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Zooplankton of Massachusetts Bay, USA, 1992–2003: relationships between the copepod *Calanus finmarchicus* and the North Atlantic Oscillation

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ABSTRACT: Zooplankton community analyses were performed on 102 µm mesh net samples from 1992 to 2003 from 2 stations, in Massachusetts Bay, USA, approximately 15 km offshore from Boston Harbor. There was significant ($p < 0.05$) negative correlation, with no temporal lag, between the boreal winter North Atlantic Oscillation (NAO) index and winter abundance of *Calanus finmarchicus* adults plus copepodites (CI to CV) at both stations. The negative correlation between the NAO Index and *C. finmarchicus* is the opposite of the positive relation emerging from other long-term studies in the Gulf of Maine (GOM) region, but is similar to the negative correlation in many areas of the NE Atlantic. Our data reflect primarily abundance of younger copepodites, which dominated our *C. finmarchicus* data. These younger copepodites had probably been produced during the first winter cohorts of *C. finmarchicus* each year, and were only weeks to months old upon capture. Previous positive correlations between *C. finmarchicus* abundance and the NAO index reported in the literature, with temporal lags of 2 to 4 yr, reflected data for larger CV and adult *C. finmarchicus*, which had probably been produced the previous year and had overwintered in deep basins in the Gulf of Maine. These older individuals would probably have been more subject to longer-term effects of NAO variability on large-scale interannual circulation patterns than the younger copepodites in our samples, which appeared to be more related to short-term climatic variability. Significant negative correlation between wind speed and abundance of *C. finmarchicus* supported this conclusion.

KEY WORDS: Zooplankton · Copepod · *Calanus finmarchicus* · North Atlantic Oscillation · Massachusetts Bay

INTRODUCTION

Large-scale climate variations can have long-term ecosystem effects. Marine ecosystems are affected primarily through variations in sea surface temperature and wind mixing, which can influence plankton and animals at higher trophic levels, including fishes. Of particular note are climatic phenomena such as the El Niño Southern Oscillation and the North Atlantic Oscillation (reviewed by Stenseth et al. 2002).

The North Atlantic Oscillation (NAO) is a large-scale atmospheric phenomenon that affects climatic variability from eastern North America through Europe to Siberia, and from the Arctic to the subtropical Atlantic (Hurrell 1995, Hurrell et al. 2001, 2003). The NAO measures the strength of westerly winds over the North Atlantic between approximately 40 and 60° N, and reflects differences in the atmospheric pressure gradient between the subtropical high centered over the Azores, and the subpolar low in the vicinity of Iceland. Effects of the NAO are particularly pronounced during winter.

Variation in the NAO can dramatically affect climate in the North Atlantic Basin and adjacent continental

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landmasses, because of differences in the intensity and storm tracks of westerly winds. Variation in the direction and strength of westerlies affects wintertime temperatures, precipitation and evaporation across the North Atlantic basin and adjacent landmasses.

During positive phases of the NAO, pressure differences are enhanced. Westerlies strengthen and storm tracks shift northward, causing increased precipitation and warmer winter temperatures over the eastern United States and adjacent NW Atlantic. During positive NAO phases, there are stormier conditions in the subpolar NW Atlantic off Greenland, and warmer wetter conditions develop over northern Europe and the adjacent NE Atlantic, with dry conditions over the Mediterranean.

During negative phases of the NAO, pressure differences are reduced. Westerlies weaken and storm tracks shift southward, leading to colder stormier conditions along the east coast of the United States and in the adjacent western Atlantic. Warmer milder conditions occur in the far NW Atlantic off Greenland, with northerlies developing over the NE Atlantic and northern Europe, resulting in cooler and dry conditions over northern Europe and the adjacent NE Atlantic, with increased precipitation over the Mediterranean (reviewed by Greene & Pershing 2000 and Stenseth et al. 2002). The boreal winter NAO index (Hurrell 1995) reflects sea level pressure differences between Lisbon, Portugal and Iceland, based on averages for December to March (index located at www.cgd.ucar.edu/~jhurrell/nao.html).

The NAO index has fluctuated significantly during the 20th century, with 3 major phases. Prior to 1935 the NAO was in a predominantly positive phase. From the late 1950s to early 1970s it was predominantly negative, and from the early 1970s to the mid-1990s, it returned to primarily positive. There was a major single-year drop in the NAO index to a negative phase in 1996, before a return to positive phases throughout the late 1990s (Greene & Pershing 2003).

Changes in the NAO have been linked to changes in plankton and other aspects of temperate marine ecosystems of the North Atlantic (reviewed by Drinkwater et al. 2003), in particular for copepods of the genus *Calanus*, which are important prey of larval and small adult fishes. In the eastern Atlantic, Fromentin & Planque (1996) found significant correlation between abundance of 2 congeners of the copepod genus *Calanus* and the NAO index in the northeast Atlantic and North Sea. *C. finmarchicus*, a cold-water species, exhibited a negative correlation with the NAO, which was attributed to higher wind stress under positive NAO conditions, leading to reduced stratification, less phytoplankton and lower copepod abundance due to food limitation. A positive correlation between the NAO and abundance of the warm-water species *C. helgolandicus* (Planque & Fromentin 1996), was attributed to warmer sea surface temperature under positive NAO conditions.

Planque & Reid (1998) generated a negative regression between abundance of *Calanus finmarchicus* and the NAO index for the northeast Atlantic for 1958 to 1992, and used it to predict abundances for 1993 to 1997. Agreement between predicted and observed abundances for 1993 to 1995 collapsed when the NAO index declined precipitously in 1996.

Since *Calanus finmarchicus* spends part of its life cycle overwintering as copepodites in deep waters, interannual variations in abundance of this copepod in continental shelf waters may be related to NAO-induced variations in convective mixing which reduce the overwintering habitat for populations in diapause (Heath et al. 1999), or changes in currents in spring when post-diapause copepods ascend to surface waters (Beare & McKenzie 1999a).

Overall, from 1960 to 1997 there was significant negative correlation between *Calanus finmarchicus* abundance and both sea surface temperature and the NAO index for the North Sea (Beaugrand 2003). However, different patterns emerge from comparable data from different areas (Planque & Taylor 1998, Beare & McKenzie 1999b), with the NAO showing a positive relationship to copepod diversity in the northern North Sea, and a negative relationship in the Atlantic west of Europe (Beaugrand & Ibañez 2002).

In the NW Atlantic, interannual variations in abundance of *Calanus finmarchicus* may also reflect variations in the North Atlantic Oscillation (Greene & Pershing 2000, 2003, Conversi et al. 2001, MERCINA Working Group 2001). However, the patterns reported thus far for the Gulf of Maine (GOM) (higher *C. finmarchicus* abundance during positive phases of the NAO index) appear to be the reverse of those most frequently found for the NE Atlantic.

One of the effects of the NAO is its influence on the shallow- and deep-water circulation in the western North Atlantic (Greene & Pershing 2000, MERCINA Working Group 2001, Greene et al. 2003a). During positive phases, convection is deeper and more intense in the Labrador Sea, and a relatively cool, fresh and thick layer of Labrador Sea water is formed. The volume transport of the Deep Western Boundary Current increases while the volume transport of the near-surface Labrador Current diminishes. During the negative phase of the NAO, these patterns are reversed, with shallower and weaker convection in the Labrador Sea, so that the Labrador Sea water becomes warmer and saltier, and volume transport of the Deep Western Boundary Current diminishes while that of the Labrador Current increases (Greene & Pershing 2000).

These changes in the NAO are also correlated with 2 other indices in the GOM (MERCINA Working Group 2001). The *Calanus finmarchicus* index of abundance in the GOM is based on continuous plankton recorder (CPR) surveys in the GOM since 1961 (Jossi & Goulet 1993). The *C. finmarchicus* index is significantly correlated with the Regional Slope Water (RSW) index for the GOM, which is an indicator of the Coupled Slope Water System (CSWS), or the extent to which southward penetration of the Labrador Current and Labrador Subarctic Slope Water (LSSW) enters deep basins of the Gulf of Maine. This RSW index is, in turn, correlated with the index for the NAO, with positive phases of the NAO correlated with warm water in the GOM, partly due to reduced penetration of Labrador Current and LSSW water from the north. Thus, the large-scale correlation between NAO and RSW appear in the *C. finmarchicus* index at regional scales in the GOM.

During the major drop in the NAO index in 1996, which was the largest of the 20th century, cold water flooded into the deep basins of the GOM during the winter, and this was correlated with reduced abundances of *Calanus finmarchicus* 2 yr later in 1998 (Greene & Pershing 2000). Thus, 1996 was similar to the situation in the 1960s of a predominately negative NAO index, minimum modal state of the CSWS (causing maximum southward intrusion of cold Labrador Sea and Labrador Subarctic Slope Water), low slope water temperatures and low abundance of *C. finmarchicus*. During the 1980s and most of the 1990s (except for 1996), these patterns were reversed, with a predominantly positive NAO index, the CSWS predominantly in its maximum modal state, warmer slope-water temperatures, and higher abundance of *C. finmarchicus*.

Conversi et al. (2001) used data from the CPR survey in the GOM (Jossi & Goulet 1993) to compare abundance of *Calanus finmarchicus*, sea surface temperature (SST) in the GOM and the NAO index for the period of 1961 to 1991. All 3 parameters exhibited overall increases over a period of 3 decades. The NAO index was significantly correlated with winter SST when SST was lagged by 2 yr relative to the NAO index. The winter SST was significantly and positively correlated with summer *C. finmarchicus* abundance, with an additional 2 yr lag. Thus, abundance of this copepod gave a consistent, significant and positive correlation with the NAO index, with a lag of 4 yr. The strongest correlations were between *C. finmarchicus* summer abundance, the same summer SST, the winter NAO index, and the winter SST of 2 yr earlier. Conversi et al. (2001) found no significant relationship between the NAO index and winter abundance of *C. finmarchicus*. The weak positive correlation for the GOM (with a 4 yr lag) for 1961 to 1989 (Greene & Pershing 2000) became non-significant when data for the 1990s were included (Greene et al. 2003a).

Thus, it appears that *Calanus finmarchicus* abundance in the GOM may reflect climate-driven changes in oceanography, as appears to be the case in the NE Atlantic. However, the correlation between abundance of this copepod and the NAO index appears to be negative in the NE Atlantic and North Sea, but positive in the NW Atlantic and Gulf of Maine (Conversi et al. 2001, Drinkwater et al. 2003, Greene et al. 2003a).

Calanus finmarchicus is a cold-water oceanic species, so its expatriate populations in shelf areas such as the North Sea and the GOM must be replenished every year through advection from offshore. Also, since this copepod overwinters as diapausing copepodites in deep waters or basins before being advected onto shelf areas in the spring, circulation and hydrodynamic changes in deep waters can affect import of this copepod into shallow waters. In the GOM, *C. finmarchicus* is probably replenished from upstream external sources such as the Labrador Sea, the Gulf of St. Lawrence and the Scotian Shelf (Miller et al. 1998). Indeed, there is low genetic diversity (mitochondrial DNA) for *C. finmarchicus* populations between the Gulf of St. Lawrence, the GOM and Georges Bank, suggesting a single interbreeding population with extensive gene flow through the region (Bucklin & Kocher 1996, Bucklin et al. 1996). Thus, NAO-related interannual changes in the characteristics or flow of slope waters into the GOM and its basins may affect abundance of *C. finmarchicus* in this region. Such fluctuations in the abundance of this copepod have also been linked to feeding conditions for, and calving success of, the endangered North Atlantic right whale *Eubalaena glacialis* in the GOM (Greene et al. 2003b, Greene & Pershing 2004).

Given the evidence of NAO influences on *Calanus finmarchicus* abundance that have emerged from CPR data on both sides of the North Atlantic, we examined our long-term zooplankton data set from Massachusetts Bay (southern GOM) for evidence of patterns. We hypothesized that the small mostly younger stage (CI to CIV) *C. finmarchicus* copepodites collected in Massachusetts Bay with 102 µm mesh nets may respond more rapidly to NAO-related changes in winter hydrography than do larger, older, overwintering CV and adult *C. finmarchicus* in the GOM that have been hypothesized to respond to large-scale, long-term fluctuations in oceanography and climate such as those described by Greene & Pershing (2000). Analyses of our Massachusetts Bay long-term (1992 to 2003) zooplankton data set afford a unique opportunity to examine the role that climate variation, as represented by the NAO, plays in interannual abundance fluctuations of important, yet frequently undersampled juvenile copepodite stages.

MATERIALS AND METHODS

Zooplankton community analyses were performed at several stations in Massachusetts Bay (southern GOM) as part of a monitoring program to examine effects of relocation of a sewage outfall from Boston Harbor to Massachusetts Bay. Zooplankton samples were collected throughout Boston Harbor, Massachusetts Bay and Cape Cod Bay (41.85 to 42.32°N, 70.22 to 71.01°W) throughout most of each year since 1992. Samples were collected with vertical tows over the upper 25 m with 0.5 m diameter, 102 µm mesh nets. From 1992 to 2003, there were 6 large-scale surveys per year (February, March, April, June, August, October) at 10 stations (see Turner 1994 for all station locations and a detailed description of the program rationale and sampling methodology). Beginning in 1995, additional surveys were added to Stns N04, N16 and N18 (Fig. 1), near the mouth of the new outfall. Samples were collected between the 6 large-scale surveys (March to December) an additional 11 times per year, for a total of 17 times per year in all months except January at Stn N16 in Massachusetts Bay (42.39°N, 70.75°W). Thus, samples for Stn N16 were taken 6 times per year from 1992 to 1994, and 17 times per year from 1995 to 1997. Beginning in 1998, Stn N18 (42.37°N, 70.78°W) was sampled 17 times per year instead of nearby Stn N16, which continued to be sampled only 6 times per year. Stn N04 (42.44°N, 70.74°W) was sampled 6 times per year during the large-scale surveys in 1992 to 1994, was not sampled during 1995, and then was sampled 17 times per year from 1996 to 2003, on the same days that Stns N16 or N18 were sampled.

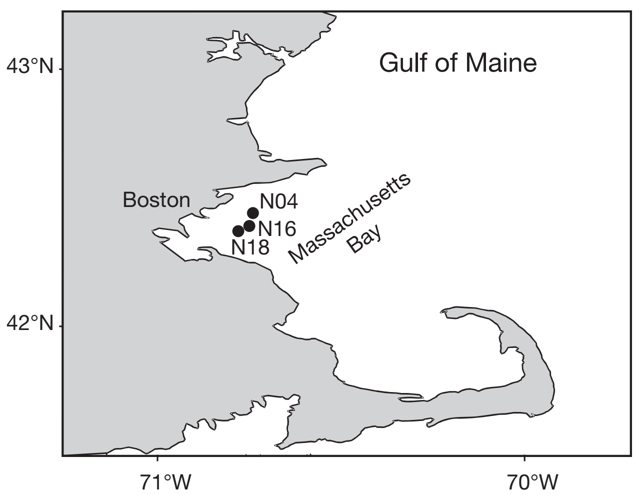

Fig. 1. Location of sampling stations in Massachusetts Bay, southern Gulf of Maine

Samples were reduced with a Folsom plankton splitter to aliquots of at least 300 individuals, and zooplankton were identified to the lowest practical taxon. For copepods, identifications were to species, with adults further identified to sex and all copepodites of a genus combined. Copepod nauplii were not identified further, and other zooplankters such as chaetognaths, fish larvae, pteropods, etc. were also not identified beyond major group. Meroplankters such as barnacle nauplii, bivalve and gastropod veligers, and polychaete larvae, were also identified only to major group.

Temperature data were collected simultaneously with zooplankton using a SeaBird CTD. Wind speed and direction data for February, March and April over the 1992 to 2003 period were obtained from the USGS Boston buoy (No. 44013) located 25.8 km east of Boston (data available at http://www.ndbc.noaa.gov/station_history.phtml). Analyses of temperature and wind data were performed with 1-way ANOVA (if data were normally distributed) or Kruskal-Wallis (non-parametric) with Tukeys post-tests. There were some gaps in the wind data. Data were missing for April 1996, and for most of February to April 2001.

All observations within a given year were averaged into monthly bins to yield monthly averages. Since no zooplankton samples were collected during the month of January, zooplankton abundance for January was linearly interpolated from the previous December and subsequent February values for each year. For each station (N04 and N16) the *Calanus finmarchicus* time-series data were decomposed into long-term trend and seasonal components, using a method similar to that used in analyzing a 34 yr time-series of North Sea zooplankton abundance (Broekhuizen & McKenzie 1995). The long-term trend was then estimated by calculating a 12-month moving-average smoother of the raw observations. At each monthly time-step, the 12-month moving-average trend was subtracted from the monthly observations to yield residuals used as initial estimates of the seasonal component of the time-series. The seasonal component estimates (monthly residuals) were then subtracted from the original monthly time-series to give a de-seasonalized time-series representing the long-term trend. This trend was smoothed by a LOWESS smoother (with a centered 6-month window) to yield the long-term de-seasonalized trends. Trend analyses require calculation of deviation about the moving averaged mean annual cycle, so trends could not be identified until completion of an entire year of sampling. Accordingly, trends are not shown until after completion of a year of sampling (1992) at Stns N16 and N04, and for another full year after the break in sampling in 1995 at Stn N04.

Correlation statistics were calculated using either SAS Version 6.12 or GraphPad Prism Version 3.00 software. Data distributions were checked for departure from normality using the Kolmogorov-Smirnov test prior to correlation analyses. Winter-averaged copepod abundance and environmental data used in these analyses were normally distributed, so Pearson's correlation coefficient was calculated to identify covarying patterns in the data.

RESULTS

Throughout the 1992 to 2003 time-series in Massachusetts Bay, several trends were apparent (Fig. 2). There was considerable seasonal and interannual variability in abundance of total zooplankton, with maxima in the summer and minima in the winter. Most of the total zooplankton were copepods (nauplii, copepodites and adults combined), and the most abundant copepods were *Oithona similis* copepodites and adults. This persistent abundance by a poikilothermic species is particularly remarkable, considering that it occurs over an annual temperature range in Massachusetts Bay that usually exceeds 20°C.

Although *Calanus finmarchicus* was generally present in Massachusetts Bay from at least February through September, its abundance was dwarfed by that of *Oithona similis* (Fig. 3). Monthly mean abundances for *C. finmarchicus* for all of Massachusetts Bay from 1992 to 2003 revealed that abundance of this species was usually 1 to 2 orders of magnitude less than abundance of *O. similis*. However, since previous correlations between the NAO index and zooplankton patterns on both sides of the North Atlantic suggest that *C. finmarchicus* responds to variations in climate, we examined patterns for this species in Massachusetts Bay in greater detail.

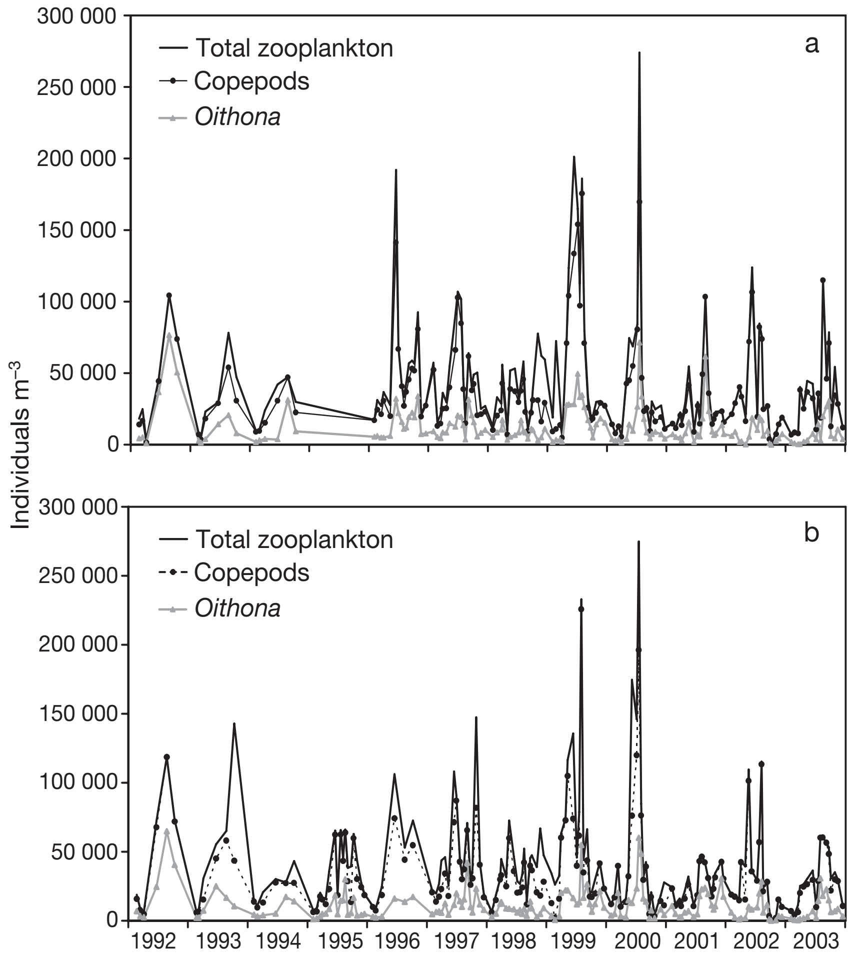

Fig. 2. Abundance of total zooplankton, total copepods and *Oithona similis* adults + copepodites (CI to CV) in Massachusetts Bay at (a) Stn N04 (42.44° N, 70.74° W) from 1992 to 2003 and (b) Stn N16 (42.39° N, 70.75° W) from 1992 to 1997 or Stn N18 (42.37° N, 70.78°W) from 1998 to 2003 (from 1998, Stn N18 was sampled instead of Stn N 16: see 'Materials and methods')

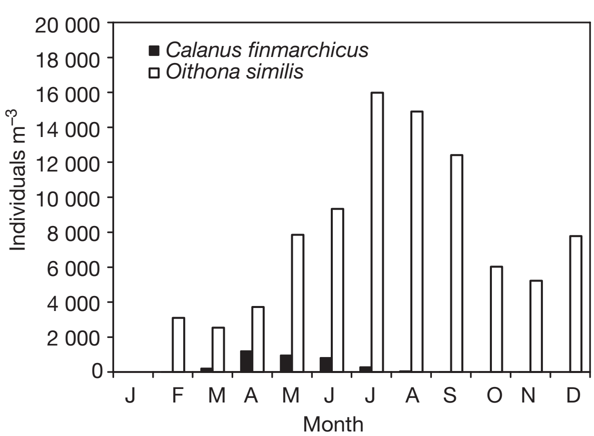

Fig. 3. *Calanus finmarchicus* and *Oithona similis*. Monthly geometric mean abundances for the entire Massachusetts Bay for adults + copepodites (CI to CV) combined, 1998 to 2003

Time-series analyses similar to those of Broekhuizen & McKenzie (1995) revealed long-term trends in the abundance of *Calanus finmarchicus* copepodites + adults from Stns N04 and N16 (Fig. 4). Abundance values were high in 1996, 2000 and 2003; 2 of these years had among the lowest winter NAO indices of the 1992 to 2003 period (range = –3.78 to +3.96, mean = 1.104), with values of –3.78 in 1996, and 0.2 in 2003. However, the winter NAO index value in 2000 was 2.8.

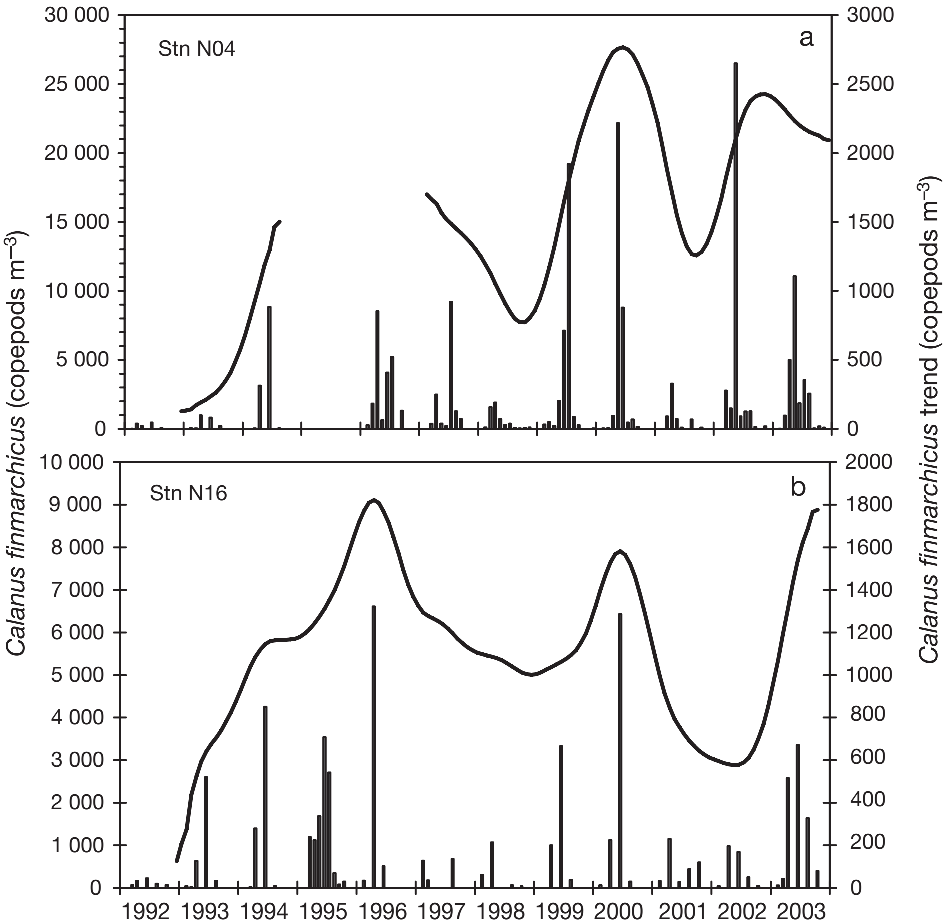

Fig. 4. *Calanus finmarchicus*. Time-series analysis of abundance of adults + copepodites (CI to CV) in Massachusetts Bay at (a) Stn N04 and (b) Stn N16. Bars are abundannce and curves are trends

Pearson's correlation coefficients for the winter NAO Index and winter means of zooplankton abundance or mean SST are presented in Table 1. There was significant negative correlation between the NAO index and abundance of *Calanus finmarchicus* at Stns N04 and N16 (Fig. 5), and between the NAO index and total copepods at Stn N04. There was no significant correlation between the NAO index and abundance of *Centropages* spp., *Oithona similis*, copepod nauplii, barnacle nauplii, and SST at either station, or between the NAO index and total copepods at Stn N04. *Pseudocalanus* spp. and *Paracalanus* spp. were not examined, since data for copepodites of these 2 genera had been combined during 1992 to 1994.

The *Calanus finmarchicus*–NAO relationship in Massachusetts Bay was highly dependent on a single year (1996), when extremely high abundance of this copepod was coupled with the lowest NAO index for the 20th century. Removal of the 1996 data resulted in a correlation that was still significant for Stn N04, but not for Stn N16. Removal of the 1996 data reduced the r^2 value from 0.71 (n = 11 yr, p = 0.0012) to 0.50 (n = 10 yr, p = 0.0218) at Stn N04, and from 0.39 (n = 12 yr, p = 0.0288) to 0.00 (n = 11 yr, p = 0.9836) at Stn N16. This dependence of the linear regression on the extreme NAO event of 1996 suggests a non-linear response of this copepod to winter climate extremes in Massachusetts Bay.

There were significant differences in mean winter (February to April) wind speed (p = 0.0002, Kruskal-Wallis test) and in mean wind direction (p = 0.0001, ANOVA) between years. Mean winter wind speed (1992 to 2003 mean = 6.5 m s^{-1}) varied from 6.0 (1998) to 7.4 (1993) m s^{-1}, and mean wind direction varied from 177°, i.e. S (1993) to 218°, i.e. SW (1999). Tukey's post-tests indicated that differences were due to pairings of the greatest wind speed in 2 yr (1992 mean = 7.3 m s^{-1}; 1993 mean = 7.4 m s^{-1}) and the slowest wind speed years (1995 mean = 6.0 m s^{-1}; 1998 mean = 6 m s^{-1}). Mean wind direction during February to April,

Table 1. Pearson's correlation coefficients for winter North Atlantic Oscillation index and winter (February to April) means of zooplankton abundance or mean sea surface temperature (SST), significance levels (p), and r^2 values, at Stns N16 and N04, 1992 to 2003. Winter means for Stn N16 based on 3 cruises per yr between February and April for the 12 yr between 1992 and 2003, inclusive. Winter means for Stn N04 based on 3 cruises per year between February and April for the 3 yr from 1992 through 1994, and 5 cruises per year between February and April, for the 8 years between 1996 and 2003, for a total of 11 yr. *Significant correlation ($p < 0.05$)

Taxon	n	Pearson's r	p	r^2
Stn N16				
Calanus finmarchicus[a]	12	−0.628	0.029*	0.394
Centropages spp.[b]	12	−0.058	0.858	0.003
Oithona similis[a]	12	+0.068	0.833	0.005
Copepod nauplii	12	−0.043	0.895	0.002
Total copepods[c]	12	−0.121	0.709	0.015
Barnacle nauplii	12	+0.077	0.813	0.006
Temperature (SST)	12	−0.130	0.687	0.017
Stn N04				
Calanus finmarchicus	11	−0.841	0.001*	0.707
Centropages spp.	11	−0.537	0.110	0.288
Oithona similis	11	−0.478	0.138	0.228
Copepod nauplii	11	−0.524	0.098	0.274
Total copepods	11	−0.633	0.037*	0.400
Barnacle nauplii	11	+0.104	0.761	0.011
Temperature (SST)	11	+0.039	0.910	0.002

[a]Adult females + males + copepodites
[b]Adult females + males + copepodites of *C. typicus* + *C. hamatus*
[c]Adult females + males + copepodites of all copepod species

1992 to 2003 was from 201° (a SSW wind). Differences in each year's February to April wind direction were from pairings of the years with more westerly winds (1994 = 215°; 1996 = 215°; 1997 = 212°, 1999 = 218°) and the 2 yr with southerly winter winds (1993 = 177°; 1998 = 182°).

Separate monthly comparisons of wind speed and direction in the February, March and April patterns with the overall 1992 to 2003 pattern for each month revealed that some months were different in different years. For February, no years had wind speed that was significantly different from the mean pattern. However, the February wind direction showed that 1996 had a significantly more westerly mean wind direction (239°) than the long-term mean of 220°, and 1998 had significantly more southerly mean wind direction (177°). For March, no years had a wind direction that was significantly different from the long-term mean. However, March wind speed (long-term mean = 6.6 m s^{-1}) was significantly different from the long-term mean in 1992 (mean = 7.6 m s^{-1}) and in 1995 (mean = 6.6 m s^{-1}). For April, wind speed was greater than the long-term mean (= 5.8 m s^{-1}) in 1993 (= 6.6 m s^{-1}) and in 2000 (= 6.8 m s^{-1}), but less than the April long-term mean in 1998 (=4 .7 m s^{-1}). April wind direction (long-term mean = 184°) was significantly more southwesterly in 1999 (206°) and more southeasterly in 1993 (137°). Thus, the abovementioned years were those in which wind speed and direction were significantly different from mean long-term patterns.

There were no significant linear relationships between mean monthly wind direction or mean monthly wind speed and monthly NAO indices during February to April (1992 to 2003) in Massachusetts Bay. However, linear relationships were found for monthly averages of wind speed and *Calanus finmarchicus* abundance at Stns N04 and N16. Wind speed was significantly correlated with *C. finmarchicus* (Pearson r = −0.50, n = 25, p = 0.011) at Stn N04 (Fig. 6), but wind speed was not significantly correlated (Pearson r = −0.41, n = 21, p = 0.069) with *C. finmarchicus* at Stn N16. No correlation was found between wind direction and *C. finmarchicus* abundance at either station. For Stn N04, a linear regression model of *C. finmarchicus* as a function of wind speed explained about 25% of the year-to-year variation in *C. finmarchicus* abundance for the February to April period. The slope of this regression (−929.9 *C. finmarchicus* m^{-3} per 1 m s^{-1} wind speed) indicates that *C. finmarchicus* abundance declines by approximately 900 individuals m^{-3} for every 1 m s^{-1} increase in mean winter wind speed (Fig. 6). At Stn N04, high *C. finmarchicus* years (1996,

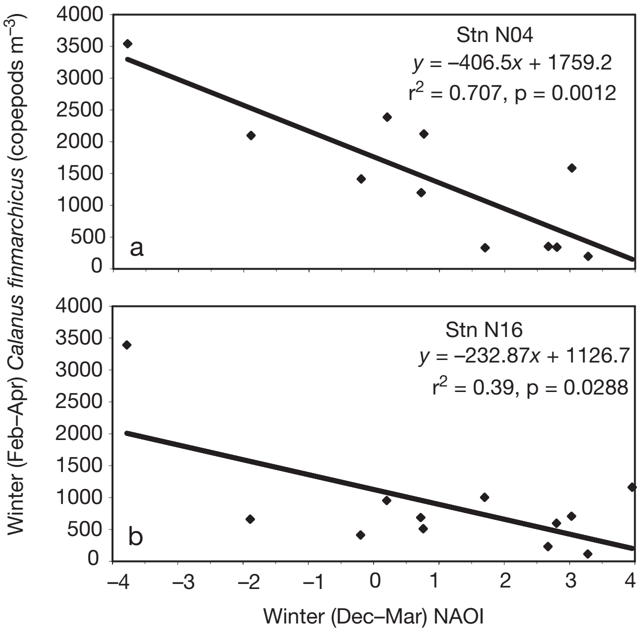

Fig. 5. *Calanus finmarchicus*. Winter (February to April) abundance of adults + copepodites (CI to CV) and boreal winter North Atlantic Oscillation Index (NAOI) in Massachusetts Bay at (a) Stn N04 and (b) Stn N16

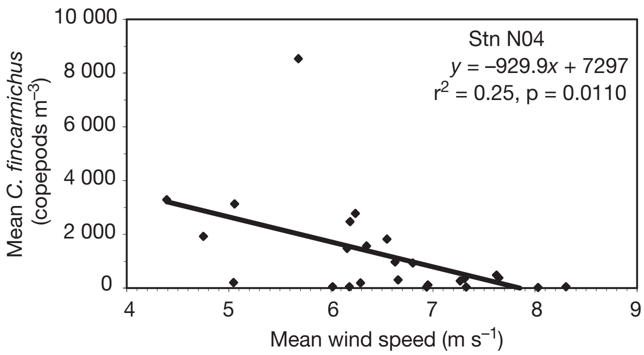

Fig. 6. *Calanus finmarchicus*. Mean winter monthly wind speed and mean monthly winter (February to April) abundance of adults + copepodites (CI to CV) at Stn N04 in Massachusetts Bay

2001, 2002, 2003) were associated with lower than mean winter wind speeds (6.5 m s^{-1}), and low *C. finmarchicus* years (1992, 1993, 1999, 2000) had above average winter wind speeds.

DISCUSSION

The significant negative correlation between winter abundance of *Calanus finmarchicus* and the winter NAO index in Massachusetts Bay is opposite to the positive correlation between abundance of this copepod and the NAO index reported for the GOM by Greene & Pershing (2000), in subsequent publications referring to the same data (MERCINA Working Group 2001, Greene & Pershing 2003, 2004, Greene et al. 2003a,b), and by Conversi et al. (2001). There are several potential explanations for this discrepancy.

Calanus finmarchicus appears to have 2 generations during the first half of the year in the GOM (Bigelow 1926, Fish 1936, Mullin 1963, Meise & O'Reilly 1996, Durbin et al. 2000a,b). The first begins in late December to early January from parents that overwintered as CV copepodites during the previous fall and early winter, possibly at depth. These CV copepodites rise to the surface layer, molt into adults, and reproduce in early winter. The resulting nauplii and early copepodites from this January generation mature throughout the spring, reaching adulthood and reproducing in late spring and early summer. This produces a second generation, which matures throughout the summer and fall, going into a resting phase as CVs at depth during the late summer and early fall. This 'overwintering' generation then remains at depth until it rises to the surface, reaches adulthood, and begins reproduction in the early winter (Durbin et al. 1997). Fish (1936) suggested that the life span of *C. finmarchicus* in the GOM was 4 mo or less in summer, but possibly 10 to 11 mo in winter. Thus, large-scale long-term oceanographic phenomena that affect water masses in deep basins in the GOM may have different effects on long-lived overwintering populations of late-stage *C. finmarchicus* than on young recently-spawned copepodites of the early winter generation linked to short-term local climatic variability. However, both short-term climatic, and long-term oceanographic variations may relate to phenomena encompassed by the NAO index.

The positive correlations (with temporal lags) of Greene & Pershing (2000), the other abovementioned studies, and Conversi et al. (2001) are all based on CPR data from 1961 to 1989 for transects across the GOM from Boston, Massachusetts, to the southern tip of Nova Scotia (Jossi & Goulet 1993). Additional CPR data for 1990 to 1999 from continuation of the CPR survey through the 1990s (Jossi et al. 2003) was presented by Greene et al. (2003a). These CPR samples were generally collected monthly, on transects that extended across the entire southern GOM. In contrast, our *Calanus finmarchicus* data are only for Massachusetts Bay and for the winter (February to April) period. The NAO index used for the Greene & Pershing (2000) and Conversi et al. (2001) analyses was the same boreal winter (December to March) index that we used.

Other differences may relate to the portions of the *Calanus finmarchicus* populations sampled in the different studies. The mesh of the net in the CPR is approximately 270 µm (Hays 1994). Thus, it collects primarily larger copepods, and the CPR data for *C. finmarchicus* was stated to be for CV copepodites and adults only (Jossi & Goulet 1993). These stages probably included many individuals that had overwintered at depth as copepodites during the previous year.

Our samples were collected with 102 µm mesh nets. Thus, smaller as well as larger stages of the *Calanus finmarchicus* population were sampled. Although copepodites were not individually staged in our data, most samples included a continuum of Copepodite Stages CI to CV, as well as a few adults. The majority of the *C. finmarchicus* copepodites were younger stages, predominantly CI to CIVs. These individuals were likely to have been only weeks to months old at the time of collection. Thus, most of the copepodites in our *C. finmarchicus* data were probably the result of recent breeding by adults that had overwintered upstream in deep basins of the NE GOM the previous year. In essence, the *C. finmarchicus* represented by the CPR data would probably have been the parents of most of the individuals represented by our *C. finmarchicus* data, had both been collected during the same winter.

The differences in age distributions of *Calanus finmarchicus* copepodites between the present study and those based on CPR data may affect the reported correlation with the NAO index. The CPR data reveal positive correlation between *C. finmarchicus* CV copepodites + adults and the NAO index with temporal lags of either 2 yr (Greene & Pershing 2000), 3 yr (MERCINA Working Group 2001) or 4 yr (Conversi et al. 2001). Greene & Pershing (2000) suggested that a reason for these patterns was that colder, less-saline Labrador subarctic slope water intruded into the deep basins of the GOM where *C. finmarchicus* copepodites overwinter, after the drops in the NAO index. This is postulated to decrease the abundance of this copepod in the GOM over the following several years. When the NAO index returns to a positive state, the deep basins of the GOM are flooded with warmer, more-saline Atlantic temperate slope-water, possibly contributing to increased abundance of *C. finmarchicus* in subsequent years.

The negative correlation we found between abundance of *Calanus finmarchicus* and the NAO index includes no temporal lag. We examined the correlation of the annual mean of *C. finmarchicus* abundance for the 3 mo February, March and April in each year compared to the mean winter boreal NAO index for December, January, February and March of the same year (Table 1). Thus, for each correlation, data are based on 12 yr for Stns N16 or N18 and 11 yr for Stn N04 (which was not sampled during 1995).

Most of the *Calanus finmarchicus* copepodites represented by these data were for individuals resulting from recent reproduction during the early winter of that year, not for individuals that had overwintered in deep basins upstream the previous year. Thus, these individuals had been subject to recent climatic or oceanographic events during the days, weeks or (at most) a few months prior to sampling, rather than to long-term large-scale hydrographic scenarios such as those proposed by Greene & Pershing (2000). The different correlation between our data and those derived from the CPR may represent different interactions between different age components of the *C. finmarchicus* population, driven by climatic and oceanographic phenomena operating on different time scales. Although our suggested explanation is different from that of Greene & Pershing (2000), there is no reason to assume that both are not correct. However, the different patterns may occur for different reasons, operating on different components of the *C. finmarchicus* population.

There is still much about interactions between plankton and climate that is not well understood. For instance, the general pattern for the North Sea and some other areas of the NE North Atlantic is that correlation between CPR-determined abundance of *Calanus finmarchicus* and the NAO index are generally negative off Europe, but generally positive in the NW Atlantic off North America (Greene et al. 2003a). Further, the weak positive correlation between *C. finmarchicus* abundance in the GOM and the NAO index (with a 4 yr lag) from 1961 to 1989, became non-significant when data from the 1990s were included (Greene et al. 2003a). Although our data for *C. finmarchicus* did not show any significant correlation with SST (Table 1), the GOM CPR data for 1961 to 1991 showed a strong negative correlation between these parameters, with no temporal lag (Licandro et al. 2001), although there was a 35-month consecutive gap in the data.

The correlation between *Calanus finmarchicus* abundance and wind speed in Massachusetts Bay is intriguing. Although there was no linear correlation between the NAO index and wind speed or direction, wind speed alone significantly explained 25% of the variance in *C. finmarchicus* abundance at Stn N04. High *C. finmarchicus* years (1996, 2001, 2002, 2003) had lower than mean winter wind speeds, while low *C. finmarchicus* years (1992, 1993, 1999, 2000) had higher than mean winter wind speeds. This suggests that wind speed is a potential link in yet unexplained climatic mechanisms leading to higher *C. finmarchicus* abundance in low NAO index years in Massachusetts Bay.

The present study was conducted for the purpose of monitoring the marine environment of Massachusetts Bay to quantify baseline variability and detect any major effects of a local large-scale sewage remediation project in Boston Harbor. Our long-term zooplankton data indicates that the plankton dynamics of this area are strongly influenced by large-scale, long-term climate phenomena, such as the North Atlantic Oscillation. Regionally-driven annual variation in winter marine climate, as represented by the NAO, appears to have greater influence on the plankton of Massachusetts Bay than does local modification of the marine habitat associated with sewage outfall relocation. In view of possible major effects of anthropogenic activities in modifying climate over the coming decades, it would seem prudent to expand long-term oceanographic and ecological monitoring programs if we are to understand the long-term effects of changing climate.

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