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# The Relationship Between Increasing Sea-surface Temperature and the Northward Spread of *Perkinsus marinus* (Dermo) Disease Epizootics in Oysters

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From its initial discovery in the Gulf of Mexico in the late 1940s until 1990, *Perkinsus marinus*, the parasite responsible for Dermo disease in the eastern oyster, *Crassostrea virginica*, was rarely found north of Chesapeake Bay. In 1990–92, an apparent range extension of the parasite led to epizootic outbreaks of the disease over a 500 km range north of Chesapeake Bay. One of the hypotheses for the range extension argues that small, undetected numbers of parasites were already present in northern oysters as the result of repeated historical introductions, and that a sharp warming trend in 1990–92 stimulated the disease outbreak. This argument was based on trends in air temperature. The present study examined this hypothesis by analysing water temperatures, rather than air temperatures, for five stations located in areas affected by the recent epizootics. At all five stations, there was a strong increasing trend in winter sea-surface temperature (SST) between 1986 and 1991. At four of the five stations, there was a smaller increasing trend in winter temperatures after 1960. There were no consistent or obvious trends in summer (August) temperatures. In Delaware Bay, which has a 40 year history of monitoring for oyster diseases, occasional findings of *P. marinus* in oysters were correlated with warming episodes that were especially notable in the winter (February) record. Empirical orthogonal function (EOF) analysis showed that winter temperatures varied consistently at the stations examined and were associated with variations in *P. marinus* prevalence. Associations using EOF analysis with August temperatures were much weaker. The SST record is consistent with the hypothesis that increasing winter water temperatures have been important in the recent outbreak of *P. marinus* epizootics in the north-eastern U.S.A.

**Keywords:** climatic changes; oyster fisheries; parasitic diseases; temperature; *Perkinsus marinus*; north-eastern United States

## Introduction

*Perkinsus marinus* is an endoparasite that causes Dermo disease in the eastern oyster, *Crassostrea virginica* (Ford & Tripp, 1996). The parasite was first discovered in the late 1940s and early 1950s over a region extending from the Gulf of Mexico along the south-eastern U.S. coast into lower Chesapeake Bay (Mackin *et al.*, 1950; Ray, 1954; Andrews & Hewatt, 1957). The parasite was also found in Delaware Bay during a period in the mid 1950s when large numbers of seed oysters were being imported from the lower Chesapeake Bay where *P. marinus* was prevalent (Ford, 1996). After an embargo on imported oysters was instituted in 1959, prevalence of the parasite in Delaware Bay decreased.

Members of the genus *Perkinsus* are warm-water parasites that infect a variety of molluscan species around the world (Perkins, 1993). They are transmitted directly from infected to uninfected hosts. *Perkinsus marinus* multiplies at temperatures above 18–20 °C, and proliferates most readily at 25 °C or higher (Chu, 1996; Ford & Tripp, 1996). Thus, the failure of *P. marinus* to persist in Delaware Bay after imports of infected oysters ceased was interpreted as an indication that temperatures were too low to sustain the parasite in that estuary (Ford & Haskin, 1982). With the exception of a few isolated findings, *P. marinus* was not detected again in Delaware Bay until 1990, although during the late 1980s, the parasite spread and intensified in Chesapeake Bay (Burreson & Ragone Calvo, 1996). In August 1990, unusual mortalities of oysters in lower Delaware Bay

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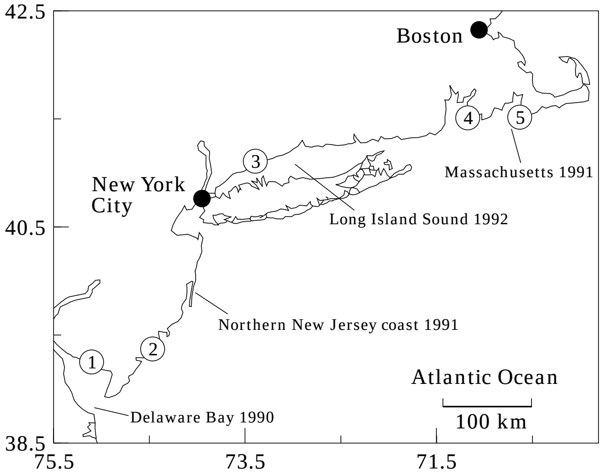

FIGURE 1. Map of north-eastern U.S., showing sea-surface temperature (SST) stations with dates and locations of new *Perkinsus marinus* observations. 1, Bivalve, NJ; 2, Atlantic City, NJ; 3, Bridgeport, CT; 4, Newport, RI; 5, Woods Hole, MA.

signalled a new outbreak of *P. marinus* infections. Within several months, infection prevalence had reached 90–100%. Equally high prevalences and consequent mortalities have occurred since then (Ford, 1996). In 1991 and 1992, additional reports of infected oysters occurred along a 500 km range from southern New Jersey to Cape Cod, Massachusetts (Figure 1). By 1995, lightly infected oysters were found as far north as Maine, and heavy infections were common in Long Island Sound and southern Massachusetts.

Hypotheses for the sudden range extension of *P. marinus* include: (1) recent introduction via the transplantation of infected oysters; (2) a change in the genetic structure of host or parasite; and (3) a change in the environment that favours the parasite. Ford (1996) reviewed evidence for and against these hypotheses and proposed that the phenomenon resulted from repeated historical introductions of *P. marinus* via many routes; survival of small, undetected populations of the parasite in oysters; and a sharp warming trend in 1990–92 that stimulated a disease outbreak. Ford's argument was based on trends in air temperature at sites near recent *P. marinus* epizootics and the observed correlations between air temperature and near-shore water temperature (Jeffries & Johnson, 1976; Southward *et al.*, 1988; Ford, unpubl. data).

In this paper, long-term sea-surface temperature (SST) records from five locations in the north-eastern U.S. were used, adjacent to sites where *P. marinus* has been detected recently, to determine whether the range extension of *P. marinus* is associated with climate-related changes in water temperature. Both long-term and short-term changes in the SST record were examined. Evidence from both Chesapeake and Delaware Bays indicates that high winter temperatures are more critical to the development or suppression of *P. marinus* epizootics than are high summer temperatures or low winter temperatures (Burreson & Ragone Calvo, 1996; Ford, 1996). For this reason, SST trends for summer and winter seasons were examined separately.

## Materials and methods

Five stations from New Jersey to Massachusetts were chosen to represent SST in the ' new ' *P. marinus* range (Figure 1, Table 1). Monthly mean water temperatures for each station were obtained from the National Oceanic and Atmospheric Administration (NOAA), with the exception of Bivalve, NJ record, which is part of a long-term data set at the Rutgers University Haskin Shellfish Research Laboratory. Historical prevalence records for *P. marinus* in Delaware Bay were taken from Ford (1996). Each station is assumed to represent the water temperature trends experienced by oysters on nearby growing grounds.

For each station, monthly SST figures were grouped into three data sets: (1) mean annual temperatures based on monthly means for each year; (2) February values representing the winter temperatures; and (3) August values representing the summer

TABLE 1. Location and length of sea-surface temperature record for each station

| Station name | Location | Lat/Long | Record length |
|---|---|---|---|
| Atlantic City | Steel Pier, Atlantic Ocean, Atlantic City, NJ | 39′21·3″N 74′25·1″W | 1950–1991 |
| Bridgeport | Tongue Pt Light, Bridgeport Harbor, Bridgeport, CT | 41′10·4″N 73′10·9″W | 1964–1993 |
| Bivalve | Haskin Shellfish Research Lab, Maurice River, Bivalve, NJ | 39′14·1″N 75′01·9″W | 1950–1993 |
| Newport | Gull Rocks Light, Narragansett Bay, Newport, RI | 41′60·3″N 71′19·6″W | 1955–1994 |
| Woods Hole | Great Harbor Light, Buzzards Bay, Woods Hole, MA | 41′31·4″N 70′40·3″W | 1950–1992 |

Data were acquired from the National Oceanographic and Atmospheric Administration and the Haskin Shellfish Research Laboratory. All temperatures were obtained by the bucket and thermometer method.

temperatures. Each data set was then analysed over three time intervals. The long-term record encompasses the entire multidecade data set for each station (Table 1). The intermediate record extends from 1960 to the end of the data set. The short-term record includes the period from 1986 to 1991. The long- and intermediate-term records were used to document trends indicative of possible climate change. The short-term record described temperature change during and just prior to the recent range expansion of *P. marinus*. Both annual and 5 year running averages of surface-water temperature were plotted for each location. The running average was used to remove some of the variability from the monthly SST data and to facilitate visualization of temperature trends.

### *Trend analysis of SST data*

To depict possible trends, a linear regression equation was calculated for each of the periods using all points for each data set. Trends were considered significant if the slopes were different from 0 at $\alpha = 0{\cdot}05$. The 30–40 year records were missing data for some months at some stations. The regression plots were calculated based on the months that were available, with no interpolation to fill in missing data.

### *Comparison of SST and* P. marinus *prevalence in Delaware Bay*

In addition to trend analysis at all stations, a more extensive investigation was performed by plotting the SST record at Bivalve against historical *P. marinus* prevalence data for Delaware Bay. The SST record, which extends from 1950 to 1994, spans the first appearance of *P. marinus* in Delaware Bay in the 1950s to the range extension in the early 1990s. The Bivalve station is about 5 miles north of the centre of the Delaware Bay leased grounds (Figure 1); however, it is immediately adjacent to oyster beds in the Maurice River, which experienced the same *P. marinus* epizootic as did oysters in Delaware Bay (Ford, 1996).

### *Empirical orthogonal function (EOF) analysis*

Another important question was whether the temporal variation was consistent among the five temperature and one *P. marinus* time series. This was accomplished using empirical orthogonal function (EOF) analysis, also known as principal component analysis (Preisendorfer, 1988), which separates multiple timeline measurements into a set of spatial patterns and allied amplitudes over time. The spatial patterns are uncorrelated in space while the temporal series are uncorrelated in time. The spatial patterns are obtained from the eigenvectors of the cross correlation matrix created from all possible pair-wise combinations of the input time series (with mean removed). The sum of the eigenvalues is equal to the sum of the diagonal terms of the correlation matrix, which is the total variance of the data. Therefore, the eigenvector associated with the greatest eigenvalue represents the largest fraction of the variance in the data. Each of the eigenvectors is then fit to the original data to create the time variation of the given pattern. Thus, EOF analysis identifies variations in contemporaneous data sets that occur with a specific temporal pattern.

All of the temperature and *P. marinus* infection data can be represented either as time series or as combinations of the EOF spatial and temporal patterns; the EOF merely changes the way they are represented. The power of EOF analysis comes from identifying a limited number of spatial patterns, or modes, that are thought to contain some information about the active processes (i.e. variations in temperature and infection levels in our analysis). There are several ways to choose significant modes. The average eigenvalue method was selected, which states that any eigenvalue larger than the arithmetic mean of all eigenvalues is considered significant. The significant modes were then used to reconstruct the time series and to compare the new series to the original measurements (Preisendorfer, 1988). Close agreement between original and reconstructed series indicate that the significant modes have captured important processes. This comparison is quantified by calculating a misfit between the original and reconstructed series. Several errors were calculated: maximum absolute difference, average absolute difference and root mean square (rms) deviation. Only the rms error is reported here, but all give basically the same result.

The analysis involved two types of data with different measurement values and range variations (i.e. degrees Celsius from $-1$ to 30 and percent *P. marinus* prevalence from 0 to 100). To allow the values for all time series equal representation in the analysis, each was divided by the square root of the variance of that series, thus giving each time series unit variance. A separate EOF analysis was performed for each temperature data set (annual, February and August SST). The *P. marinus* time series was the same for each temperature series.

## Results

### *Sea-surface temperature and* P. marinus *prevalence in Delaware Bay*

The most extensive records of both SST and prevalence are for the Delaware Bay system. During the last

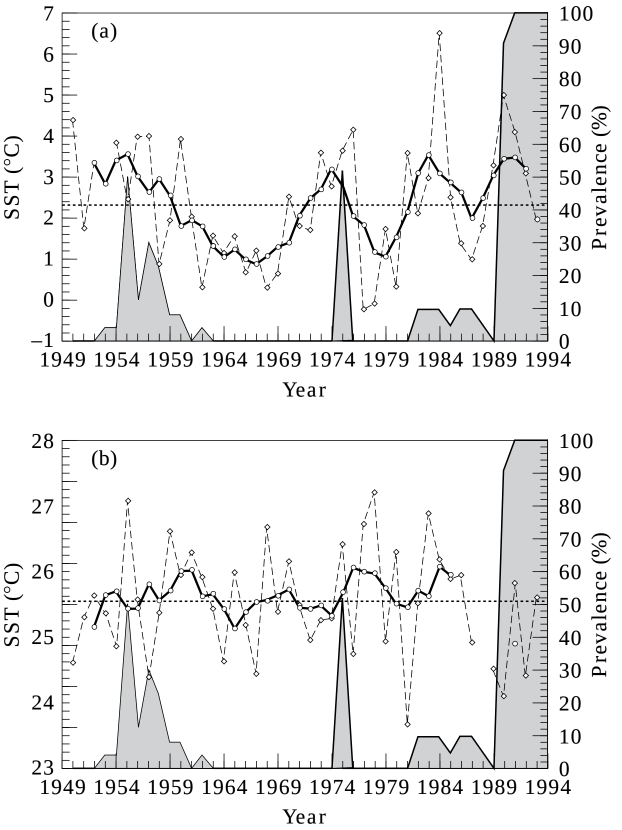

FIGURE 2. Annual (– – –) and 5 year averaged (——) (a) February and (b) August SST for Bivalve, NJ superimposed with prevalence of *P. marinus* in Delaware Bay oysters (shaded area) from Ford (1996). Horizontal dotted line represents the mean sea-surface temperature (SST) for 1950–1994.

45 years, winter temperatures have varied considerably and the prevalence of *P. marinus* appears to be related to both short- and long-term cycles [Figure 2(a)]. The 5 year running average shows that February SST decreased steadily from 1955 to 1966. Although temperatures increased again after 1966, they remained below the long-term average for the entire decade of the 1960s. From 1953 to 1958, oysters infected with *P. marinus* were being repeatedly introduced into Delaware Bay (Ford, 1996). Infection prevalence was initially high, then gradually decreased. Importation of oysters into the Bay was prohibited in 1959, and *P. marinus* became undetectable after 1963 [Figure 2(a)].

The 5 year running average showed that between 1970 and 1987, two complete cycles of February SST variation occurred, with peaks in 1974 and in 1984 [Figure 2(a)]. These warming events were associated with localized outbreaks of *P. marinus*, the most severe of which occurred in 1975. A third winter warming episode began in 1988 and lasted through 1991, years preceding and including the recent *P. marinus* epizootic.

Examination of the August SST record for Bivalve showed little, if any, relationship with prevalence data for Delaware Bay [Figure 2(b)], and no pronounced cyclic pattern compared to the winter record [Figure 2(a)]. Some *P. marinus* outbreaks did occur during periods of increasing August SST (e.g. mid 1980s), whereas others, including the severe epizootic and range extension in 1990, did not. Although the mean annual SST record for Bivalve is incomplete, the years available show more similarity to the February record than to the August record (Figure 3).

Regression analyses using the long- and intermediate-term Bivalve data sets showed a slight increasing trend in both the mean annual and February temperatures (Table 2). Neither slope, however, was statistically different from zero. Regression plots for the mean annual and February short-term (1986–91) records, however, had steep positive slopes, although only the winter temperatures showed a statistically significant trend. Plots for August SST had negative slopes indicating slight decreasing trends, but none was significantly different from zero.

### *Other north-eastern sites*

As the other north-eastern sites examined in this study (Figure 1) do not have a historical record of *P. marinus* prevalence comparable to that in Delaware Bay, we analysed only the SST record for these locations. As with the Bivalve data, long-, intermediate- and short-term records were examined using trend analysis.

The SST trends at Atlantic City, NJ were consistent with those at nearby Bivalve, namely decreasing temperatures during the 1950s and 1960s and increasing values in the most recent years [Figure 4(a–c)]. Regression analysis applied to the Atlantic City data showed an increase in the mean annual, August and February SST over the entire record, as well as the period since 1960 (Table 2). The trends for both February and mean annual temperatures since 1960 were statistically significant. The short-term plot showed a slight negative trend in the August data, and an increasing trend in the February and mean annual SST. Only the February temperatures, however, showed a statistically significant trend.

The SST data set at Bridgeport, CT is shorter than at other stations (Table 1) and the entire record from 1964 to 1993 is equivalent to the intermediate-term records at other stations. This record showed decreasing trends for all data sets, with statistical significance for August and annual data [Figure 5(a–c) Table 2].

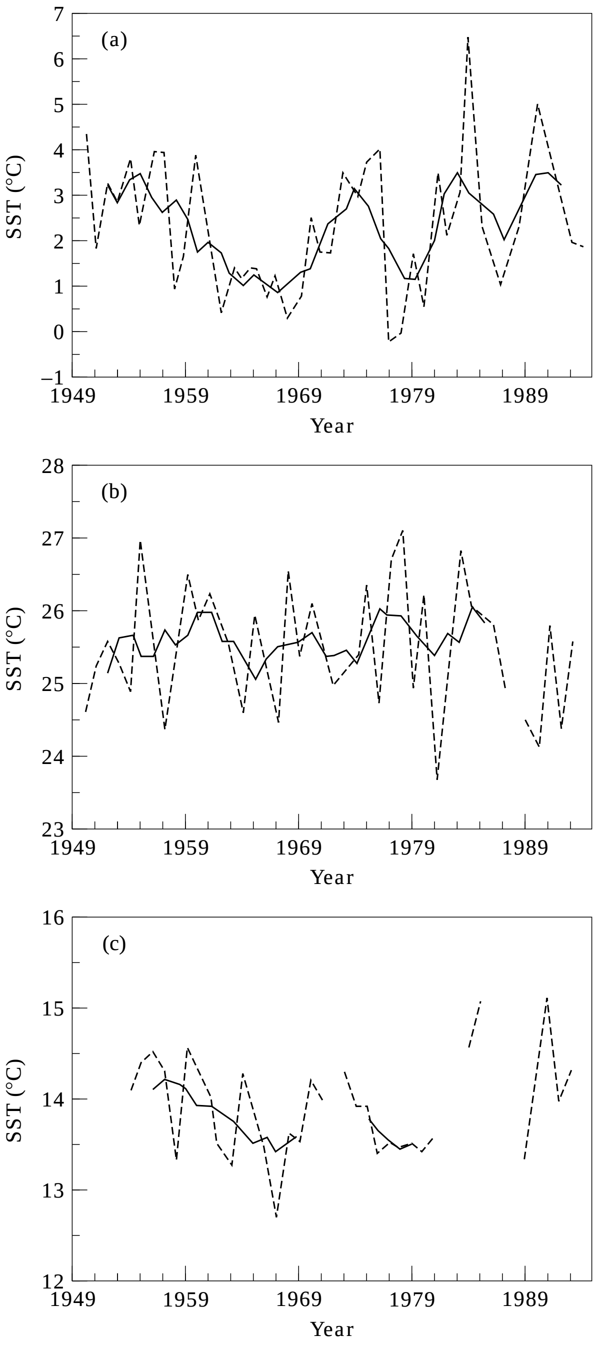

FIGURE 3. Annual (– – –) and 5 year averaged (——) (a) February, (b) August, and (c) mean annual sea-surface temperature (SST) for Bivalve, NJ.

It is difficult to compare the intermediate-term trends at Bridgeport with the other stations because there were no data for the early 1960s when SSTs were low at the other four stations. The short-term record, which is complete, showed a well-defined increase in August, February and mean annual SST. The February trend was statistically significant.

Records for Newport, RI, are complete except for the decade of the 1970s. Five year running averages displayed the same general pattern as the New Jersey sites; decreasing SST during the late 1950s and into the 1960s, and increasing temperatures since the mid to late 1960s [Figure 6(a–c)]. The regression slopes for the long- and intermediate-term data were positive and significantly different from zero (Table 2). The temperature increase over the short-term was even more pronounced, although the trend was not statistically significant.

For Woods Hole, MA, SST trends were similar to those at Newport, RI [Figure 7(a–c)]; (Table 2). Regression analysis of the long-term records showed an increasing, but not statistically significant, trend for all data sets. Increasing temperature trends observed since 1960, however, were statistically significant. The short-term regression plots and the 5 year running averages also showed increasing trends, with statistically significant slopes for the February and mean annual temperatures.

## *EOF analysis*

For each data set (annual, February and August), there were six time series so the EOF analysis produced six modes. For all of these cases, two modes were significant (i.e. had eigenvalues above the mean of all eigenvalues). All of the EOF analyses produce similar results.

The first mode from the analysis using annual mean temperatures explained 60% of the variance (Table 3). It indicated that the temperatures at all stations, except Bridgeport, increased or decreased in unison with about the same amplitude (Table 4). Prevalence of *P. marinus* changed in concert with these temperatures, increasing with increasing temperature. Temperatures at Bridgeport, according to the first EOF mode, decreased when other temperatures increased, although with a somewhat smaller amplitude. The second mode from the annual analysis explained 17% of the variance and represents mainly the Bridgeport temperature with some contribution from Atlantic City and Woods Hole and *P. marinus* prevalence, although *P. marinus* changes were opposite to the temperature changes. This mode represents a different timing of temperature changes at Bridgeport compared to the other stations. In a sense, it corrects the first mode results by making Bridgeport temperatures increase and decrease with the other temperature series, but with a slightly different time pattern. The error made by representing the time series with just the first two modes is between 15 and 30% of the largest deviation from the mean in each time series

TABLE 2. Trend analysis of February, August and mean sea-surface temperature (SST) computed for each station

| | Bivalve | | | Atlantic City | | | Bridgeport | | | Newport | | | Woods Hole | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Station | *n* | *m* | *P* | *n* | *m* | *P* | *n* | *m* | *P* | *n* | *m* | *P* | *n* | *m* | *P* |
| February | | | | | | | | | | | | | | | |
| 1950–end | 41 | 0·007 | 0·732 | 37 | 0·005 | 0·755 | 0 | na | na | 31 | **0·074** | 0·0001 | 42 | 0·008 | 0·586 |
| 1960-end | 32 | **0·060** | 0·045 | 27 | **0·050** | 0·020 | 24 | −0·030 | 0·396 | 27 | **0·093** | 0·0001 | 32 | **0·059** | 0·003 |
| 1986–1991 | 6 | **0·768** | 0·015 | 6 | **0·610** | 0·006 | 6 | **0·373** | 0·012 | 6 | 0·265 | 0·265 | 6 | **0·486** | 0·026 |
| August | | | | | | | | | | | | | | | |
| 1950–end | 41 | −0·001 | 0·931 | 40 | 0·005 | 0·797 | 0 | na | na | 32 | **0·024** | 0·036 | 40 | **0·016** | 0·071 |
| 1960–end | 31 | −0·011 | 0·527 | 30 | 0·047 | 0·136 | 28 | **0·105** | 0·0001 | 27 | **0·037** | 0·003 | 30 | **0·037** | 0·003 |
| 1986–1991 | 5 | −0·104 | 0·661 | 6 | −0·011 | 0·986 | 6 | 0·142 | 0·554 | 6 | 0·145 | 0·309 | 6 | 0·263 | 0·154 |
| Mean | | | | | | | | | | | | | | | |
| 1950–end | 35 | 0·005 | 0·538 | 32 | 0·008 | 0·413 | 0 | na | na | 30 | **0·044** | 0·0001 | 40 | **0·011** | 0·109 |
| 1960–end | 27 | 0·018 | 0·115 | 22 | **0·040** | 0·010 | 22 | **0·064** | 0·004 | 26 | **0·054** | 0·0001 | 30 | **0·037** | 0·0001 |
| 1986–1991 | 4 | 0·343 | 0·247 | 6 | 0·217 | 0·324 | 6 | 0·129 | 0·355 | 6 | 0·133 | 0·394 | 6 | **0·230** | 0·049 |

na, not available.
The number of data points (*n*), the slope (*m*), and the probability that the slope is different from zero (*P*) for the regression equation are given. A positive value denotes an increasing trend in SST record and a negative value denotes a decreasing trend in SST record. Slopes with a statistically significant *P* value are in bold. (Note: Newport record begins in 1955, Bridgeport record begins in 1964).

(Table 5). Visually, the reconstructed time series resembled the original time-temperature series, with strong multiyear cycles, but with slightly different amplitudes [Figure 8(a)].

The results from analysis of February temperatures were similar to those for the annual-temperature analysis. However, mode 1, which explained 60% of the variance (Table 3), showed consistent variations in temperature and *P. marinus* across the data set (Table 4). The Bridgeport temperatures now changed in concert with the other stations, but with a magnitude about half of the other stations. The second mode explained 21% of the variance and represents temperature changes at Bridgeport with opposite changes in *P. marinus* prevalence. The reconstructed time series for February temperatures resembled that for mean annual temperatures [Figure 8(b)], but had somewhat smaller errors, ranging from 15 to 25% (Table 5).

The final analysis examined the relationship between August temperatures and *P. marinus* prevalence. The first mode, which explained 36% of the variance (Table 3), showed that temperatures and *P. marinus* prevalence fluctuated in concert and that Bridgeport temperatures changed opposite to other stations (Table 4). Curiously, the temperature at Bivalve did not seem to be represented in this mode. The second mode, representing 26% of the variance, showed consistent temperature change at all stations except Atlantic City. Infection prevalence changed in the opposite direction, but with a small amplitude. The reconstructed time series showed no strong multiyear cycles [Figure 8(c)]. The error in the reconstructed series ranged from 17 to 30% (Table 5), which is comparable to the annual-temperature analysis and higher than the February-temperature analysis. There was also a weaker relationship between *P. marinus* and summer temperatures compared to the other analyses (error=30 *vs* 18–20%; Table 5).

## Discussion

At all north-eastern U.S. locations examined in this study except Bridgeport, CT, there were increasing trends in mean annual and February SSTs for the long-term and intermediate-term intervals. Over the short-term, February SSTs showed an increasing trend at all five stations, including Bridgeport. The increasing temperature trend was least pronounced for the long-term record (40–45 years) and most striking for the 6 year period from 1986 to 1991, immediately preceding the apparent *P. marinus* range extension. The strongest trend, as indicated by statistical significance of the slopes, was for the winter period. Between 1960 and the early 1990s, winter SST increased at a rate of 0·05–0·09 °C year$^{-1}$ (Table 2). Over the 6 year period from 1986 to 1991, the increase was much more dramatic, ranging from 0·27 to 0·77 °C year$^{-1}$. In contrast to winter SSTs, summer temperatures showed fewer significant trends, which were both increasing and decreasing.

In addition to the trend analyses, our investigation showed that periodic localized outbreaks of *P. marinus* in Delaware Bay occurred during winter SST warming cycles and that the parasite receded during winter cooling periods. As in the trend analysis, there was

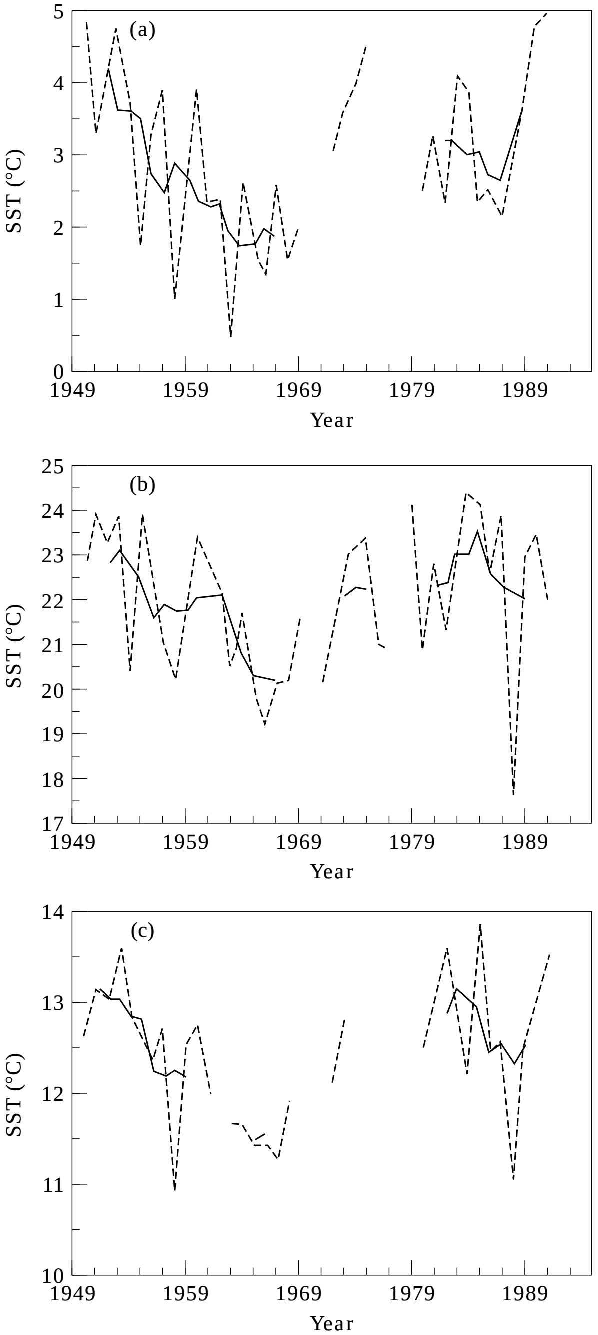

FIGURE 4. Annual (– – –) and 5 year averaged (——) (a) February, (b) August, and (c) mean annual sea-surface temperature (SST) for Atlantic City, NJ.

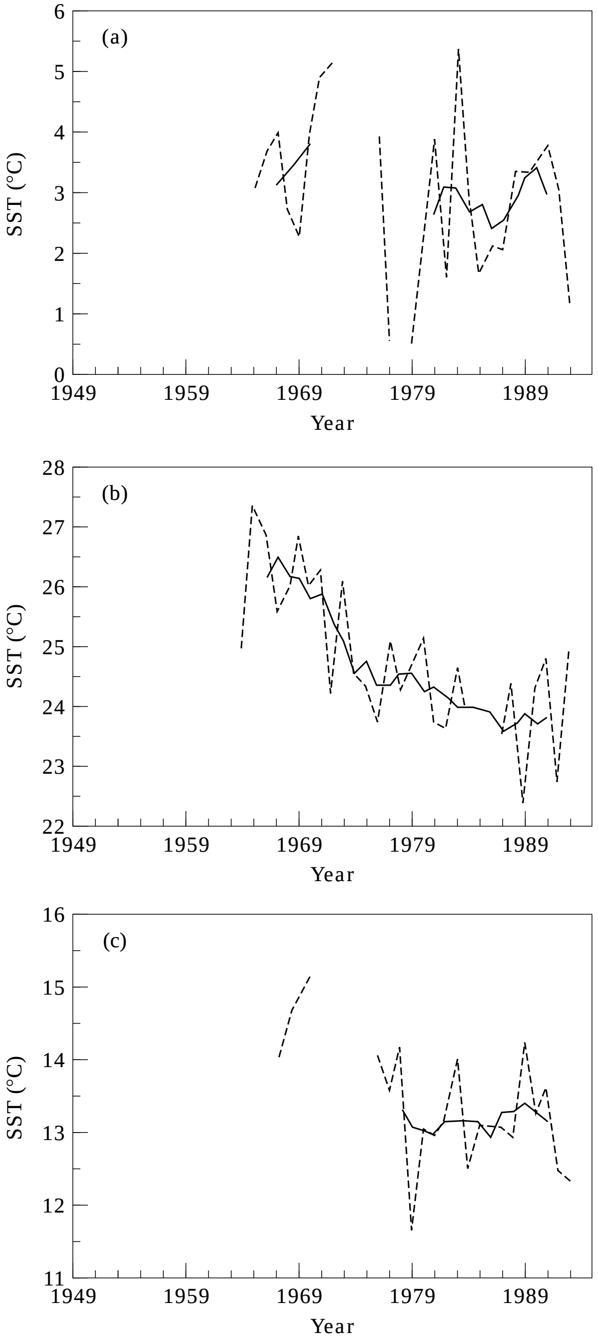

FIGURE 5. Annual (– – –) and 5 year averaged (——) (a) February, (b) August, and (c) mean annual sea-surface temperature (SST) for Bridgeport, CT.

no similar association with summer temperatures as represented by August data.

Empirical orthogonal functional analysis corroborated these results. It showed that temperature variations at the stations examined were generally consistent in time and space, and were moderately well associated with variations in *P. marinus* prevalence. The fact that the first two EOF modes explained 60–80% of the total variance indicates a broad-scale pattern that controls both sea-surface temperature variation and *P. marinus* infections in the north–eastern U.S. The strongest relationship among temperatures at the five stations and infection prevalence was made using the February SST data.

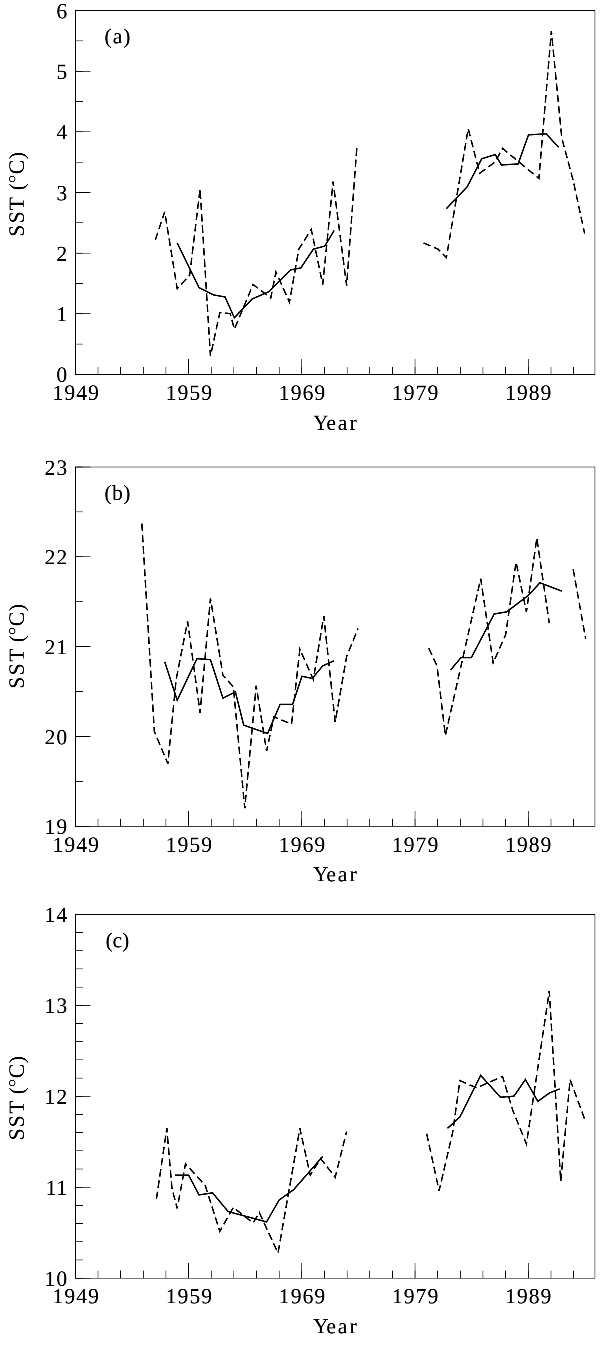

FIGURE 6. Annual (– – –) and 5 year averaged (——) (a) February, (b) August, and (c) mean annual sea-surface temperature (SST) for Newport, RI.

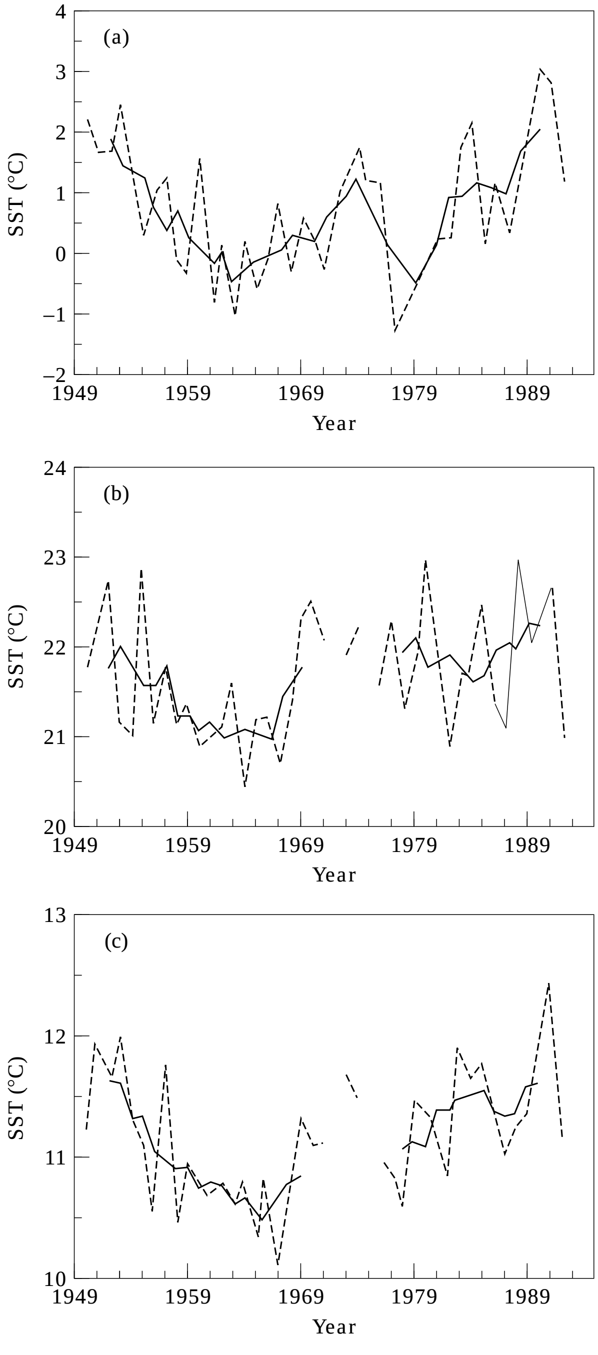

FIGURE 7. Annual (– – –) and 5 year averaged (——) (a) February, (b) August, and (c) mean annual sea-surface temperature (SST) for Woods Hole, MA.

The associations measured using the August temperature series were considerably weaker, further confirming observations that *P. marinus* epizootics are influenced more by winter temperatures than by summer temperatures.

The argument that the range extension of *P. marinus* into northern waters is related to a warming trend that was especially strong during the several years immediately before and during the recent disease outbreaks, is consistent with the results of our study. Our analyses also substantiate conclusions from other studies that high winter temperatures are more critical to the development of *P. marinus* epizootics than are high summer temperatures (Ford, 1996; Powell *et al.*,

TABLE 3. Percent variance explained by each spatial pattern (mode) in empirical orthogonal functional (EOF) analysis

| | Mode | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Annual | 59·7 | 17·4 | 11·0 | 7·5 | 4·3 | 0·0 |
| February | 59·3 | 21·0 | 9·7 | 6·5 | 2·2 | 1·3 |
| August | 36·1 | 26·1 | 16·0 | 12·8 | 6·1 | 2·8 |

Each value is the eigenvalue divided by the total variance of the observations multiplied by 100.

TABLE 4. Eigenvectors for each data series for the two significant modes resulting from empirical orthogonal functional (EOF) analysis

| | Time series | | | | | |
|---|---|---|---|---|---|---|
| | BV | AC | BP | NP | WH | *P. marinus* |
| Annual | | | | | | |
| 1 | 0·42 | 0·43 | −0·27 | 0·50 | 0·48 | 0·30 |
| 2 | 0·05 | 0·40 | −0·59 | −0·05 | −0·28 | 0·64 |
| February | | | | | | |
| 1 | 0·45 | 0·50 | 0·24 | 0·42 | 0·51 | 0·25 |
| 2 | 0·13 | 0·15 | 0·66 | −0·39 | 0·05 | −0·61 |
| August | | | | | | |
| 1 | 0·06 | 0·42 | −0·38 | 0·60 | 0·42 | 0·38 |
| 2 | 0·52 | −0·33 | 0·56 | 0·27 | 0·47 | −0·11 |

The amplitude of each eigenvector is represented by the magnitude of the number and the direction is represented by the sign. BV, Bivalve; AC, Atlantic City; BP, Bridgeport; NP, Newport; WH, Woods Hole.

TABLE 5. Error measurements for time series reconstructed from the two significant modes

| | Time series | | | | | |
|---|---|---|---|---|---|---|
| | BV | AC | BP | NP | WH | *P. marinus* |
| Annual | 0·28 | 0·24 | 0·31 | 0·16 | 0·17 | 0·18 |
| February | 0·18 | 0·16 | 0·24 | 0·18 | 0·16 | 0·20 |
| August | 0·32 | 0·24 | 0·24 | 0·17 | 0·27 | 0·30 |

The error measure is the root mean square (rms) of the deviation between actual measurements and reconstructed observations divided by the maximum absolute value of the data series. This is the root mean square fractional error. BV, Bivalve; AC, Atlantic City; BP, Bridgeport; NP, Newport; WH, Woods Hole.

1996). Although we did not analyse trends in salinity, we believe that changes in salinity *per se* have relatively little to do with the observed range extension because most of the locations where *P. marinus* has been detected recently have salinity that is normally high enough to favour the parasite.

As there is an oyster bed in the Maurice River at the Bivalve station, which is known to have experienced the *P. marinus* epizootic that began in 1990, we can investigate this record for actual temperature values in addition to trends. Examination of the February data shows that SST reached a maximum (6·5 °C) in 1984, 6 years before the epizootic began. No severe outbreaks of *P. marinus* occurred at this time, however, and this high value is probably anomalous as it derives from only two readings, taken on consecutive days. In fact, air temperatures for the period from January to March of that year were slightly below normal, so that the high-temperature episode represented by the 1984 peak was evidently short-lived. In contrast, during the period preceding the recent range extension, the February SST maximum (5·0 °C), which occurred in

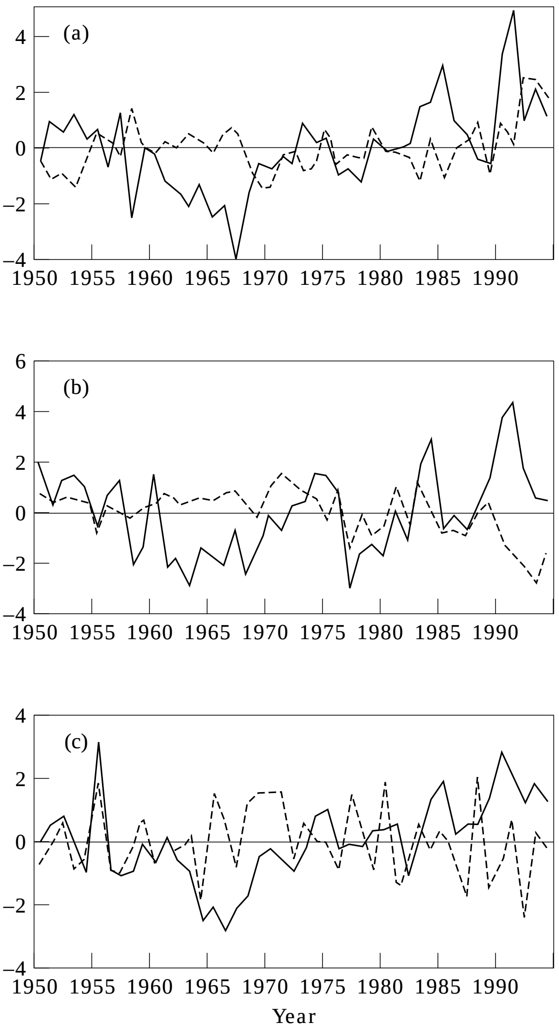

FIGURE 8. Reconstructed time series using the two significant modes (mode 1, ——; mode 2, – – –) from empirical orthogonal function (EOF) analyses, including the percent of total variance explained by each of the modes. The analysis was performed for (a) mean annual, (b) February, and (c) August temperatures using temperatures at each station and *Perkinsus marinus* prevalence in Delaware Bay. The *y*-axis indicates relative amplitude of the EOF pattern. Total variance explained by each mode: (a) mode 1, 59·7%, mode 2, 17·4%; (b) mode 1, 59·3% mode 2, 21·0%; (c) mode 1, 36·1%, mode 2, 26·1%.

1990, was part of a 4 year period (1989–92) when February SST was approximately 1–2 °C warmer each year than the long-term (1950–1994) mean of 2·4 °C. These results suggest that extreme, but short-term temperature increases are less effective triggers for *P. marinus* epizootics than are more sustained although less extreme changes. It should be noted that maximum February SST at Atlantic City, Newport and Woods Hole, was not reached until 1991, and in each case it was part of a multi-year interval in which temperatures were 1–2 °C above the long-term mean.

In a 1976 review, Cushing and Dickson (1976) concluded that the ‘ simplest ’ (biological) response to climate change is the appearance of exotic species. These and other authors have provided ample evidence that temperature change is typically accompanied by the appearance of new species and the disappearance of existing species, often in a cyclic fashion, as climate fluctuates over long periods (Southward *et al.*, 1975, 1988; Jeffries & Johnson, 1976; McGowan, 1990; Barry *et al.*, 1995). Barry *et al.* (1995) documented the appearance or increased abundance of eight southern species in a rocky-intertidal habitat on the California coast between 1931–33 and 1993–94. Water temperature over the same period increased 0·75 °C, or slightly more than 0·01 °C year$^{-1}$. The yearly rate of increase for the mean annual SST at our stations with the longest records (42–44 years) averaged somewhat less than this (0·005–0·011 °C year$^{-1}$). Temperatures have increased at a much greater rate over the last 30 years of north-eastern U.S. record (0·02–0·05 °C year$^{-1}$), however, which translates into a total increase of 0·6–1·5 °C. When the interval from 1986 through 1991 is considered, the change is even greater; 1·17–2·06 °C in just 6 years. Thus, the rate of change has accelerated recently and most likely represents short-term natural variability superimposed on the longer-term trend.

There is always a question of whether temporal changes in temperature are really due to long-term climate change or are merely temporary aberrations in an otherwise stationary climate. Our finding that coastal-water temperature in the north-eastern U.S. appears to have increased since 1950 is supported by a longer-term record showing that air temperatures in the same region have increased 2–3 °C over the last century (Karl *et al.*, 1996). This data set shows that most of the increase in annual air temperatures after the 1970s occurred during the winter and spring, which concurs with our observation that increases in the February SST have been more pronounced, and have occurred with more consistency across stations, than increases in the August temperatures.

Whereas the outbreaks of *P. marinus*-caused disease in the northeast are clearly associated with a warming period, the question of how long the parasite itself was present in the new range before it caused disease epizootics remains open. Oysters have been transplanted from south to north along the Atlantic seaboard for more than a century and *P. marinus* is suspected to have been resident in southern waters for at least a century (Ford, 1996). Small pockets of the parasite clearly remained in Delaware Bay between its apparent ‘ disappearance ’ in the early 1960s and its massive reappearance in 1990, but there is no concrete evidence that it was present in Long Island Sound or New England at that time. Failure to detect a microscopic endoparasite like *P. marinus* does not necessarily mean that it is not present, because diagnostic assays and sample collection methods are typically not adequate to detect very light infections, very low prevalences, or both (Bushek *et al.*, 1994). Consequently, undetected parasites may have been present in northern waters long before 1990 and the superimposition of short-term and intermediate-term warming trends may have enhanced the overwintering capacity of *P. marinus* even before its expansion in the early 1990s.

Alternatively, the range extension may have occurred much more recently. A conceptual model of spatial variation in zooplankton biomass associated with events of differing time scales indicates that occurrences such as an El Niño episode lasting 1–3 years, may produce a biomass change registered over 100–1000 km (McGowan, 1990). Presumably this would occur as a combination of transport of animals into, and their increased survival within, the new range. Infective stages of *P. marinus* are present in the water column and if they behave like plankton, much of the observed range extension over about 500 km may have been due to increased survival of infective stages transported by water currents during a relatively short interval. However, because the near-shore currents between Cape Cod, Massachusetts and Delaware Bay are primarily southward, the case for significant large-scale movement of infective particles in a northerly direction is weakened.

Regardless of how the parasite arrived in northern waters, increasing SST in that region supports the hypothesis that the environment has become more favourable to *P. marinus*, a southern parasite. The analysis of air temperatures by Ford (1996) showed that over nearly a 2 year period in 1990 and 1991, each consecutive month was warmer than average in the ‘ new ’ *P. marinus* range. The water temperature data from the present study demonstrated that there was also a pronounced warming trend for several years before this, during which parasite populations may have been gradually building up before the epizootic outbreaks in 1990–92.

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