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Environmental factors affecting zooplankton in Cape Cod Bay: implications for right whale dynamics

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ABSTRACT: Cape Cod Bay is the only known winter-feeding ground of the highly endangered North Atlantic right whale *Eubalaena glacialis*, and is thus a critical habitat for right whales. As with most coastal ecosystems, Cape Cod Bay is a dynamic system with a high degree of variability in both physical and biological parameters. However, the extent of these fluctuations and their effect on the suitability of the bay as a right-whale feeding ground are not known. This study was conducted to address variability in the biological and physical environment of the bay and the possible impacts of this variability on the right whales' use of the area as a feeding ground. This study synthesized data collected from January to May, in 2000 to 2003. During 2002, the whales made very limited use of the bay compared to the other 3 yr, providing a unique opportunity for comparing conditions in the bay during this change in pattern of usage by the whales. Data on the physical and biological environment of Cape Cod Bay were collected during weekly cruises. These data indicated that there was significant interannual variation in the wind-forcing affecting Cape Cod Bay. Coincident with this variation were changes in the hydrography of the bay, suggesting that circulation patterns changed during the course of the study. Circulation changes affected the zooplankton prey of the whales either directly through changes in advection, or indirectly by affecting the production of the zooplankton.

KEY WORDS: *Eubalaena glacialis* · Zooplankton · Cape Cod Bay · Hydrography · Wind patterns · Interannual changes · Advection · Copepod production

INTRODUCTION

Cape Cod Bay is a semi-enclosed embayment that forms the southern part of Massachusetts Bay (see Fig. 1). Like most coastal ecosystems, it is a very productive region with a high degree of seasonal and interannual variability in both physical and biological characteristics (Toner 1984, Geyer et al. 1992, Turner 1994). This region has become the focus of attention recently because of its use as a feeding ground by the North Atlantic right whale *Eubalaena glacialis*, a species considered to be the most endangered large cetacean. With only approximately 300 individuals remaining in the population in combination with an estimated negative population growth rate, the North Atlantic right whale is in serious danger of extinction (Caswell et al. 1999, Kraus et al. 2001, Fujiwara & Caswell 2001, IWC 2001).

It is important to understand the factors governing the productivity of the feeding grounds of right whales because environmental factors such as inadequate nutrition may be affecting the survival of this species (Best et al. 2001, Cooke et al. 2001, IWC 2001). Despite the inherent physical variability of the waters of Cape Cod Bay, this region has consistently yielded a food resource adequate to attract roughly one-fourth of the population of North Atlantic right whales during the

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winter and early spring (Brown et al. 2002). This, however, changed in 2002. Based on aerial survey data collected since 1998, both the number of right whales observed in the bay and their total residency time declined dramatically in 2002 compared to all other years (Brown et al. 2002, 2003).

Previous studies have shown the importance of the abundance and quality of the food resource in determining right-whale distribution (Murison & Gaskin 1989, Mayo & Marx 1990, Wishner et al. 1995, Baumgartner et al. 2003). Right whales feed primarily on calanoid copepods, particularly the lipid-rich, older developmental stages of *Calanus finmarchicus* (Murison & Gaskin 1989, Wishner et al. 1995, Baumgartner et al. 2003), although other species such as *Centropages typicus* and *Pseudocalanus moultoni* are also targeted by the whales in Cape Cod Bay (Mayo & Marx, 1990). Because the food resource is thought to be the main factor that attracts the right whales to the bay each winter (Mayo et al. 2001, 2002), understanding the factors affecting this food resource is vital to understanding the interannual variability in the right whales' use of the bay.

The Cape Cod Bay–Massachusetts Bay region is influenced both by events in the offshore waters of the Gulf of Maine and by more coastal waters moving through the inshore waters of Massachusetts Bay into Cape Cod Bay (Signell et al. 2000). Additionally, there is a strong seasonal cycle in the physical environment of Cape Cod Bay. During the fall and winter months, winds are generally from the NW and are stronger and more variable than the SW winds of spring and summer (Geyer et al. 1992). The temperature, salinity, and stratification of the bay waters are affected by these events and will thus change with season.

The zooplankton assemblage of Cape Cod Bay likewise exhibits a strong seasonal cycle. In terms of biomass 3 of the dominant species are the copepods *Centropages typicus*, *Pseudocalanus moultoni* and *Calanus finmarchicus* (Mayo et al. 2000). Of these, *Centropages typicus* and *P. moultoni* are more closely associated with coastal waters (Smith & Lane 1988, Frost 1989, Davis & Alatalo 1992, Durbin 1997, Kane 1999, Bucklin et al. 2001) and are present year-round in Cape Cod Bay (Toner 1984, Turner 1994). *Calanus finmarchicus* is considered to be an oceanic species and does not occur year-round in the bay (Toner 1984, Turner 1994), but enters a state of diapause for part of the year in the colder, deeper, offshore waters (Bigelow 1926). Although there is overlap among these 3 species, there is separation in the period of peak abundance of each. Typically, *Centropages typicus* and *P. moultoni* are more abundant and comprise the fall and winter food resource for the right whales, while *Calanus finmarchicus* comprises their food resource in early spring (Mayo & Marx 1990).

In this study, the interrelatedness of the physical environment (wind stress, hydrography) and the zooplankton assemblage (abundance, composition) of Cape Cod Bay was investigated over the course of four years. These data were further analyzed in the context of the right whales' use of the bay to investigate the possible factors leading to the virtual abandonment of this feeding ground during 2002.

MATERIALS AND METHODS

Data collection and processing. Data were collected during cruises aboard the RV 'Shearwater' from December 1999 through May 2003. Beginning in December and continuing through May of each year, sampling was carried out approximately once a week (weather permitting) at stations previously established by the Center for Coastal Studies (Fig. 1), as well as opportunistically in the presence of right whales *Eubalanea glacialis*. All stations were not sampled during each cruise, but several were sampled frequently during the course of the year, providing adequate data on spatial and temporal variation (Table 1).

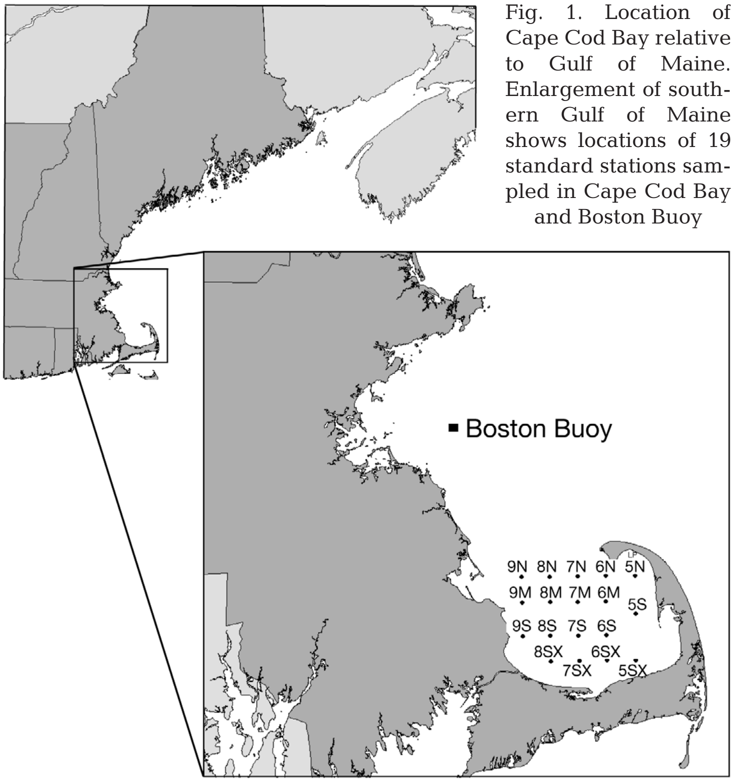

Fig. 1. Location of Cape Cod Bay relative to Gulf of Maine. Enlargement of southern Gulf of Maine shows locations of 19 standard stations sampled in Cape Cod Bay and Boston Buoy

Table 1. Number of zooplankton samples taken from each station in Cape Cod Bay during each sampling year. Other: stations opportunistically sampled in the presence of right whales

Year	Station no.																			
	LP	5N	5S	5SX	6N	6M	6S	6SX	7N	7M	7S	7SX	8N	8M	8S	8SX	9N	9M	9S	Other
2000	25	6	9	1	5	13	8	5	2	7	4	5	1	3	1	4	0	1	1	25
2001	21	4	13	6	11	11	13	1	5	7	1	5	4	1	0	4	0	0	5	45
2002	16	7	13	4	10	11	16	6	7	9	1	6	5	0	4	4	1	0	3	8
2003	21	6	19	4	8	15	11	3	10	6	9	3	10	9	5	1	0	0	7	11
Total	83	23	54	15	34	50	48	15	24	29	15	19	20	13	10	13	1	1	16	89

A Seabird SBE 19 conductivity-temperature-depth (CTD) recorder was used to measure temperature and salinity of the water column at each station. Zooplankton samples were collected coincident with CTD casts by towing a 333 µm mesh conical net (30 cm diameter opening) horizontally in the upper 1 m of the water column. The net was equipped with a General Oceanics helical flow meter to determine volume filtered. The net was towed for approximately 5 min at a speed of 1.5 m s^{-1}. Samples were preserved in 5% buffered formalin for later enumeration. On return to the laboratory, zooplankton samples were diluted to a known volume and then subsampled with a 1 or 2 ml Hensen Stemple pipet. Using a dissecting microscope, organisms were identified to species and stage when possible. Sufficient subsamples were counted to enable at least 300 organisms per sample to be identified. Counts were converted to organisms m^{-3}.

The zooplankton assemblage was dominated by 3 species during this study: *Centropages typicus*, *Pseudocalanus moultoni* and *Calanus finmarchicus*. *Centropages typicus* was staged as female, male or copepodid, and all 6 stages (Copepodid I, II, III, IV, V, and adult) of *Calanus finmarchicus* were counted separately. *P. moultoni* was not staged consistently throughout the study.

Data on wind speed and direction were obtained from the Boston Buoy, ID 44013, located 30 km east of Boston. This buoy is part of a network of buoys maintained by the National Data Buoy Center (NDBC), an agency within the National Weather Service (NWS) of the National Oceanic and Atmospheric Administration (NOAA). The data recorded at the buoy are archived and made available online by the NOAA Marine Environmental Buoy Database.

Data analysis. ***Wind data:*** The averaging technique for wind speed and direction for each time interval of interest followed that of the NDBC. The average wind speed (U) was calculated as a simple scalar average:

$$U = \Sigma U_i / N$$

Where U_i is the instantaneous wind speed and N is the number of observations. Variation among years and among months of each year was determined using a 1-way analysis of variance (ANOVA).

The average wind direction was calculated as a unit-vector average, with the length of the vector equal to 1 and the orientation of the vector equal to the observed wind direction, using the following equations:

$$V_e = \Sigma[U_i \sin(A_i)]/N$$

$$V_n = \Sigma[U_i \cos(A_i)]/N$$

$$AV = \arctan(V_e/V_n)$$

Where U_i is the instantaneous wind speed (= 1), A_i is the instantaneous wind direction, N is the number of observations, V_e is the mean E–W component of the wind, V_n is the mean N–S component of the wind, and AV is the resultant mean wind direction.

Possible correlations between average weekly zooplankton abundance (*Centropages typicus*, *Pseudocalanus moultoni*, *Calanus finmarchicus* and total zooplankton) and average weekly wind speed were also examined using a cross-correlation analysis with variable lag times.

Physical data: The CTD data from all stations were used to examine patterns in surface hydrography. Although CTD casts recorded data throughout the entire water column, only surface data were analyzed. Surface CTD data provided information on the physical environment from which the surface zooplankton tows were collected. Also, since the waters were well-mixed during the major part of the study period (Geyer et al. 1992), surface data accurately represent the physical environment of Cape Cod Bay. From the perspective of evaluating the feeding environment of the whales, we focused on surface data because of the relatively high frequency with which right whales skim-feed on the surface in Cape Cod Bay. Although feeding at depth is also thought to occur, observations and data collections are not as exact as when the whales are feeding at the surface. The surface zooplankton samples and associated environmental data unequivocally capture the conditions to which the whales are exposed while feeding at the surface.

Temperature and salinity data collected in the top 1.5 m were analyzed for differences among years and among months using 1-way ANOVA. Surface temperature and salinity values were plotted (T–S plots) for 6 of the standard stations to examine temporal (seasonal and interannual) and spatial variability of different water masses present in the bay. Density was calculated from temperature and salinity values recorded throughout the entire water column. The difference in the minimum and maximum values of density (sigma-t) in the water column from each cast was used as an index of the degree of stratification and analyzed for monthly and yearly variation. Additionally, correlation coefficients were calculated between zooplankton abundance (for each species and for total zooplankton) and each environmental factor (surface temperature, surface salinity, degree of stratification). This was accomplished using MATLAB's corrcoef function to calculate a normalized measure of linear relationship strength between these variables (MathWorks 2000).

Zooplankton: Variability in total zooplankton abundance and abundance of the 3 prevalent species (*Centropages typicus*, *Pseudocalanus moultoni*, *Calanus finmarchicus*) was analyzed for differences among years, within years, and among months using 1-way ANOVA. ANOVA was also used to compare, among years, the average proportion of each stage comprising the population on each sampling date for *Centropages typicus* and *Calanus finmarchicus*. Correlations among species were examined as described above.

Multivariate analysis: We employed 2 different types of multivariate analyses to investigate the interrelatedness of the variables measured in this study. All data (wind speed, wind direction, surface temperature, surface salinity, stratification, abundances of *Centropages typicus*, *Pseudocalanus moultoni* and *Calanus finmarchicus*) were converted to weekly averages so that data could be matched both temporally and spatially. For example, zooplankton samples were collected approximately once a week at several stations throughout the bay. Wind data were recorded hourly at 1 location. To have corresponding wind and zooplankton data, all data collected during a 7 d period were averaged and these averages represented 1 wk. Each sampling period covered 26 wk (December 1 to May 31).

A cluster analysis was done on the weekly averages of wind speed, wind direction, temperature, salinity, stratification and abundance of the 3 copepod species. All data were standardized and a similarity matrix was calculated using the Bray-Curtis index of similarity.

To tease out the possible associations between the environmental conditions and biological patterns, a BIO-ENV procedure was used (Clarke & Warwick 2001). In this analysis, the environmental variables (wind speed and direction, surface salinity and temperature, degree of stratification) were separated from the biological (abundance of *Centropages typicus*, *Pseudocalanus moultoni*, and *Calanus finmarchicus*). Draftsman plots of the variables were done to reveal any multivariate normality. A similarity matrix of each of the prevalent zooplankton species was calculated using Euclidean distance. For the environmental data, similarity matrices using normalized Euclidean distance were calculated for each of the possible combinations of environmental variables. A measure of agreement between the 2 similarity matrices (the fixed biological matrix and each of the possible environmental matrices) was determined by rank-correlating the matching elements in the 2 matrices using a standard Spearman rank correlation.

RESULTS

Wind data

A comparison of wind data averaged over the entire sampling period (December to May) indicated that wind speeds varied significantly among years (Table 2). Compared to the other 3 yr, 2002 had much lighter winds throughout the study (Fig. 2a). A comparison among years of individual months also indicated

Table 2. Statistical differences (p-values) calculated using ANOVA for comparisons among years and between months of study period. Significant values in boldface

Parameter	By year	By month					
		December	January	February	March	April	May
Wind speed	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Temperature	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.018**	**<0.001**
Salinity	**<0.001**	0.411	0.991	**<0.001**	**0.003**	**<0.001**	**<0.001**
Stratification	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**
Centropages typicus	0.054	**0.019**	0.086	**0.012**	0.105	0.188	**0.033**
Pseudocalanus moultoni	**0.013**	0.200	**<0.001**	**0.044**	0.127	**0.039**	0.06
Calanus finmarchicus	0.054	N/A	0.858	0.246	0.219	**0.038**	**0.019**
Total zooplankton	**<0.001**	**0.038**	**0.015**	**0.018**	**0.035**	**0.032**	0.067

significant differences for all months (Table 2). There was typically a decrease in wind speed in spring (April, May) versus winter (December to March) (Fig. 3). Although this was observed for all years, in 2002 the decrease was not as dramatic due to lower than average winter winds and higher than average spring winds. For 2000, 2001 and 2003, winds decreased on average approximately 4 m s^{-1} from winter to spring. For 2002 the decrease was less than 2 m s^{-1} over the course of the sampling period.

The year 2002 also differed with respect to the direction of winds, especially during the winter months (Fig. 4). Mean monthly wind direction was more often from the SW during 2002 compared to other years. The average direction for all winter months (December, January, February) of the 2002 sampling period was

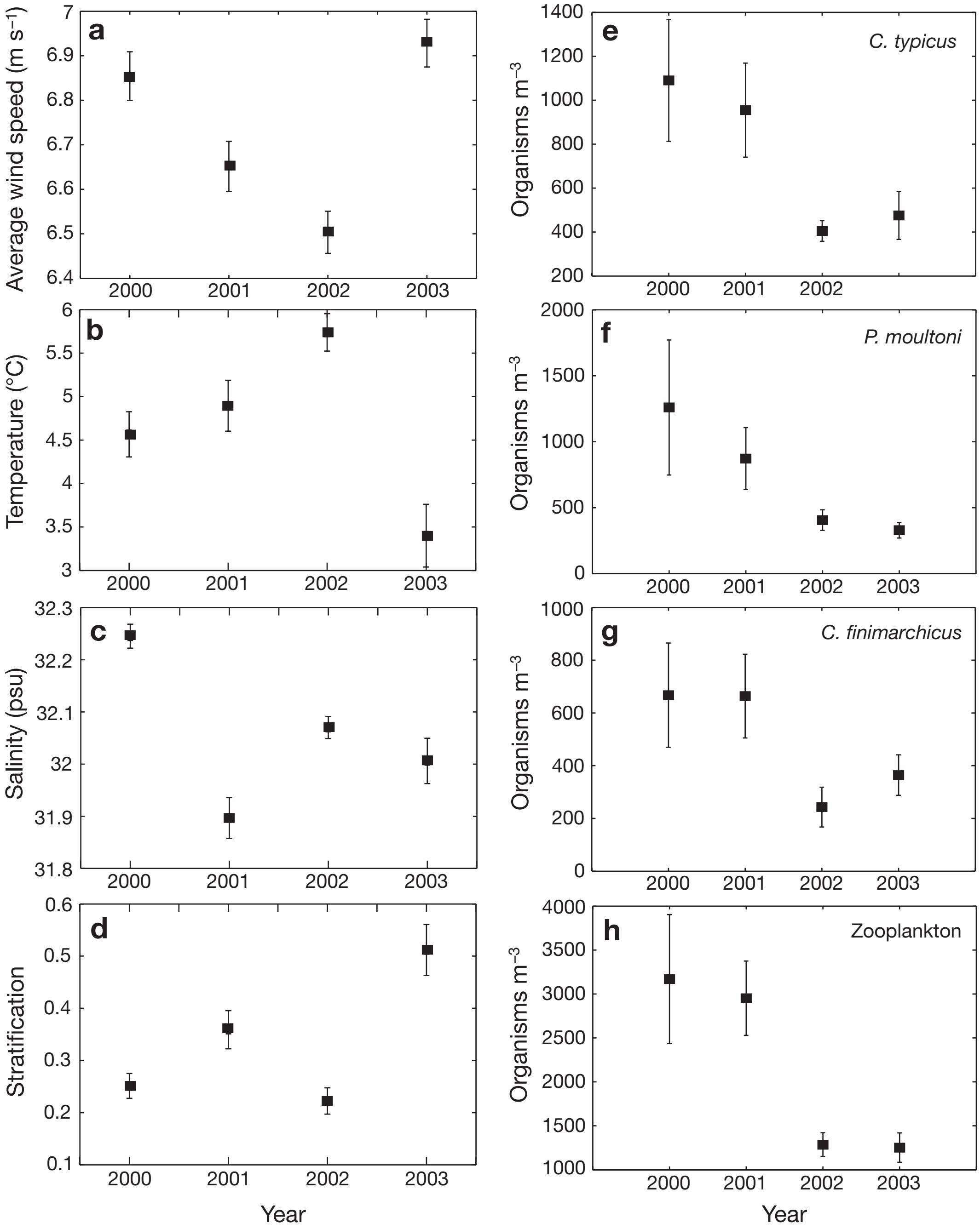

Fig. 2. Mean ± SE values for (a) wind speed, (b) surface temperature, (c) surface salinity, (d) stratification strength, (e) *Centropages typicus* density, (f) *Pseudocalanus moultoni* density, (g) *Calanus finmarchicus* density, (h) total zooplankton density for each year of study

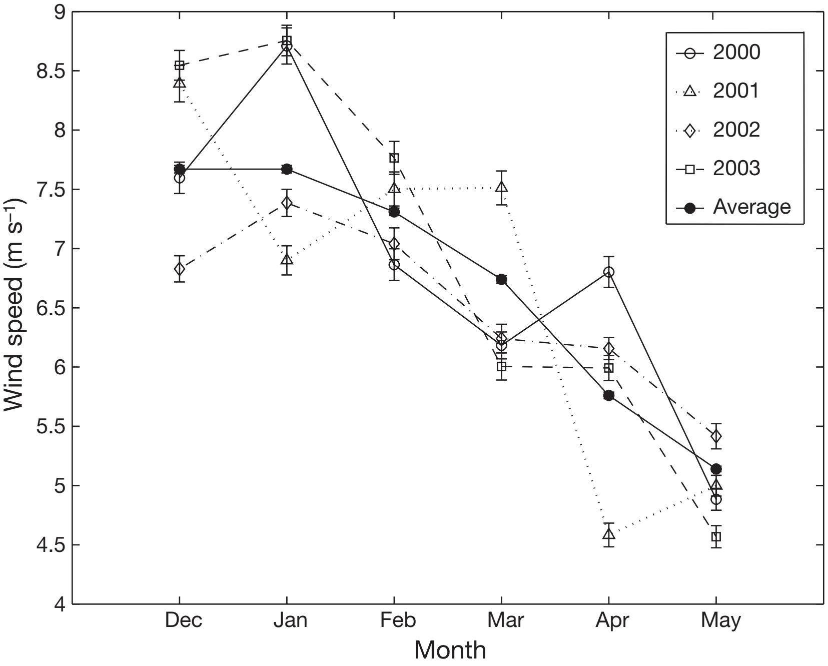

Fig. 3. Mean ± SE. Monthly wind speed measured at Boston Buoy for each sampling period. (●) average of monthly wind speeds recorded since 1984

SW, whereas for all other years the average direction of winter winds was NW. Average direction of winds during the spring months (April, May) was variable.

Total zooplankton abundance did not show a strong relationship with wind speed (Fig. 5a). This relationship was confounded by a number of factors, in particular because cruises were weather-dependent and sample collection was biased towards periods of lighter winds. Additionally, different species showed different relationships with wind speed (Fig. 5b–d). For all years, *Centropages typicus* showed a positive correlation with wind speed at variable lag times, *Calanus finmarchicus* showed a negative correlation, and there was no relationship between *Pseudocalanus moultoni* and wind speed at any lag time.

Changes in wind direction from one year to the next in relation to zooplankton abundance were also analyzed. As mentioned above, 2002 appeared different

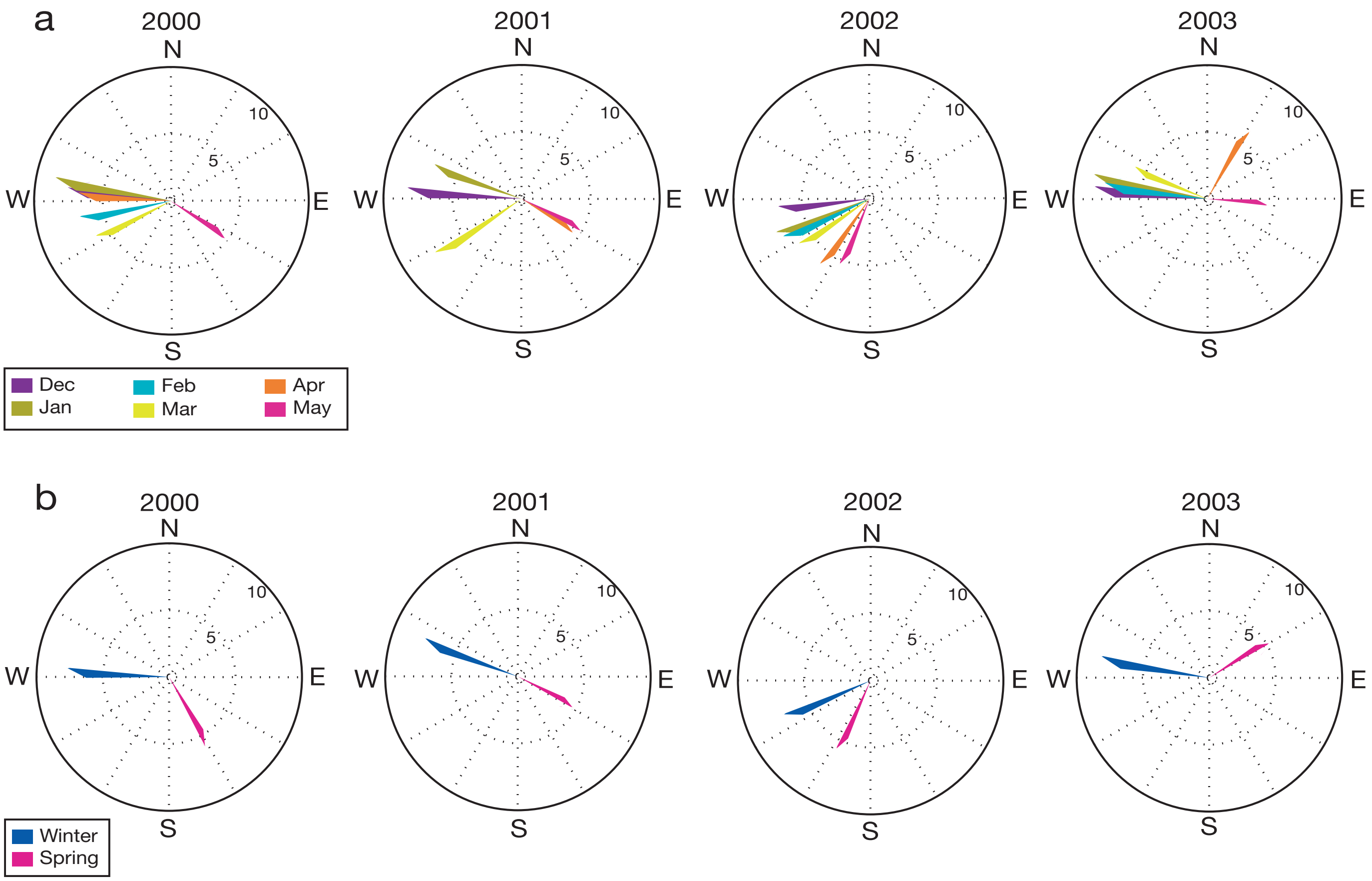

Fig. 4. Average wind direction and speed (m s^{-1}) for (a) each month and (b) winter and spring. 5,10 refer to wind speed

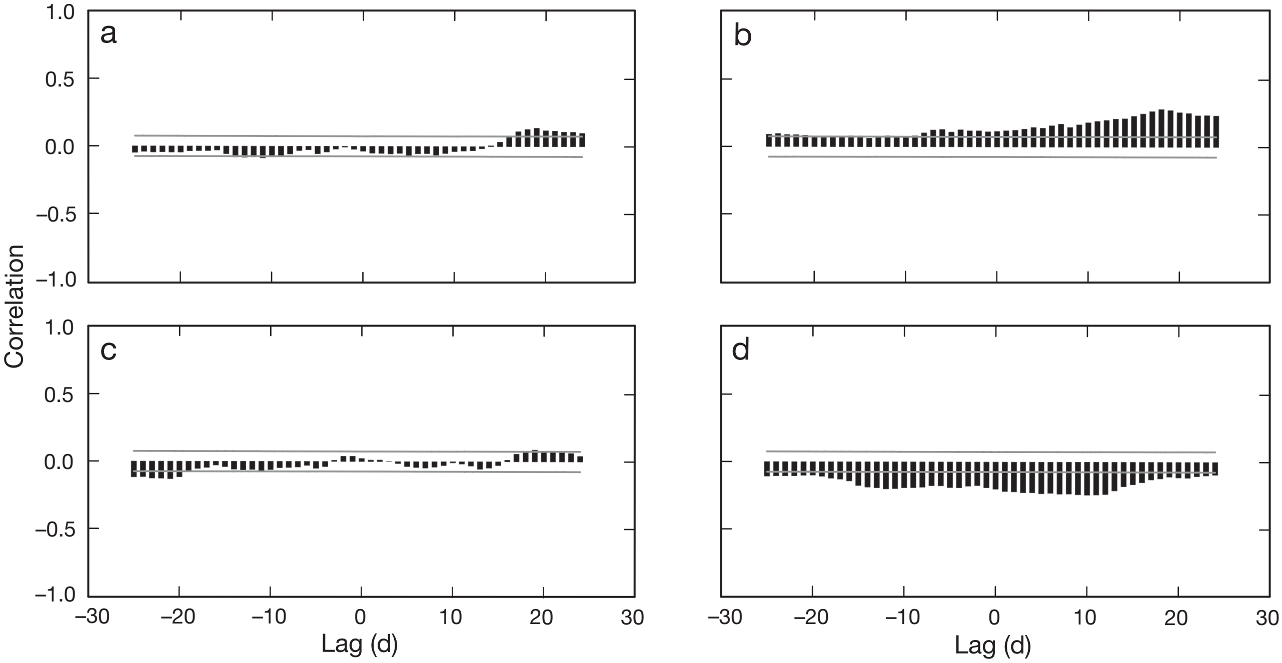

Fig. 5. (a) Total zooplankton, (b) *Centropages typicus*, (c) *Pseudocalanus moultoni* and (d) *Calanus finmarchicus*. Cross correlation plots at variable lag times of wind speed with zooplankton abundance

from other years, having more of a southerly influence during the winter than is typically observed. Zooplankton abundance was also lower during this year, as will be discussed later.

Physical data

Temperature

There were significant differences among years in surface temperatures measured in Cape Cod Bay (Table 2). The year 2002 was significantly warmer than 2000 and 2001, while 2003 was significantly cooler (Figure 2b). This is also reflected in the monthly averages among the four years of the study, with 2002 average monthly temperatures generally higher and 2003 generally lower than during the first 2 yr (Fig. 6a). The temperature change over the course of the sampling period was least in 2002, increasing by only 6.7°C, and greatest in 2003, increasing by almost 9°C.

Surface salinity

Yearly, average surface salinities differed significantly among years (Table 2, Fig. 2c). There were no significant differences among years in December and January (Table 2). The range in salinity among years began to increase during the late winter months, and was largest during spring (Fig. 6b). The least change in salinity over the course of the sampling period was in 2002, with salinity values remaining lowest in February and March.

Stratification

The degree of stratification varied significantly among years (Table 2, Fig. 2d). Comparisons among years of average monthly stratification showed significant differences in all months except December (Table 2). Degree of stratification typically increased over the course of the sampling period, with the strongest degree of stratification occurring during May 2003 (Fig. 6c).

Correlations with zooplankton abundance

In all years, surface values for temperature and salinity were negatively correlated with each other (Table 3). This was expected because, as the season progresses, temperatures increase, and snowmelt increases freshwater inflow, decreasing the surface salinity. Similarly, as the season progresses, the water column becomes increasingly stratified, explaining the positive correlation of stratification with temperature and the negative correlation with salinity.

Calanus finmarchicus abundance was positively correlated with temperature, negatively correlated with salinity, and positively correlated with stratifica-

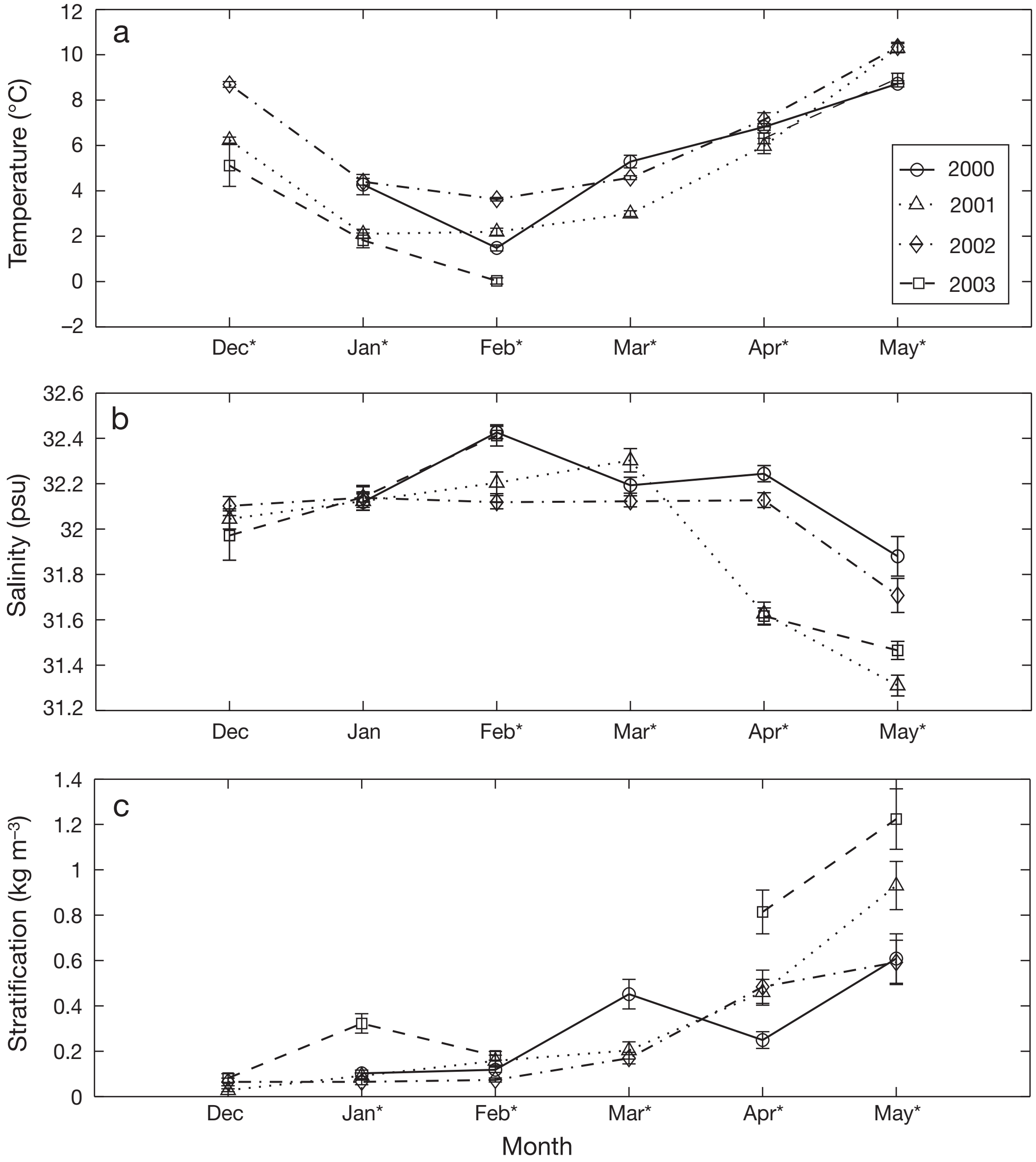

Fig. 6. Mean ± SE (a) sea-surface temperature, (b) surface salinity and (c) stratification strength measured in Cape Cod Bay during study period. *Significant difference ($p < 0.05$) between years

tion. Typically this species does not appear in Cape Cod Bay waters until early spring, and so should be associated with warmer, lower-salinity surface waters that are just beginning to become stratified (Fig. 7a). Abundance of *Pseudocalanus moultoni* did not show any strong correlations, positive or negative, with temperature, salinity, or stratification. This species is found throughout the year in moderate numbers and is therefore more of a euryhaline, eurythermal species (Fig. 7b). In direct contrast to *Calanus finmarchicus*, abundance of *Centropages typicus* was negatively correlated with temperature and positively correlated with salinity. This species is a late-fall, early-winter species, and would be expected to be associated with cooler, higher-salinity waters with little stratification (Fig. 7c). The correlation of physical characteristics and total densities of zooplankton varied among years, depending on which species contributed most to the zooplankton assemblage. For example, in 2000, *Centropages typicus* contributed most (correlation coefficient with total zooplankton = 0.83), and therefore total zooplankton was associated with characteristics similar to that of this species, i.e. cooler temperature, higher salinity.

Spatial and temporal variation

Temperature–salinity plots from several of the stations (LP, 5S, 6M, 6N, 6S, 7M) indicated that the bay was spatially homogenous in that T–S characteristics were similar at all stations (Fig. 8). Temporally, however, at these stations there was considerable variation, both during each year and among all 4 yr. Warming and freshening of the surface waters occurred at all stations as the year progressed. Interannual variation was observed, particularly during the month of February, when water mass properties during 2002 were both warmer and fresher than in the other years of this study.

Zooplankton

Total zooplankton and *Pseudocalanus moultoni* abundances varied significantly among years, abundances of *Centropages typicus* and *Calanus finmarchicus* did not (Table 2, Fig. 2e–h). A comparison of the

Table 3. Correlation coefficients for relationships between physical and biological characteristics. Significant correlations ($p < 0.05$) in boldface

Characteristic	Temperature	Salinity	*Calanus finmarchicus*	*Pseudocalanus moultoni*	*Centropages typicus*	Total zooplankton	Stratification
All data (2000–2003)							
Temperature	1.00						
Salinity	**–0.59**	1.00					
C. finmarchicus	**0.25**	**–0.23**	1.00				
P. moultoni	0.01	0.02	**0.34**	1.00			
C. typicus	**–0.14**	**0.14**	–0.05	**0.34**	1.00		
Total zooplankton	–0.01	0.02	**0.44**	**0.73**	**0.77**	1.00	
Stratification	**0.56**	**–0.60**	**0.22**	–0.03	**–0.12**	–0.03	1.00
2000							
Temperature	1.00						
Salinity	**–0.58**	1.00					
C. finmarchicus	**0.31**	–0.18	1.00				
P. moultoni	0.06	0.11	**0.38**	1.00			
C. typicus	**–0.23**	**0.21**	–0.05	**0.38**	1.00		
Total zooplankton	–0.04	0.14	**0.42**	**0.76**	**0.83**	1.00	
Stratification	**0.56**	**–0.52**	0.18	–0.03	–0.15	–0.06	1.00
2001							
Temperature	1.00						
Salinity	**–0.76**	1.00					
C. finmarchicus	**0.31**	**–0.37**	1.00				
P. moultoni	–0.03	–0.05	0.13	1.00			
C. typicus	**–0.25**	**0.23**	–0.13	0.17	1.00		
Total zooplankton	–0.03	–0.05	**0.38**	**0.60**	**0.47**	1.00	
Stratification	**0.76**	**–0.72**	**0.29**	0.05	**–0.28**	0.00	1.00
2002							
Temperature	1.00						
Salinity	**–0.36**	1.00					
C. finmarchicus	**0.48**	**–0.48**	1.00				
P. moultoni	**–0.35**	0.09	**–0.17**	1.00			
C. typicus	–0.09	0.05	–0.10	**0.49**	1.00		
Total zooplankton	0.16	**–0.30**	**0.49**	**0.55**	**0.72**	1.00	
Stratification	**0.58**	**–0.38**	**0.48**	**–0.35**	**–0.18**	0.04	1.00
2003							
Temperature	1.00						
Salinity	**–0.78**	1.00					
C. finmarchicus	**0.35**	**–0.36**	1.00				
P. moultoni	0.13	–0.13	**0.52**	1.00			
C. typicus	**–0.26**	**0.22**	**–0.22**	–0.09	1.00		
Total zooplankton	0.15	–0.18	**0.71**	**0.88**	**0.21**	1.00	
Stratification	**0.72**	**–0.64**	**0.27**	–0.04	**–0.31**	–0.03	1.00

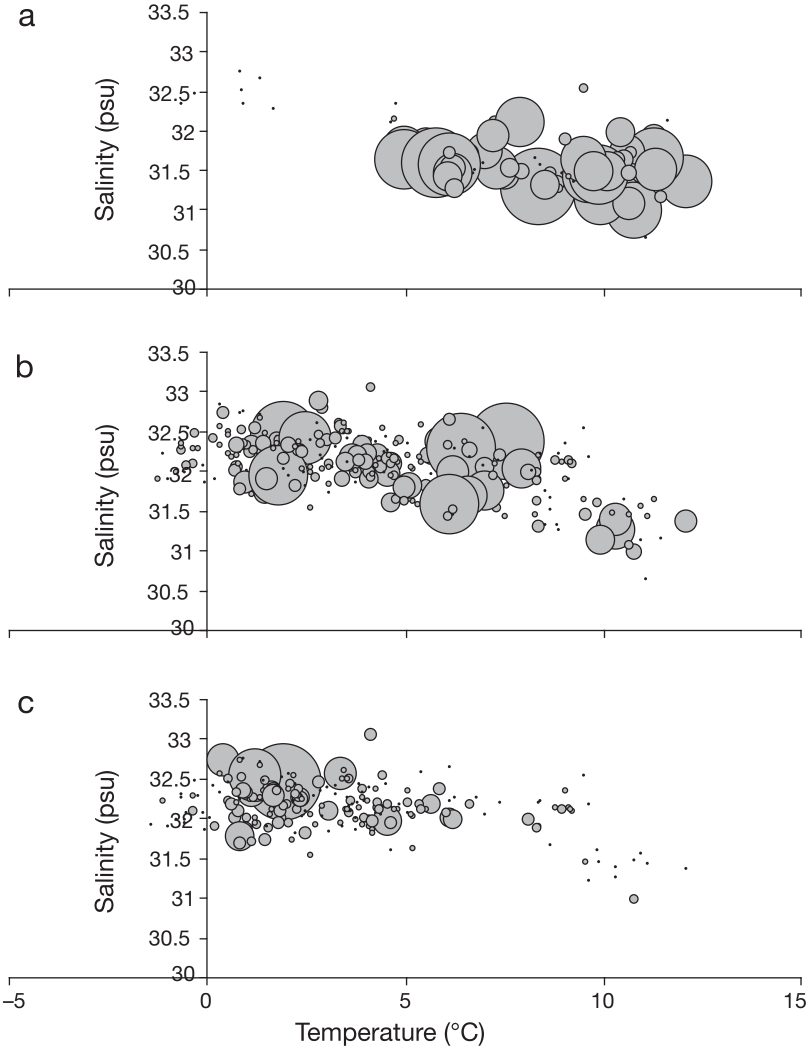

Fig. 7. (a) *Calanus finmarchicus*, (b) *Pseudocalanus moultoni* and (c) *Centropages typicus*. Distribution as a function of temperature and salinity. Circles represent density of each of the species as individuals m^{-3}, the larger the circle, the higher the abundance of the relevant species (ranges = *C. finmarchicus* <1 to 14 700, *P. moultoni* <1 to 22 000, *C. typicus* <1 to 54 900)

abundance of each species of zooplankton averaged over each month of the study period yielded significant differences among years for most species (Table 2). Exceptions to this occured primarily when the species were not very abundant.

During each of the four years of the study, a seasonal progression in the dominant species of zooplankton was observed (Fig. 9). *Centropages typicus* occurred during the early part of the sampling period (December to February), followed by peak abundances in *Pseudocalanus moultoni* during late winter and into early spring (February to April), and finally *Calanus finmarchicus*, which was strongest during the spring months (April to May). Despite the seasonal trends, there was some overlap among these species, as is seen in the positive correlations between *Centropages typicus* and *P. moultoni* and between *P. moultoni* and *C. finmarchicus* (Table 3).

Staging of *Centropages typicus* and *Calanus finmarchicus* allowed a limited examination of the age structure of these populations during the 4 years. Due to the large size of the mesh used in sampling (333 µm), only older stages of *Centropages typicus* were captured. For *Calanus finmarchicus*, although all stages were seen, the larger mesh size used did not representatively capture the younger stages (E. Durbin pers. comm.). Despite these limitations to the data, some interesting patterns emerged.

During the winter months, when *Centropages typicus* is a dominant member of the zooplankton, copepodids comprised roughly 40% of the population (Fig. 10). During 2002, this percentage dropped in mid-February to only 14% and remained significantly lower throughout March ($p < 0.001$, based on ANOVA comparing all four years). This decline was not observed in the other years and was coincident with the anomalous low-salinity, warmer waters observed during 2002.

To compare the age structure of the population of *Calanus finmarchicus* among years, data collection and analysis of the 2002 data were extended an additional month (through June) to account for the late appearance of *C. finmarchicus* during this year. A comparison of all 4 years indicated that the proportion of each stage of the population of *C. finmarchicus* did not differ significantly among years (ANOVA, $p > 0.05$) (Fig. 11).

Multivariate analyses

Draftsman plots of the individual environmental variables revealed a roughly linear relationship and symmetric distribution of points, indicative of multivariate normality; therefore, no transformation was necessary. No variables were highly correlated, so all were included in the subsequent analyses.

The dendrogram produced from the cluster analysis of the weekly averages of environmental variables (wind speed, wind direction, temperature, salinity,

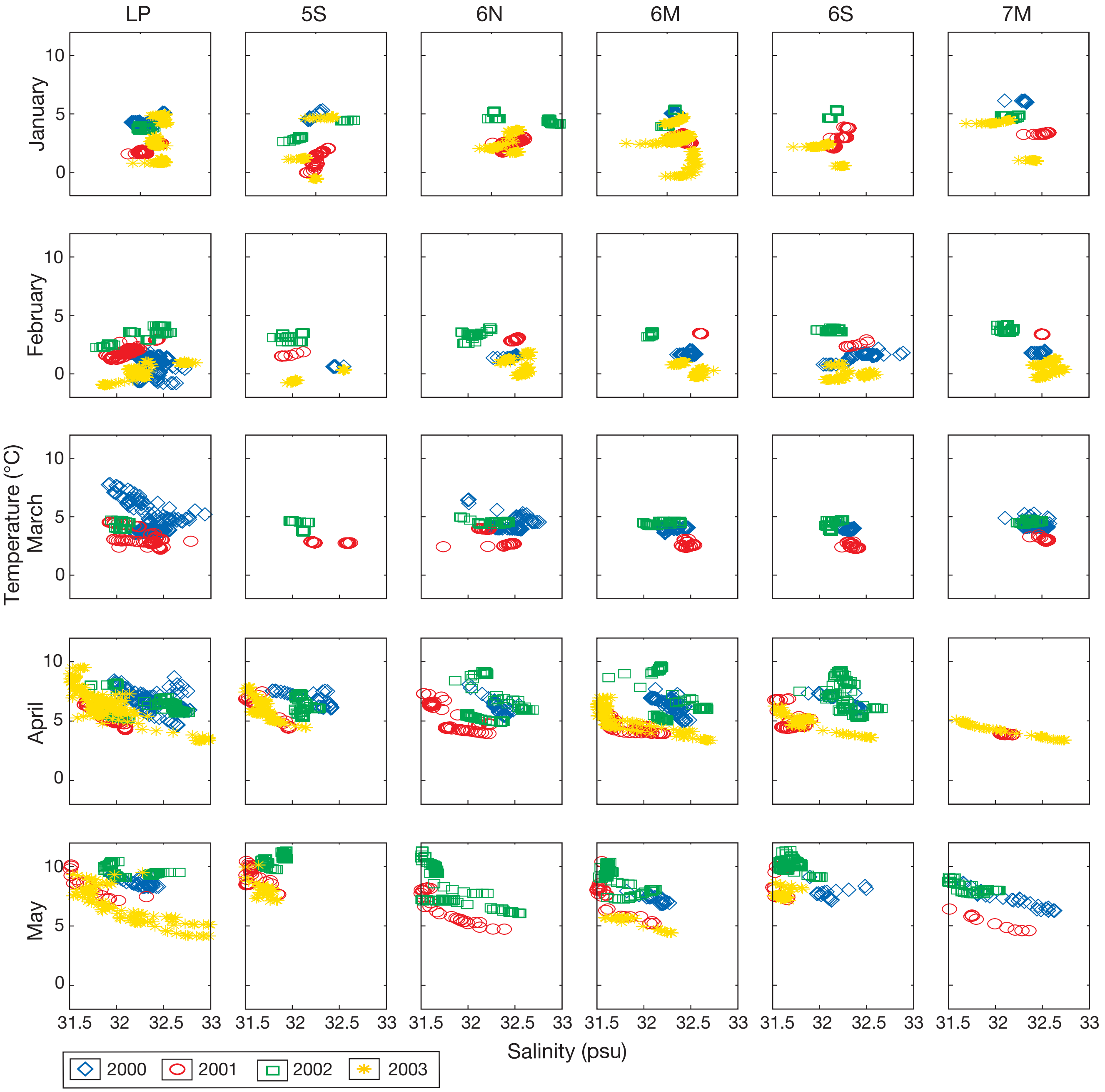

Fig. 8. Temperature–salinity plots for 6 stations sampled during the study period

stratification) and zooplankton abundance (*Centropages typicus*, *Pseudocalanus moultoni*, *Calanus finmarchicus*) reveals some interesting contrasts among weeks (Fig. 12). There are 3 large groups that appear to be separated mostly by time. Group A is comprised primarily of samples taken late in the sampling period (late April and May); Group B contains samples taken early in the sampling period (December to February); Group C consists mostly of samples taken during the middle of the sampling period (March and early April). These separations most probably result from seasonal changes in both the physical characteristics of the water as well as the zooplankton assemblage. When additional information on whale presence is considered, the dendrogram separates those weeks when whales were present in the bay from those weeks in which there were no whales. This is apparent not only in the more general grouping of Clusters A, B and C, but also in subgroups within these larger clusters. When environmental data were excluded, and the analysis was done solely with zooplankton data, separation was not as clear.

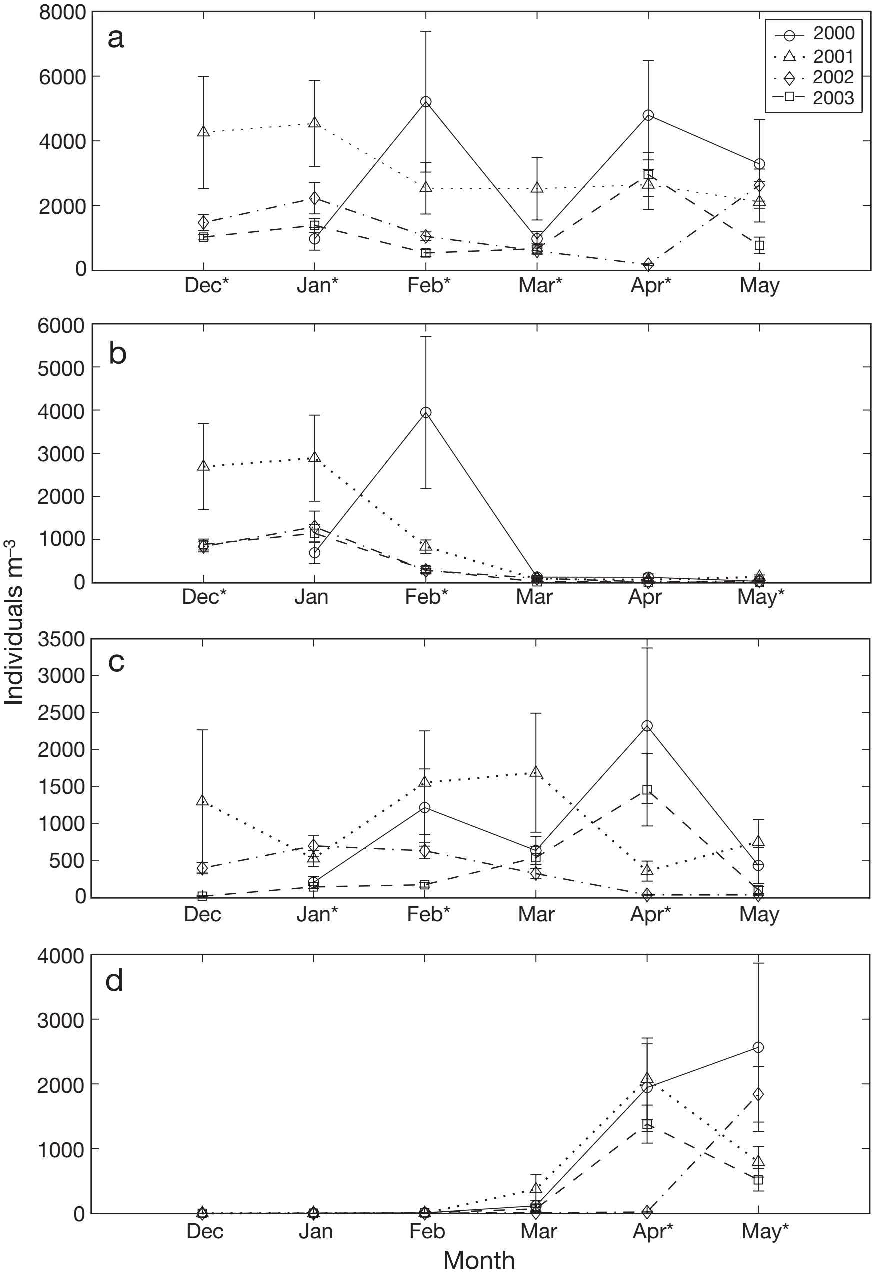

Fig. 9. Mean ± SE monthly zooplankton densities in Cape Cod Bay during study period. (a) All species combined, (b) *Centropages typicus*, (c) *Pseudocalanus moultoni*, (d) *Calanus finmarchicus*. *: significant differences ($p < 0.05$) between years

Finally, the BIO-ENV procedure was used to examine the interrelatedness of environmental conditions and the abundance patterns of the 3 prevalent species of zooplankton in Cape Cod Bay. Table 4 presents the 5 best results for each species determined by this procedure. *Calanus finmarchicus* abundance was most influenced by environmental parameters. Salinity and stratification best explained the observed patterns in abundance of this species (p = 0.607). Neither *Centropages typicus* nor *Pseudocalanus moultoni* were as strongly related to any of the environmental parameters measured. For *C. typicus* the 2 best parameters were wind direction and temperature (p = 0.121), for *P. moultoni* wind direction and salinity (p = 0.075).

DISCUSSION

The zooplankton species assemblage of Cape Cod Bay is comprised of populations that are self-sustaining within the bay as well as populations that are more transient. Therefore circulation patterns and the resulting changes in the physical environment are important in structuring the zooplankton community.

Cape Cod Bay forms the southern part of Massachusetts Bay and is open to and influenced by the circulation dynamics of the Gulf of Maine. During the early 1990s, several studies addressed the circulation patterns of Massachusetts Bay (Geyer et al. 1992, Irish & Signell 1992, Blumberg et al. 1993). Much of what Bigelow (1927) showed with drifter bottles was confirmed with moored current measurements as well as with different types of drifters in these more recent studies (Geyer et al. 1992). The mean circulation pattern of Cape Cod Bay (and the whole of Massachusetts Bay) is a counter-clockwise flow, driven primarily by the larger-scale forcing of the Gulf of Maine (density and mean westerly-wind stress). Superimposed on this mean flow pattern are the more variable forcings that influence circulation in most coastal environments: winds, tides, and river discharge. The variation in these factors is primarily on a seasonal or annual scale.

This study was conducted during the winter and spring of each year, 2000 to 2003. A change in the factors driving circulation accompanies the transition from winter (December to March) to spring (April to May). Large-scale, seasonal circulation in the Gulf of Maine is weaker and less defined during the winter than in the spring, resulting in longer time scales of circulation during the winter months (Geyer et al. 1992, Xue et al. 2000). In Cape Cod Bay, because the water column is well-mixed throughout the winter (Fig. 6) and run-off events do not have a strong influence, wind stress is the only significant force operating on the circulation pattern. Winds from the NW are most common (Fig. 4) and help to reinforce the Gulf of Maine's mean counter-clockwise circulation pattern in Cape Cod Bay (Geyer et al. 1992). April is the month of transition from NW winds and cooling in winter to SW winds and warming in summer (Xue et al. 2000). Similarly, in Cape Cod Bay, April and May are characterized by SW winds (Fig. 4). Winds from this direction can inhibit the mean cyclonic circulation pattern (Geyer et al. 1992, Robinson et al.: available at: people.deas.harvard.edu/leslie/MBST98/index_rtime.html) and, as observed in this study, can have a distinct effect on the physical and biological environment of Cape Cod Bay.

Because of the importance of atmospheric forcing on the circulation regime, variations in the seasonal pattern of winds would be expected to have a large effect on the physical environment of Cape Cod Bay. This was observed during the study. The winter months of 2002 in particular were atypical, being dominated by light southerly winds and lacking the stronger NW winds characteristic of the winter wind regime of this

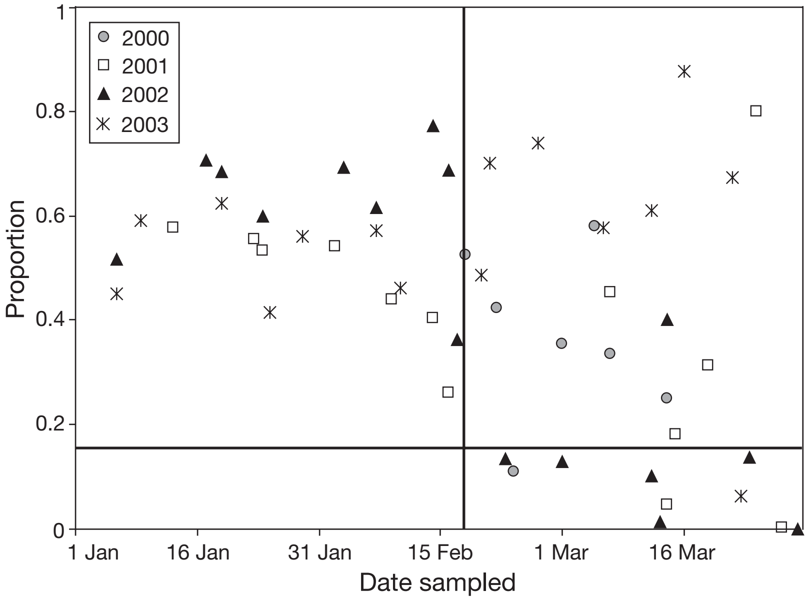

Fig. 10. *Centropages typicus*. Proportion of copepodids in population sampled each year. Vertical line indicates date after which proportion of copepodids declined significantly during 2002, and horizontal line that, on all but one sampling date during 2002, copepodids comprised <18% of population. During other years, copepodids typically averaged around 40% of population

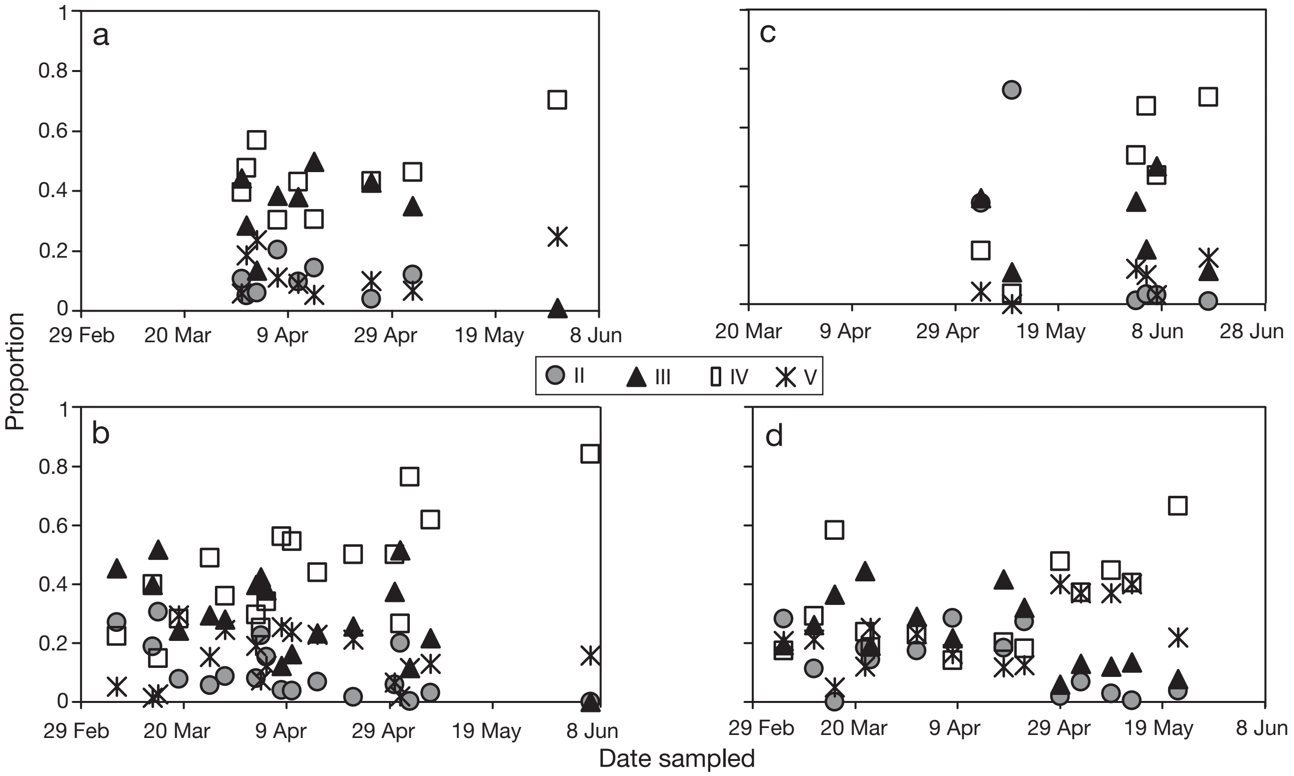

Fig. 11. *Calanus finmarchicus*. Proportion of each stage comprising population during (a) 2000, (b) 2001, (c) 2002 and (d) 2003

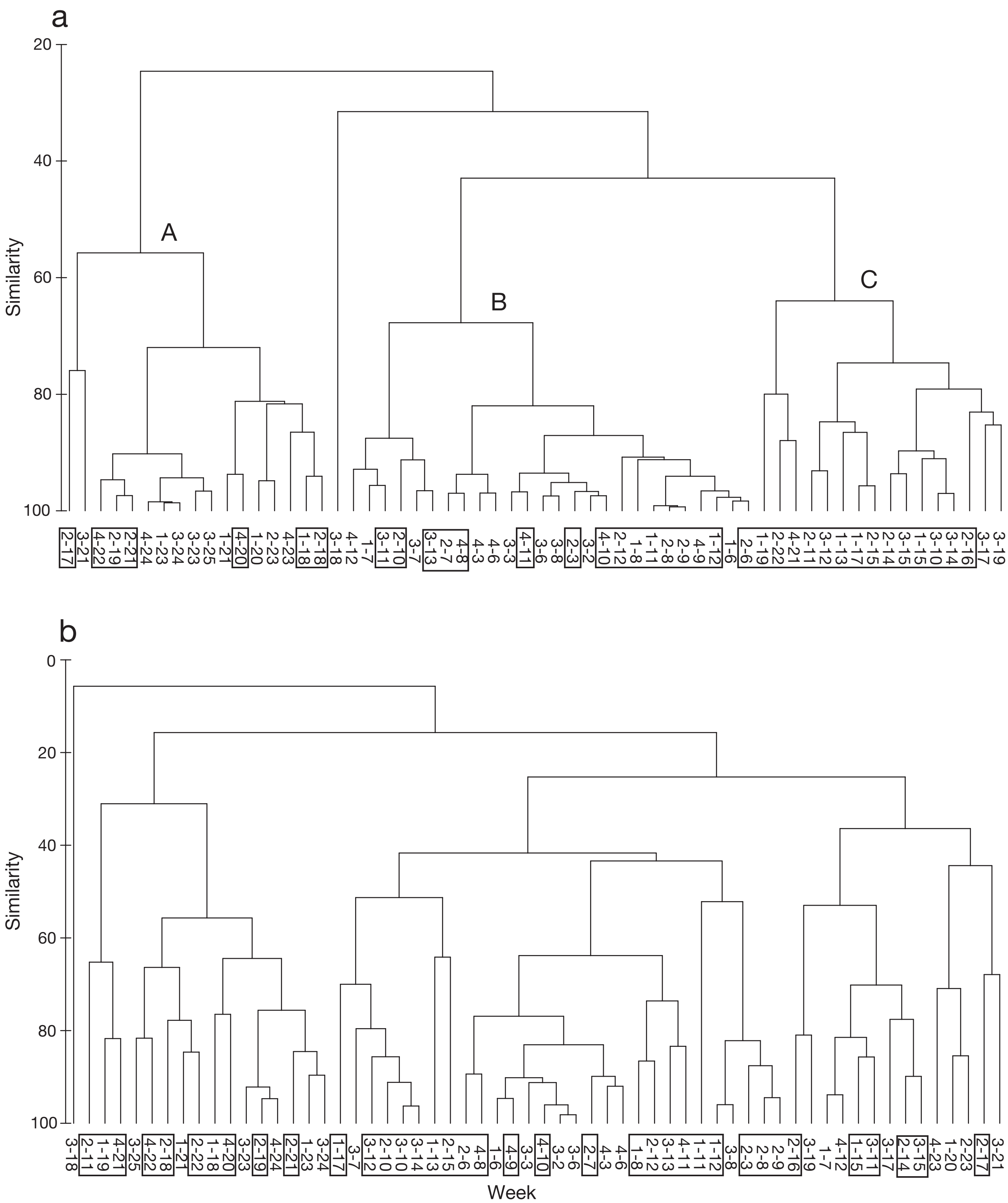

Fig. 12. Dendrogram produced from cluster analysis of (a) all data (environmental and zooplankton species abundances) and (b) zooplankton species abundances only. Abscissa labeling represents number of the sampling period (1 = 2000, 2 = 2001, 3 = 2002, 4 = 2003) followed by the week of that year (e.g. 2-17 = 17th week of 2001 sampling period). Boxed numbers indicate weeks when right whales *Eubalaena glacialis* were present in Cape Cod Bay. Subclusters A, B, and C in (a) represent temporal separation of data

Table 4. *Centropages typicus*, *Pseudocalanus moultoni* and *Calanus finmarchicus*. Results of BIO-ENV procedure indicating variables that best explain variation in each species, abundance, and corresponding correlation coefficient

Correlation	Selected variables
Centropages typicus	
0.121	Wind direction, temperature
0.118	Wind speed, wind direction, temperature
0.11	Wind speed, wind direction
0.07	Wind direction
0.06	Wind speed, temperature
Pseudocalanus moultoni	
0.075	Wind direction, salinity
0.07	Wind direction, salinity, stratification
0.057	Salinity
0.056	Salinity, stratification
0.045	Wind direction
Calanus finmarchicus	
0.607	Salinity, stratification
0.592	Stratification
0.574	Temperature, salinity, stratification
0.53	Wind speed, temperature, salinity, stratification
0.522	Wind speed, salinity, stratification

region (Figs. 3 & 4). Both the decline in magnitude and the change in direction during the winter could result in a more stagnant circulation regime (Geyer et al. 1992). Under these conditions, bay waters would not be replenished as often by the waters of the Gulf of Maine. Consequently, Cape Cod Bay was both warmer and less saline during the winter months of 2002 (Fig. 8). The seasonal changes in the physical characteristics over the course of the 2002 sampling period were also much less than in other years, probably as a result of weaker circulation patterns. Neither surface temperature nor salinity changed as much as in the other years between December and May; as a result, stratification strength was also lower (Fig. 6).

Annual differences in the populations of the 3 species of copepods were less dramatic than those in the physical environment. Yearly averages indicated no statistical difference for either *Centropages typicus* or *Calanus finmarchicus*, and only a slight difference for *Pseudocalanus moultoni*, with abundance in 2000 being greater than in 2002. A finer-scale comparison of monthly averages, however, did indicate differences for each of the 3 populations. Peak abundance of *Centropages typicus* occurred between December and February (Fig. 9b), *P. moultoni* typically peaked in April (Turner 1994), although there was considerable variation from year to year (Fig. 9c), and *Calanus finmarchicus* typically peaked in the spring before water temperatures got too warm (Marshall & Orr 1955, Davis 1984, Turner 1994, and present Fig. 9d). The significant differences observed in monthly abundances of these species (Table 2) suggests that timing of peaks in the populations varied among years, although total yearly abundances did not (Fig. 9).

An examination of the physical characteristics that coincided with the peak abundance of each species explained some of the observed variation in abundances during the four years. *Centropages typicus* appeared to be most abundant during years with temperatures around 2°C, salinities greater than 32 , average wind speeds around 7 m s^{-1}, and less prevalent southerly winds. These characteristics best describe the conditions during February 2000 and January 2001. As indicated by the BIO-ENV analysis, wind direction and temperature were the most important factors structuring this species (Table 4). Looking solely at these 2 characteristics, 2002 was too warm during the early winter and had a higher percentage of southerly winds, while 2003 was an unusually cold year with water temperatures well below those of 2000 and 2001. This could in part explain the lower abundance of *C. typicus* during these years.

Factors explaining variations in the populations of *Pseudocalanus moultoni* during these four years are harder to identify. The physical environment during peak abundances of *P. moultoni* was highly variable among years and no environmental characteristics more conducive for the occurrence of this species could be distinguished. Correspondingly, multivariate analysis indicated that none of the measured environmental characteristics explained the variation in this population (Table 4). Temperature could perhaps play a role, in that population peaks occurred early (January, February) during the warmer year (2002) and later (April) during the cooler year (2003) (Fig. 9c).

Seasonal fluctuations in the *Calanus finmarchicus* population are more closely tied to environmental conditions than those of the other 2 species, as seen in the BIO-ENV analysis (Table 4). The initial increase in *C. finmarchicus* abundance began in most years during April, coinciding with surface temperatures around 6°C, decreasing surface salinities, increasing southerly winds, increasing stratification, and decreasing wind stress. Since there were no significant differences in yearly abundances, monthly variation in abundances among years is best attributable to timing of peak occurrence. For example, in April 2000, abundances were significantly greater than in April 2002, because *C. finmarchicus* did not increase until May of that year (Fig. 9d). Similarly, in May 2000, abundances were greater than in May 2003. Whereas in most years the population declined dramatically after a couple of weeks, in 2000 it was sustained into a second month and therefore was significantly higher than in the other years. This could be due in part to the slight increase in surface temperature during 2000 of < 2°C compared to other years, when the temperature increase was closer to 3–4°C (Fig. 6a).

By definition, plankton organisms drift under the influence of the currents. Therefore, circulation patterns are one of the primary factors contributing to their distribution. As previously discussed, the circulation regime of Cape Cod Bay is an extension of the Gulf of Maine. The Maine coastal current is therefore a key factor in structuring both the hydrography and the plankton community of Cape Cod Bay via advective processes.

Calanus finmarchicus in particular appears to be driven primarily by advective processes (Gaard & Hansen 2000, Pershing et al. 2001). A comparison among years of the data collected on the abundance and age structure of the *C. finmarchicus* population sampled in Cape Cod Bay supports this conclusion. During the 2002 sampling period, the peak in abundance of *C. finmarchicus* and the development of the population were delayed by approximately 1 mo (Fig. 9d). During the other 3 yr of sampling (2000, 2001, 2002), the *C. finmarchicus* population followed the development patterns characteristically observed for the *C. finmarchicus* population of the Gulf of Maine (Durbin et al. 1997, 2000), with increasing numbers of Stage III through late April, and increasing numbers of Stage IV throughout May (Fig. 11).

Variation in circulation patterns induced by wind-forcing is important in controlling the interannual variability of *Calanus finmarchicus* populations in shelf waters (Gaard & Hansen 2000). Data collected in this study could also implicate wind as a factor controlling *C. finmarchicus* abundance and population structure in Cape Cod Bay. The changes in wind, the resulting (hypothesized) changes in circulation, and the possible effects on the observed differences in temperature and salinity measured during 2002 compared to the other years have already been addressed. This can be extended a step further to encompass the *C. finmarchicus* population. Slower circulation induced by weaker, southerly winds could have been a factor in delaying the development of the *C. finmarchicus* population in Cape Cod Bay in 2002.

In addition to variability in advection from the Gulf of Maine, other factors could be equally important in structuring the population dynamics of *Centropages typicus* and *Pseudocalanus moultoni*. These species are not as transient as *Calanus finmarchicus* in Cape Cod Bay, but are resident, productive components of the plankton assemblage throughout the year. Therefore, not only are the abundances of these species driven by advection, but observed population fluctuations could also be a response to changes in the physical environment of the bay and subsequent changes in rates of production. Thus, it is not unexpected that *Centropages typicus*, a species more constrained by the physical regime, had greater fluctuations in abundance than did *P. moultoni*, a species thought to be more tolerant of changes in temperature and salinity.

Not only is the total population of *Centropages typicus* affected by its physical environment, but variability in the age structure of this population also appears to be related to the physical regime of Cape Cod Bay. Copepodids made up an extremely low percentage of the population in February 2002 (Fig. 10), when the bay waters were anomalously warm. During this same time period in 2003, a much cooler year, *C. typicus* copepodids comprised a very high percentage of the population. The years 2000 and 2001 were average years with respect to both temperature and the proportion of *C. typicus* copepodids. There is an inverse relationship between temperature and development in *C. typicus* (Smith & Lane 1985, 1987). Based on this, development times would have been shortest during 2002 and longest during 2003. Assuming production to be negligible at this time (Bigelow 1926, Smith & Lane 1987), longer development times would result in a greater proportion of copepodids late in the sampling period (as seen in 2003), and shorter development times would result in a smaller proportion (as seen in 2002).

It should be noted that the underlying assumption of this study is that the zooplankton samples collected gave an indication of the food resource available to the whales. Therefore, it is assumed that when low densities of zooplankton were detected in the study area, it is because either physical (circulation patterns) or biological (low production levels) mechanisms prevented the population of each of the species from developing in Cape Cod Bay. Other regions were not sampled for zooplankton simultaneously with Cape Cod Bay, so nothing can be said about the zooplankton resource available to these whales in other feeding grounds. However, during 2002, when numbers of right whales observed in Cape Cod Bay were low, higher numbers of right whales were observed in the Great South Channel and along the backside of Cape Cod (Brown et al. 2002).

Several studies have suggested that zooplankton densities are a determining factor in the whales' distribution in the NE Atlantic (Murison & Gaskin 1989, Mayo & Marx 1990, Wishner et al. 1995). This study indicates that the physical environment is equally important. For example, the cluster analysis separated samples based on whale presence or absence better when environmental data were included (Fig. 12).

Although zooplankton abundance and species composition are likely to influence how long right whales will utilize Cape Cod Bay as a feeding ground, it is the physical environment that gives these whales cues on whether to visit and explore the area initially. During 2002, changes in the physical environment and zooplankton assemblage (Figs. 2 to 4, 6, 8 & 9) corresponded with both low numbers of right whales and a shorter duration of occupancy of Cape Cod Bay (Brown et al. 2002, 2003). In 2003, the physical environment returned to conditions similar to those of the first 2 yr, yet zooplankton densities remained low (perhaps because the system had to recover from some stress, and the physical environment was able to rebound faster than the zooplankton). The increased number of whales sighted in Cape Cod Bay in 2003 (Brown et al. 2003) suggests that something attracted them to the bay. Their low residence time (Brown et al. 2003) suggests that the food resource was not adequate. Environmental cues such as temperature or salinity are easier to detect at a longer range than aggregations of zooplankton would be (Kenney et al. 2001). Therefore, the physical environment could indicate to the whales if conditions are conducive for high abundances of zooplankton and thus function as the initial factor attracting the whales into Cape Cod Bay. The existence of an adequate food resource would then prolong their stay in the bay.

In conclusion, several studies have attempted to identify links between the physical environment and higher trophic levels (e.g. Meise-Munns et al. 1990, Pershing et al. 2001, Baumgartner et al. 2003). Few have found conclusive results. The results of this study are also far from definitive; however, they do suggest some interesting inter-relationships among the physical environment, the zooplankton community, and the right whales in Cape Cod Bay:

- Interannual changes in wind patterns were coincident with changes in the hydrography of Cape Cod Bay, suggesting that circulation patterns changed during the course of the study.
- Of the 3 species of zooplankton considered in this study, *Calanus finmarchicus* is a transient species advected into the bay each year and greatly influenced by the circulation regime; *Pseudocalanus moultoni* and *Centropages typicus* are more permanent members of the zooplankton assemblage and are affected indirectly by circulation via its effects on the physical environment of the bay.
- Periods of peak abundance of each species varied significantly among years and were closely coupled with the physical environment; however, interannual changes in the abundances of these 3 species of zooplankton were not as distinct as changes in the physical environment.
- Modeling the physical environment in addition to the zooplankton provides a better indicator of the right whales' seasonal occurrence in Cape Cod Bay than evaluating the zooplankton alone.

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