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UNDERSTANDING THE SUCCESS AND FAILURE OF OYSTER POPULATIONS: PERIODICITIES OF *PERKINSUS MARINUS*, AND OYSTER RECRUITMENT, MORTALITY, AND SIZE

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ABSTRACT   Ten-year time series (1992 to 2002) of salinity, Dermo disease, and size-class structure and mortality measured for an eastern oyster (*Crassostrea virginica*) population at a reef in Bay Tambour, Terrebonne Parish, LA, were analyzed using wavelet techniques to determine dominant frequencies and correlations. Along the Gulf Coast of the United States, Dermo disease (caused by *Perkinsus marinus*) responds to the El Niño-Southern Oscillation (ENSO) climate signal through its response to salinity. During the La Niña portion of ENSO, decreased rainfall leads to an increase in salinity, which triggers a rise in Dermo disease prevalence and intensity, producing increased oyster mortality. Although disease responds to the 4-y periodicity of ENSO and salinity, the oyster population dynamics do not appear to be controlled by disease at this site. A significant 4-y coherency exists between recruitment and salinity, with recruitment being higher during periods of high salinity. Recruit numbers and submarket numbers also exhibit a strong 4-y periodicity. However, a relationship between the recruit time series and the subsequent change in market-size abundance did not exist. The complexity of postsettlement processes and the extended time over which these processes interact decrease the predictability of the recruit-to-market transition. Even the strong pulse of recruits associated with La Niña and its locally elevated salinities did not result in an exceptional abundance of market oysters. Understanding the environmental and biotic factors that favor the production of large oysters is critical because large oysters not only supply the fishery, but, upon their death, contribute the bulk of the shell required for reef sustainability.

KEY WORDS: oyster, *Crassostrea virginica*, *Perkinsus marinus*, climate, wavelet analysis, recruitment, mortality, sustainability

INTRODUCTION

The success of oyster populations is determined by a complex interaction between environmental variables and population attributes such as recruitment, growth, and juvenile and adult mortality. Along the Gulf Coast of the United States, eastern oyster (*Crassostrea virginica*) populations are distinguished by prodigious recruitment, rapid growth, and high mortality. Gulf Coast oysters generally spawn early and often (Hopkins et al. 1953, Hayes & Menzel 1981). They reach sexual maturity in as little as 1 mo, and the spawning season in the northern Gulf can extend from April to November (Hopkins 1955). Major spawning events typically occur during the spring and/or fall, although intermittent multiple spawns are possible throughout the summer (Hopkins et al. 1953, Hopkins 1955, Hayes & Menzel 1981, Gauthier & Soniat 1989, Hofmann et al. 1994). The time required for growth from newly settled spat to harvest-legal adult ($\geq$75 mm) can be as short as 12 mo, is rarely more than 24 mo, and is typically about 18 mo (Hopkins et al. 1953, Hopkins 1955).

Mortalities of market-size Gulf oysters resulting from the endoparasitic protozoan *Perkinsus marinus*, which causes Dermo disease, often exceed 50% (Mackin 1961, Mackin 1962). Dermo-related mortality is size dependent, with smaller oysters generally showing lower prevalence and intensity of disease (Mackin 1951). However, populations of juvenile oysters in enzootic areas can acquire disease prevalence and intensity that exceed those of the adult population (Ray 1987). In addition to disease, predation from mud crabs (*Eurypanopeus depressus, Panopeus herbstii*), blue crabs (*Callinectes sapidus*), stone crabs (*Menippe adina*), black drum (*Pogonias cromis*), and oyster drills (*Stromonita haemastoma*) is a significant source of mortality for Gulf Coast oysters. Predation, like disease, is typically greater at higher salinities. However, unlike disease mortality, smaller size classes experience greater predator mortality. The interaction of predation with salinity and prey size is more complex than simple relationships with size or salinity. Some predators are broadly euryhaline (e.g., *C. sapidus, E. depressus, P. herbstii*) whereas others are relatively stenohaline (e.g., *M. adina, S. haemastoma*), and differences exist in the maximum size of exploited prey of the various predators (White & Wilson 1996, Shirley et al. 2004). For example, adult *P. herbstii* can open oysters up to about 25 mm in length (Bisker & Castanga 1987), whereas black drum consume oysters up to 80 mm long (White & Wilson 1996).

Despite heavy mortalities, Gulf Coast oyster populations persist and support a viable fishery. The sustainability of oyster populations results from a balance between recruitment and mortality. Assuming adequate spawning stock and suitable substrate, recruitment is largely a function of salinity, with greater recruitment occurring at higher salinity (Hopkins et al. 1953, Hopkins 1955, Cake 1983, Chatry et al. 1983, Ray 1987). Furthermore, high-salinity events and recruitment are closely linked in time. However, the response time from the transition of recruits to market oysters is greater than a year, during which time multiple and interactive factors of mortality are operating differentially on the various size classes.

In a previous study (Soniat et al. 1998), we combined field observations with numerical modeling to investigate the complex basis for population structure. We described key environmental and biological interactions, and their spatial and temporal variation. In a second contribution (Soniat et al. 2005), we investigated a particularly critical and likely causal sequence that links water salinity to prevalence and intensity of *P. marinus*. In the current study, time series of salinity, Dermo disease prevalence and intensity, and oyster size and mortality, measured from February 1992 to February 2002 at a reef in Bay Tambour, Terrebonne Parish, LA (Fig. 1), were examined for relationships among recruitment, mortality, and environmental factors that influence sustainability of oyster populations. Emphasis is placed on identifying conditions that potentially result in an exceptional abundance of market-size oysters that support the fishery upon their harvest and disproportionately supply substrate upon their death.

The following section describes the data sets and statistical method used for analysis of the time series. This is followed by results that show relationships among salinity, oyster recruitment, oyster numbers, Dermo disease intensity, and oyster mortality. The Discussion places these results in the context of sustainability of exploited oyster reefs.

MATERIALS AND METHODS

Data Sets

Environmental variables were measured weekly, and oysters (*C. virginica*) were sampled monthly from February, 2, 1992, to February, 14, 2002, at a single reef. The site (29°11.18′ N, 90°39.93′ W) lies at the intersection of Bayou Petit Calliou and Bay

Tambour, Terrebonne Parish, LA (Fig. 1). Water depth varied from about 0.3–0.6 m.

Water was sampled from 0.3 m above the reef. Salinity was measured weekly to the nearest 0.5 using a refractometer (Beherns 1965). Oyster population parameters were measured monthly. About 0.13 m^3 of reef material was collected using hand-operated tongs from a 5.1-m skiff. Live oysters, boxes (articulated shells), and single shells were separated. Live oysters and boxes were counted and assigned to 25-mm size classes (0–24 mm, 25–49 mm, and so on). Single shells, boxes, and live oysters were examined for the presence of spat, which were also counted and assigned to a size class. Mortality fraction, the ratio of dead to live oysters, was calculated for submarket oysters (25–74 mm) and market oysters (≥75 mm) by dividing the number of boxes by the number of live oysters in the respective size class.

Each month, 10 market-size (≥75 mm) live oysters were culled, cleaned of epifauna, and measured (anterior to posterior length) to the nearest millimeter. A small piece (about 4 mm^2) of mantle tissue was used to assay *P. marinus* (Ray 1966). Level of infection was scored using Mackin's 0–5-point scale as modified by Craig et al. (1989). Disease prevalence as percent infection and infection intensity (*II*) were determined, where

$$II = \frac{sum\ of\ Mackin's\ disease\ code\ numbers}{number\ of\ infected\ oysters}.$$

For each time series the mean, median, and range was calculated (Table 1). Salinity showed the range of variability expected for a midlatitude temperate estuary. The submarket and market boxes were about 10–15% of the number living for each category. This gives average mortality fractions of 0.07–0.13, which are within values for oyster populations that are not undergoing major population changes (Powell et al. 2009);
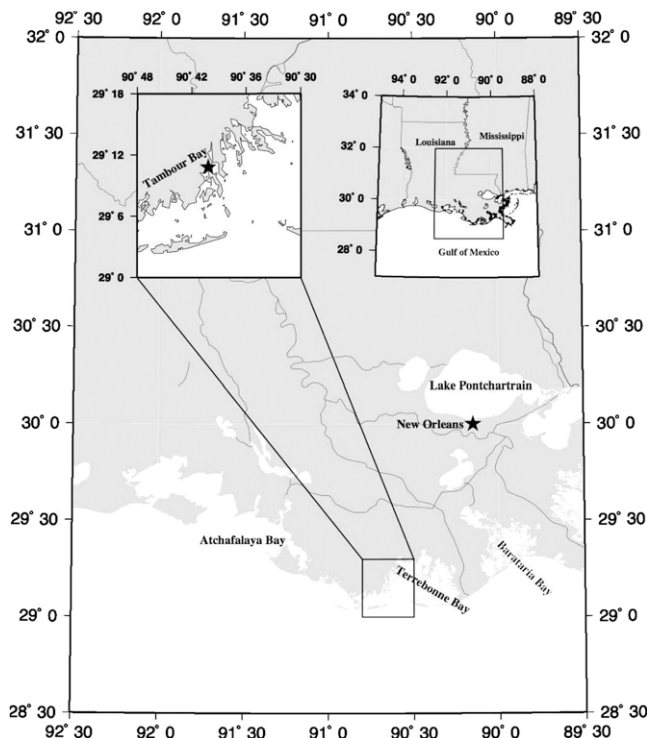
Figure 1. The location of the Bay Tambour sampling site in central coastal Louisiana.

TABLE 1.

Mean, median, and range computed for the 10-y time series of environmental and oyster population parameters measured in Bay Tambour from 1992 to 2002.

Parameter	Mean	Median	Minimum	Maximum
Salinity	15.23	15.25	0.5	29.5
Infection intensity	0.95	0.87	0.00	2.96
Percent infection	79.30	85.45	0.00	100
Recruit numbers	52.24	45	12	233
Submarket numbers	34.86	33	8	97
Submarket boxes	3.50	2.81	0	23
Market numbers	32.64	33	13	60
Market box numbers	4.76	4.50	0	16
Market mortality fraction	0.13	0.12	0.00	0.41
Submarket mortality fraction	0.07	0.06	0.00	0.33
Niño 3.4 index	0.03	−0.07	−1.85	2.80

The El Niño 3.4 index was obtained from the Climate Prediction Center, National Center for Environmental Prediction (www.cpc.ncep.noaa.gov/data/indices/sstoi.indices).

however, because the rate of disarticulation may be greater in the Gulf of Mexico than in more northern climes (Christmas et al. 1997, Ford et al. 2006), these mortality estimates are likely to be conservative. Similarly, the measured percent infection and infection intensity are within values expected for Gulf coast oyster populations (Soniat 1996). Thus, the oyster population used for this study was not undergoing major expansions or contractions and had characteristics typical of a normally growing population (Powell et al. 2009).

Data Analysis

Wavelet analysis (Daubechies 1992, Torrence & Compo 1998) was used to investigate interannual relationships among water salinity, oyster disease, and oyster size-class structure and mortality. This technique uses sets of data filters (wavelets) that are designed to extract estimates of the amplitudes of specific frequencies from time series. This approach identifies oscillation periods in the time series even if the amplitude of the oscillation is variable. Defining a particular mother wavelet sets the character of the frequency analysis, which in turn leads to a series of functional forms that extract the oscillatory behavior of the time series. In this analysis, a Morlet mother wavelet was used because it provides the best resolution in the frequency domain at the cost of minimal smearing of signals in the time domain. The wavelet analysis considered both the frequency content of individual time series as well as correlations between time series in the frequency domain (i.e., cross-wavelet analysis). The latter analysis evaluated the correlation between the periodicity of 2 variables.

For this analysis, the Niño 3.4 sea surface temperature index was used (National Weather Service, Climate Prediction Center: www.cpc.ncep.noaa.gov/data/indices/sstoi.indices/) to represent large-scale climate variability (Soniat et al. 2005). Local environmental variability was represented by the salinity time series. Responses of the oyster population to large-scale and local environmental variability were represented by time series of recruit numbers, submarket numbers, and market numbers. Oyster population mortality was partitioned into a submarket mortality fraction and a market mortality fraction. Time series of disease infection intensity provided a measure of the contribution of disease to oyster mortality. The time series were analyzed independently (Table 2) as well as jointly (Table 3) to understand size-class dynamics and to determine correlations between environmental and biological processes, which suggest causative linkages.

RESULTS

Individual Time Series

The salinity time series shows a significant periodicity at 4 y (Fig. 2, Table 2), which reflects the periods of high salinity (>20) in 1992 and 1994 to 1996, and the extended high salinity from 1999 to 2001 (Fig. 2, Table 2). The other environmental time series, the Niño 3.4 index, also shows a dominant periodicity at 4 y (Table 2); it is manifest of the ENSO cycle, because it typically influences the Gulf coast (Douglas & Englehart 1981, Schmidt & Luther 2002, Soniat et al. 2005, Bergquist et al. 2006).

The recruit numbers (oysters <25 mm) time series shows a significant periodicity at 4 y as well as at 1 y (Fig. 3, Table 2). The 1-y periodicity results from the annual spawning cycle, which is seen as an increase in recruit numbers in each year of the time series (Fig. 3). The 4-y periodicity is driven by the increase in recruit numbers in the latter part of the time series and suggests

TABLE 3.

Significantly correlated periodicities, or lack thereof, between population attributes as revealed by cross-wavelet analyses.

Time Series	Period (y)					
	0.5	1	1.5	2	3	4
Salinity × Niño 3.4 index				*		**
Salinity × recruit numbers			*			**
Niño 3.4 index × recruit numbers						**
Salinity × submarket numbers				*		
Niño 3.4 index × submarket numbers						
Salinity × market numbers			**	**		
Niño 3.4 index × market numbers						
Recruit numbers × submarket numbers	**	*	*	**		
Recruit numbers × market numbers						
Submarket numbers × market numbers	**	*	*	*		*
Infection intensity × submarket mortality fraction						*
Infection intensity × market mortality fraction			*			*

* P < 0.10, ** P < 0.05.
Blank table cells indicate the absence of a significant cross-correlation at α = 0.10.

TABLE 2.

Significant periodicities obtained from wavelet analysis of individual time series.

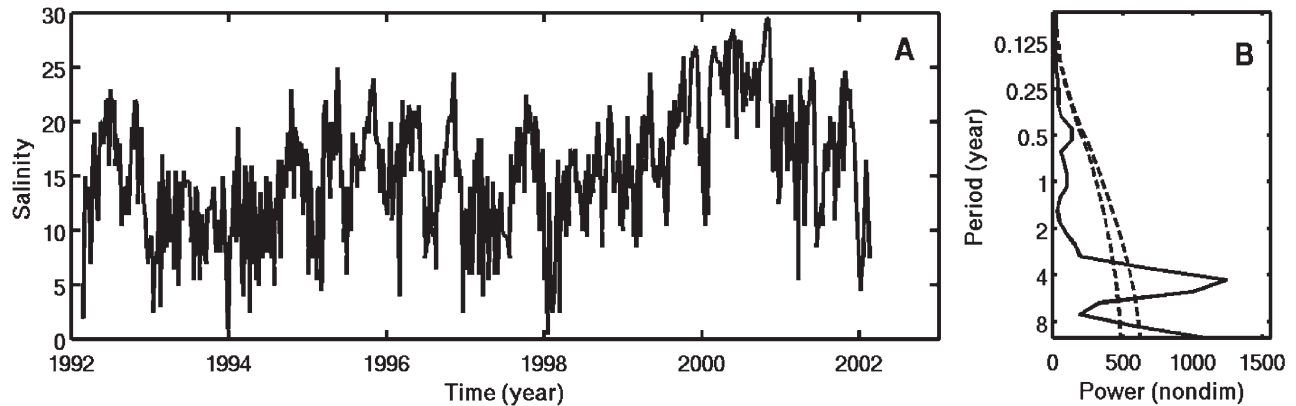| Time Series	Period (y)						
	0.5	1	2	3	4	5	6
Salinity					**		
Niño 3.4 index					**		
Recruit numbers		**			**		
Submarket numbers		*	*				**
Submarket mortality fraction					**		
Market numbers							**
Market mortality fraction		*					**
Infection intensity	*	*			*		*

* P < 0.10, ** P < 0.05.

Figure 2. (A) Time series of the zero-mean unit-variance salinity derived from weekly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained for the salinity time series from the wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.

a possible relationship with the ENSO cycle and salinity. The only other oyster population characteristic that shows a 4-y periodicity was the submarket mortality fraction (Table 2). Population Dermo infection intensity shows 4 significant periodicities, one of which also was 4 y (Table 2). Analysis of the time series of submarket numbers, market numbers, market mortality fraction, and infection intensity show evidence of a 6-y periodicity (Table 2). However the 10-y time series is too short to resolve a 6-y periodic signal from a temporal shift trending through the time series.

Cross-wavelet Analysis

Cross-wavelet analysis using the Niño 3.4 index and locally measured salinity gave the expected significant 4-y signal and a lesser 2-y signal (Fig. 4, Table 3). Phase analysis of the 4-y signal (Fig. 4C) shows that the Niño 3.4 index and salinity are nearly 180° out of phase. High salinities follow a low Niño 3.4 index by about 2 y (phase/360 × period, or 180/360 × 4). The higher salinities are associated with low values of the Niño 3.4 index, the La Niña condition. La Niña is associated with lower precipitation across the northern Gulf of Mexico and hence higher salinity in Gulf coast bays (Douglas & Englehart 1981, Ropelewski & Halpert 1986, Schmidt & Luther 2002).

The cross-wavelet analysis between the salinity time series and recruit numbers shows significant periodicities at 1.5 y and 4 y (Fig. 5, Table 3). A significant coherency at 4 y is also observed between recruit number and the Niño 3.4 index (Fig. 6, Table 3). The phase shift between the recruit number 4-y cycle and the salinity 4-y cycle is near 0° (Fig. 5C). Recruitment is higher at times of high salinity. The 4-y cycle between salinity and recruit abundance is not recapitulated in cross-wavelet analysis between salinity and submarket abundance; instead, a 2-y cycle is apparent (Table 3). As in the cross-wavelet analysis between salinity and submarket numbers, the 4-y cycle is absent in the cross-wavelet analysis between the Niño 3.4 index and submarket abundance (Table 3).

Cross-wavelet analysis confirms the absence of a 4-y cyclic interaction between salinity and market abundance. Rather, salinity and market abundance show significant coherency at periods of 1.5 y and 2 y (Fig. 7, Table 3). Phase analysis shows that a change in market abundance lags about 1 y behind a change in salinity. The timescales, 1.5 y and 2 y, are consistent with the 18-mo, more or less, growth time from recruitment to market size, but also are consistent with modeling that suggests a multiyear trajectory for Dermo disease epizootic development and decay (Powell et al. 1996). Paralleling the lack of correspondence between salinity and market numbers (Fig. 7), the
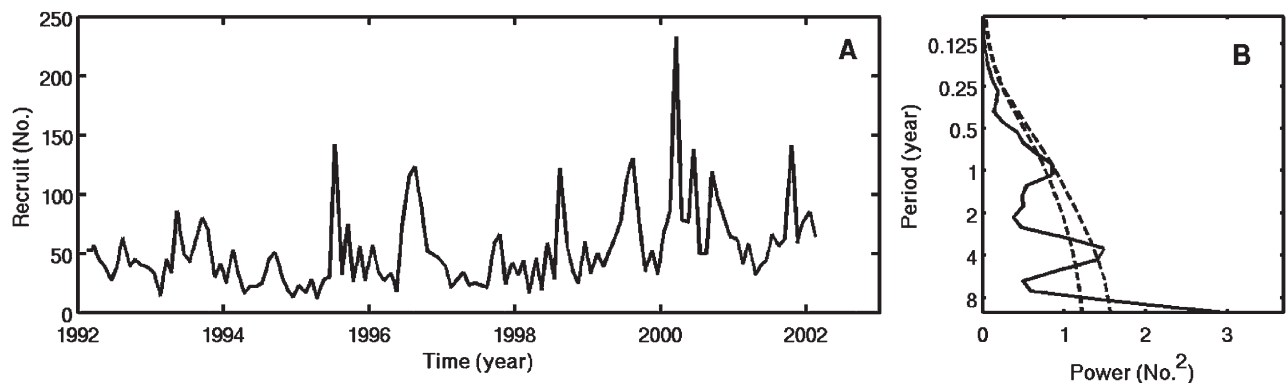

Figure 3. (A) Time series of the zero-mean unit-variance recruit numbers derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained for the recruit numbers time series from the wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.

Figure 4. (A) Time series of the zero-mean unit-variance salinity (solid line) and Niño 3.4 index (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0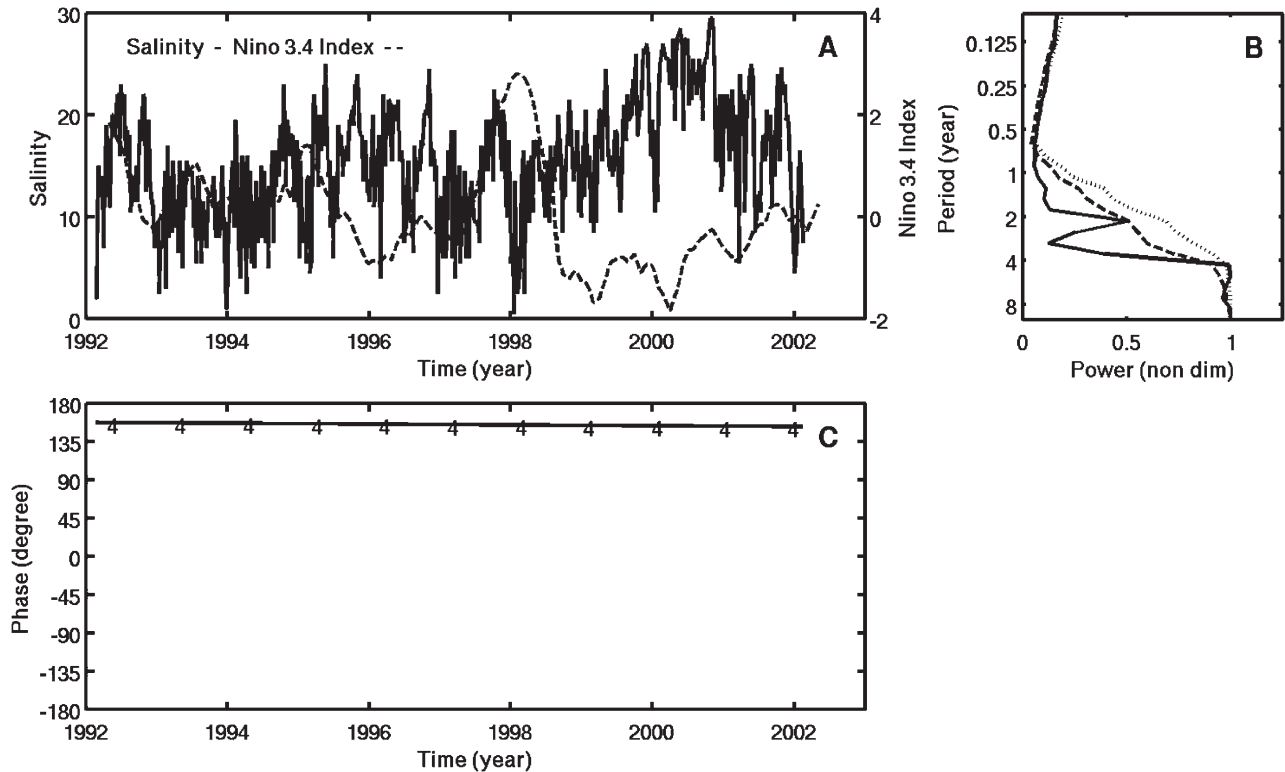.05$ (right) significance levels. (C) Phase diagram. Note that for the 4-y periodicity, salinity and the Niño 3.4 index are nearly 180° out of phase.

results of the cross-wavelet analysis between the Niño 3.4 index and market numbers revealed no significant coherency (Fig. 8, Table 3).

Although peaks in recruit numbers corresponded to peaks in the number of submarket oysters, there was no correspondence between recruit numbers and market oyster numbers. Cross-wavelet analysis of the recruit number time series with the submarket number time series showed dominant periods of 2 y or less (Fig. 9, Table 3), but no significant periodicity with the market number time series (Fig. 10, Table 3). Cross-wavelet analysis of the time series of the submarket numbers and market numbers also showed significant periodicities at the shorter timescales as well as at 4 y, in this case (Fig. 11, Table 3). Oysters recruit and grow to adult size in 18 mo, more or less; hence, the dominance of these shorter timescales is expected. Indeed, phase analysis shows that the submarket index lags the recruit index by about 0.75 y, a typical time for growth from spat size to submarket size. For the submarkets, the 4-y signal shows that submarket abundance leads to market abundance in about a year, a time frame consistent with growth dynamics of the oyster in the Louisiana region. Interestingly, the same phase analysis shows a shift in the 2-y signal throughout the time series, in that the cycles begin 0.5 y out of phase early in the time series and come into phase later (Fig. 11C). This behavior offers one possible explanation for the failure of the recruit time series and market time series to show significant periodicities. Phase analysis of recruit and market abundance shows that the 2-y

relationship between these time series is in phase (0°) early in the time series, and out of phase (180°) later in the time series (Fig. 10C). This is consistent with the inferred trend in market abundance throughout the course of the time series, which suggests an evolving relationship between recruitment and market abundance.

Dermo disease is strongly influenced by salinity (Hofmann et al. 1995, Powell et al. 1996). Cross-wavelet analysis of the time series of Dermo disease infection intensity with the 2 time series for submarket and market mortality fraction show significant periodicities at 4 y for submarket mortality (Fig. 12), and at 4 y and 1.5 y for market mortality (Fig. 13). In both cases, an increase in Dermo infection intensity leads to an increase in mortality by about two thirds of a year. This lag time is consistent with the time to development of lethal infection levels observed empirically and experimentally (Soniat 1985, Saunders et al. 1993, Soniat et al. 1998). The 4-y periodicity corresponds to that of the high-salinity phase of ENSO when oyster mortality from Dermo is elevated along the Gulf coast (Powell et al. 1992, Wilson et al. 1992, Kim & Powell 1998).

DISCUSSION

Perspective on Periodicity

The oyster population examined in this study is characterized by 3 distinct periodicities. The dominant periodicity was at
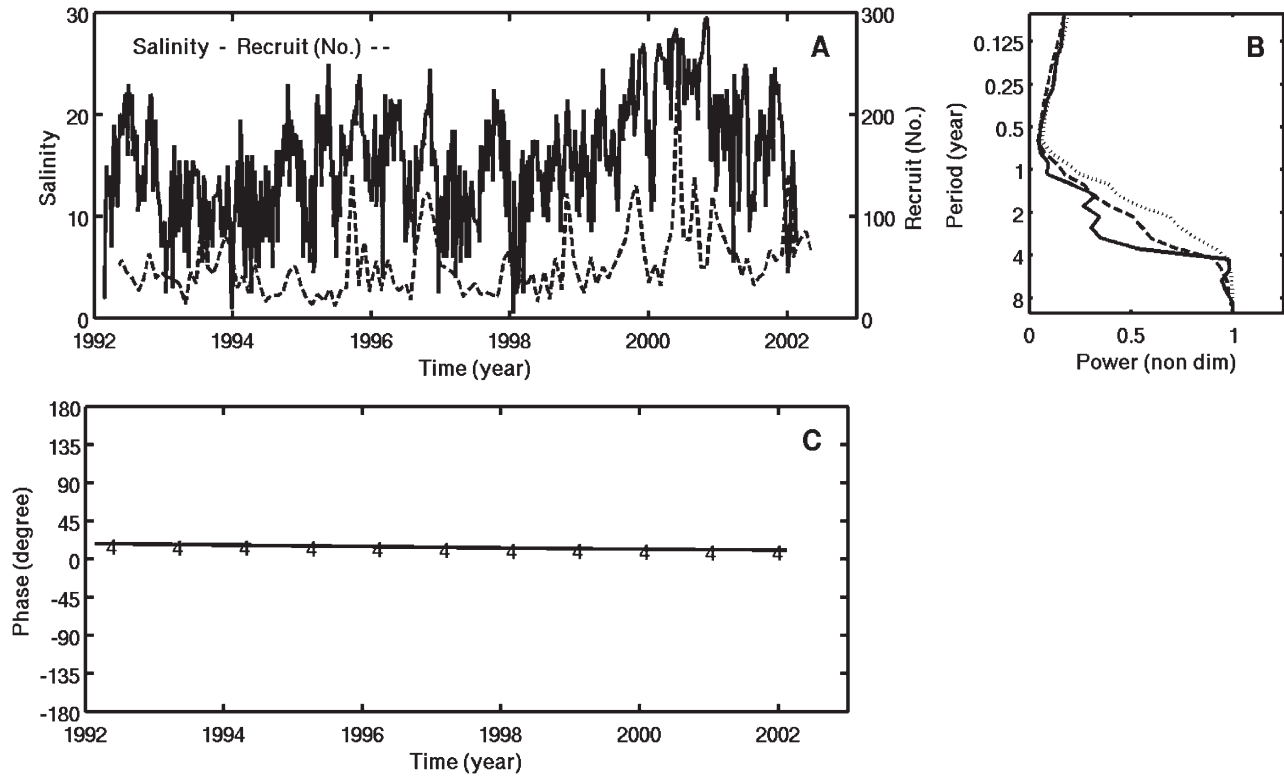
Figure 5. (A) Time series of the zero-mean unit-variance salinity (solid line) and recruit numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels. C) Phase diagram. Note that for the 4-y periodicity, salinity and recruit numbers are nearly in phase.

4 y and occurred in the recruit and submarket abundances, Dermo infection intensity, and submarket mortality fraction time series, and in the ENSO and local salinity time series. Shorter term periodicities (1–1.5 y) were associated with the transitions from recruit to submarket to market size for the oyster and the proliferation rate of Dermo disease. Cross-wavelet coherency fit the expected time frame for oyster growth and Dermo proliferation for Gulf coast oyster populations. Market abundance showed a longer term periodicity. Shorter term

coherences revealed by cross-wavelet analysis between other population attributes and market abundance showed phase shifts throughout the time series; that is, the relationships were not stable temporally. This behavior reinforces the conclusion that market abundance followed a different trajectory from other population attributes. The evolution of the oyster population at this Bay Tambour site was, therefore, influenced by a range of cyclic signals, one of which—the 4-y cycle—was obviously explained by the environmental variables included in
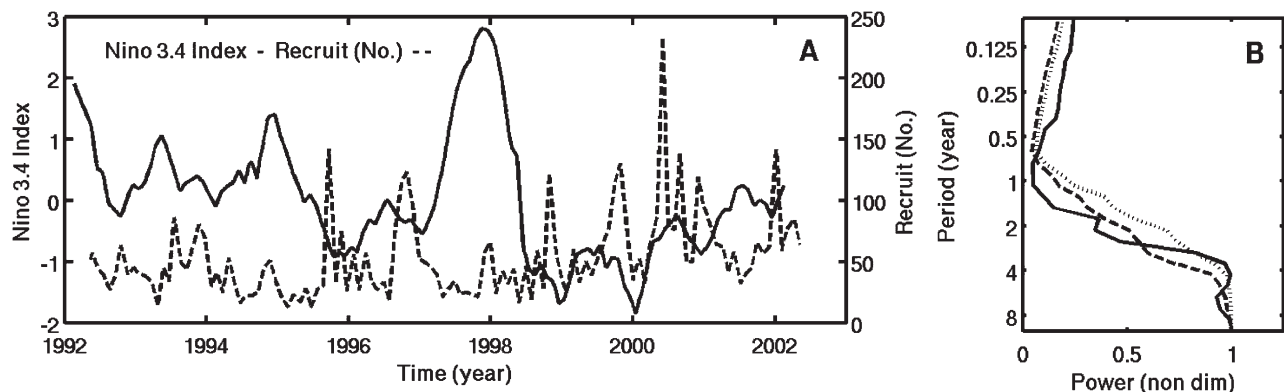

Figure 6. (A) Time series of the zero-mean unit-variance Niño 3.4 index (solid line) and recruit numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.

Figure 7. (A) Time series of the zero-mean unit-variance salinity (solid line) and market numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.
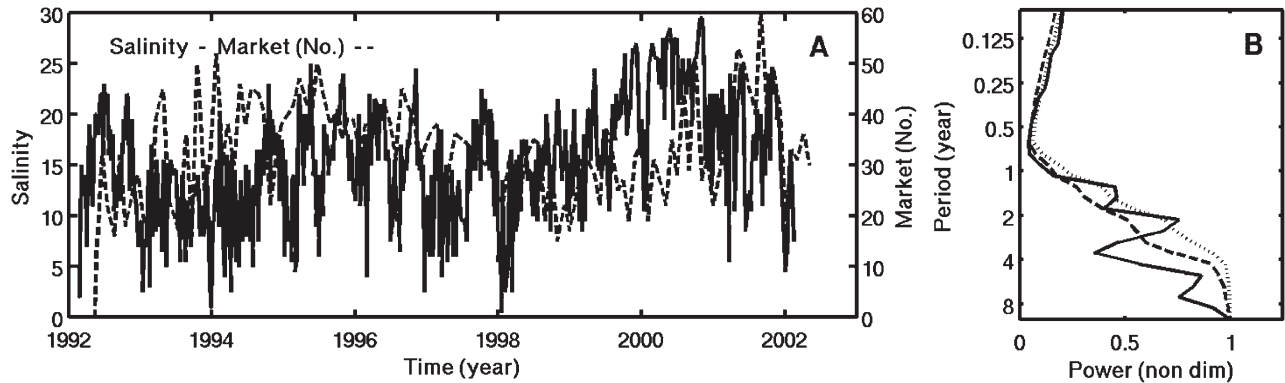
the analysis, and another (the short-term periodicities) was an integral manifestation of the life cycle of the oyster and its disease.

Large-Scale Climate and Mortality

Previous analyses of coincident environmental, oyster, and disease data sets from Gulfwide (Powell et al. 1992, Wilson et al. 1992, Kim & Powell 1998, Kim et al. 2001) and local sites (Soniat et al. 2005) identified significant correlations between ENSO and Dermo disease in Gulf of Mexico oyster populations. These studies showed essentially the same correlations at the large and local spatial scales. During the La Niña portion of ENSO, which influences the Gulf of Mexico at approximately 4-y intervals, decreased rainfall leads to increased salinity, which triggers a rise in Dermo disease prevalence and intensity. Increased disease burden then results in increased mortality. The results from the current study are consistent with these other studies. The 4-y periodicity in Dermo infection intensity, and its coherence with the submarket and market mortality fraction observed in the cross-wavelet analysis, highlights the underlying influence of ENSO in this Bay Tambour oyster population. However, the relationship between Dermo and oyster mortality is less clear. Increased

disease infection intensity affected the submarket and market mortality fractions, but not the submarket and market numbers (Table 3). This suggests that Dermo may influence the number of market-size boxes present; however, the resulting increment in mortality rate imposed by Dermo was insufficient to produce a clear decline in the abundance of market-size oysters at the study site.

The salinity regime of the Bay Tambour study site is favorable for oyster growth and production (Cake 1983, Chatry et al. 1983, Soniat & Brody 1988), and does not necessarily support epizootic levels of Dermo disease. The study site has not experienced recent killing floods, salinity typically remains within an optimal range for oysters, and frequent lower salinity events have kept disease in check (www.oystersentinel.org). Therefore, in the absence of a simple and straightforward control of oyster mortality by salinity and its effect on Dermo disease, the population is likely controlled by multiple factors of mortality interacting in complex ways. For example, the suite of predators changes with changing salinity. These predators impact oysters of different size classes differentially. Background predation at low salinity (5–15) is likely the result of euryhaline crabs such as mud crabs (*E. depressus, P. herbstii*) and blue crabs (*C. sapidus*). At salinities greater than 15, oyster drills (*S. haemastoma*) and
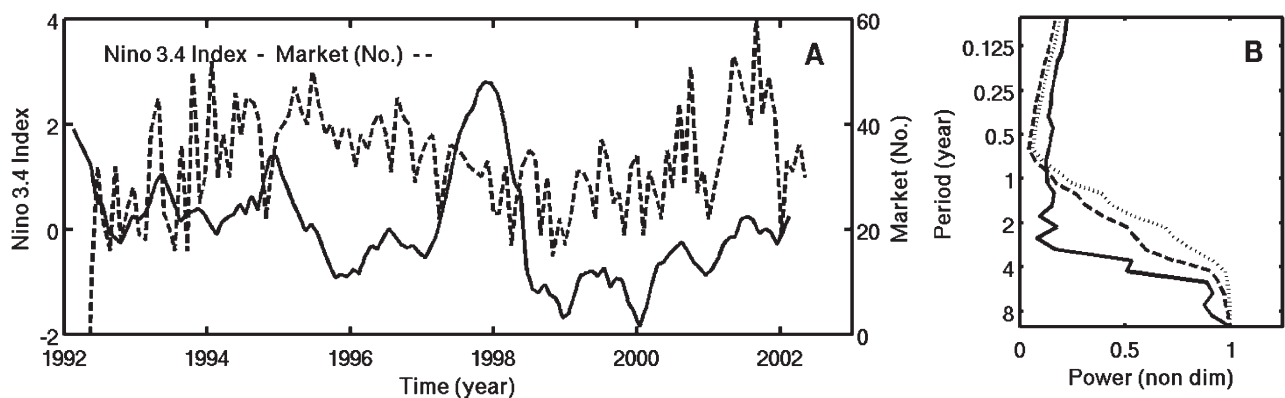

Figure 8. (A) Time series of the zero-mean unit-variance Niño 3.4 index (solid line) and market numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.
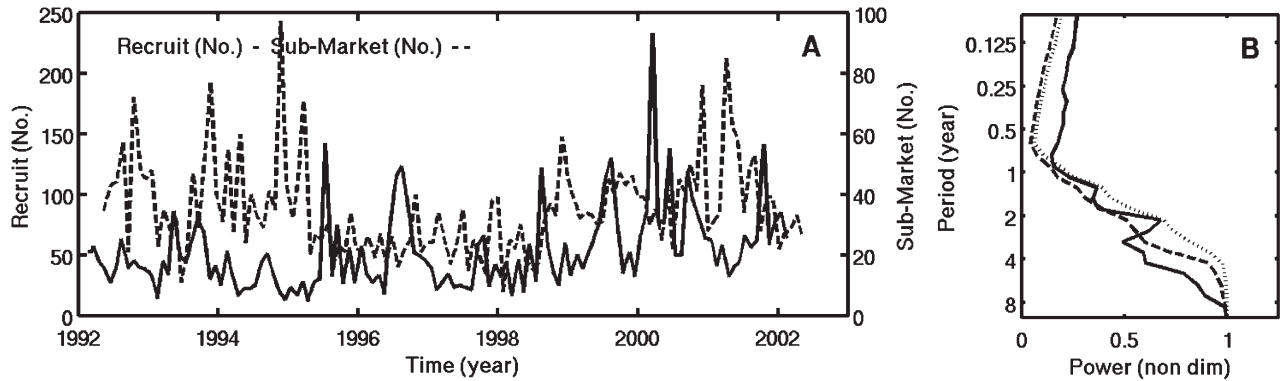
Figure 9. (A) Time series of the zero-mean unit-variance recruit number (solid line) and submarket numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.

other predators (e.g., *P. cromis* and *M. adina*) become more abundant, and at salinities greater than 20, Dermo becomes an additive factor of mortality (Mackin 1962, Bisker & Castanga 1987, White & Wilson 1996, Hofmann et al. 1995, Shirley et al. 2004).

Oyster Recruitment and Growth

Rapid growth and heavy recruitment are the principal defenses against parasites for many host populations, including oysters (Hofmann et al. 1995, Powell et al. 1996). Rapid growth of the host "dilutes" the parasite, and recruitment replaces the old, diseased, and dying with the young, uninfected, and robust. Populations of Gulf oysters, because they grow quickly and recruit often and prodigiously, seem especially resistive to parasitic demise.

Our analysis identifies a significant relationship between recruitment and salinity (Fig. 4, Table 3), with the recruitment rate being higher during periods of high salinity. Recruit numbers and submarket numbers also exhibit a strong 4-y signal. Higher
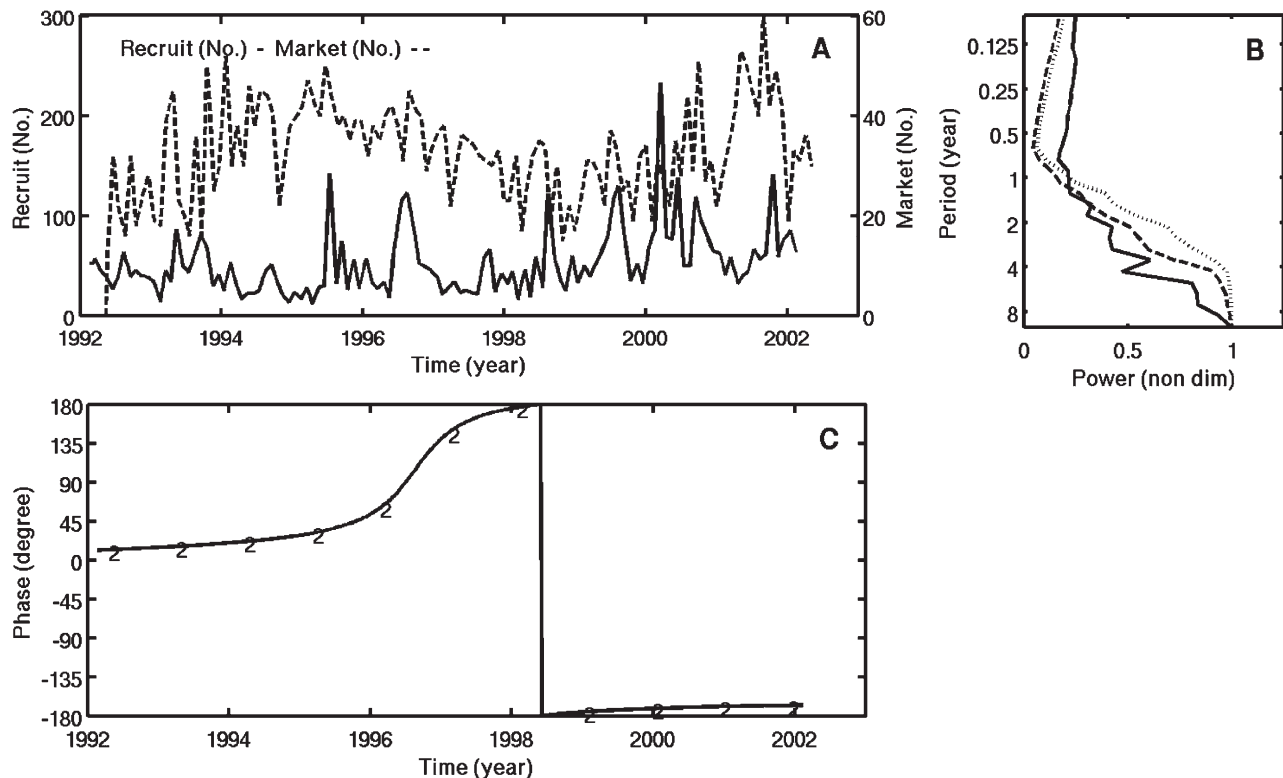

Figure 10. (A) Time series of the zero-mean unit-variance recruit numbers (solid line) and market numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels. (C) Phase diagram. Note the phase shift over the time series for the 2-y periodicity of recruit numbers and market numbers.
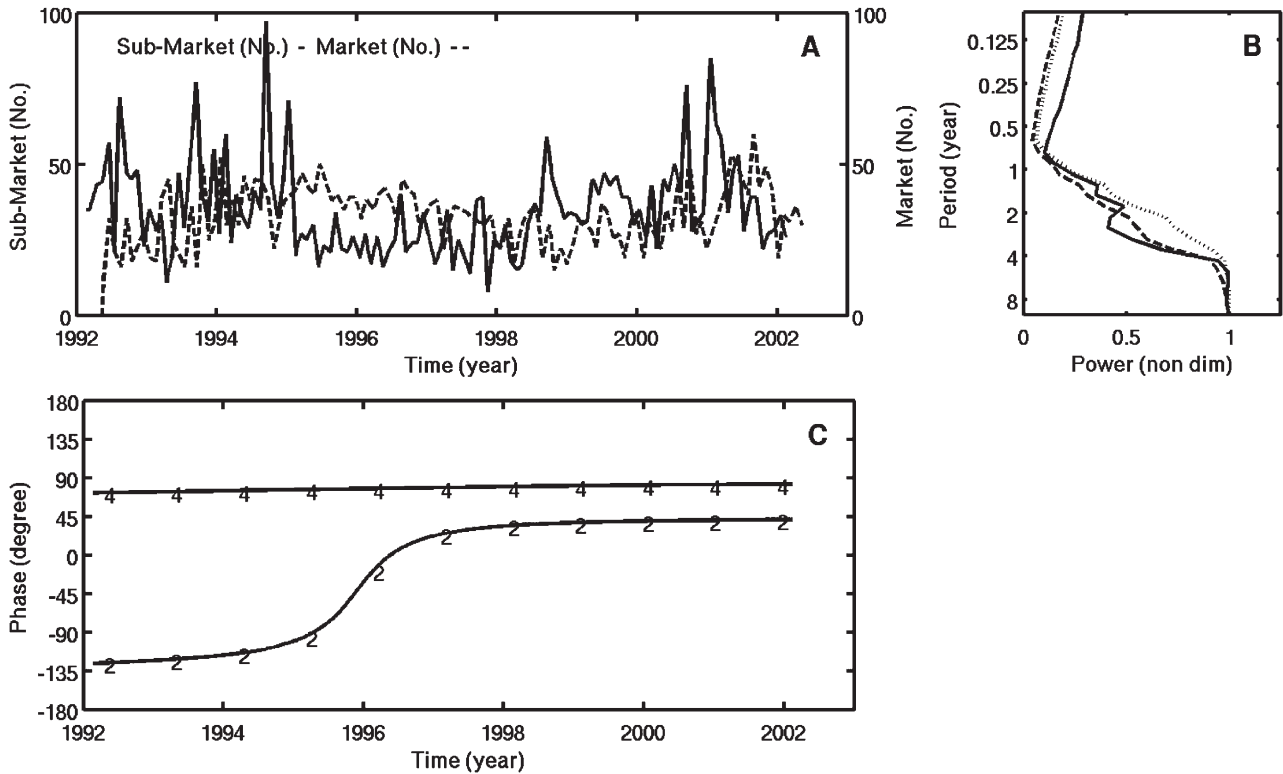
Figure 11. (A) Time series of the zero-mean unit-variance submarket number (solid line) and market numbers (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the *P* < 0.10 (left) and *P* < 0.05 (right) significance levels. (C) Phase diagram. Note that for the 4-y periodicity, submarket numbers and market numbers are nearly 90° out of phase throughout the entire time series; in contrast, the phase of the 2-y periodicity shifts throughout the time series.

(more optimal in this case) salinity supports increased recruitment and, after a lag for growth, increased submarket abundance. In general, oyster larvae are influenced positively by higher salinity, with growth rates increasing with increasing salinity (Dekshenieks et al. 1993). A relationship between salinity and oyster recruitment has been noted for other Gulf coast bays (Hopkins et al. 1953, Hopkins 1955, Cake 1983, Chatry et al. 1983, Ray 1987).

However, although a pattern in the transition of recruits to submarket oysters (Fig. 9, Table 3), and submarkets to market-size oysters (Fig. 11, Table 3), is apparent from cross-wavelet analysis, the data fail to reveal a relationship between the recruit time series and the subsequent change in market-size abundance (Fig. 10, Table 3). This apparent disconnect may arise because the market-size oysters consist of multiple cohorts accreted over a number of years. No recruitment event, not even

Figure 12. (A) Time series of the zero-mean unit-variance Dermo infection intensity (II; solid line) and submarket mortality fraction (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the *P* < 0.10 (left) and *P* < 0.05 (right) significance levels.
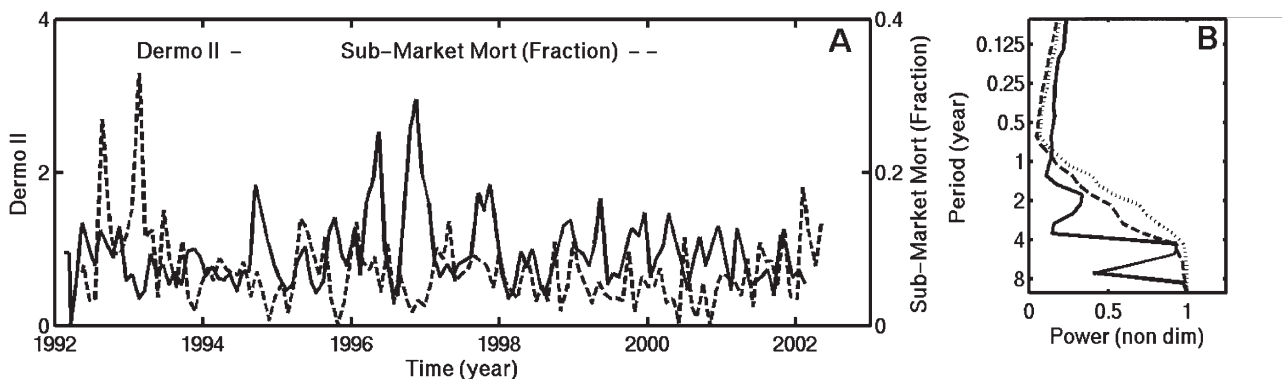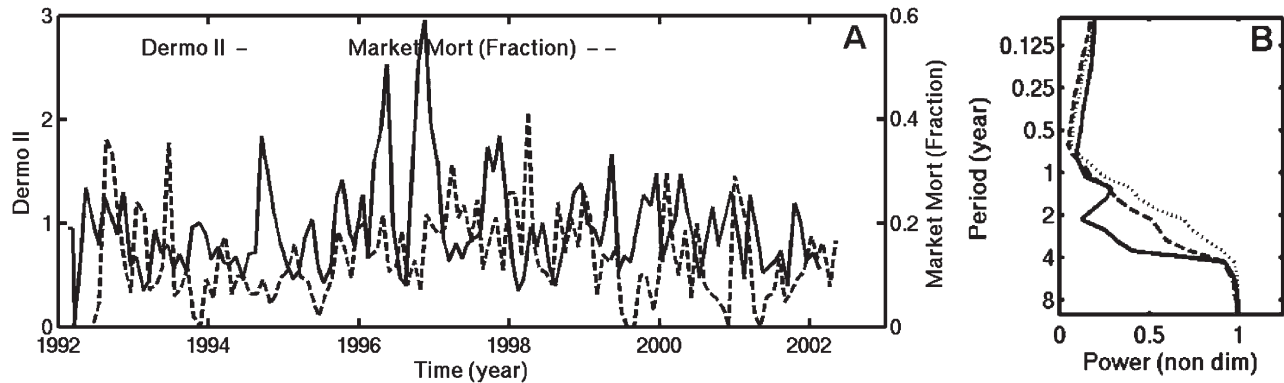
Figure 13. (A) Time series of the zero-mean unit-variance Dermo infection intensity (II; solid line) and market mortality fraction (dashed line) derived from monthly measurements made in Bay Tambour, LA. (B) Power and periodicity (solid line) obtained from the cross-wavelet analysis. The amplitude of the peak represents the strength of the signal. The dashed lines represent the $P < 0.10$ (left) and $P < 0.05$ (right) significance levels.

the one that follows the ENSO cycle (Fig. 6, Table 3) is sufficient to affect market-size abundance significantly.

The Conundrum of Market Abundance

The absence of a 4-y signal in market abundance belies the strength of the ENSO signal in modulating recruitment and early growth. The transition time from recruits to market oysters is longer than the transition time of recruits to submarket oysters or submarket oysters to market oysters. The complexity of postsettlement processes and the extended time over which these processes interact, decreases the predictability of the recruit-to-market transition. Thus, even the strong pulse of recruits associated with La Niña and its locally elevated salinities did not result in an exceptional increase in abundance of market oysters. One possible explanation is that the enhanced mortality from Dermo disease, also associated with the La Niña phase, more or less balances the increased recruitment. Growth and disease proliferation occur on similar timescales, which would allow this compensation to occur at subannual timescales.

The relationship between recruit and market oysters may prove predictable in this way and thus minimize the effect of the 4-y cycle on market-size abundance, but longer term changes in market abundance also occur. Market-size oysters are produced almost continuously from submarket-size individuals (Fig. 11, Table 3), but a large pulse in the number of market oysters is rare. The wavelet analysis suggests either a 6-y cyclicity or a long-term trend in the submarket numbers, market numbers, market mortality fraction, and Dermo infection intensity data (Table 2). This longer periodicity is not apparent in any of the other population or environmental characteristics followed in this study. The large influx of market oysters does not coincide with the 4-y periodicity associated with salinity, ENSO, and recruit number (Table 2). The pulse in market numbers is presaged by the low-frequency, interannual 6-y pulse of submarkets (Table 2).

A pulsed production of large numbers of market-size oysters promotes sustainability of commercially exploited reefs. When the abundance of these larger animals exceeds the market demand, they remain as part of the reef habitat and, upon their death, provide the bulk of the shell required for reef maintenance (Powell et al. 2006, Powell & Klinck 2007). The results from this analysis suggest that that production of large numbers of market-size oysters is a rare event that is explained inadequately by trends in salinity, which explain so much of the oyster population dynamics. Dermo disease also did not offer any explanatory power, perhaps because of the limited importance of the disease in mortality and the need for near-lethal infection levels to reduce growth and reproduction (Choi et al. 1989, Paynter 1996, Dittman et al. 2001). Thus, no simple combination of environmental and biological factors seems to result in the production of market-size oysters at this site. Enhanced production of market (large) oysters is important for maintaining use of the resource while also maintaining the reef habitat. Understanding how this happens requires extensive, long-term monitoring of oyster reef systems at sites that represent a range of environments. The central dilemma for oyster fisheries management is balancing the goals of fishing, which removes animals and their shells, with reef maintenance, which requires large oysters to die and remain in place (Mann et al. 2009, Powell et al. in press). This latter need emphasizes the requirement of understanding the controls on market abundance.

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