water depth 0.3 to 0.6 m. Site 2 (Bay Cocodrie) is an exposed bay-edge, low-salinity location with a depth of 0.6 to 0.9 m. Site 3 (Bay Tambour) is higher in salinity and semiprotected (bayou side of a marsh island in an open bay), water depth 0.3 to 0.6 m.

Environmental Variables

Environmental variables were measured weekly. Water temperature was measured to the nearest 0.1°C with a mercury thermometer. Salinity was determined (nearest 0.5‰) using a refractometer (Beherns 1965).

Seston

Water was sampled weekly from 0.3 m above the reef with a hand-operated peristaltic pump. Between 100 and 250 mL (depending upon turbidity) was filtered through 47-mm Gelman A/E glass fiber filters. The filters and filtrate were dried for 1 h at 103°C to obtain seston dry weight and subsequently ashed at 550°C for 15 min to determine particulate inorganic and particulate organic matter (POM) (American Public Health Assoc. 1971). Twenty-five mL of water was filtered through 25-mm Whatman GF/F glass fiber filters, extracted in 60:40 v:v 90% acetone: dimethyl sulfoxide, and read on a Turner Designs Model 10 fluorometer to measure chlorophyll a (Shoef and Lium 1976).

Food potentially available for oysters was estimated in three ways. First, measured POM was used directly. Second, chlorophyll a was converted to phytoplankton biomass using a chlorophyll-to-mg carbon conversion of 40 (Parsons et al. 1961) and a mg carbon-to-mg dry weight conversion of 2.14 (Widdows et al. 1979) as described by Wilson-Ormond et al. (1997). Third, food was estimated using a regression equation relating total labile carbohydrate, total protein, and total lipid to chlorophyll a obtained from studies in Galveston Bay, Texas (Soniat et al. 1984).

$$\text{Food} = \text{Total carbohydrate} + \text{Total lipid} + \text{Total protein}$$

$$= 0.088 * \text{chlorophyll a} + 0.520$$

where chlorophyll a is in $\mu L\ L^{-1}$, and food is in mg DW L^{-1}. This third method has the interesting attribute of increasing oyster food supply above that estimated by chlorophyll a and also increasing food supply disproportionately during the winter, when chlorophyll a values are normally low.

Oysters

About 0.13 m^3 of reefal material (enough to fill a 13.2-L bucket) was collected monthly by tonging. Live oysters, boxes (dead articulated shells), and single shells were separated. Live oysters were tallied and assigned to a 25 mm size class (e.g., 0 to 24 mm, 25 to 49 mm). Shells and live oysters were examined for the presence of spat.

Ten commercial-size (≥76 mm) live oysters were culled, cleaned of attached epifauna, and anterior-to-posterior length was measured to the nearest mm. Displacement volume before and after shucking was used to calculate mantle cavity volume (Galtsoff 1964). Gonadal thickness and adductor muscle diameter were measured with vernier calipers (nearest 0.1 mm) to calculate gonadal index.

$$\text{Gonadal Index} = \frac{\text{average gonadal thickness (mm)}}{\text{average diameter adductor muscle (mm)}} \cdot 100$$

(Soniat and Ray 1984). Sex was determined by blotting gonadal material onto a glass slide and observing the tissue at 100 X. Dry weight was determined by drying at 80 to 85°C to constant weight. Condition index was calculated as follows.

$$\text{Condition Index} = \frac{\text{oyster dry weight (g)}}{\text{mantle cavity volume (mL)}} \cdot 100$$

(Hopkins 1949).

A small piece of mantle tissue (about 4 mm^2) was used to assay for *Perkinsus marinus* (Ray 1966). Infection intensity was scored using Mackin's (1962) 0-to-5-point scale as modified by Craig et al. (1989). Population infection intensity was calculated as weighted incidence (WI).

$$\text{WI} = \frac{\Sigma \text{ Mackin's disease code number}}{\text{n}}$$

Oyster Perkinsus marinus *Model*

The oyster population dynamics model consists of separate components for the postsettlement oyster population and *Perkinsus marinus*. The two model components are coupled by the relationships that describe the removal of oyster energy by the parasite to support its metabolic needs, relationships that relate rates of parasite cell division and mortality to host mortality, and the influence of *P. marinus* on oyster physiology. The postsettlement component, as described by Powell et al. (1995), consists of a size-structured model that includes the processes regulating growth, reproduction, and death of oysters from newly settled juveniles to adults. These processes include assimilated ingestion as it depends on filtration rate, ambient food supply, and assimilation efficiency; filtration rate as a function of oyster size, temperature, salinity, turbidity, and current flow; respiration as it depends upon size, temperature, and salinity; and the apportionment of net production into somatic and reproductive growth as a function of temperature and time of year. The *Perkinsus marinus* component, as described by Hofmann et al. (1995), consists of processes controlling cell division and cell mortality as a function of temperature, salinity, and cell density; transmission rate as a function of oyster population density, *P. marinus* prevalence, and *P. marinus* infection intensity; and host mortality as a function of cell density. A flowchart of the coupled oyster disease model appears as Figure 1.

The model was solved numerically using an implicit (Crank-Nicolson) tridiagonal solution technique with a 1-day time step. Environmental forcing factors in the model are salinity, temperature, current flow, food supply, and turbidity. Environmental variables were input into the model from measured time series at each of the three sites. Daily values used by the model were obtained by linear interpolation between each measurement and the next. The model simulates oyster biomass, rather than length. Model results were expressed as length using a dry weight-to-length relationship obtained from the three studied populations.

$$\text{Dry weight(g)} = 2.4 \times 10^{-6} \text{ Length(mm)}^{2.935}$$

All simulations began on January 1 (Julian day 1) or May 20 (Julian day 140) and ran for 6 years. Each simulation was initialized with an oyster size-frequency distribution representative of the sampled site or by permitting the settlement of spat on day 140. The oyster population was initialized with a *P. marinus* prevalence of 50% to reduce the time required to bring the model into equilibrium with the environmental variables. Typically, this took about 12 to 18 months of simulation. Thus, discussion focuses on the final 4 years of the 6-year simulation. Specific variables set for each simulation are shown in Table 1.

RESULTS

Field Measurements

Environmental Variables

Temperature was similar at all three sites and varied from 12°C in December to 31°C in July (Fig. 2). Salinities were highest at Bay Tambour (site 3, Fig. 2c), often ≥5‰ above sites 1 and 2. Salinity remained above 10‰, except during the winter months. Salinities were similar at sites 1 and 2 and hovered around 10‰ except during the winter, when salinities below 5‰ were frequently recorded (Fig. 2a,b). Salinity was more variable on short time scales in Bay Cocodrie (site 2).

Site 1 was typically the least turbid (Fig. 3a). Total seston rarely exceeded 60 mg L^{-1}. No seasonal pattern was evident. Total seston was generally higher at sites 2 and 3, often exceeding 40 mg L^{-1} (Fig. 3b,c). Again, no seasonal pattern was evident.

Food Supply

A moderately distinct bloom occurred during May to July at all three sites. Chlorophyll a concentrations exceeded 20 μg L^{-1} during some of this period (Fig. 3), however highest values did not occur simultaneously. Values were higher earlier (in May) in Bay Tambour (site 3), but rose to peak values in July at the lower-salinity sites (Savin Canal, Bay Cocodrie). Concentrations fell to persistently low levels (<10 μg L^{-1}) for the remainder of the year at all three sites. No fall bloom was evident at any site.

Particulate organic matter was correlated with total seston, rather than chlorophyll (POM vs. seston: r^2 = 0.86, 0.94, 0.89; POM vs. chlorophyll: r^2 = 0.02, 0.10, 0.05; stations 1, 2, and 3, respectively [Fig. 4]). Values routinely were 10% or less of total seston.

Oysters

Most oysters were 25 to 99 mm long (Fig. 5) and the size–frequency distribution remained stable throughout the year. No oysters exceeded 150 mm. Site 1 had the smallest oysters, on average. By the end of the study, oysters were somewhat larger at site 3 than at sites 2 or 1. Juvenile oysters (0–24 mm) were most abundant in early spring and late summer, and were normally most abundant at site 3.

At all stations, gonadal index peaked in April or May and was lowest in November (Fig. 6). Second, smaller peaks occurred in July at site 1, August/September at site 2, and September at site 3. Sex was indeterminant from November through February coincident with low values of gonadal index; otherwise, the commercial-size oysters were predominantly female. Condition index paralleled gonadal index in being highest in April/May and lowest in November (Fig. 6). However, condition index was relatively lower during the second peak in gonadal index than during the spring, and particularly low at site 3.

Perkinsus marinus prevalence was highest at the higher-salinity site (Bay Tambour, site 3) and lowest at site 2 (Bay Cocodrie), where frequent low-salinity events occurred. Prevalence rarely

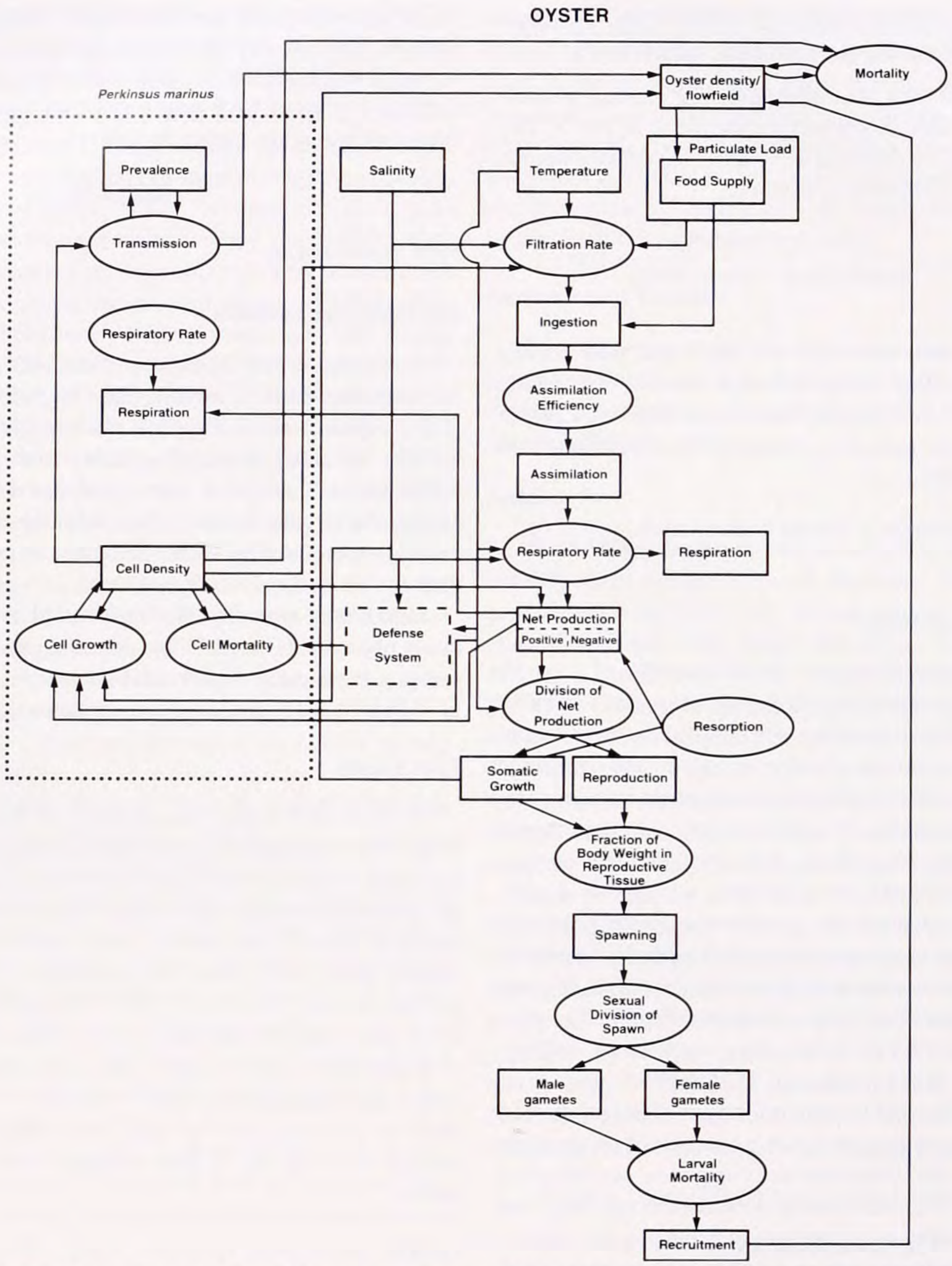

Figure 1. Flow chart for the *Crassostrea virginica-Perkinsus marinus* model described by Powell et al. (1995) and Hofmann et al. (1995). Note the following corrections to Table 3 of Hofmann et al. (1995): $\beta = 3.2454 \times 10^{8}$, $\varepsilon = 9.57 \times 10^{-10}$, $\zeta = 1.16 \times 10^{-4}$.

dropped below 50% at site 3 and never rose above 40% at site 2 (Fig. 7). Weighted incidence followed the same general trend, never exceeding 0.35 at site 2 and 0.9 at site 1, but averaging above 0.5 at site 3. Weighted incidence was lowest during the winter at sites 1 and 3. Weighted incidence was much more variable at site 2, coincident with the more variable salinity at this site. Overall, *P. marinus* prevalence and infection intensity followed the expected pattern with temperature and salinity at these sites. Lowest infection levels occurred at the lower salinity sites and during the colder periods of the year.

Model Simulations

Food Supply

The first set of simulations examined the adequacy of various measures of food supply. A crucial prediction, in judging the adequacy of an input variable describing food supply, is the size frequency of the simulated adult population. In oysters, adult size is environmentally controlled, and, within a local area, food supply will be a significant determining factor of adult size (Hofmann et al. 1994). A second important parameter is the spawning season and the pattern of spawns. The amount of energy devoted to gamete production is sensitive to oyster net production, which is largely determined by the availability of food (Hofmann et al. 1992).

The size frequencies of three simulated populations obtained using the environmental conditions for site 3 (Bay Tambour) and the three different food supplies are shown in Figure 8. Other model parameters were set, as given in Table 1. Simulations for sites 1 and 2 yielded qualitatively similar results. In comparison to the actual population shown in Figure 5, particulate organic matter yields a simulated size frequency of adults much too large: standard estimates of phytoplankton biomass from chlorophyll yields a simulated size frequency much too small. Using an estimate of

TABLE 1.

Parameters used for simulations.

Simulation	Site[a]	Day 1[b]	Size Frequency[c]	Food[d]	*P. marinus*	Rate of Recruit[e]	Mortality Size Range[f]	Rate of Mortality[g]	Sampling Frequency[h]	Figure
1.	1	b	a	POM	Absent	0	none	0.	week	8,9
2.	2	b	a	POM	Absent	0	none	0.	week	8,9
3.	3	b	a	POM	Absent	0	none	0.	week	8,9
4.	1	b	a	Chl	Absent	0	none	0.	week	8,9
5.	2	b	a	Chl	Absent	0	none	0.	week	8,9
6.	3	b	a	Chl	Absent	0	one	0.	week	8,9
7.	1	b	a	LPC	Absent	0	none	0.	week	8,9,10
8.	2	b	a	LPC	Absent	0	none	0.	week	8,9,10
9.	3	b	a	LPC	Absent	0	none	0.	week	8,9,10
10.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	week	11,12,13
11.	3	a	b	LPC	Present	2.	1–4	.0208	week	14,15,16
12.	1	a	b	LPC	Present	2.	1–4	.0208	week	14,17
13.	1	a	b	LPC	Present	6.	1–4	.0192	week	15,16
14.	1	a	b	LPC	Present	2.	1–3	.0128	week	17
15.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	mon	18,19,20
16.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	week	18,19,20
17.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	1st	21,22,23,24
18.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	2nd	21,22,23,24
19.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	3rd	21,22,23,24
20.	3,2,1	a	b	LPC	Present	3.9	1–4	.0192	4th	21,22,23,24

[a] Multiple sites indicate that the site environmental time series were used sequentially in the order listed, for one year at a time, during the model run.
[b] a, simulation begun on January 1; b, simulation began May 20.
[c] a, simulation initialized with a settlement of spat on day 140; b, simulation initialized with a population size-frequency distribution typical of the simulated site.
[d] POM, particulate organic matter; Chl, phytoplankton biomass directly estimated from chlorophyll; LPC, food estimated from a regression between chlorophyll and total lipid, labile carbohydrate, and protein.
[e] Fraction recruited listed as the number of successful recruits per 10^9 larvae spawned.
[f] Size classes exposed to postsettlement mortality. Size class designation refers to the 11 size classes as defined in Figure 8, none, no postsettlement mortality.
[g] in day^{-1}.
[h] Mon, one sample per month (average of the four weekly samplings) used to define conditions present on the 15th day of each month and daily values obtained by linear interpolation between these monthly values; week, the weekly measurements with conditions imposed on the day of collection with linear interpolation between collection times; 1st, 2nd, 3rd, 4th, the weekly value for that week assumed to be a monthly sample defining conditions present on the 15th day of each month and daily values obtained by linear interpolation between these monthly values.

food that includes a nonchlorophyll-explained food resource based on lipid, labile carbohydrate, and protein yields a size frequency that is similar to field observations.

We compare the pattern of spawning and the amount of gonadal tissue present in simulated oyster populations at site 3 (Bay Tambour) under the three different food supplies (Fig. 9). Simulations for sites 1 and 2 yielded qualitatively similar results. The actual population shown in Figure 6 spawned in May to July and possibly in September to October, as suggested by the gonadal index (Fig. 6). Condition index was highest in April to June. The spawning season for a simulated population in which particulate organic matter was used for food begins and ends too late in the year (Fig. 9). Spawning season in the simulated populations using chlorophyll directly to estimate phytoplankton biomass or as a surrogate for total lipid, labile carbohydrate, and protein better approximates field conditions. Gametic tissue, however, is no longer present in the simulated population at the end of August, when the direct conversion of chlorophyll to phytoplankton biomass is used to estimate the primary food resource. Using total labile carbohydrate, protein, and lipid extends the time gametic tissue is present into October, as seen in the field, and suggests that the September/October decline in gonadal index (Fig. 6) may be attributable to gonadal resorption rather than spawning. Once again, the simulation in which food supply contains a nonchlorophyll-explained portion based on measures of total lipid, labile carbohydrate, and protein, provides results most similar to field observations.

Comparison Across Environmental Gradients

For these simulations, we assumed that the only difference between the three sampling sites was in the time-history of the environmental variables that were measured: temperature, salinity, food supply, and turbidity. All other processes, such as larval survivorship and juvenile mortality, were kept constant (Table 1). The three sites represent a substantial salinity gradient (from 2 to 1 to 3, Fig. 2). Turbidity is highest at site 2 (Fig. 3). Lower salinity and high turbidity should restrict adult size at site 2. By the end of the study, oysters were somewhat larger at site 3 than at sites 2 or 1, as might be anticipated from the salinity gradient (Fig. 5). Increased turbidity at site 2 did not, however, seem to influence adult size. The simulated oyster population size–frequency distributions conform to both of these observations (Fig. 10).

Comparing simulated reproductive effort with observation is

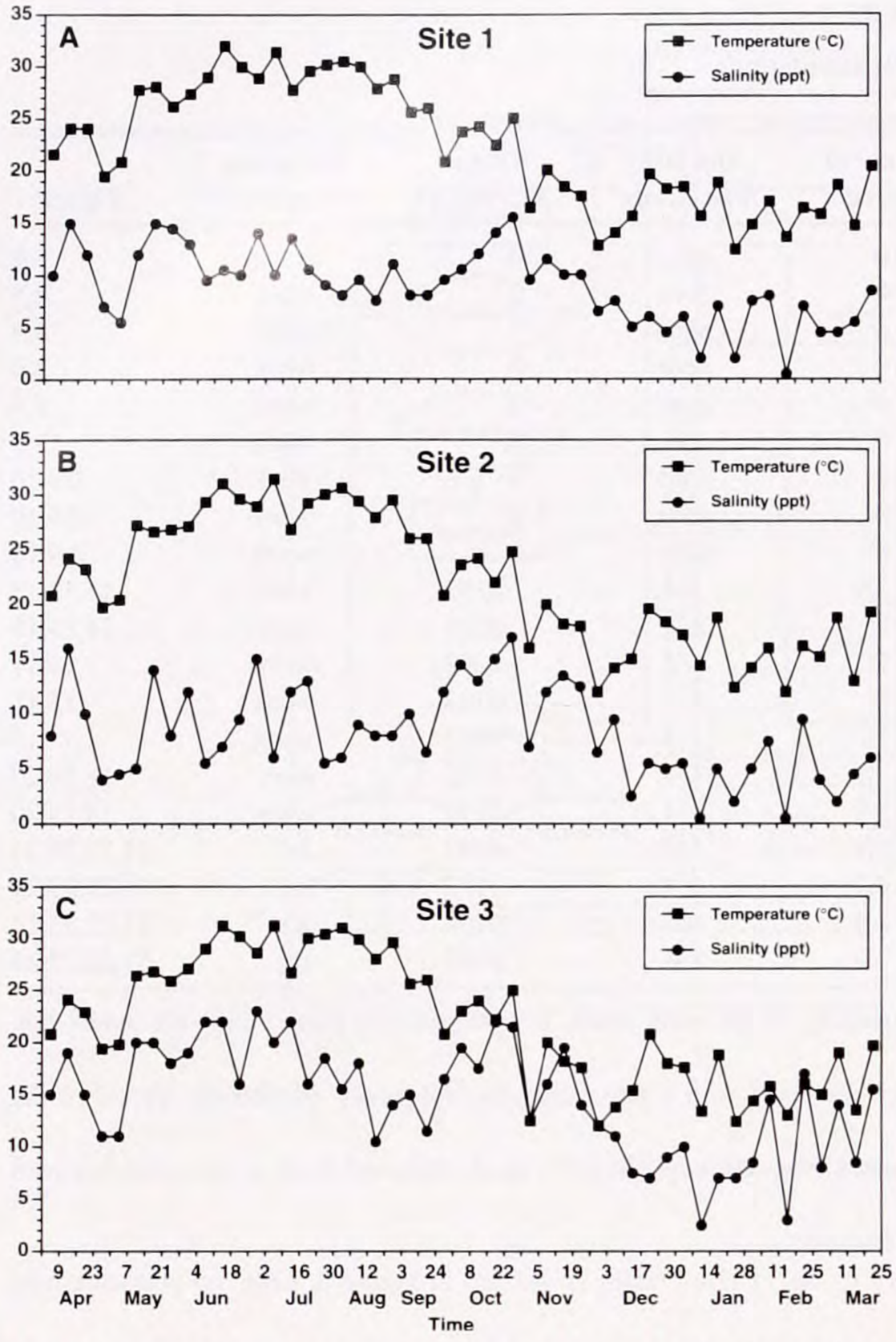

Figure 2. Field measurements of salinity and temperature; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

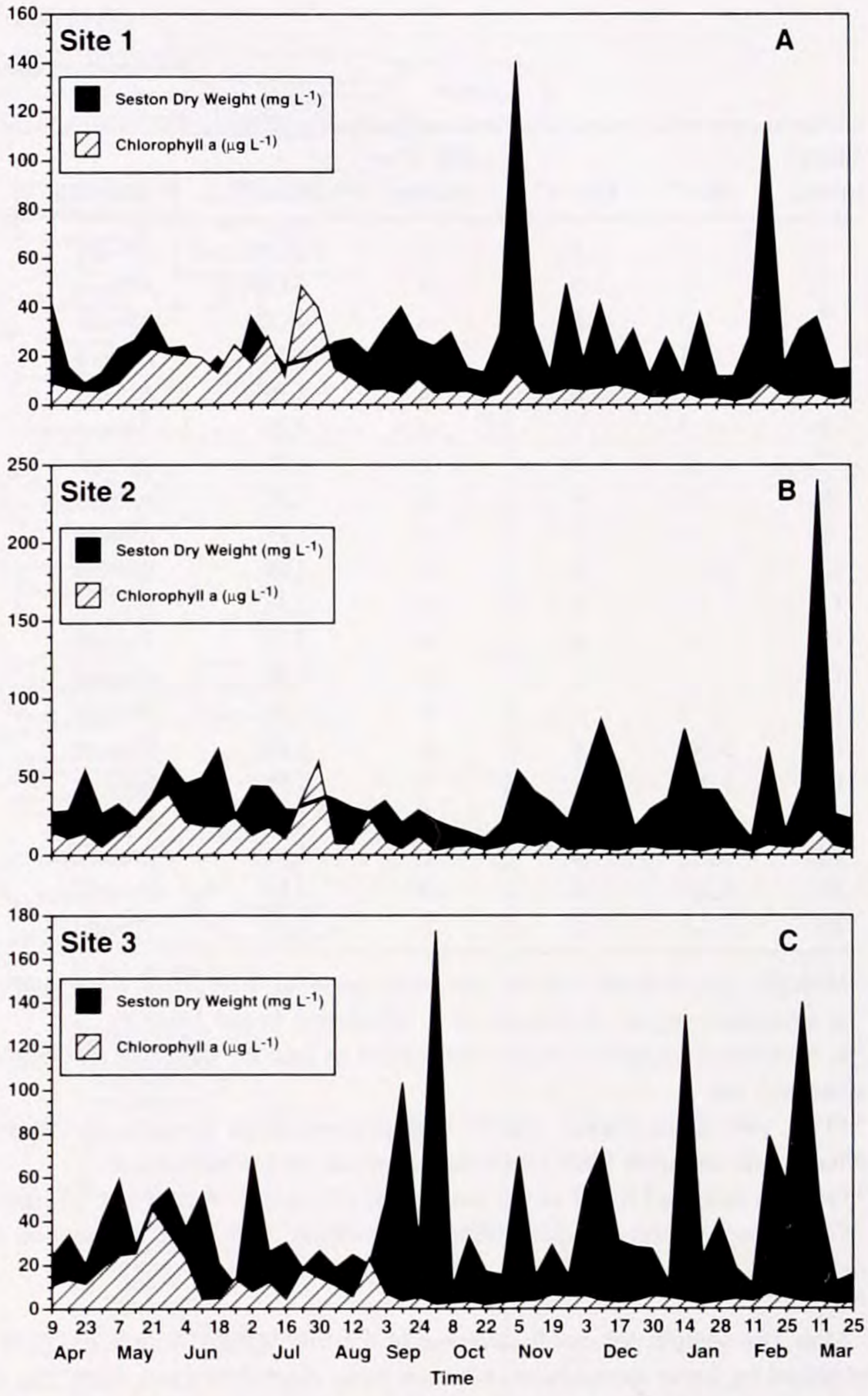

Figure 3. Field measurements of chlorophyll a and total seston; note that the *y*-axis scale differs between plots; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

difficult, because the number of gametes spawned is readily calculated in the model, but not readily measured in the field. Field observations of gonadal index must be used to evaluate spawning. Simulating the reproductive cycle is also more complex than simulating adult oyster size, because spawning and fecundity are sensitive to a large number of environmental and biological factors. *P. marinus* infection intensity, for example, can have a significant impact on fecundity. Therefore, the influence of the environmental gradient on an oyster population infected with *P. marinus* was examined by sequentially exposing the population to environmental conditions for the three sites 1 year at a time. The basis for this sequential juxtaposition of time series is discussed in a subsequent section. Spawning season is longer and fecundity is higher in the simulated population during the years when the site 3 time series was used (Fig. 11). Gonadal index averages lower at site 2. Spawning season inferred from gonadal index seems to be shortest at site 1. The early fall increase in gonadal index at sites 2 and 3 is observed in simulations of sites 2 and 3. Thus, to the extent that a comparison of gonadal index to fecundity permits, the simulated population follows trends observed in the field data.

P. marinus prevalence and infection intensity usually are strongly influenced by salinity gradients. In particular, both should be lower at low salinities. The simulated *P. marinus* prevalences (Fig. 12) and infection intensities (Fig. 13) show these general trends. Simulated *P. marinus* summer prevalence averages between 60 and 80% at site 3, about 20% at site 2, and between 30 and 50% at site 1, very similar to field observations (Fig. 7). Summer infection intensity averages 2 to 3 at site 3, less than 0.5 at site 2, and about 1 at site 1 for market-size oysters; in each case slightly above field observations. Infection intensity in the simulated entire population is even more similar to field observation, particularly for sites 2 and 3 (Fig. 7).

Overall, the model reasonably approximated adult size, spawning pattern, and population disease intensity across the salinity gradient represented by sites 2, 1, and 3.

Biological Processes and Population Instability

Qualitatively, the environmental gradients are adequately simulated by the model. However, achieving the degree of similarity between simulation and observation shown in Figures 10 to 13 required cycling the oyster population sequentially through the environmental time series from the three sites (Table 1). For simplicity, we present results for only one of a number of possible sequences (i.e., 3, 2, 1, Table 1). Any population is a product of the time-history of environmental change. Oyster populations are in-

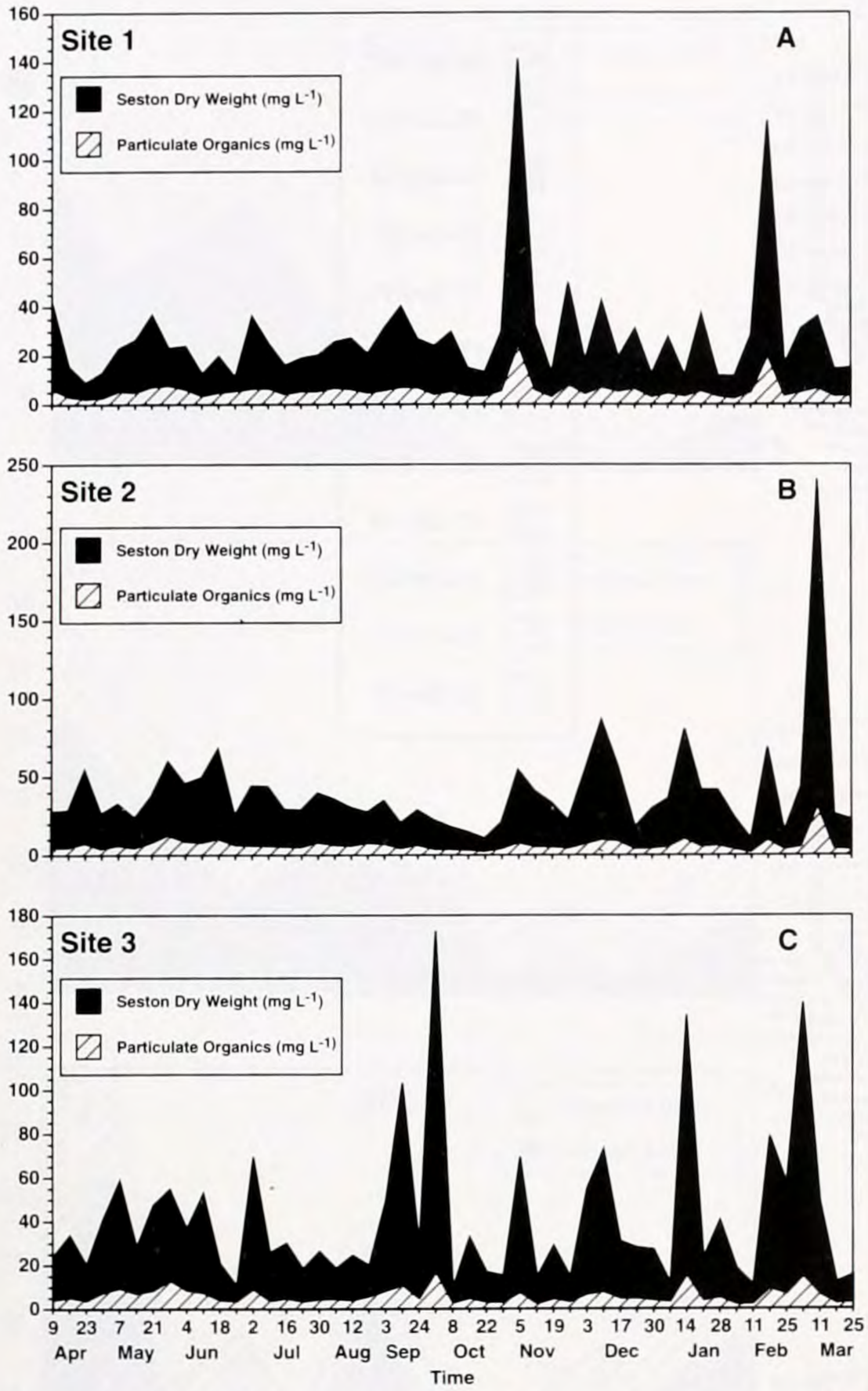

Figure 4. Field measurements of particulate organic matter and total seston. Note that the *y*-axis scale differs between plots; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

herently unstable, either expanding or contracting based on variations in environment and external forces, such as larval influx from distant brood stock. Realistic simulations, such as depicted in Figures 10 to 13, require continual transitions between conditions promoting expansion and contraction.

Figure 14 shows an example of simulated populations exposed continuously to the same set of conditions over several years. Local biological factors did not vary among these simulations; e.g., the same rate of larval survival and juvenile mortality. Environmental conditions at site 1 result in population extinction over several years; whereas, environmental conditions at site 3 result in population expansion. Population stability can be achieved by varying such biological factors as the rates of recruitment and mortality. If, for example, the rate of subadult recruitment at site 1 is higher than site 3 because of a proportional increase in recruitment and lower juvenile mortality, site 1's population persists over several years, just as does site 3's (Fig. 15). Thus, modifying the rate of subadult recruitment achieves much the same result as was achieved by cycling the environmental time series. However, Figure 16 shows that both simulations result in a slow increase in *P. marinus* infection intensity, unlike field observations. By year 6, epizootic conditions are evident in both simulated populations. Variations in the rate of juvenile mortality as a result of varying predator abundance can also result in oyster populations that expand or contract over a period of years (Fig. 17). Varying predator abundance can also achieve stability in population abundance and size structure (simulation not shown), but, once again, *P. marinus* infection intensity does not stabilize.

Overall, these three sets of simulations show that several consecutive years of the same environmental conditions always result in a simulated oyster population that fails to resemble field observations of all population variables. Varying such biological factors as the rates of recruitment and mortality markedly improves the simulation, but does not result in an acceptable simulation of disease. Only if the environmental time series include substantial year-to-year environmental change, do the simulated populations correspond closely to field observations at the three Terrebonne Basin sites.

Time Scale of Monitoring (Weekly vs. Monthly)

Most routine sampling is conducted monthly. For many studies, weekly sampling would be feasible. Technological advancement has permitted the sampling of some variables much more frequently. The question is, then, how frequently are samples needed to resolve the processes controlling oyster population structure adequately? The effect of measurement frequency was tested by inputting weekly or monthly (calculated as the mean of the 4 weekly measurements) observations and interpolating these to daily values (Figs. 18–20). In all cases, for all important biological attributes used to characterize an oyster population (e.g., oyster density, spawning pattern, *P. marinus* infection intensity), monthly averages produce simulated populations that compare poorly to field observations. The monthly values tend to overestimate population abundance (Fig. 18), reproduction (Fig. 19), and disease intensity (Fig. 20). Weekly measurements produce simulated populations much more similar to field observations (Figs. 18–20).

The Importance of Sampling Time

In many routine monthly monitoring regimens, the time of sampling is not firmly set. Nevertheless, the single measurements taken are usually assumed to be indicative of conditions during the entire month. We examined the consequences of ignoring the time of month that the measurement was made in a series of simulations in which the observations from each of the 4 weeks of the month were assumed to be representative of the entire month (Table 1). The simulated oyster population density (Fig. 21), spawning pattern (Fig. 22), and *P. marinus* infection intensity (Figs. 23,24) obtained for each of the four cases show that the oyster populations do consistently better as later weeks in the month are taken as the characteristic monthly value. Only in week 3, are the population attributes even remotely comparable to those observed using the weekly samples (cf. Figs. 18–20).

DISCUSSION

Food Supply

Food supply was estimated from measures of total particulate organic matter, phytoplankton biomass estimated from measures of chlorophyll a, and total labile organic matter estimated from a regression between measurements of chlorophyll a and total labile carbohydrate, lipid and protein. The third was clearly superior.

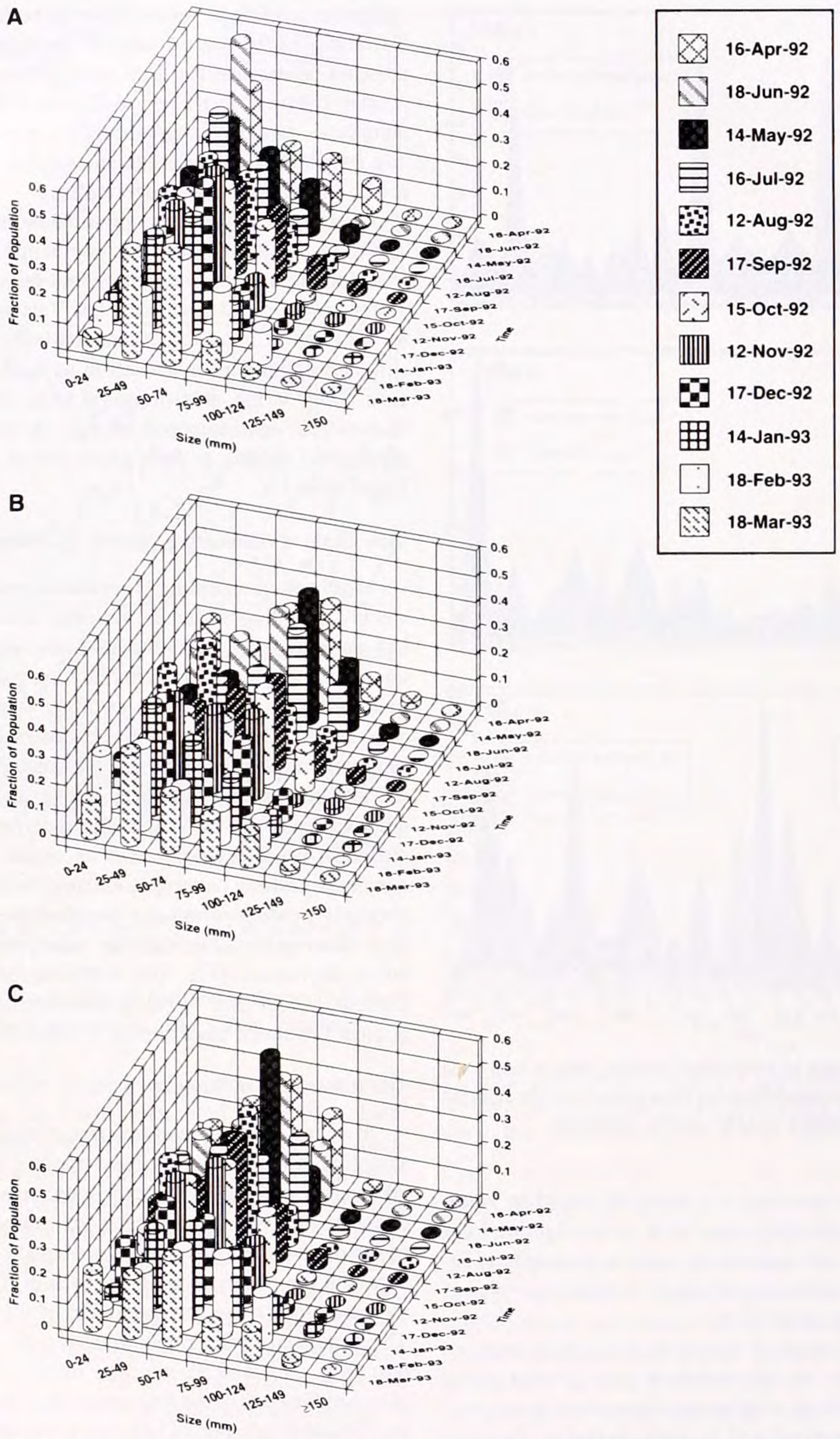

Figure 5. Size-frequency distribution of oysters obtained from the three sampling sites over the study period; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

POM produced a simulated adult population that far exceeded the observed population in adult size. Total particulate organic matter is a poor measure of food supply unless a low assimilation efficiency is assumed. Langdon and Newell (1990) and Crosby et al. (1990) measured a low assimilation efficiency for refractive organic matter, and it is probable that POM from the Louisiana sites, like Galveston Bay (Wilson-Ormond et al. 1997), is mostly refractive. Assimilation efficiency was set at 75% in our simulations. Thus, a lower assimilation efficiency might be used to provide simulated results more similar to field observations. However, as in Galveston Bay, the fraction of POM that is labile probably varies significantly during the year as phytoplankton biomass varies, and, in particular, the impact of the spring bloom on growth and reproduction in April to June could not be reproduced using POM. This spring/early summer event is crucial in determining population success (Hofmann et al. 1992). Thus, POM and

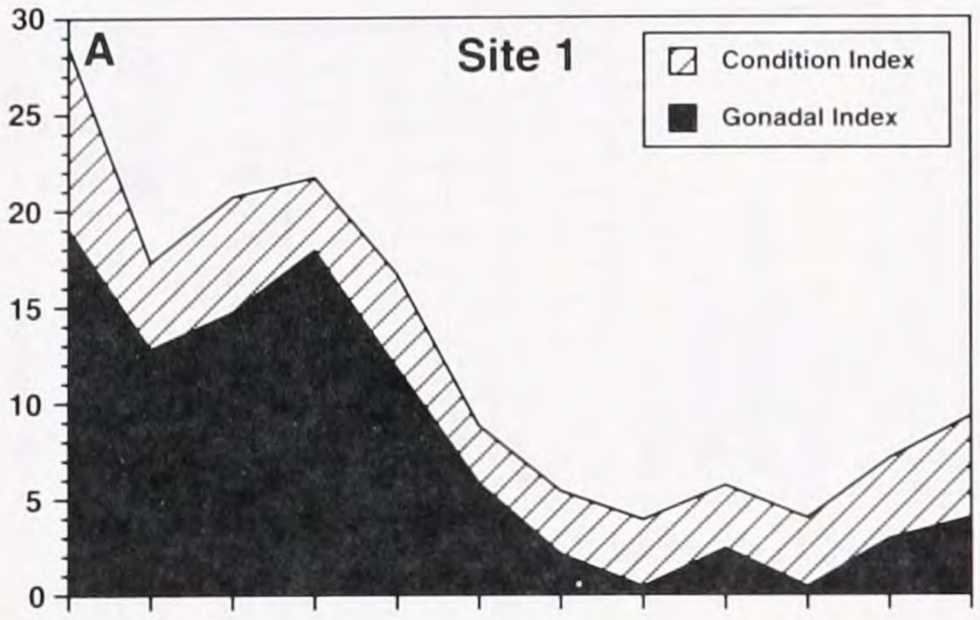

Figure 6. Gonadal index and condition index of oysters from the three sampling sites over the study period. Note that the *y*-axis scale differs between plots; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

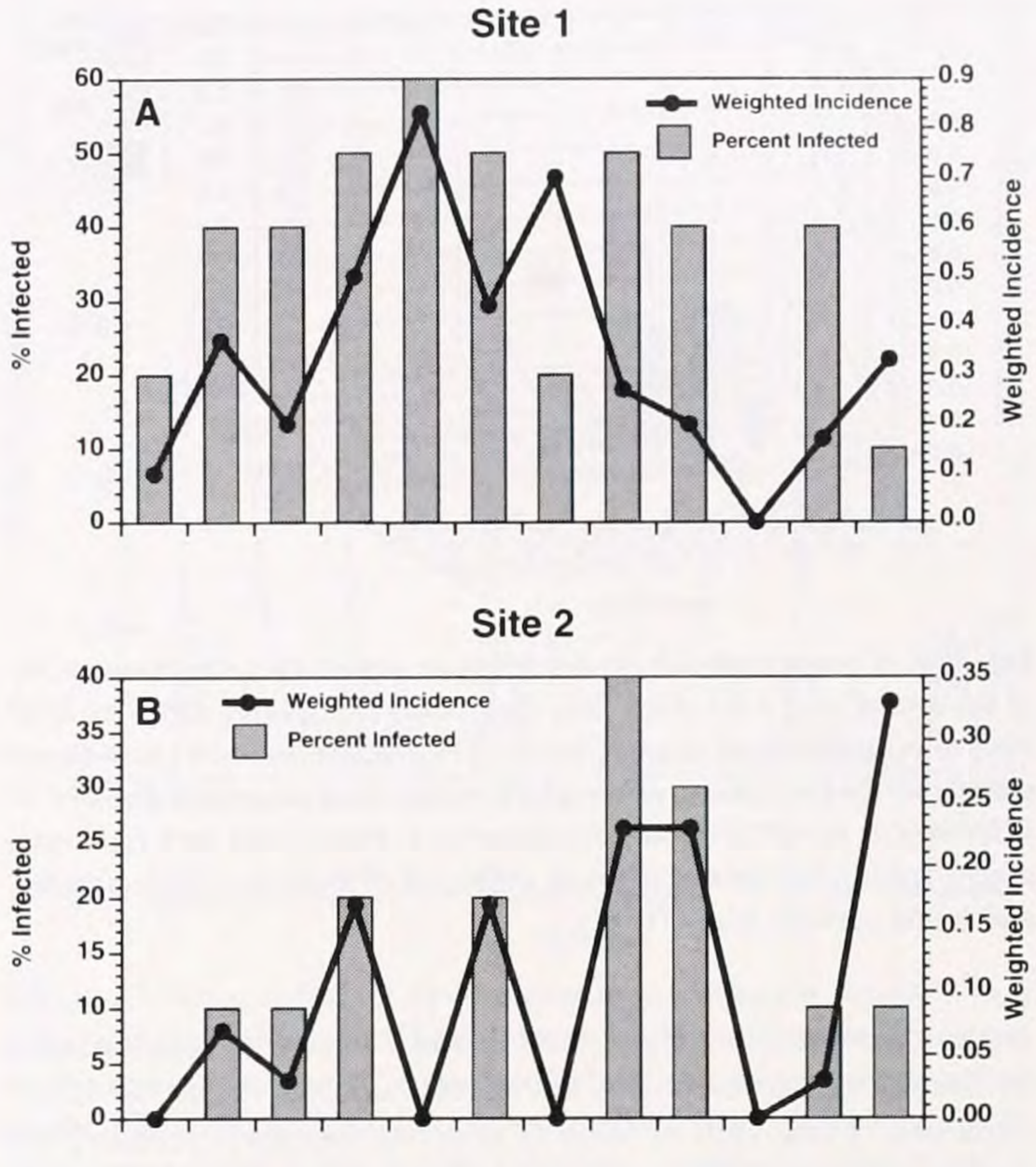

Figure 7. *Perkinsus marinus* prevalence and infection intensity for oysters from the three sampling sites over the study period; note that the *y*-axis scale differs between plots; (A) site 1, Savin Canal; (B) site 2, Bay Cocodrie; (C) site 3, Bay Tambour.

a low assimilation efficiency cannot produce a realistically simulated oyster population because the timing of the seasonal variation in food supply would be incorrect.

Chlorophyll a certainly measures an important component of oyster food (Berg and Newell 1986, Epifanio and Ewart 1977). Estimating food supply as phytoplankton biomass generates most important seasonal events in the oyster's life cycle. Growth, reproductive development, and spawning all occur at approximately the correct time in simulated populations, unlike that observed when POM was used. However, phytoplankton biomass simply does not provide an adequate food supply. Oysters remain too small, and reproductive development ends too early in the fall, coincident with the decline in phytoplankton standing stocks observed after July. Literature values will not support a higher assimilation efficiency (75% in these simulations) (Powell et al. 1992b, Tenore and Dunstan 1973, Valenti and Epifanio 1981). Thus, phytoplankton biomass is not a complete measure of oyster food.

Soniat et al. (1984) and Soniat and Ray (1985) demonstrated the importance of including a nonchlorophyll-explained food resource in the estimate of oyster food supply. They used the sum of three labile organic fractions: lipid, protein, and labile carbohydrate. In every test, this estimate of oyster food supply produced simulated oyster populations that most closely resembled those observed in the field. Similar results were obtained in simulations of oyster populations from Delaware Bay (Powell et al. 1997), Galveston Bay (Powell et al. 1994a), Gulf of St. Lawrence (unpubl. results), Chesapeake Bay (unpubl. results), and for a second oyster species, *C. gigas* (Kobayashi et al. 1997). The regression equation also has the interesting attribute of increasing oyster food

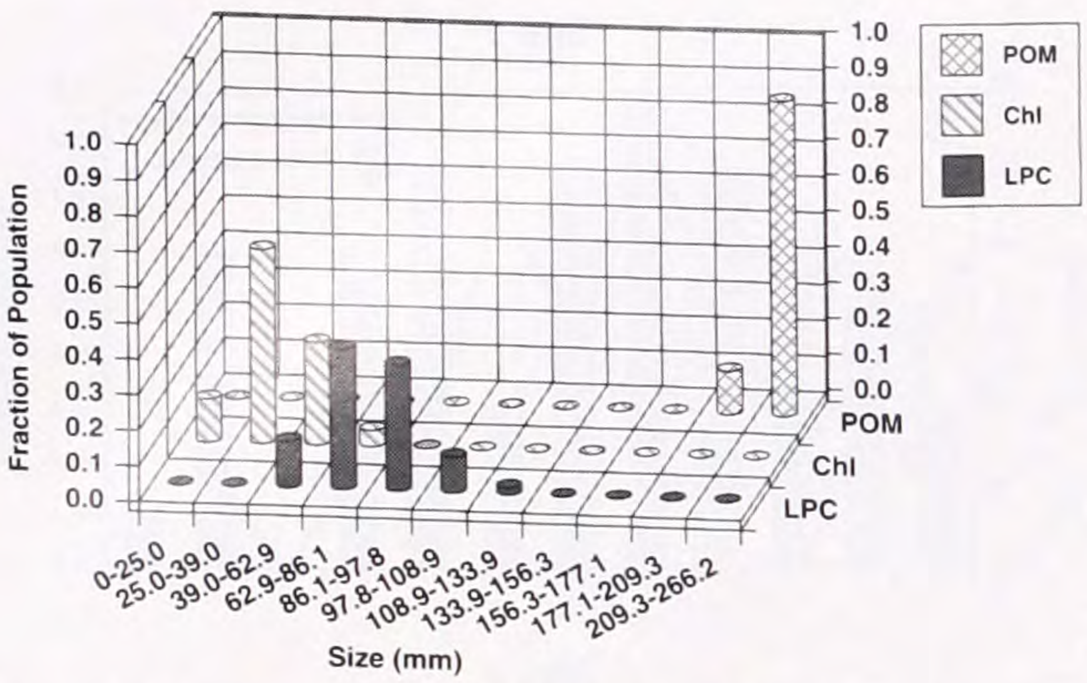

Figure 8. Comparison of simulated oyster population size frequencies at the end of year 6 for site 3 (Bay Tambour) using three different food resources: particulate organic matter (POM); phytoplankton biomass estimated directly from chlorophyll using the conversion factors of Widdows et al. (1979) and Parsons et al. (1961) (Chl); and food estimated from a regression between chlorophyll and total lipid, protein, and labile carbohydrate (LPC).

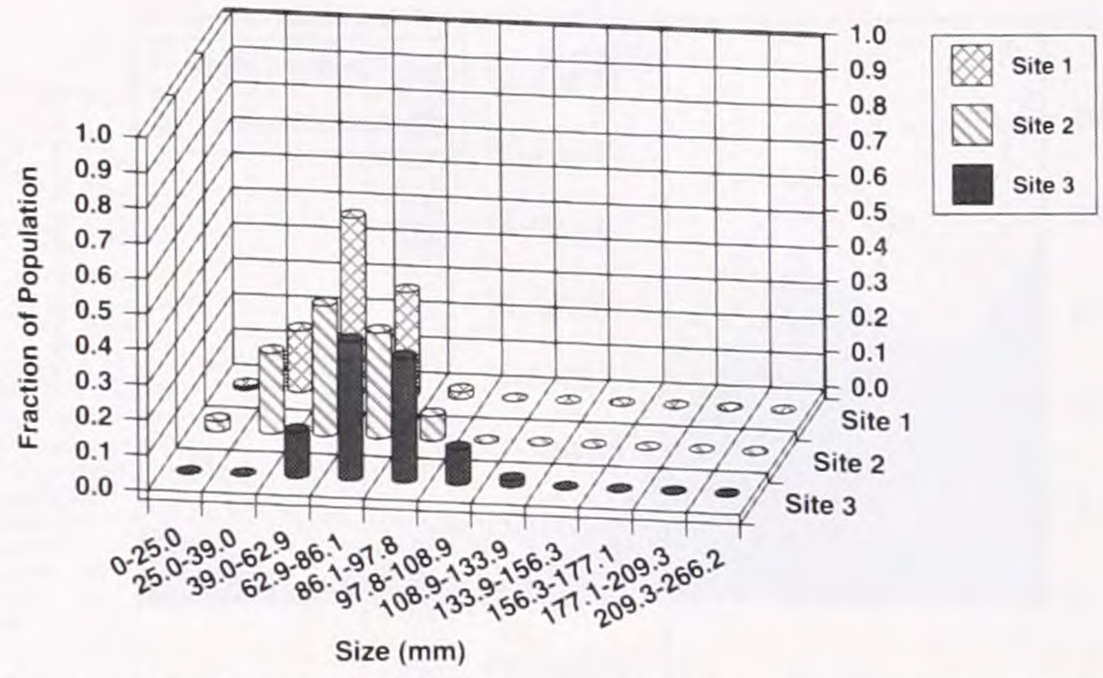

Figure 10. Comparison of the simulated size frequencies of oyster populations from the three sites at the end of year 6. Total lipid, protein, and labile carbohydrate was used as the food supply; (site 1) Savin Canal; (site 2) Bay Cocodrie; (site 3) Bay Tambour.

supply disproportionately in the fall and winter when phytoplankton stocks fall to seasonally low levels, as observed at the Louisiana sites. In the Gulf of Mexico, water temperatures remain high enough throughout the winter that oysters remain active for much of the time. Although a loss of condition is typically observed in larger animals (e.g., Fig. 6), growth may continue in juveniles. Phytoplankton biomass as the sole food resource produces an unacceptably large drop in biomass in simulated populations during the winter and does not produce the observed growth in juveniles. Appropriate winter population dynamics only occur if total labile organic matter is used.

Data and simulation both suggest that oysters depend upon a nonchlorophyll-explained food resource to supplement their diet and that this dependency is disproportionately important during the fall and winter in the Gulf of Mexico when phytoplankton stocks are low. Measures dependent upon direct conversion of chlorophyll to phytoplankton biomass, now the measures in routine use, do not adequately describe oyster food supply in the field, and may not adequately describe the seasonal variation in food supply any more than they do the absolute value.

Environmental and Biological Variables

Some years are wetter than others. Thus, sessile populations will experience differing salinity regimes as isohalines migrate up and down the estuary over the years. This year-to-year variability may provide a degree of stability, because some good years may permit populations to expand enough to survive lean years. In fact, oyster populations, in particular, may be stabilized by the year-to-year changes in environmental conditions that slow population expansion in the lean years and slow adult mortality in the better ones.

Simulated populations given the same environmental conditions year after year normally fall to extinction or increase in

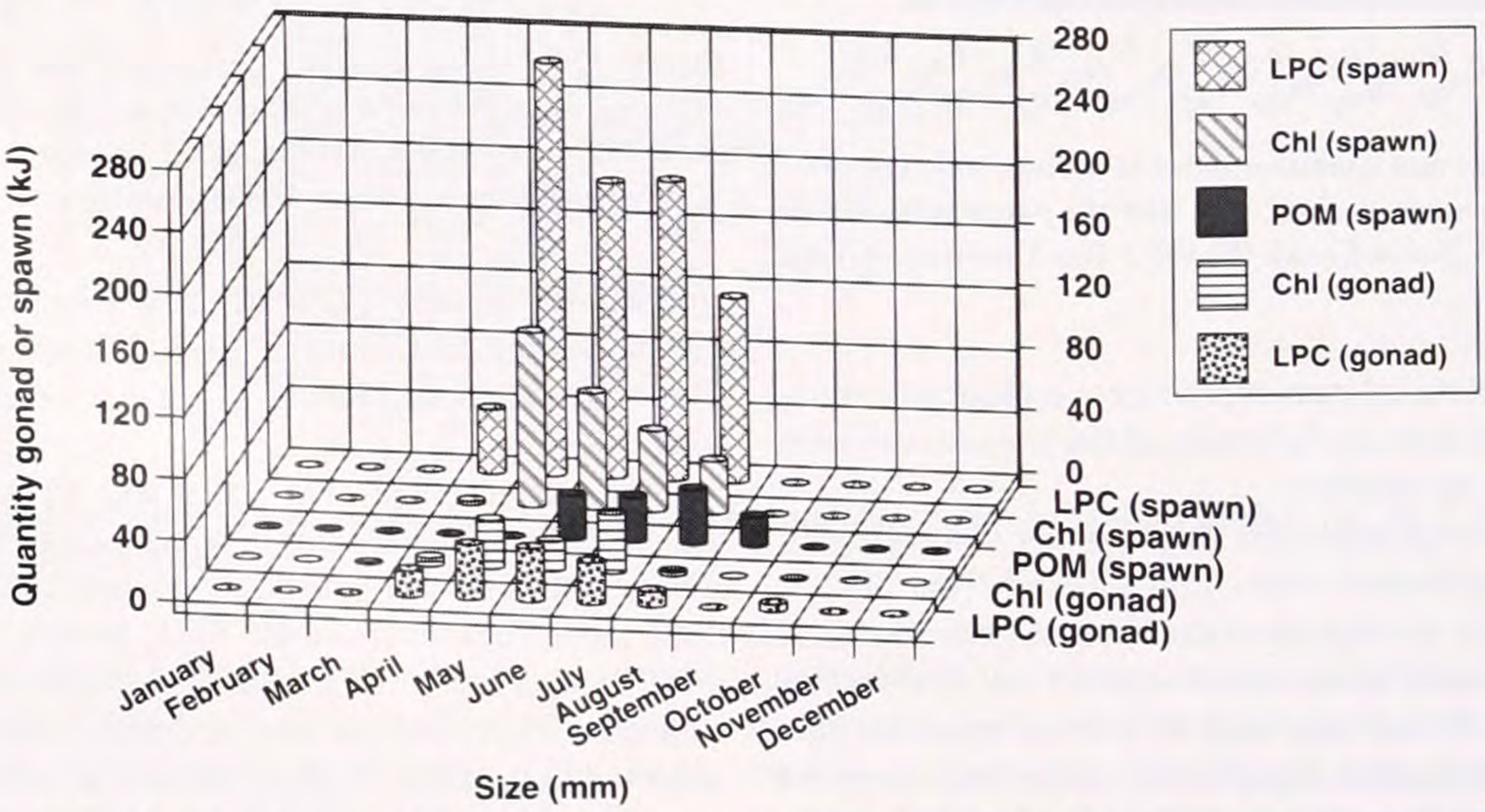

Figure 9. Comparison of simulated oyster population spawning pattern (monthly total of kJ of gametes spawned) and gonadal quantity (kJ gametic tissue). Spawning values represent the monthly total spawned by 10 oysters. Gonadal quantity represents the amount of gametic tissue present in 10 oysters on the last day of each month. Simulation results are for year 6 for site 3 (Bay Tambour) using three different food resources: particulate organic matter (POM); phytoplankton biomass estimated directly from chlorophyll using the conversion factors of Widdows et al. (1979) and Parsons et al. (1961) (Chl); and food estimated from a regression between chlorophyll and total lipid, protein, and labile carbohydrate (LPC).

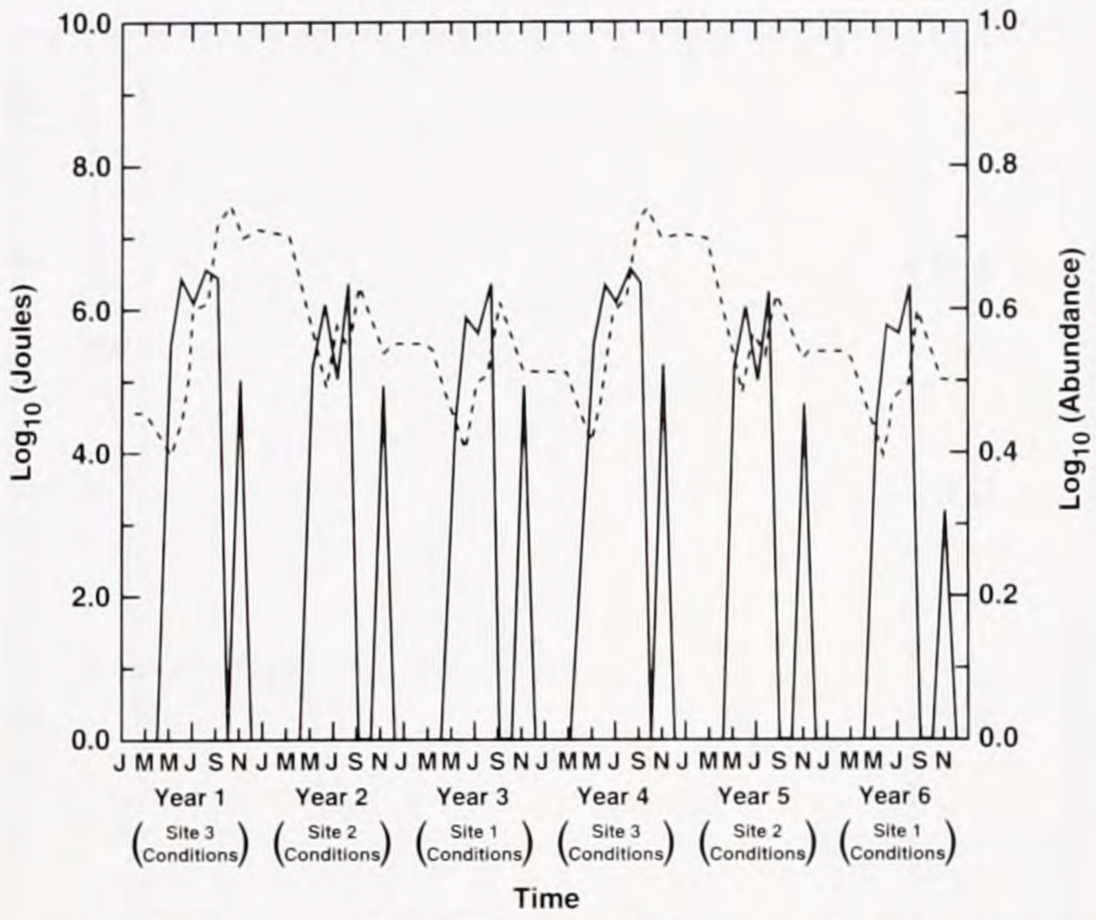

Figure 11. Comparison of oyster density [dashed line – $\log_{10}$(abundance)] and reproductive effort defined as the amount of gametic tissue spawned [solid line in $\log_{10}$(joules)] in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions.

abundance to abnormally high densities. Expansion and contraction are primarily a function of fecundity, larval survival, and postsettlement mortality. Distant brood stock supplying larvae may also play a significant role. Oyster population dynamics are characterized by thresholds that bound conditions yielding expansion or contraction and that prevent the existence of long-term equilib-

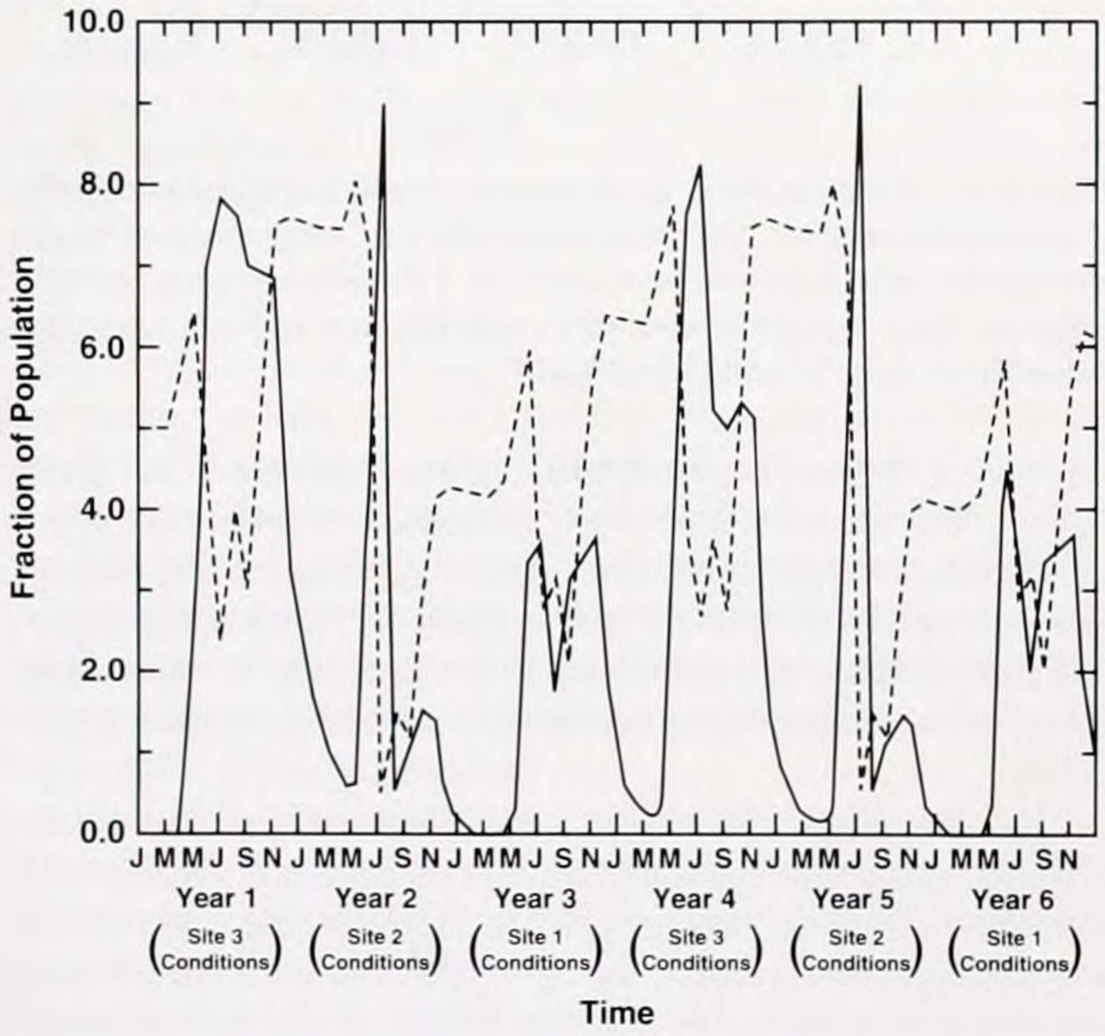

Figure 12. Comparison of *Perkinsus marinus* prevalence in a population exposed sequentially to the three environmental time series. Dashed line, the entire population. Solid line, the market-size portion of the population with prevalence calculated by assuming that oysters with <4,000 cells g dry wt^{-1} are recorded as uninfected. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions.

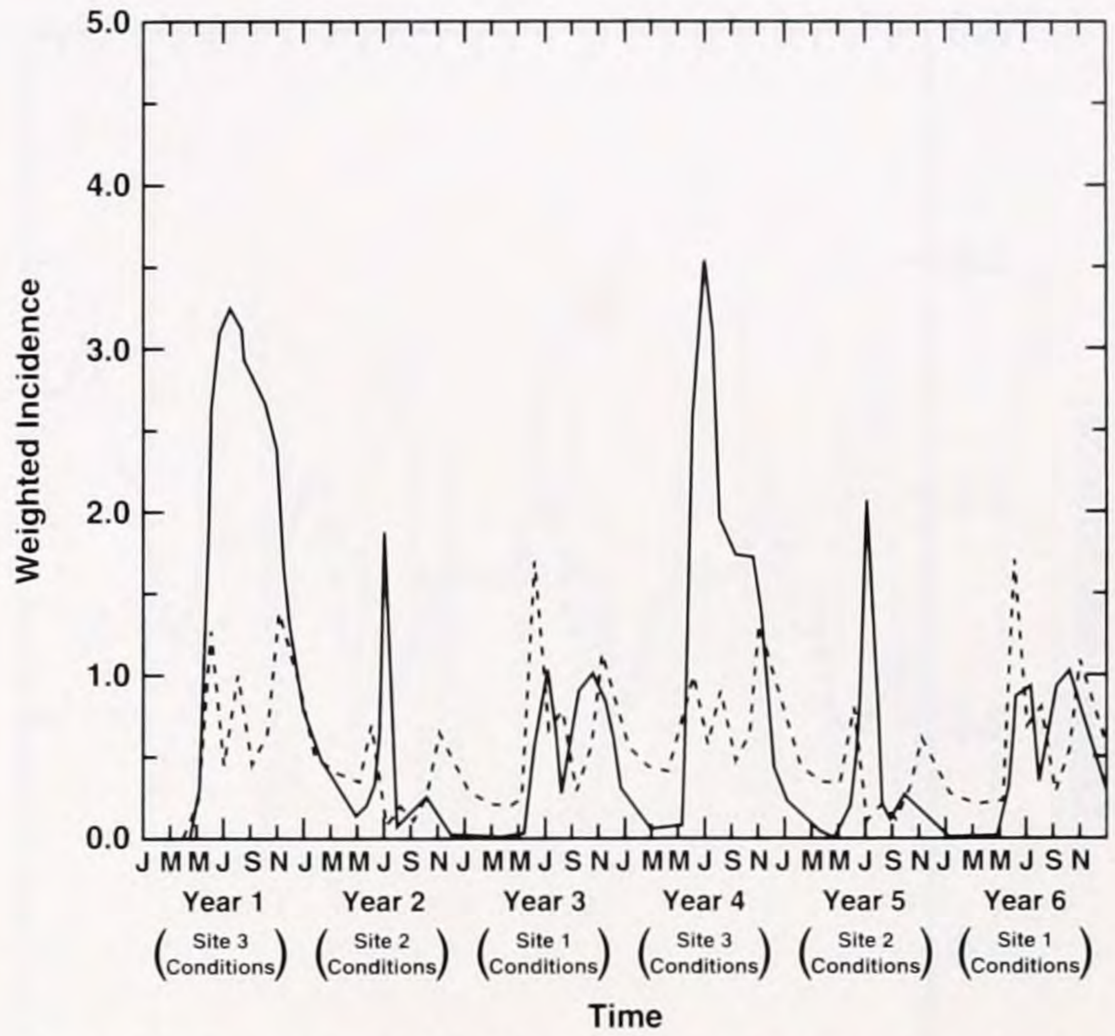

Figure 13. Comparison of *Perkinsus marinus* infection intensity in a population exposed sequentially to the three environmental time series for market-size oysters (≥76 mm) (solid line) and the entire population (dashed line). Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions.

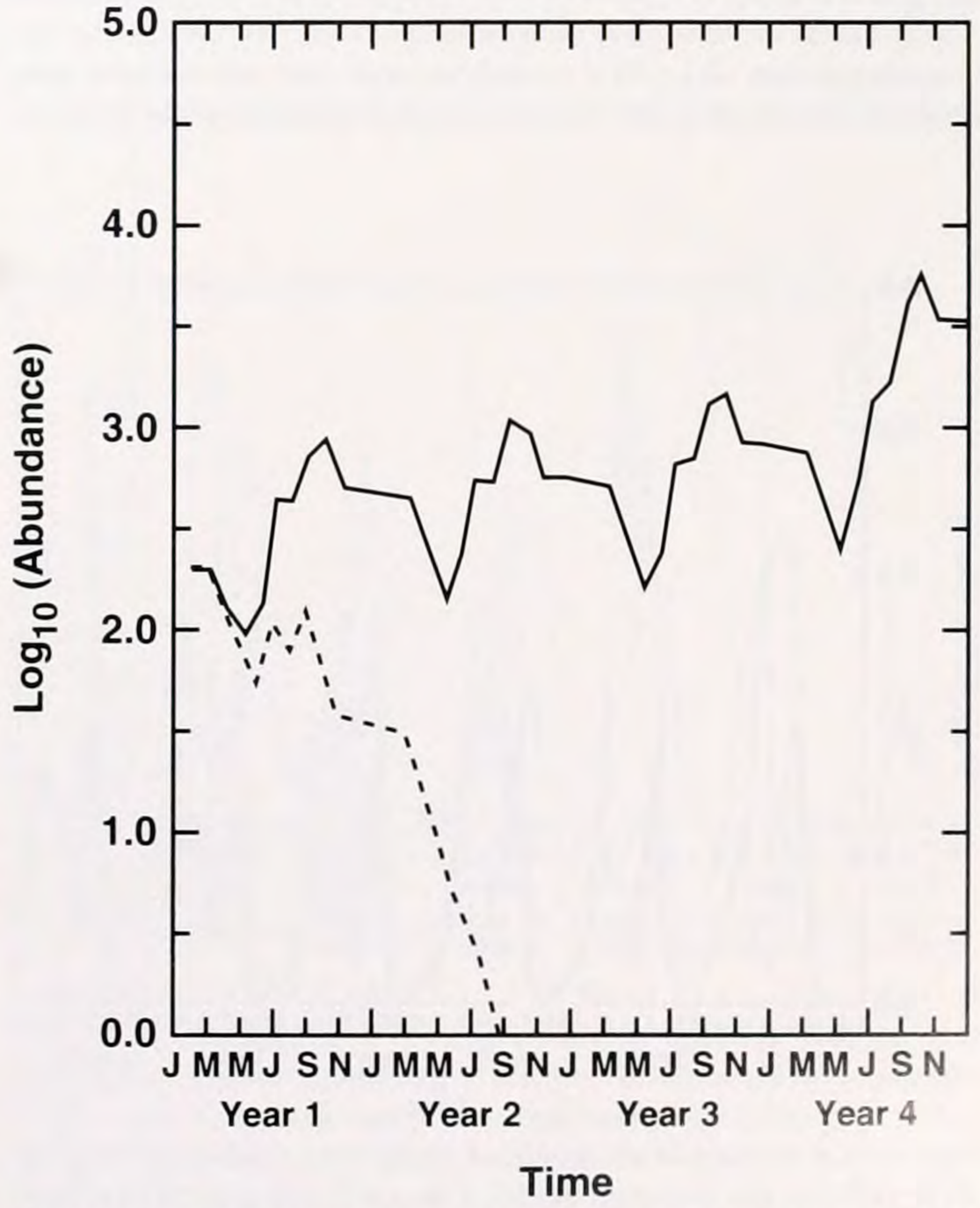

Figure 14. Comparison of simulated total population density [$\log_{10}$(abundance)] of oysters at sites 1 (Savin Canal, dashed line) and 3 (Bay Tambour, solid line) exposed to the respective site-specific environmental time series for 4 continuous years, but with identical rates of larval survival and juvenile mortality at both sites.

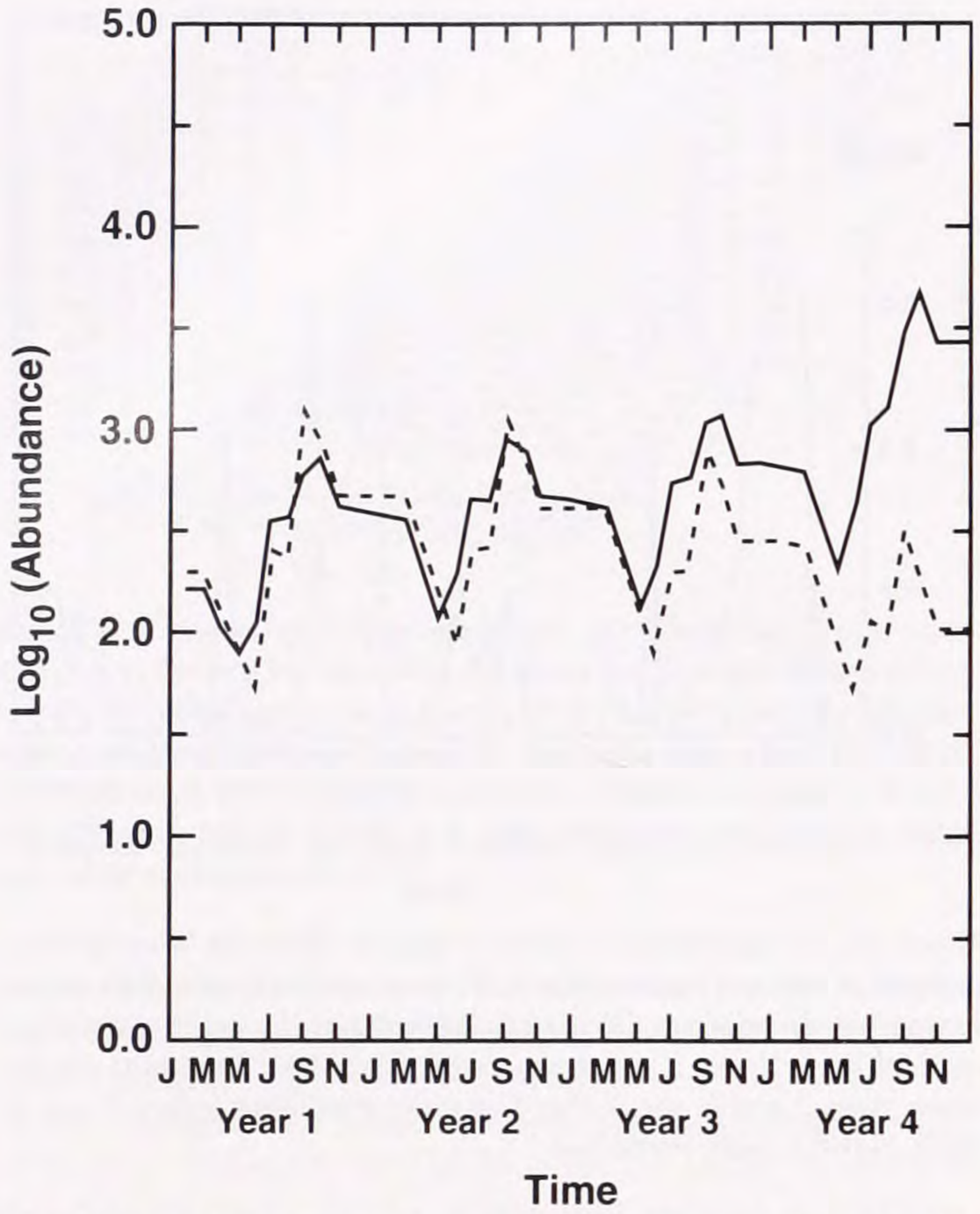

Figure 15. Comparison of simulated total population density [$\log_{10}$(abundance)] of oysters at sites 1 (Savin Canal, dashed line) and 3 (Bay Tambour, solid line) exposed to the respective site-specific environmental time series for 4 continuous years, but with a higher rate of larval survivorship and a lower rate of juvenile mortality at site 1.

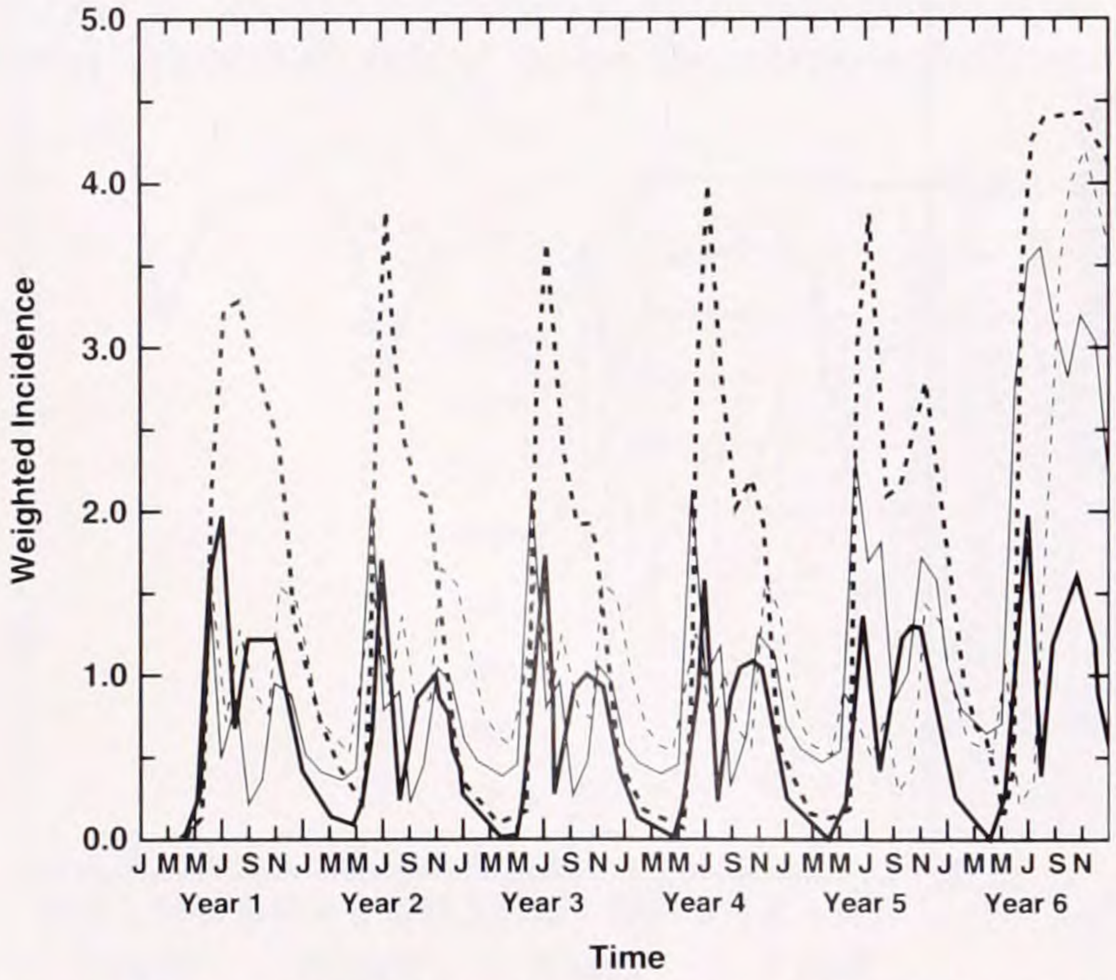

Figure 16. Comparison of simulated *Perkinsus marinus* infection intensity of oyster populations at sites 1 (Savin Canal) and 3 (Bay Tambour) exposed to the respective site-specific environmental time series for 6 continuous years, but with a higher rate of larval survivorship and a lower rate of juvenile mortality at site 1; solid line, site 1 (Savin canal); dashed line, site 3 (Bay Tambour); thin line, entire population; thick line, market-size oysters.

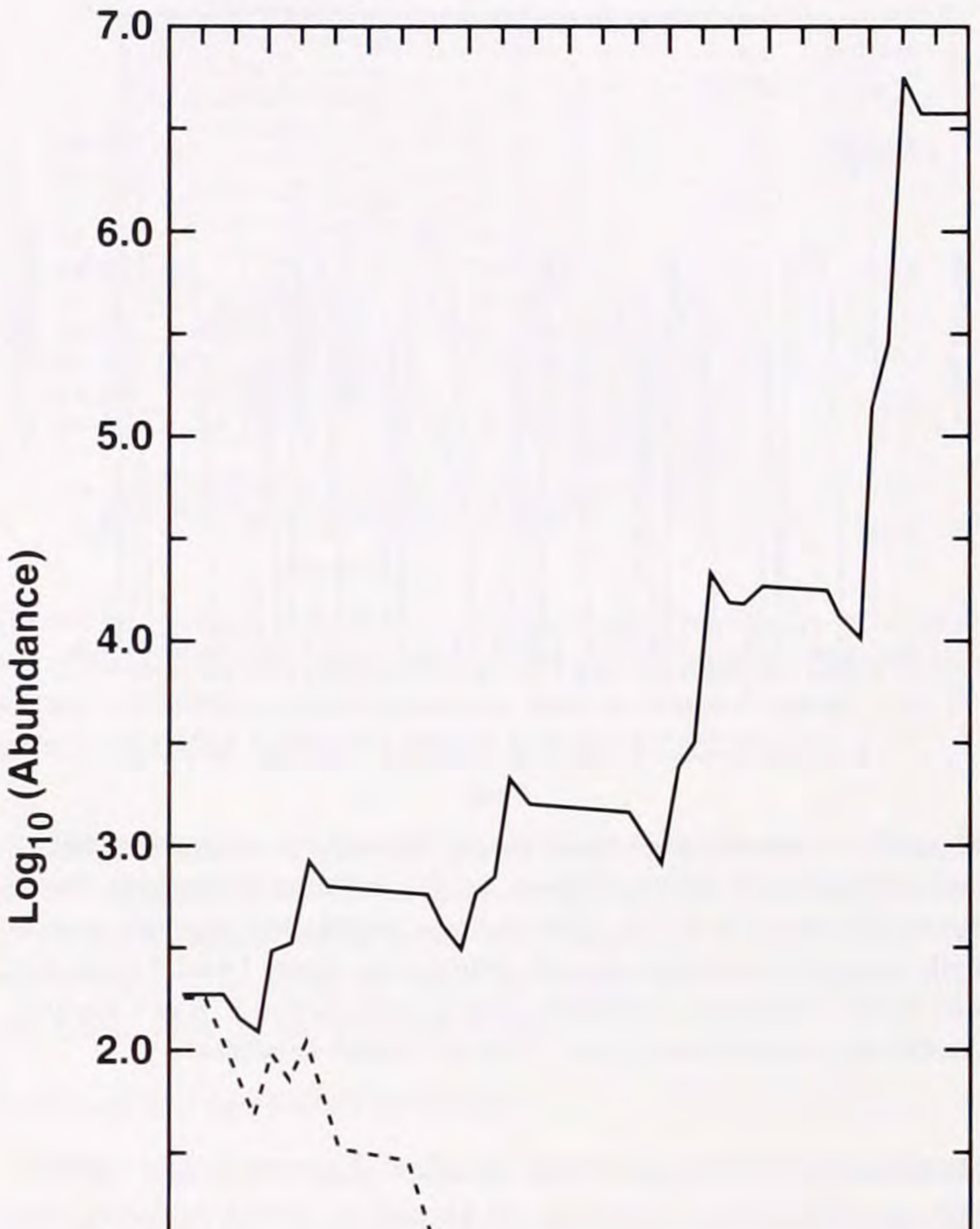

Figure 17. Comparison of simulated total population density [$\log_{10}$(abundance)] of oysters at site 1 (Savin Canal) exposed to the site-specific environmental time series for 4 continuous years, but with differing rates of juvenile mortality; solid line, low juvenile mortality; dashed line, high juvenile mortality.

ria under a constant environmental regime, as shown in our simulations. The inference from these simulations is that oyster populations are normally either expanding or contracting and that the year-to-year variations in environment are overwhelmingly important in restricting the time alloted to each process. It follows that multiyear sampling of environmental variables is extremely important.

The short-term effect of such environmental variables as the effect of an increase in temperature on the rate of *P. marinus* cell division is relatively easy to simulate. However, many population attributes integrate a longer history of environmental change. Any population is a product of the time-history of the environmental and biological processes that have occurred over a number of generations, and these processes will change seasonally and from year to year. Thus, a detailed comparison between simulation results and field observations will always yield inconsistencies because of the limited time span of the environmental data and, because the repetition of environmental data from one year to the next is unlikely to mimic field conditions. In particular, simula-

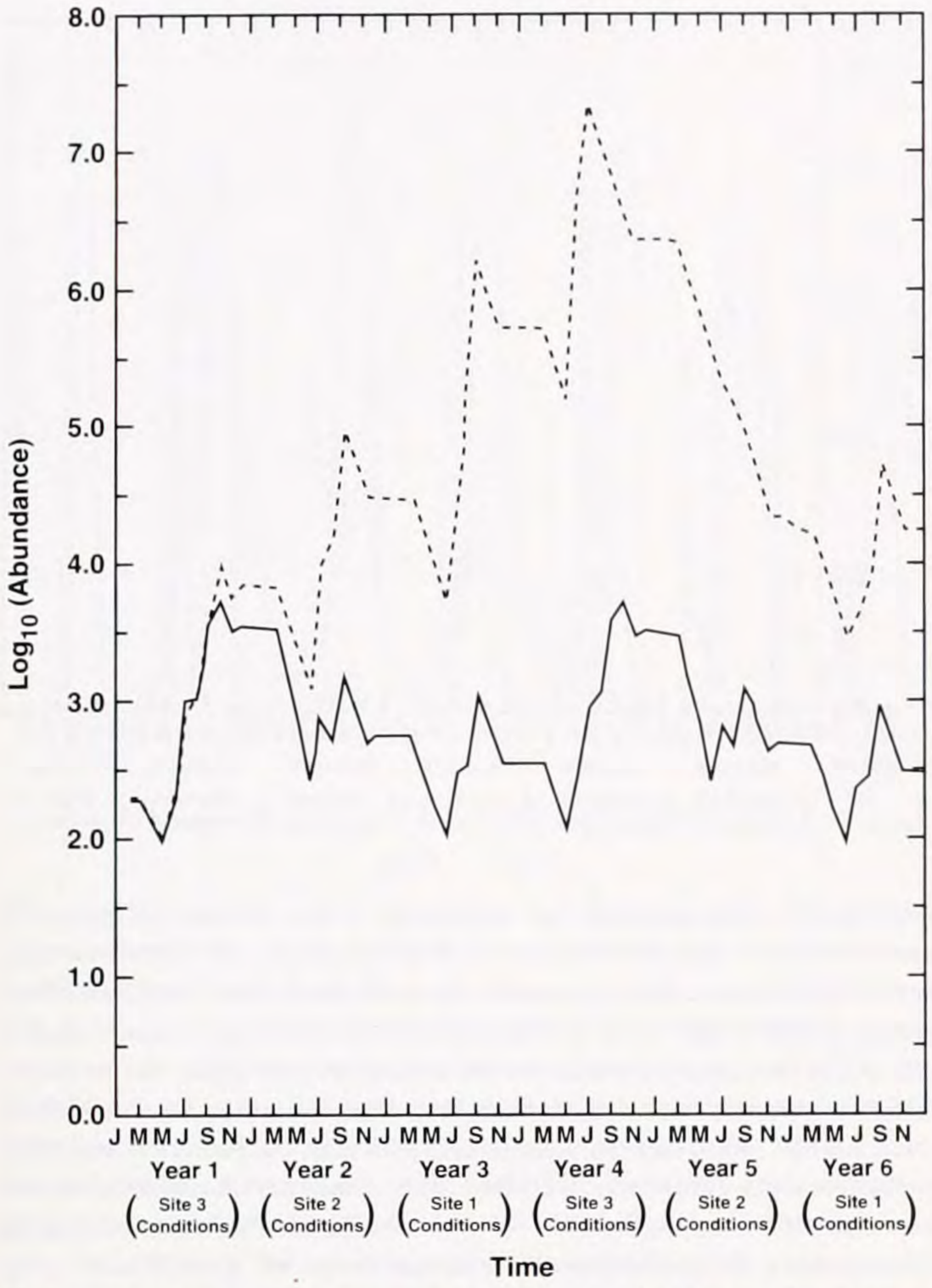

Figure 18. Comparison of simulated oyster densities [$\log_{10}$(abundance)] in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the weekly environmental measurements with daily values obtained by linear interpolation between measurements; dashed line, results using the average of four weekly samplings to define the monthly value and daily values obtained by linear interpolation between the 15th of each month.

tions should be more accurate using longer time series, and a direct correlation between environment and many population attributes should not be anticipated. Most studies of oyster populations using long-term time series have identified significant lag effects of months to years in duration, for this reason (Ulanowicz et al. 1980, Allen and Turner 1989, Wilson-Ormond et al. 1997, Powell et al. 1992a). Our simulations and those of, for example, Powell et al. (1996), which focused on *P. marinus* epizootics, have shown the importance of multiyear history.

To examine the influence of multiyear time series and relative influence of the most recent year in the time series, we appended the environmental variables for the three sites so that the environmental conditions of site 3 were followed by those for site 2 and then those for site 1. For brevity, we show results only for this sequence, which is a high-low-moderate salinity time series. The results emphasize the importance of multiyear environmental time series in describing the time-history of a relatively long-lived species. Only with a multiyear time series introducing interannual environmental variation did the simulated populations at each site conform to field observations. The results also emphasize that the most recent year exerts the strongest impact, as anticipated, par-

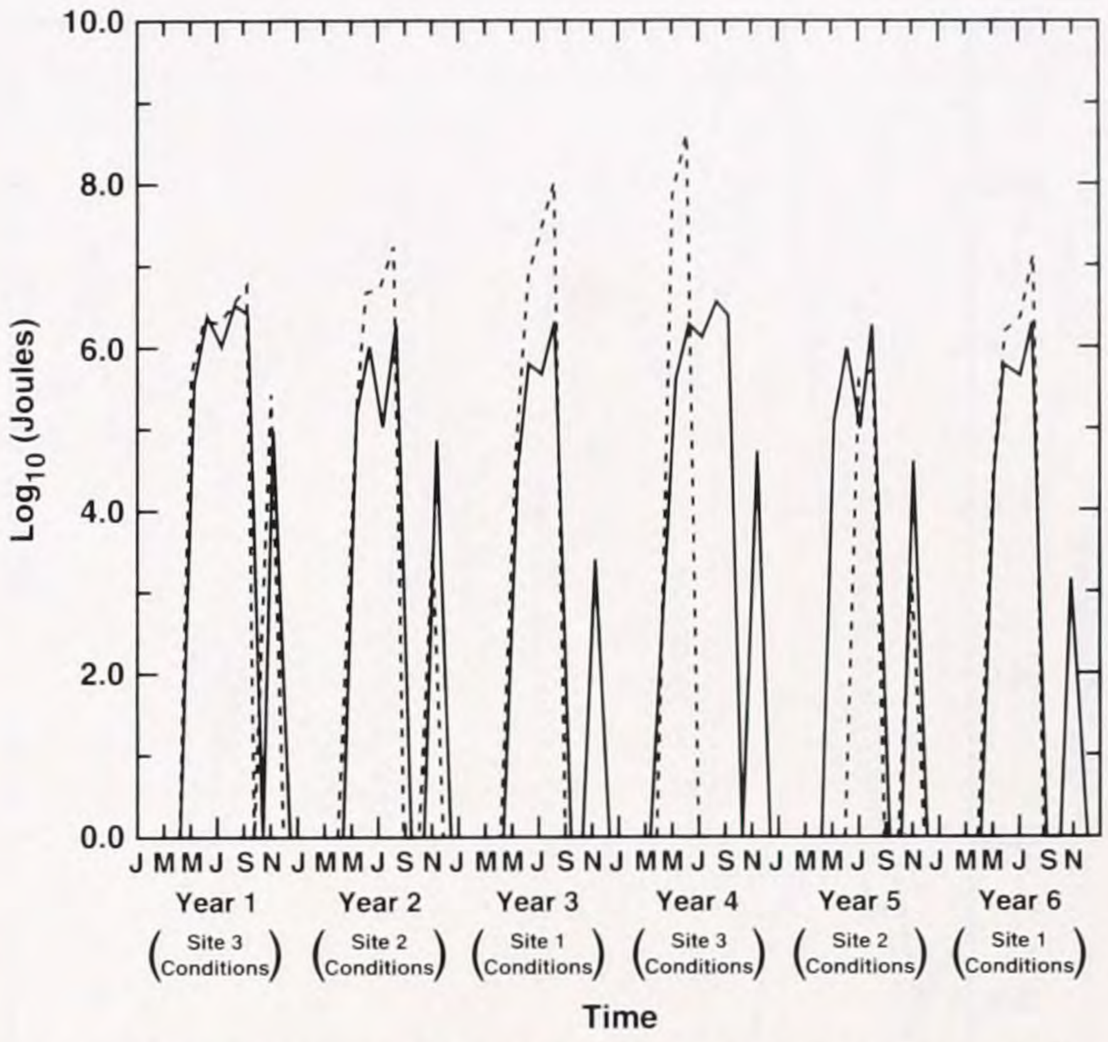

Figure 19. Comparison of spawning [$\log_{10}$(joules)] in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the weekly environmental measurements with daily values obtained by linear interpolation between measurements; dashed line, results using the average of four weekly samplings to define the monthly value and daily values obtained by linear interpolation between the 15th of each month.

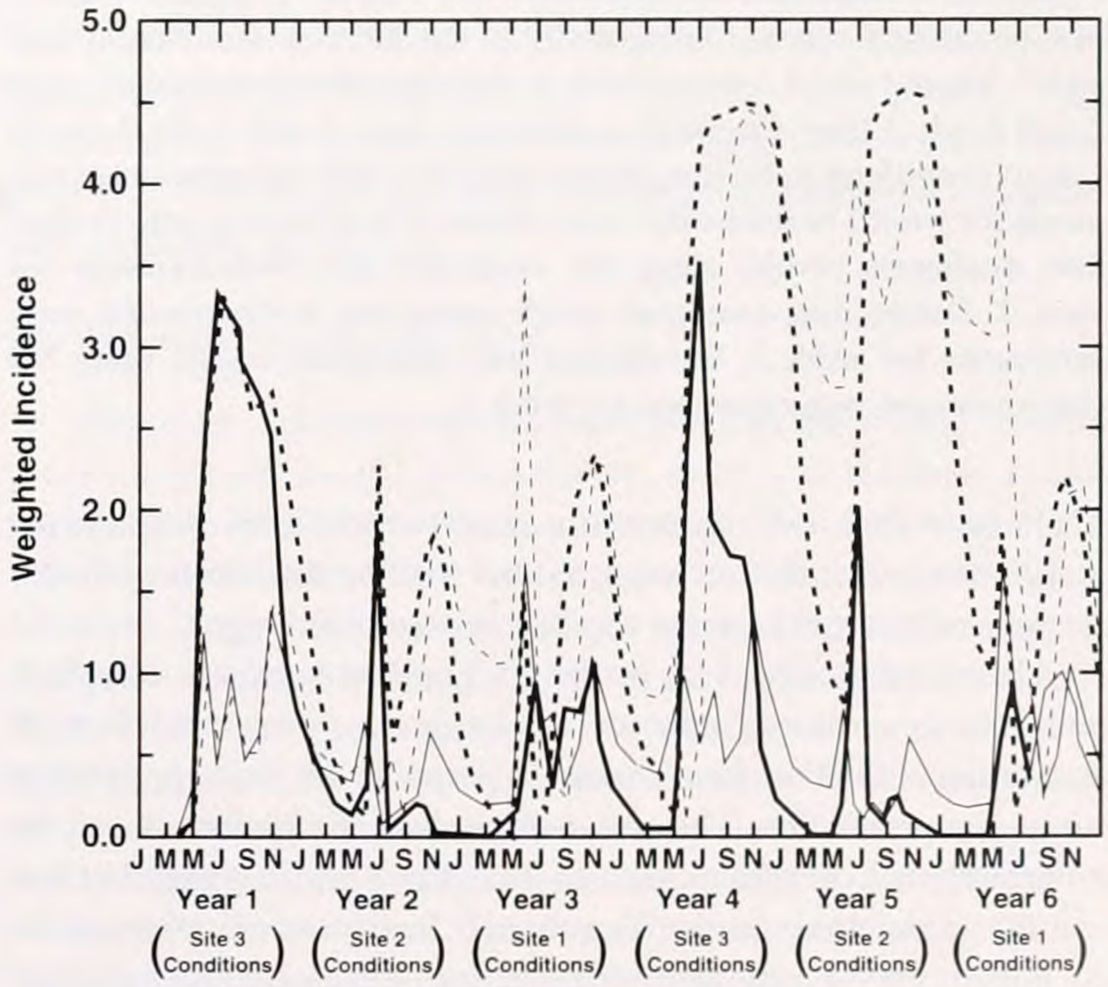

Figure 20. Comparison of *Perkinsus marinus* infection intensity in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the weekly environmental measurements with daily values obtained by linear interpolation between measurements; dashed line, results using the average of four weekly samplings to define the monthly value and daily values obtained by linear interpolation between the 15th of each month. Thin line, the entire population; thick line, the market-size population.

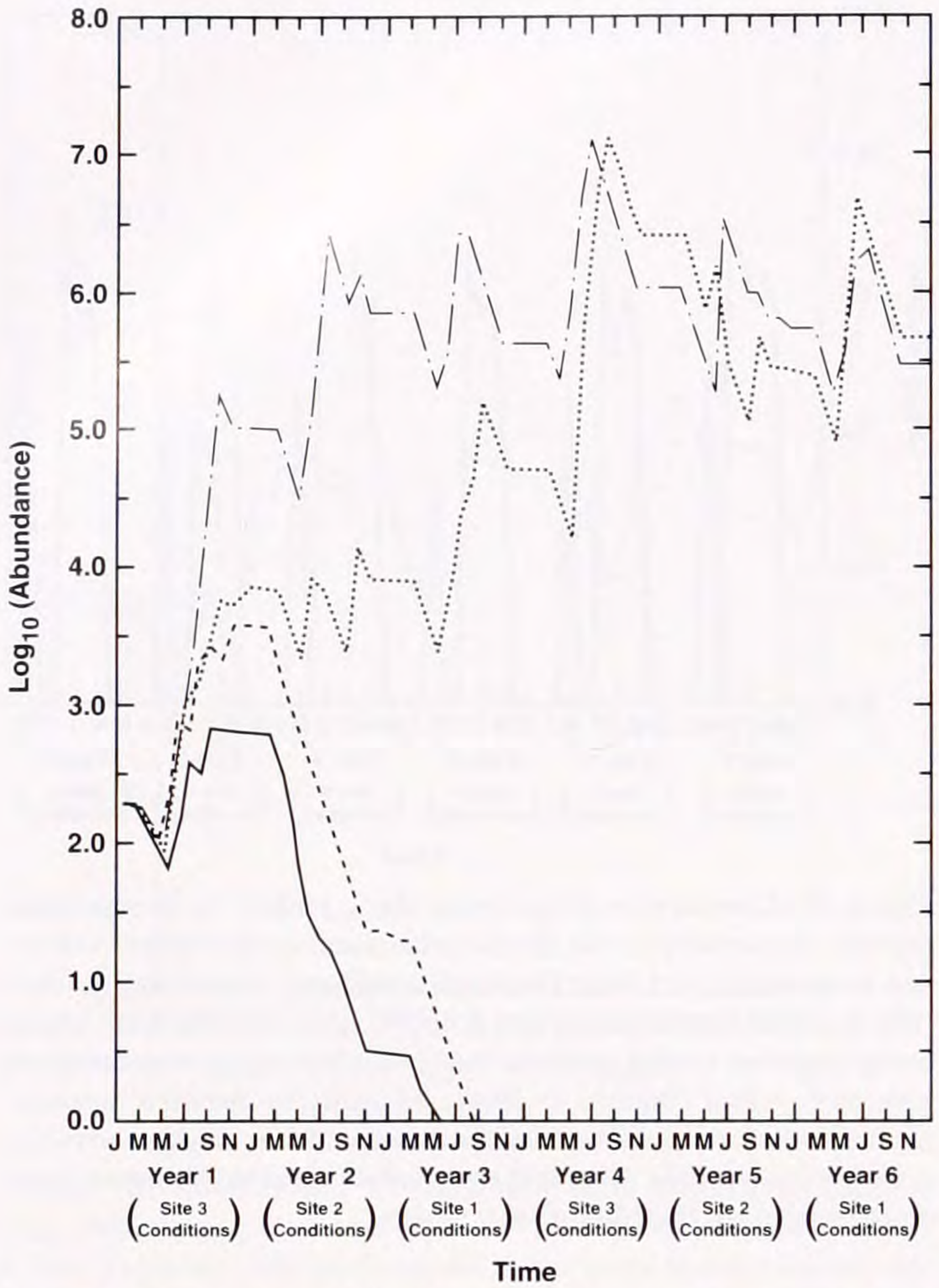

Figure 21. Comparison of simulated oyster densities [$\log_{10}$(abundance)] in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) conditions; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the environmental measurements for week 1 to define the value on the 15th of each month. Dashed line, analogous results using the environmental measurements for week 2. Dotted line, analogous results using the environmental measurements for week 3. Dot-dashed line, analogous results using the environmental measurements for week 4.

ticularly in such environmentally sensitive variables as spawning and *P. marinus* infection intensity, but that the time-history modulates the effect of the most recent environmental signal.

The simulations reveal a distinct gradient between sites 3, 1, and 2 in the susceptibility of populations to local extinction. In particular, site 3 is better able to support its own population through reproduction. The simulations show the importance of the environmental conditions measured at site 3 and suggest that low salinity populations in the Terrebonne Basin are sustained either by outside larval settlement or by year-to-year variability in environmental conditions, providing that good years occur frequently enough. Achieving a persistent population at site 2 requires either higher larval survival or lower postsettlement mortality than at site 3, if the salinity regime remains constant. Although the present field data cannot distinguish the two alternatives, because the number of predators is unknown, it is likely that site 2 and probably site 1 require an external source of larvae during consecutive low-salinity years to limit the chance of local extinction.

It is interesting that a reasonable simulation is achieved by sequentially juxtaposing the environmental time series, while

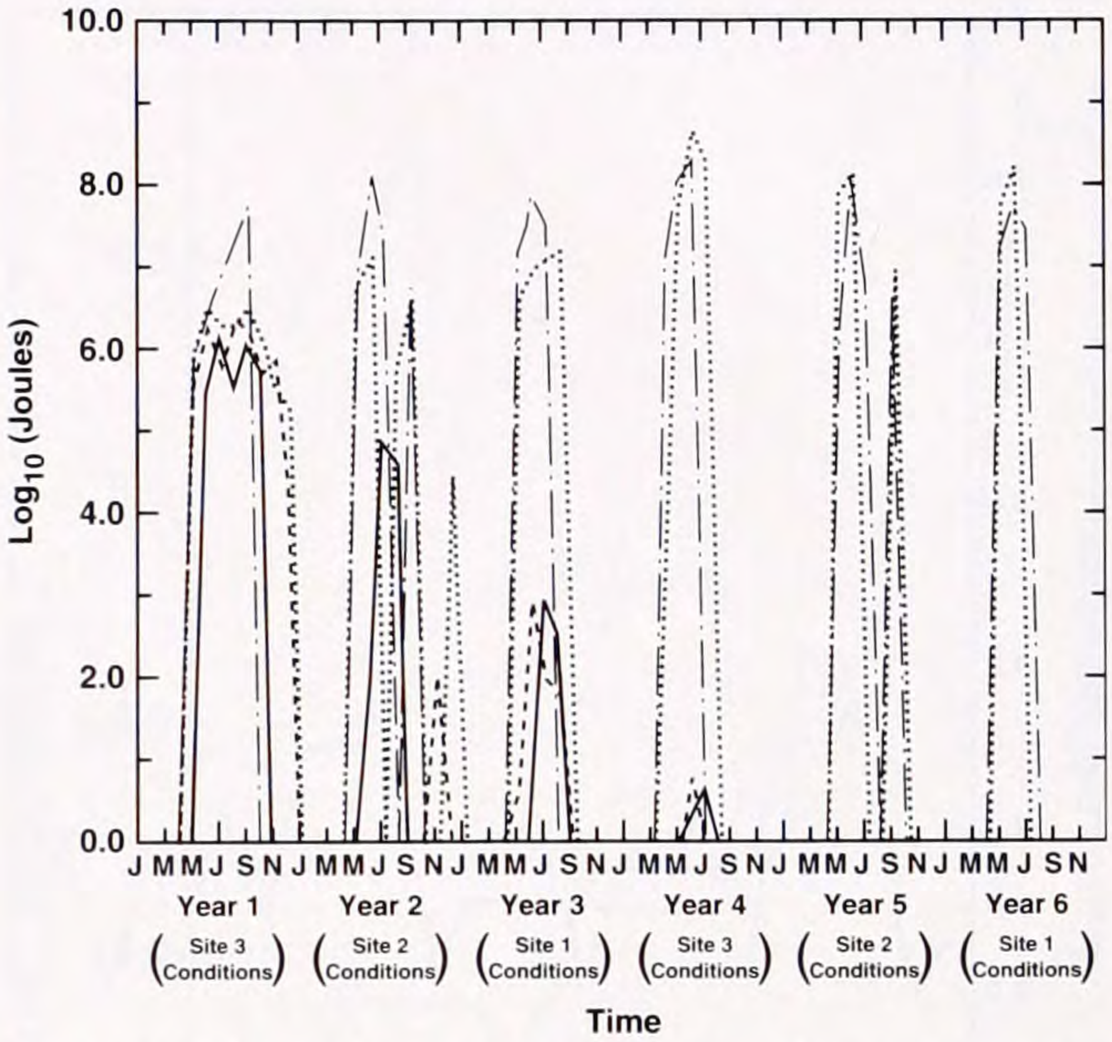

Figure 22. Comparison of spawning [$\log_{10}$(joules of gametes spawned)] in a population exposed sequentially to the three environmental time series. Years 1 and 4 represent site 3 (Bay Tambour) time series; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the environmental measurements for week 1 to define the value on the 15th of each month. Dashed line, analogous results using the environmental measurements for week 2. Dotted line, analogous results using the environmental measurements for week 3. Dot-dashed line, analogous results using the environmental measurements for week 4.

maintaining the same biological characteristics for the oyster population (e.g., rates of larval survival and juvenile mortality). Population persistence and, therefore, adequate simulations can be created by persistent shifts in the environment or by biological gradients in larval settlement, juvenile mortality, etc. Very likely, sequential shifts in environmental regime are also associated with changes in predator abundance and rates of larval recruitment; however, the simulations indicate that simple sequential shifts in environmental variables adequately explain the observed population attributes in these Terrebonne Basin sites. This indicates, for example, that fecundity during good years (= site 3 conditions) may be sufficient to permit population persistence during bad years (= site 2 conditions) in this area. Whether populations persist without an external larval supply will depend upon the relative frequency of these good and bad years. The suggestion from these simulations is that population dynamics at these sites is most influenced by the time-history of environmental change and less influenced by variations in predator abundance and larval survivorship.

However, these populations are heavily influenced by disease and, on occasion, by low-salinity mortality, which adds an important mortality gradient at these sites and in the simulations. Nondiseased populations or populations where disease is a minor contributor to mortality would certainly behave differently. Furthermore, all three sites are in areas where oyster drills are probably not a major source of mortality; whereas, crabs are. Crab densities are less influenced by environmental gradients (Powell et al. 1997), and, thus, rates of crab-induced mortality may be similar among all three sites. Therefore, the data and simulations do not completely discount the importance of determining predator abun-

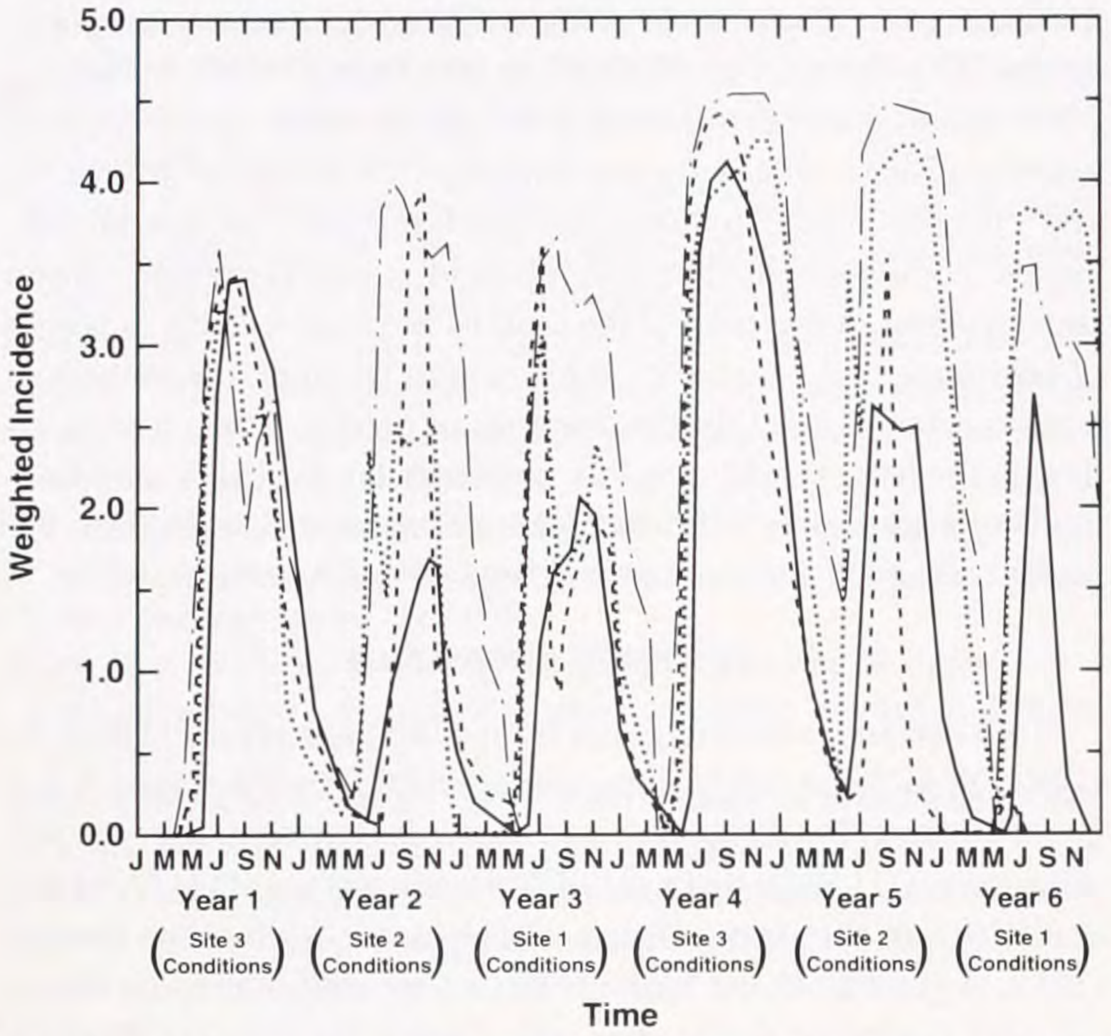

Figure 23. Comparison of *Perkinsus marinus* infection intensity in market-size oysters in a population exposed sequentially to the three environmental conditions. Years 1 and 4 represent site 3 (Bay Tambour) time series; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the environmental measurements for week 1 to define the value on the 15th of each month. Dashed line, analogous results using the environmental measurements for week 2. Dotted line, analogous results using the environmental measurements for week 3. Dot-dashed line, analogous results using the environmental measurements for week 4.

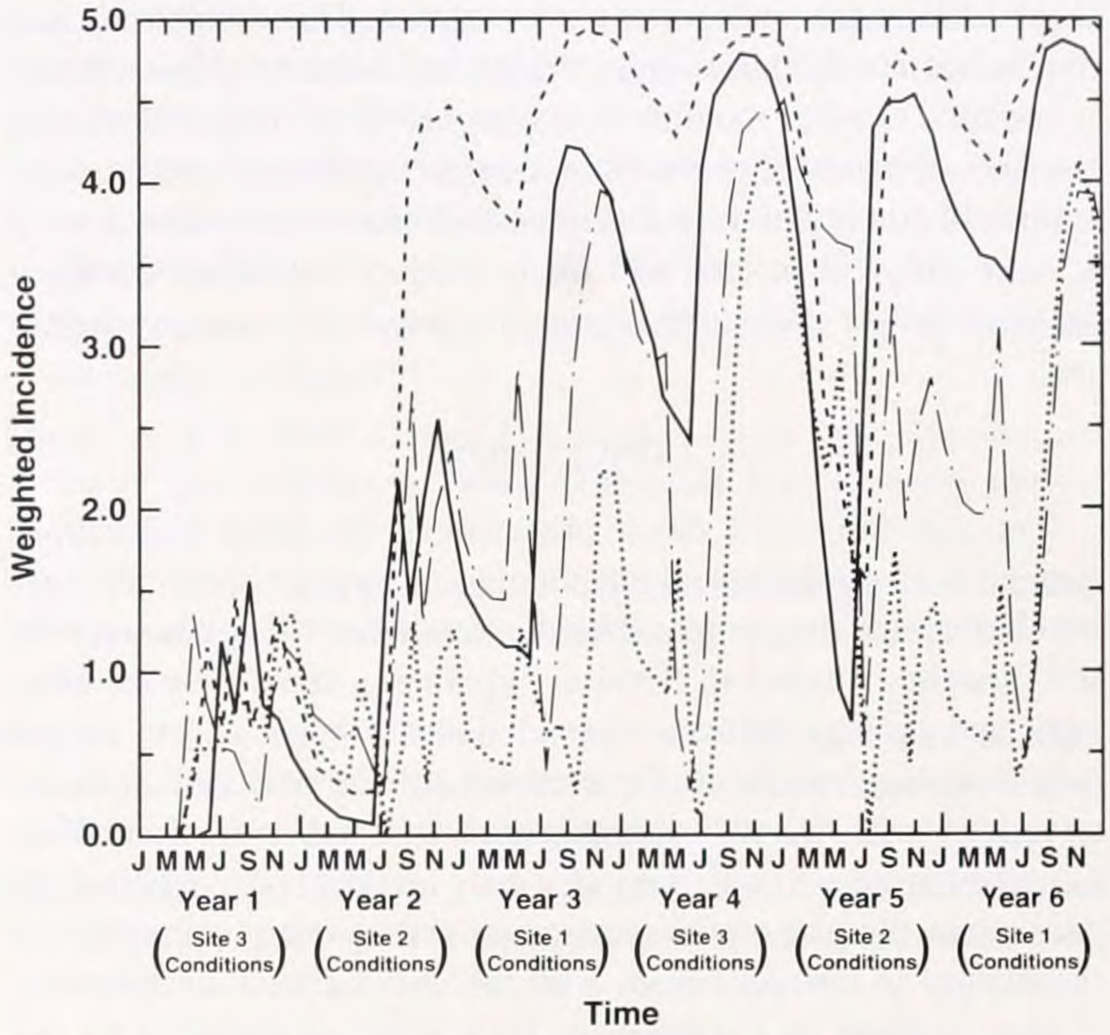

Figure 24. Comparison of *Perkinsus marinus* infection intensity in the entire population of oysters exposed sequentially to the three environmental conditions. Years 1 and 4 represent site 3 (Bay Tambour) time series; years 2 and 5, site 2 (Bay Cocodrie) conditions; years 4 and 6, site 1 (Savin Canal) conditions. Solid line, results using the environmental measurements for week 1 to define the value on the 15th of each month. Dashed line, analogous results using the environmental measurements for week 2. Dotted line, analogous results using the environmental measurements for week 3. Dot-dashed line, analogous results using the environmental measurements for week 4.

dances in understanding the mechanisms producing the observed oyster population attributes, but they do emphasize the necessity of a long-term series of environmental conditions.

Our results indicate the power of combining field research and simulation modeling in understanding the processes producing observed population structure. In this case, the combination of the two has distinguished the potential importance of environmental shifts and biological interactions and suggested further research to test these hypotheses. In addition, the combination has permitted estimation of the sensitivity of these populations to local extinction and the likely mechanisms. Of course, many of these inferences could have been obtained by examining a very long-term dataset for these populations, but resources normally preclude the long-term collection of the intensive dataset on population attributes required for observational inference.

The Importance of Adequate Sampling

Sampling frequency is often determined by funding. In planning a field research program on oyster population dynamics, the immediate question is: how intensive must sampling be to permit an adequate evaluation of observed population attributes or to produce adequate model simulations? A comparison of monthly versus weekly data in the time series clearly shows that field observations are not adequately simulated using monthly environmental data, at least for these Terrebonne Basin sites. Whether even shorter time-scale sampling would provide a further improvement over weekly sampling is untested, but has been assumed in recent modeling studies in Galveston Bay (Powell et al. 1994a) and Delaware Bay (Powell et al. 1997), where hourly or daily environmental data have been used. Regardless, obviously, weekly sampling provides a quantum leap in accuracy over monthly data in simulations and, presumably, a fundamental improvement in the ability to evaluate the mechanisms determining population structure in natural populations.

The Importance of Sampling Time

Very little consideration has been given to the timing of sampling during the month. In the spring, week 1 is routinely colder than week 4. In the fall, the opposite is true. However, much of the population attributes of the oyster population for the year are established in the crucial period of the spring when temperature is rising, as is food supply (Hofmann et al. 1992). Colder temperatures do not permit oysters to take advantage of the increase in food supply, and, on the average, more food is available in the later weeks of each spring month. Hofmann et al. (1992) discussed the crucial nature of the timing of the spring bloom and the rise in temperature in the spring. The opposite conditions in the fall are less important, because oyster metabolism slows down, and food supplies are normally low. Thus, sampling time and frequency are important, particularly in the spring, and, as important, is the recognition that explicit sampling time must be retained in all analyses rather than permitting a monthly sampling to pertain simply to the entire month.

In this study, a sampling fell no more than 10 days from the middle of the month in the most extreme case; however, simulation accuracy was substantially degraded if these values were assumed indicative of the entire month. The simulations emphasize the importance of a change in environmental signal over a few weeks

or less during the spring and early summer. The simulations also emphasize that the temptation of applying monthly measurements at one time to other monthly data obtained at an independent time must be eschewed. For example, comparing monthly mean environmental conditions with a single event stock assessment a week or more different in time will likely produce inaccurate comparisons that fail to clarify the reasons for population success or failure.

CONCLUSIONS

The comparison of direct observations of oyster populations through field sampling and the population attributes obtained from simulation modeling emphasizes the importance of combined field and modeling studies to develop hypotheses about how environment and biology influence population attributes and to design field sampling programs. Simulations only approached field observations with weekly sampling and with the correct food resource estimated. Simulations also only approached field observations when the assumption was made that oyster populations are chronically in disequilibrium with the environment so that year-to-year changes in environment contribute substantially to observed population attributes. This latter finding, of course, is well documented in a number of studies of time series in oyster populations (Ulanowicz et al. 1980, Allen and Turner 1989). Finally, in these simulations, the influence of environment and *Perkinsus marinus* disease seemingly overwhelmed the influence of year-to-year changes in predator abundance or larval survival in establishing the population attributes in the field at our Terrebonne Basin sites. At least in this area of the Gulf of Mexico, weekly sampling of environmental variables would seem to be more important than a more detailed monthly enumeration of predator abundances, although the latter would certainly be beneficial. Probably, this finding is typical of the Gulf coast, where *P. marinus* is prevalent, but it may not apply throughout the range of the American oyster.

ACKNOWLEDGMENTS

This research was supported by institutional grant NA89-AA-D-SG128 to Texas A&M University (TAMU) by the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, grant DACW64-91-C-0040 from the Army Corps of Engineers, Galveston District Office, a grant from the Nicholls State University Research Council, and computer funds from the Center for Coastal Physical Oceanography at ODU. We appreciate this support.

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