

Multivariate analysis of the copepod community of near-shore waters in the western Gulf of Maine

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ABSTRACT: Abundance patterns were described for 15 species of planktonic copepods in coastal waters of the western Gulf of Maine, NW Atlantic, between April 2002 and March 2003. Vertically stratified sampling was carried out at 4 stations along a 12 km cross-shelf transect ranging from 60 m to 105 m depth offshore of Portsmouth, NH, USA. Temporal and spatial patterns of distribution and abundance were described for adult copepods, and multivariate analyses were used to assess trends in community composition. Three species, *Oithona similis*, *Temora longicornis*, and *Centropages typicus*, dominated the community numerically, comprising 72.1% of all copepods identified. The abundances of 7 species exhibited strong seasonal variation, in contrast to 5 species which were abundant throughout the year. As shown by non-metric multi-dimensional scaling (MDS), the composition of the community changed in a cyclical pattern over the 1 yr period, suggesting a clear seasonal cycle. There was significant vertical partitioning of the copepod community, with significant differences among depth strata at all but the shallowest station. In contrast, significant horizontal spatial variation was evident only in the deepest stratum; surface and mid-depth samples did not differ among the 4 stations. Although many of the same species found in this study are also known from Georges Bank and Massachusetts Bay, their seasonal patterns of abundance differed notably among the regions. Such dissimilarities emphasize the importance of sampling at appropriate time and space scales in order to accurately assess population and community dynamics of coastal zooplankton assemblages.

KEY WORDS: Zooplankton · Copepods · Coastal processes · Multi-dimensional scaling · Gulf of Maine

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INTRODUCTION

Planktonic copepods in the Gulf of Maine have been extensively sampled (Bigelow 1924, Davis 1987, Kane 1993, Licandro et al. 2001), yet patterns of distribution and abundance in the coastal waters of Maine and New Hampshire are not completely known. Copepods consistently dominate the zooplankton assemblages of this region both in numbers and biomass (Bigelow 1924, Kane 1993). As phytoplankton grazers and active predators, copepods play an important role in the transition of energy from primary producers to higher consumers. Larval stages of many commercially important fish species prey primarily on copepods (Sherman et al.

1998), and copepod abundance directly affects recruitment success of these fish. Quantifying the temporal and spatial abundance patterns of copepods in coastal areas of the Gulf of Maine is thus essential to understanding the regional ecosystem.

The Gulf of Maine is enclosed by shallow coastal waters of the United States and Canada to the north and west. The Western Maine Coastal Current tends to flow south along the coasts of Maine and New Hampshire, herein termed the Western Maine Coastal Region (WMCR). This region is stratified in summer months and mixed to a depth of approximately 100 m in winter (Bisagni et al. 1996). It is a nutrient rich zone with high phytoplankton productivity (Durbin 1997)

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that in turn supports an abundant copepod community (Bigelow 1924, Turner 1994). Water from the WMCR may feed Massachusetts Bay and Georges Bank, acting as a supply for copepod species to these areas (Durbin 1997), although the degree to which this occurs is still debated (McGillicuddy et al. 1998). To date, the WMCR has not been as comprehensively sampled as Georges Bank or Massachusetts Bay. As a result, it is unclear how similar the patterns of variation in the WMCR copepod community will be to patterns described for these other shallow, productive areas in the Gulf of Maine.

The behavior of planktonic copepods can significantly influence how they are transported by local water currents. Copepods can swim strongly enough to overcome diffusive processes and potentially even turbulent mixing (Wiafe & Frid 1996, Lagadeuc et al. 1997), enabling them to control their vertical location in the water column to some extent (Ambler & Miller 1987, Incze et al. 2001). This is significant because water currents often vary in both speed and direction across vertical gradients in the water column. Two copepods at the same location, vertically separated by only 50 m, may be transported kilometers apart within 24 h. The vertical distribution of individual species is thus critical to understanding and predicting copepod population dynamics.

For 2 cryptic species in the WMCR, *Pseudocalanus moultoni* and *P. newmani*, very little knowledge of seasonal and spatial patterns exists. The species have not been differentiated in most zooplankton studies due to

their morphological similarity. They can now be readily identified using a species-specific polymerase chain reaction (SS-PCR) that has been used to discriminate these species in studies on Georges Bank (Bucklin et al. 1998, Bucklin et al. 2001). The objectives of this study are to describe individual species' patterns of distribution and abundance in the WMCR and to determine the degree of change in the composition of the copepod community over monthly time scales and small (1 to 10 m) to coarse (10 to 100 m) space scales. We report here the results of analysis of monthly zooplankton collections at appropriate horizontal and vertical resolution, characterization of hydrographic structure of the water column, and molecular discrimination of cryptic species, in order to provide a detailed picture of the dynamics of the copepod community of the WMCR.

MATERIALS AND METHODS

Samples were collected at approximately monthly intervals from 4 stations along a cross-shelf transect in the coastal waters offshore of Portsmouth, NH, USA from April 2002 to March 2003 (Fig. 1). The length and position of the transect was chosen to minimize sampling of estuarine output; stations were located at 60, 80, 90, and 105 m depth. Zooplankton samples were collected using a 1/4 m² Multiple Opening Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1985), with 150 µm mesh nets and inte-

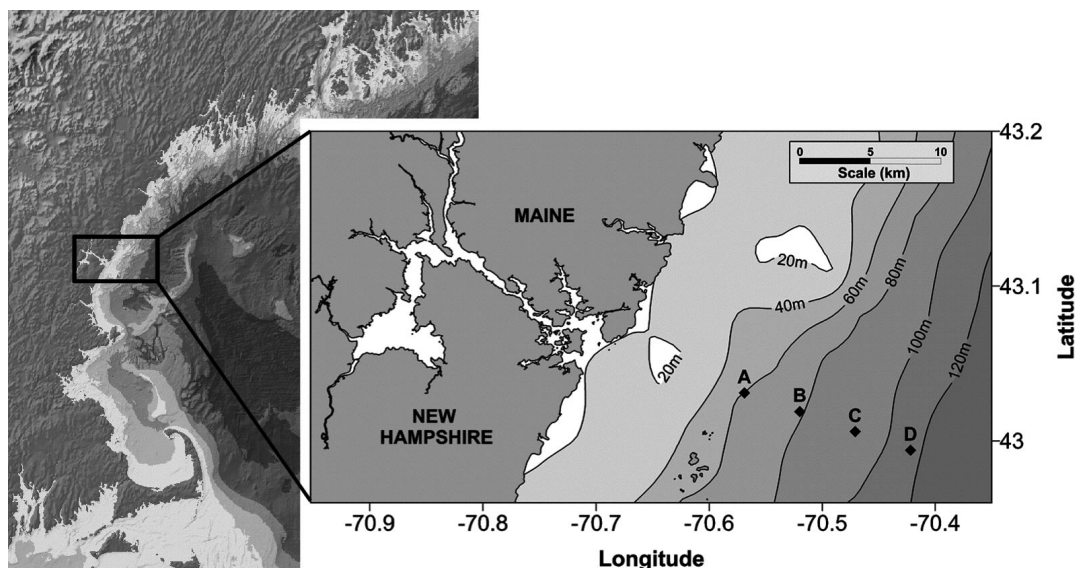


Fig. 1. Location of sampling stations, indicated by A, B, C, and D. Station coordinates are as follows: Stn A: 43.031° N, 70.569° W; Stn B: 43.019° N, 70.519° W; Stn C: 43.011° N, 70.472° W; Stn D: 42.994° N, 70.422° W. (Gulf of Maine image by E. Roworth and R. P. Signell)

grated CTD. The volume of water sampled by each net was determined using a flow meter mounted on the net frame and an on-board inclinometer to record the area of the net opening. Real-time CTD data relayed to the ship as the MOCNESS was lowered were used to locate the pycnocline (defined as a sharp gradient in temperature and/or salinity separating 2 depths of different densities) and thus to select the depths of 3 discrete samples taken during the uphaul. Samples were taken within 5 m of the bottom to 5 m below the pycnocline (the 'deep' sample), through the pycnocline ('midwater'), and from 5 m above the pycnocline to the surface ('surface'). If no pycnocline existed, the water column was equally divided between the 3 samples. On average, the surface net sampled down to 19 m, the midwater net sampled between 19 and 42 m, and the deep sample was from 42 to within 5 m of the bottom. Zooplankton samples were preserved in 95% ethanol immediately after retrieval and the ethanol was changed after 24 h.

A Folsom plankton splitter was used to divide an aliquot of approximately 200 adult copepods from the original sample (mean aliquot size = 212 copepods, SD = 97.0), requiring splits of 1/8 to 1/1024. All adult copepods in this aliquot were identified to species and counted. Species count data were transformed into densities (number per m³) using the dilution factor of the subsample and the volume of water sampled by that net. Copepod biomass was estimated using the formula determined by Davis & Wiebe (1985):

$$\text{Wet weight (mg)} = 0.086 (\text{Length}^{2.809})$$

Lengths used in the formula were average prosome lengths (mm) taken from previously published work (Wilson 1932, Johnson 1934, Lawson & Grice 1970, Murphy & Cohen 1978, Frost 1989, Gerber 1999).

Pseudocalanus spp. were identified to species utilizing a multiplexed, competitive species-specific polymerase chain reaction (SS-PCR, Bucklin et al. 2001). Female *Pseudocalanus* spp. were sorted from the subsample and 24 individuals were randomly chosen for identification by SS-PCR. At least 20 successful PCR identifications were done for samples in which *Pseudocalanus* spp. comprised at least 5% of adult copepods. Densities for each species were determined by the proportion of SS-PCR identified *P. moultoni* and *P. newmani* in each aliquot multiplied by the total number of *Pseudocalanus* spp. counted in the original subsample. Differences in vertical distribution between the 2 species of *Pseudocalanus* were tested using split-plot analysis of variance (ANOVA). The response variable used in the ANOVA was the abundance of a species in the deep strata subtracted from the abundance of that species in the surface strata, calculated for each individual MOCNESS tow. Two ANOVA were performed:

one for periods of water column stratification (April 2002–October 2002), and one for periods of mixing (November 2002–March 2003).

Patterns of species diversity were assessed by evaluating 2 characteristics of each sample: species richness (i.e. number of species found in a sample) and evenness (see Pielou 1975). Pielou's evenness index (J') ranges from near 0 (indicating the community is heavily dominated by 1 species) to 1 (indicating that all species have identical abundances).

Copepod densities for the 15 most numerous species were visualized in section plots generated using Surfer version 7 (Golden Software), with interpolation by linear kriging. An anisotropy ratio of 0.16, which compensates for the discrepancy in the scales of the axes, was selected after analyzing copepod densities to determine correlation length scales in both the horizontal (i.e. station to station) and vertical (i.e. average depth sampled by each net) dimensions. On average, a horizontal change of 8 km was equivalent to a vertical change of 50 m. Multivariate data analysis and diversity analysis was done using PRIMER (Plymouth Routines In Multivariate Ecological Research) version 5.2.9 (PRIMER-E). For multivariate analyses, the absolute densities of each species were natural log [$\ln(x+1)$] transformed, to reduce the potential effect of sampling error. Bray-Curtis similarities were used to generate a similarity matrix of all pair wise comparisons of samples, based on the transformed densities.

Non-metric multi-dimensional scaling (MDS) was used to analyze temporal and spatial changes in the copepod community. MDS plots are generated from a ranked similarity matrix, such that the distance from one point to another is representative of the similarity between those points (Clarke 1993). The closer 2 points are in the resulting plot, the more similar the copepod assemblages between those samples. The degree to which the distances between all points in the plot accurately represent the similarity between them is measured by the stress value. A stress value of less than 0.1 indicates the plot accurately represents similarities, while a stress value of greater than 0.3 indicates the points are close to being randomly placed (Clarke 1993).

The significance of both temporal and spatial variation in community composition was tested using a 2-way crossed Analysis of Similarities for unreplicated data (ANOSIM2) routine in PRIMER (Clarke & Warwick 1994). This analysis generates an average Spearman correlation coefficient, ρ , for all pairwise comparisons between ranked similarity matrices of among-treatment groups in each block. For example, when testing the significance of depth and sample date at Stn A, ranked similarity matrices of all depths at each sample date are compared (using only samples

taken at Stn A). The resulting p value is close to zero when there is no correlation in the order of ranked similarities; a value of 1 indicates perfect correlation of the ranked similarities in all matrices. Significance levels are determined by comparison with values produced by random permutations of the data.

RESULTS

The water column was stratified from April to October 2002 and was completely mixed from November 2002 to March 2003. Temperature ranged from a minimum of 2.5°C on 27 February 2003 to a surface

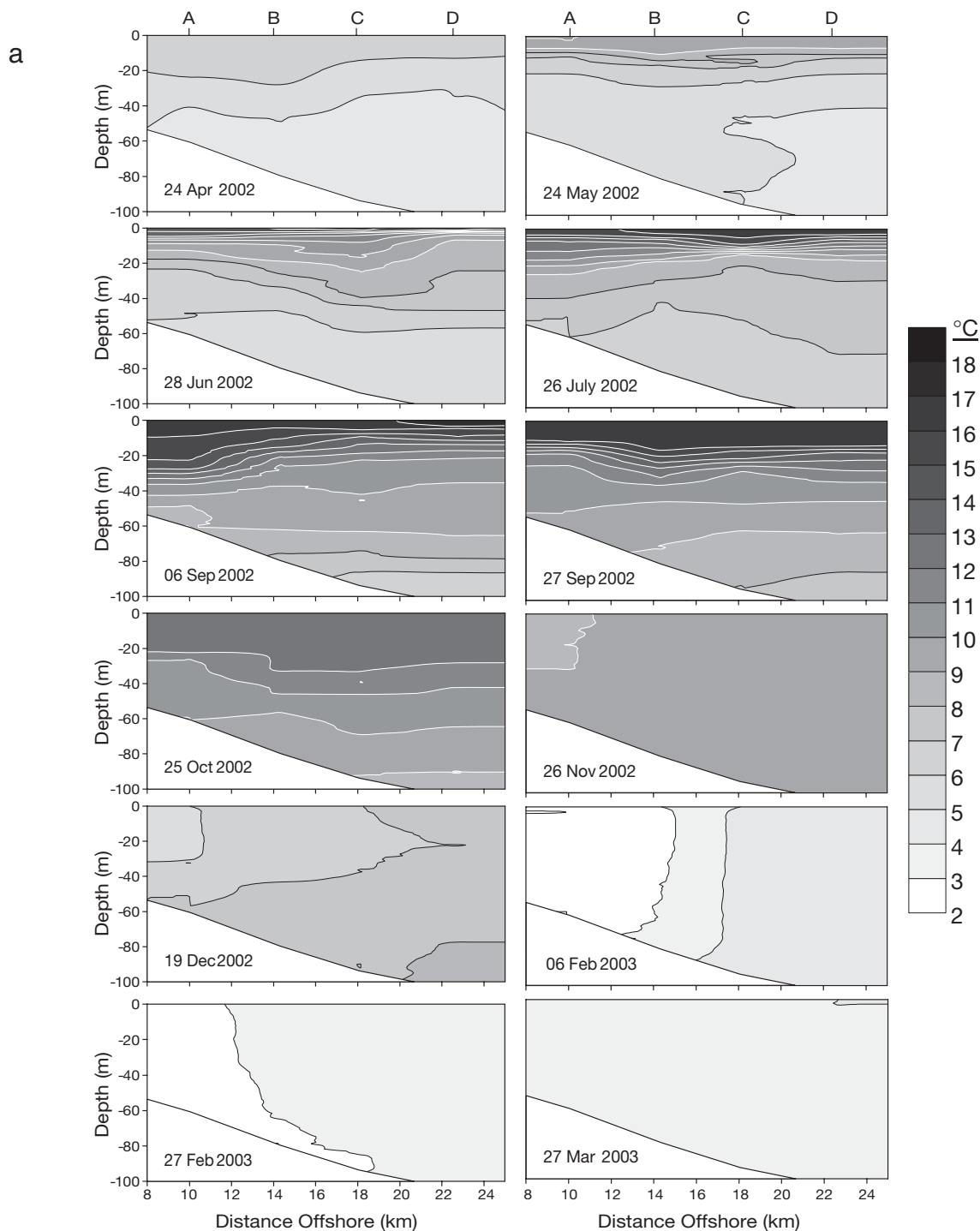


Fig. 2. Above and facing page. Section plots of (a) temperature, and (b) salinity, as sampled by MOCNESS tows at each station

maximum of 18°C on 6 September 2002 (Fig. 2a). Salinity ranged from a surface low of 30.4 ppt on 24 May 2002 to a maximum of 33.2 ppt on 6 February 2003 (Fig. 2b). Data for water currents at 6 different depths were obtained from the Gulf of Maine Ocean Observing System (GOMOOS; www.gomoos.org)

Buoy B, located approximately 16 km NNE of the transect. Over the period of this study flow was generally SSE, paralleling the coastline (Fig. 3). Surface (2 m) currents had velocities up to 5 times greater than deep (54 m) currents; the direction of flow was similar at all depths.

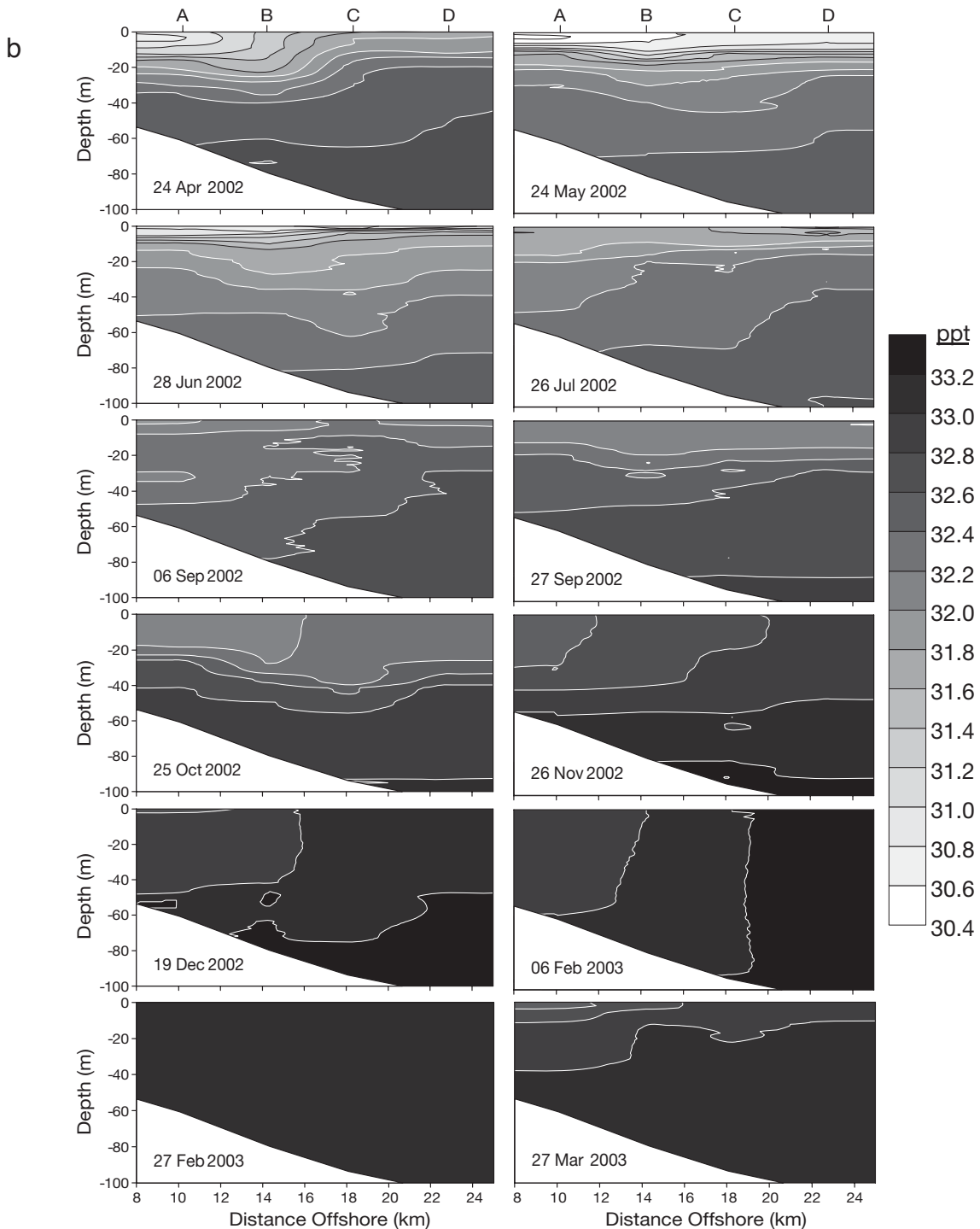


Fig. 2. (continued)

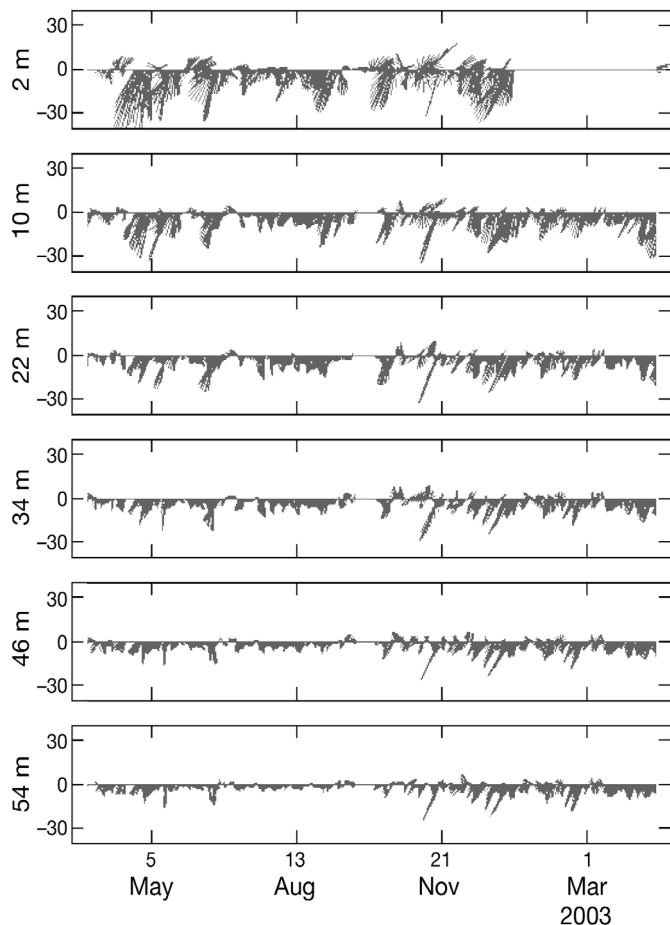


Fig. 3. Residual ocean currents for 6 depths as recorded by GOMOOs Buoy B, located roughly 16 km NNE of transect (43.181°N, 70.428°W). Data for this plot were filtered by GOMOOs to remove tidal currents. Direction of line indicates compass direction of current; for example, a line pointing straight up indicates a flow due north, while a line pointing to the right would indicate a flow to the east. y-axis scale is in cm s^{-1} . (Courtesy of www.gomooos.org.)

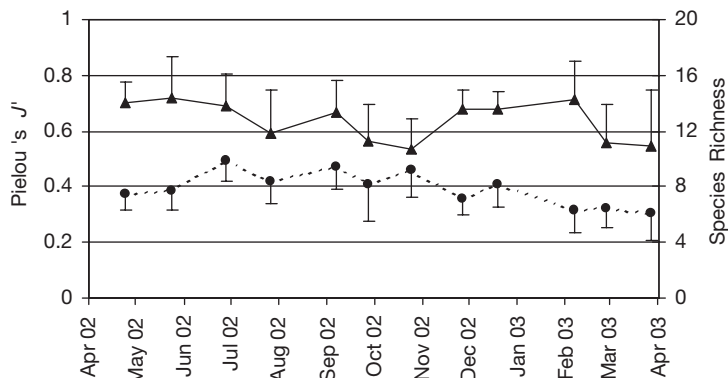


Fig. 4. Pielou's J' (evenness, indicated by solid line) and species richness (number of species, indicated by dashed line) averaged for each sample date. Error bars are 1 standard deviation; they are shown only above or below the line for clarity

Adults of 21 copepod species were recorded in the plankton samples taken from the WMCR. The average species richness found in an aliquot was 7.87 (SD = 2.00), and the average evenness (Pielou's J') was 0.637 (SD = 0.142). Species richness was highest in summer and fall samples; evenness did not fluctuate significantly by season (Fig. 4). *Oithona similis*, *Temora longicornis*, and *Centropages typicus* comprised 72% of all copepods identified; *T. longicornis*, *Calanus finmarchicus*, and *C. typicus* made up 78% of total biomass, considering adults only (Table 1). Total

Table 1. Contribution of each species to overall density and biomass

% total	Species
Density	
30.47	<i>Oithona similis</i>
26.06	<i>Temora longicornis</i>
15.57	<i>Centropages typicus</i>
5.97	<i>Acartia longiremis</i>
5.93	<i>Pseudocalanus newmani</i>
3.81	<i>Pseudocalanus moultoni</i>
3.52	<i>Calanus finmarchicus</i>
2.16	<i>Acartia hudsonica</i>
1.85	<i>Paracalanus parvus</i>
1.29	<i>Microcalanus pusillus</i>
1.21	<i>Centropages hamatus</i>
0.74	<i>Oithona atlantica</i>
0.64	<i>Eurytemora herdmani</i>
0.57	<i>Metridia lucens</i>
0.53	<i>Clausocalanus pergens</i>
0.13	<i>Microsetella norvegica</i>
0.04	<i>Tortanus discaudatus</i>
0.02	<i>Parvocalanus crassirostris</i>
0.02	<i>Acartia tonsa</i>
0.002	<i>Paraeuchaeta norvegica</i>
0.001	<i>Euchaeta marina</i>
Biomass	
31.85	<i>Temora longicornis</i>
24.91	<i>Calanus finmarchicus</i>
21.45	<i>Centropages typicus</i>
4.34	<i>Acartia longiremis</i>
3.90	<i>Oithona similis</i>
3.79	<i>Pseudocalanus moultoni</i>
2.97	<i>Pseudocalanus newmani</i>
1.93	<i>Metridia lucens</i>
1.52	<i>Acartia hudsonica</i>
1.37	<i>Centropages hamatus</i>
0.56	<i>Paracalanus parvus</i>
0.43	<i>Eurytemora herdmani</i>
0.42	<i>Oithona atlantica</i>
0.19	<i>Tortanus discaudatus</i>
0.18	<i>Clausocalanus pergens</i>
0.17	<i>Microcalanus pusillus</i>
0.15	<i>Paraeuchaeta norvegica</i>
0.02	<i>Microsetella norvegica</i>
0.02	<i>Acartia tonsa</i>
0.006	<i>Euchaeta marina</i>
0.004	<i>Parvocalanus crassirostris</i>

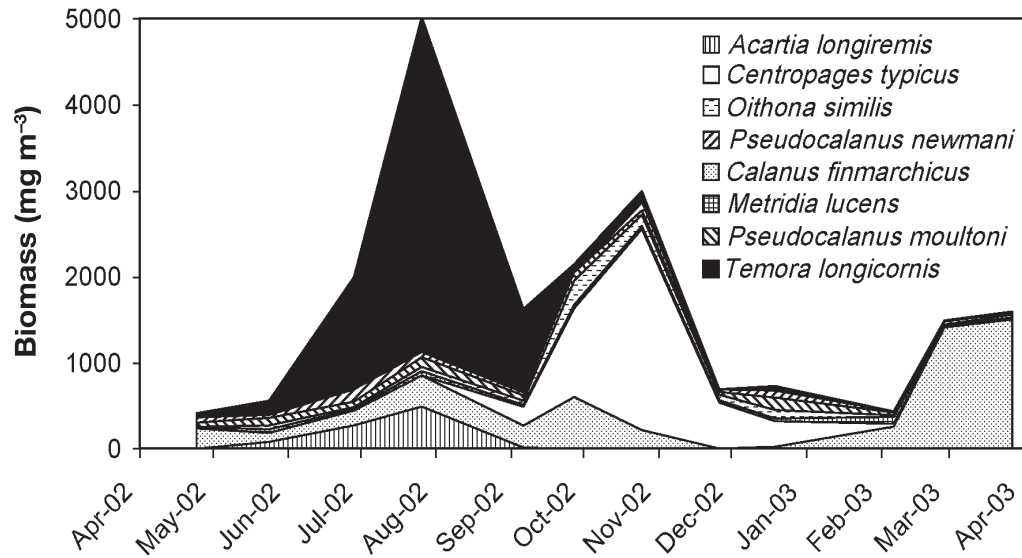


Fig. 5. Total biomass of the 8 most abundant species of planktonic copepods, averaged across station and depth

adult copepod biomass in this study peaked in July (Fig. 5). This sample date also had the highest total density, largely due to the abundance of *Temora longicornis*.

Copepod species in the study were categorized based on their temporal and spatial abundance patterns: adult *Oithona similis*, *Metridia lucens*, and *Microcalanus pusillus* were recorded year-round and showed significant vertical abundance gradients. *O. similis* was generally found in higher numbers in the surface net (Fig. 6a), while *M. lucens* and *M. pusillus* were relatively more abundant in deep samples and almost absent from surface samples (Fig. 6b and c, respectively). *Calanus finmarchicus*, *Oithona atlantica*, *Pseudocalanus moultoni*, and *P. newmani* were present throughout the year but showed no consistent pattern of vertical distribution. *C. finmarchicus* was more prevalent in deep samples from late spring through fall, but was much more abundant in early spring in surface water (Fig. 7a). *O. atlantica* was sporadically present throughout much of the sampling period and showed no clear pattern of vertical distribution (Fig. 7b). The 2 species of *Pseudocalanus* showed different vertical distributions during periods of stratification (ANOVA, $p < 0.05$), but were not significantly different after the water column was mixed. *P. moultoni* was more abundant in deep samples when the water column was stratified and *P. newmani* more abundant in surface samples throughout the year (Fig. 7c and d, respectively).

The remaining species exhibited strong seasonal changes in abundance: *Acartia hudsonica*, *A. longiremis*, *Centropages hamatus*, *Eurytemora herdmani*,

and *Temora longicornis* were most abundant in June and July, and formed a distinct summer community. *A. hudsonica* and *A. longiremis* had similar seasonal patterns of vertical distribution: both were most abundant in surface samples in spring and were present throughout the water column at their summer peak (Fig. 8a and b). When present, *C. hamatus* and *E. herdmani* were more abundant in surface samples (Fig. 8c and d). *T. longicornis* reached greater density in July than any other species over the course of the study, with highest densities closer to shore (Fig. 9a). *Centropages typicus*, *Clausocalanus pergens*, and *Paracalanus parvus* had highest abundances in October and November and differentiated the fall community (Fig. 9b–d). *C. typicus* and *P. parvus* were more abundant in surface samples, while *C. pergens* was uniformly vertically distributed.

The multi-dimensional scaling plot of all samples described a cyclical seasonal pattern of community composition; with few exceptions, there was a clockwise progression from one month to the next (Fig. 10a,b). Individual MDS plots for each month showed that samples generally clustered by depth, indicating the community had less variability among stations than among depth strata (Fig. 11).

The patterns visible in the MDS plots were statistically supported by the ANOSIM2 test (Table 2). Sample date had a significant effect on copepod composition at each individual station and depth (i.e. the ranked similarities of samples from all collection dates tended to follow the same month-to-month pattern at each station, and at each depth). The effect of depth was significant at Stns B, C, and D, which indicated the

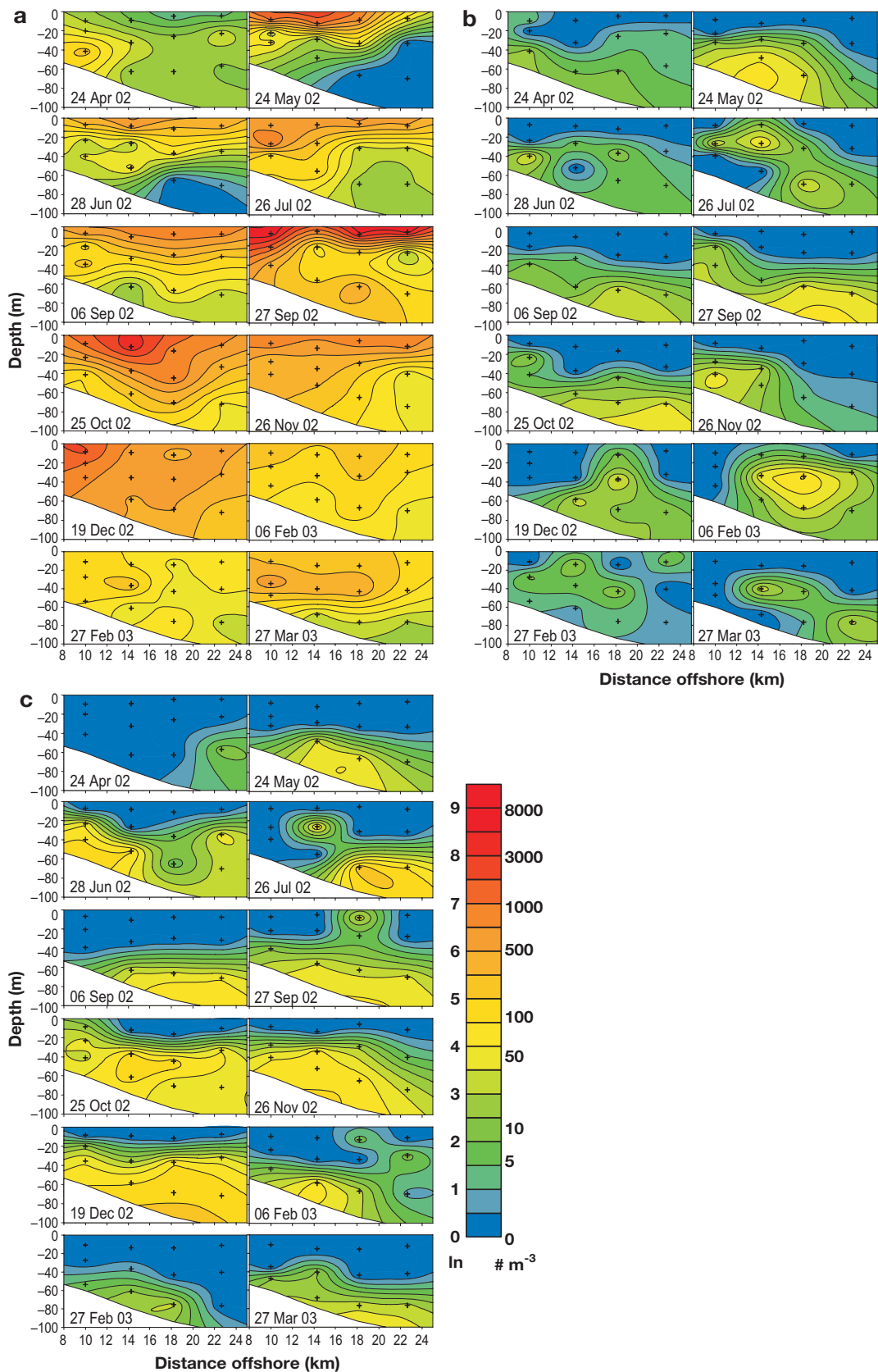


Fig. 6. Monthly section plots of individual species' densities. +: average depth sampled by each MOCNESS net. Copepod densities are shown at the same scale in each figure. (a) *Oithona similis*; (b) *Metridia lucens*; (c) *Microcalanus pusillus*

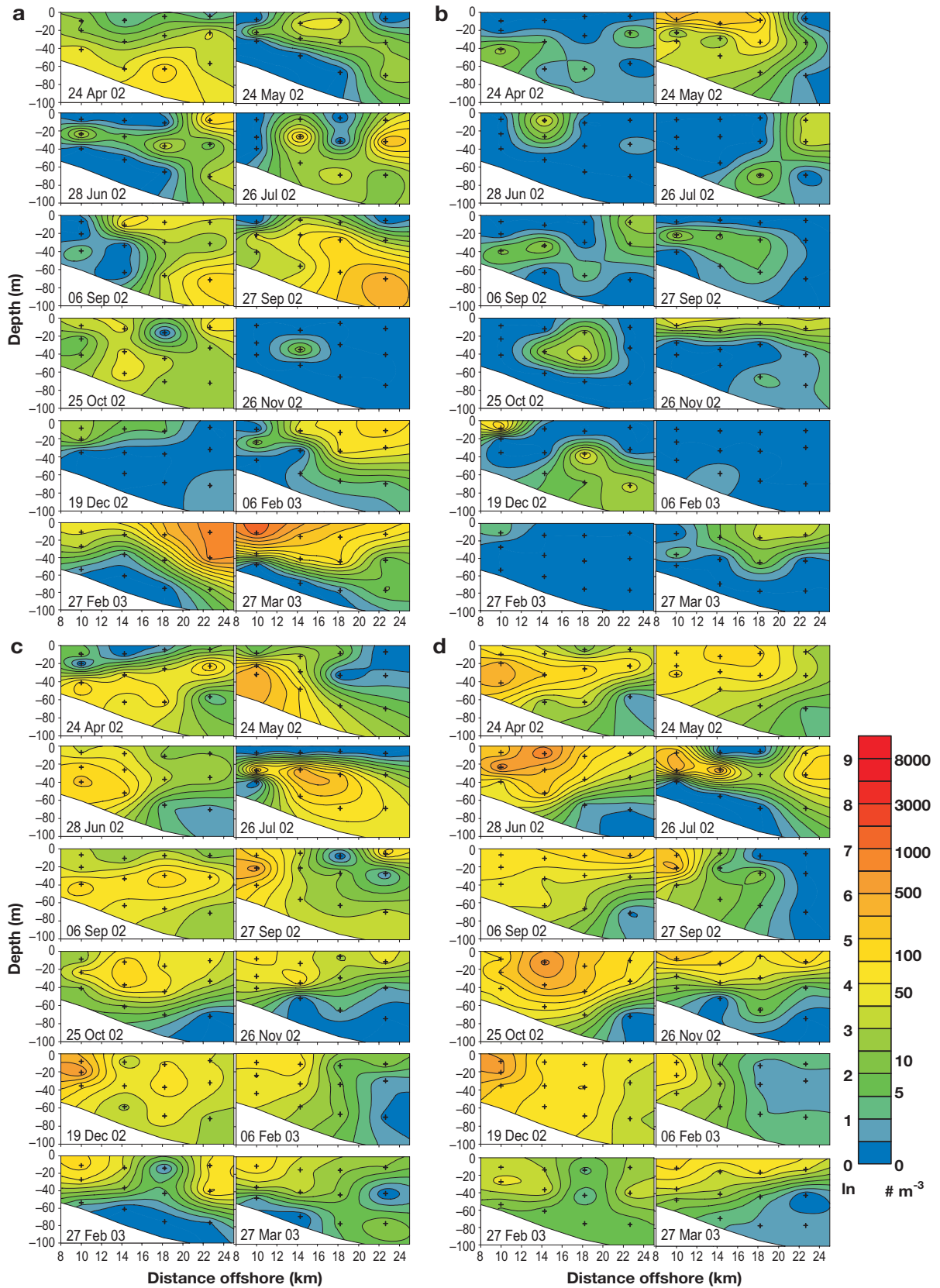


Fig. 7. Section plots as in Fig. 6. (a) *Calanus finmarchicus*; (b) *Oithona atlantica*; (c) *Pseudocalanus moultoni*; (d) *P. newmani*

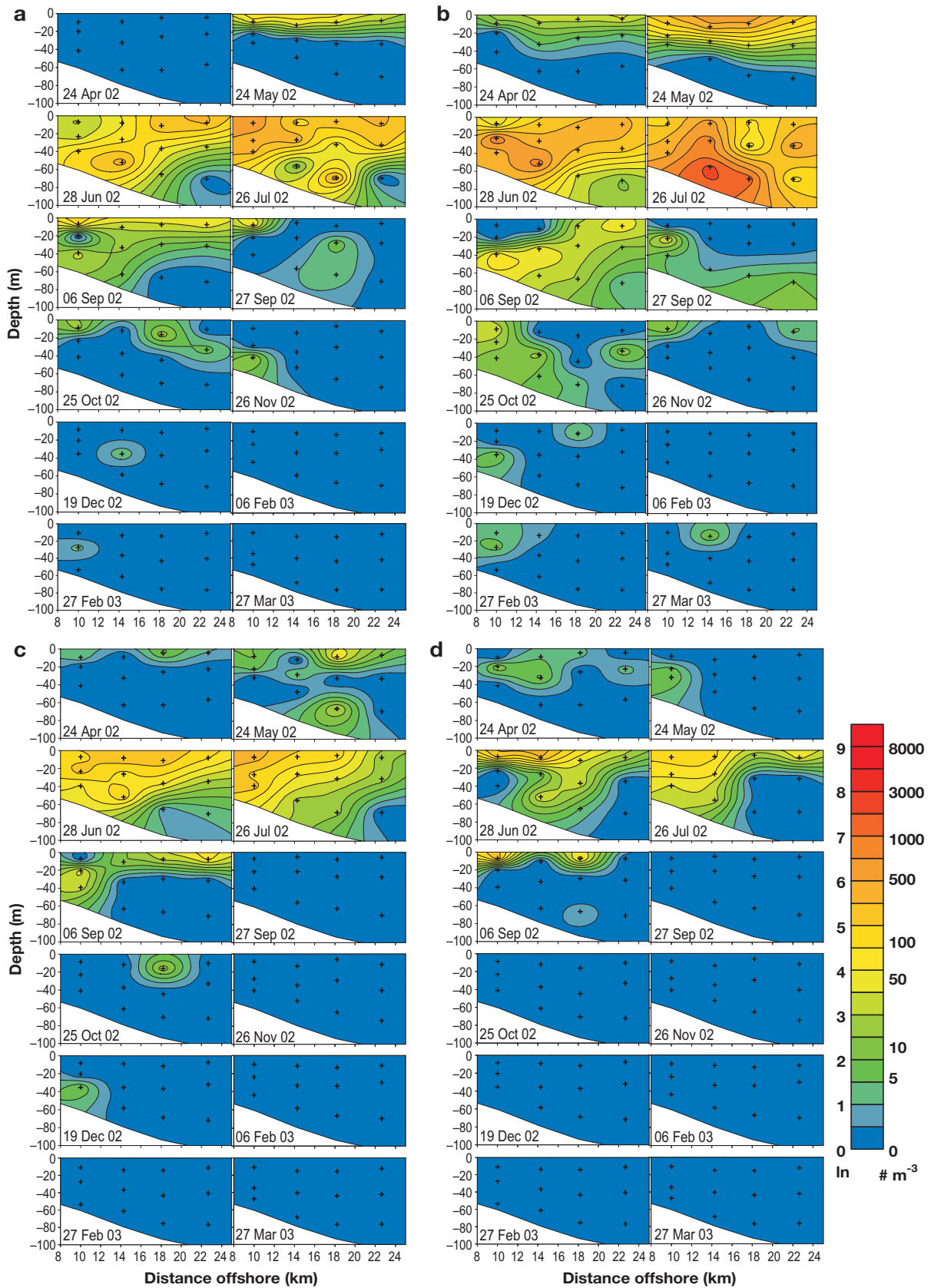


Fig. 8. Section plots as in Fig. 6. (a) *Acartia hudsonica*; (b) *A. longiremis*; (c) *Centropages hamatus*; (d) *Eurytemora herdmani*

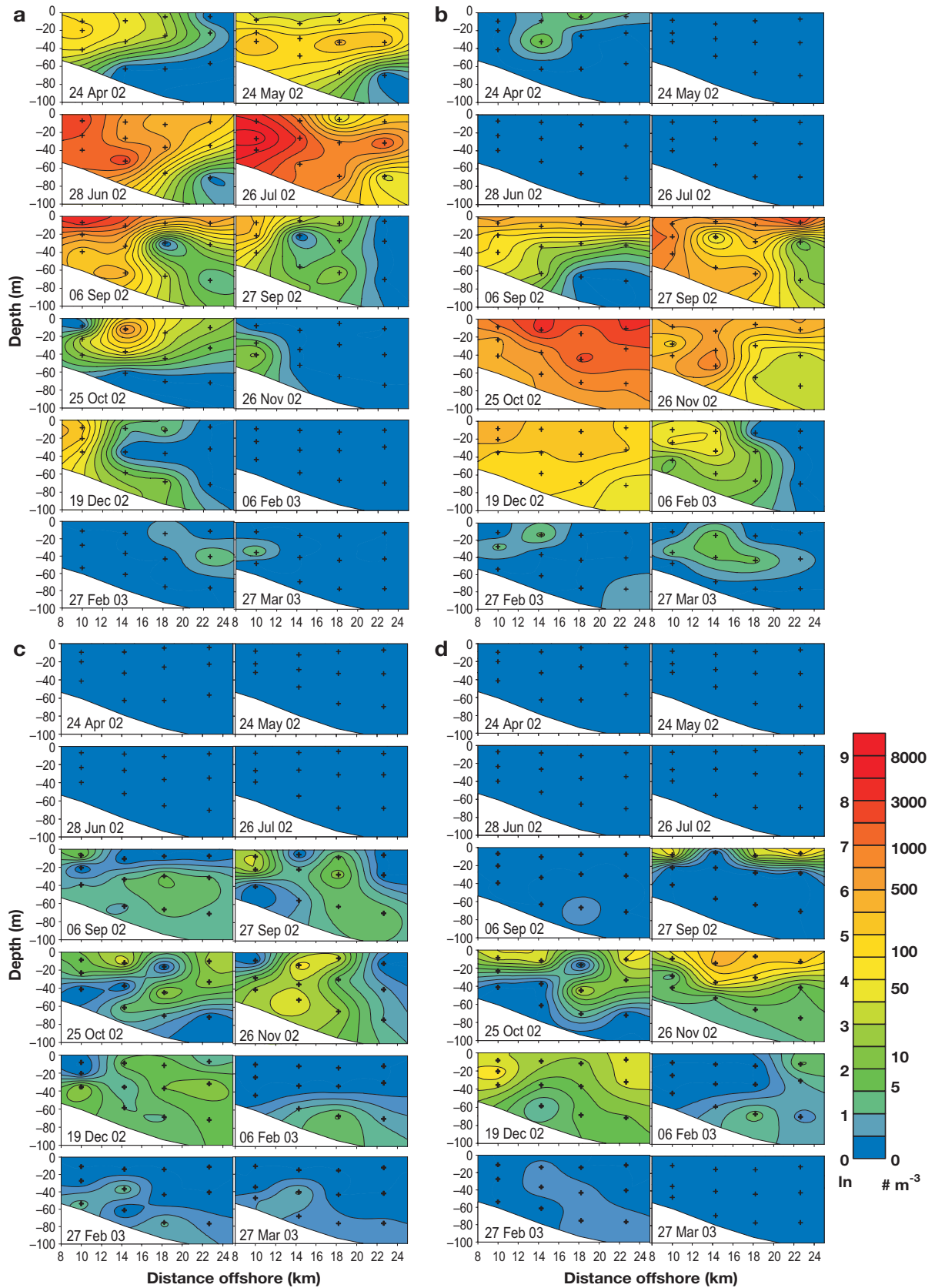


Fig. 9. Section plots as in Fig. 6. (a) *Temora longicornis*; (b) *Centropages typicus*; (c) *Clausocalanus pergens*; (d) *Paracalanus parvus*

community had consistent vertical structure at those stations. There was a significant effect of station only among the deep samples. In the surface and midwater samples (which were approximately the same depth range at each station), there was no consistent change in species composition among stations.

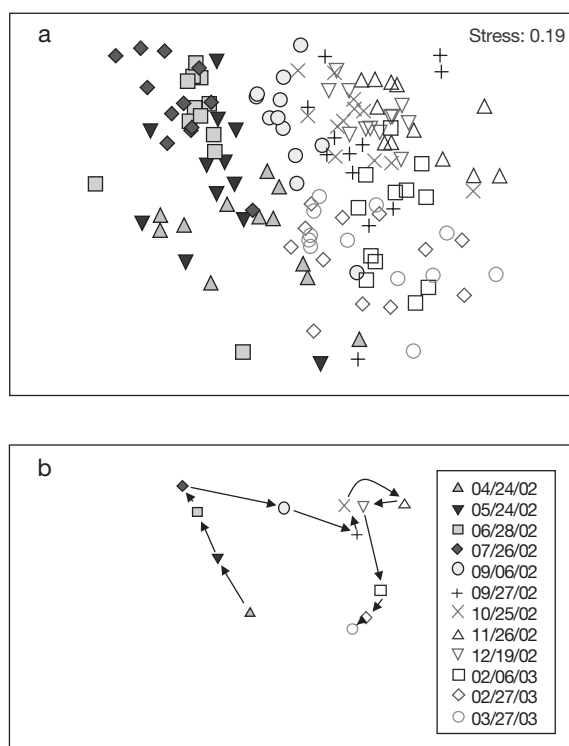


Fig. 10. MDS plots illustrating temporal variation in community structure. Greater proximity of points in the plot corresponds to greater similarity. (a) All samples. (b) Euclidian average for each month, showing generally cyclical pattern consistent with a seasonal cycle. Dates given as mo/d/yr

DISCUSSION

Temporal patterns of species' abundance

The greatest variation in the composition of the WMCR copepod community was associated with temporal change. On average and considering only the adults, the number of species recorded in the WMCR was higher from July to November than other times of the year. This was largely due to the presence of seasonally abundant species that were absent during winter months. Seven of the species sampled in this study had seasonal abundance peaks, with periods of scarcity or absence; 5 species were abundant year-round, with minimal seasonal fluctuation. A clear sea-

sonal cycle of species' abundances is revealed by the MDS plot, in which the points are clustered by sample date rather than by depth or station (Fig. 10). If the pattern had been driven by spatial variability, the MDS plot would have shown clustering of the samples collected at each station. Importantly, the 4 stations were sufficiently closely spaced to reveal the temporal, rather than spatial, variability of the WMCR.

What factors enable one species to exist as adults year-round, while others do not? Seasonal specialization may be a result of a physiological limitation, such that individual mortality is dramatically higher outside a certain time period. Biological limitation may also drive seasonal peaks in abundance, through predatory control of population growth in the short term, and natural selection to avoid seasonally abundant predators (such as larval fish) in the long term. Physical transport controlled by the direction and speed of the Western Maine Coastal Current likely has a large influence over seasonal patterns as seen in the WMCR. Weak summer currents may allow copepod populations to bloom locally before being advected south by stronger fall currents (Fig. 3). The transport of organisms through the study site prevents us from concluding that the observed seasonal patterns are characteristic of patterns throughout a species' range. Additionally, though interannual variation in species' abundances in the WMCR is likely to be high (Sherman et al. 1998, Licandro et al. 2001, Plourde et al. 2002), the order and timing of peak abundances observed in this study may accurately represent the typical pattern of community dynamics for the region (Mazzocchi & Ribera d'Alcala 1995).

Horizontal spatial variability of species' abundances

There was no significant variation among stations in species' abundances for surface and mid-water samples (Table 2). The similarity of samples at these depth strata indicated that horizontal patchiness did not alias the observed temporal patterns significantly. It is possible that patches were either large enough, so the 4 stations consistently fell within the same patch, or small enough, so the tow length integrated across several patches (see Haury & Wiebe 1982). In either case, considerable variation in community structure may have been missed by the sampling used in this study. Future studies of the region will benefit by increasing both the vertical and horizontal resolution of sampling.

In contrast, there was significant variation among stations for the deep stratum (Table 2). The significant influence of station on the community sampled in the

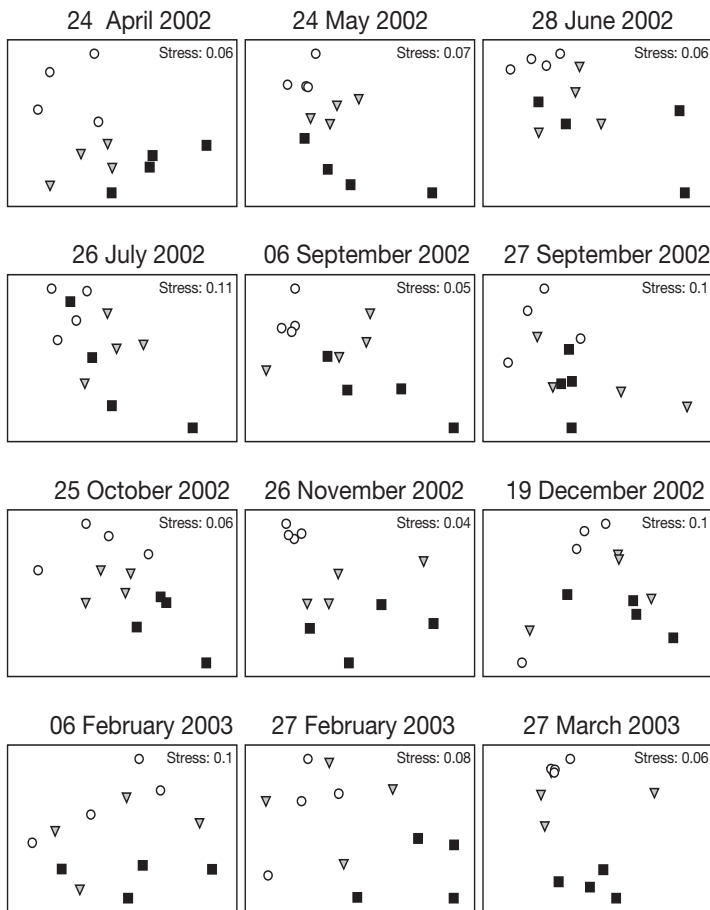


Fig. 11. MDS plots of individual months, showing surface (○), midwater (▽), and deep (■) samples for each station. Greater proximity of points in the plot corresponds to greater similarity. In many months, clustering of the same depth among the 4 stations is apparent

deep strata was likely driven by the increasing depth of the cross-shelf transect. Stn D was deeper than 100 m and the deep sample at this station may be more typical of the Gulf of Maine basins than the coastal current.

Vertical partitioning of species' abundances

Vertical position in the water column is of considerable ecological significance for zooplankton, since this may markedly impact the direction and speed of advective transport, due to differences in currents throughout the water column (Hannah et al. 1997). Species found primarily in surface waters may be transported through the WMCR up to 5 times more rapidly than species found at depth (Fig. 3).

Many copepod species in the WMCR exhibited strong vertical gradients in abundance, which ap-

peared to be influenced by the stratification of the water column. The significant vertical partitioning of the copepod community was indicated by the tendency of samples to cluster by depth rather than by station in the monthly MDS plots (Fig. 11). The significant differences among depths at Stns B, C, and D were mostly due to a consistent set of species, including *Oithona similis*, *Metridia lucens*, *Microcalanus pusillus*, *Eurytemora herdmanni*, and both species of *Centropages*, which showed strong affinities for certain depths. Considered together, these findings clearly revealed the significance of depth—rather than horizontal placement—in determining copepod species abundances.

The observed spatial patterns may result from active swimming behaviors of individual copepods responding to physical cues, and/or from passive transport in a distinct water mass. For example, *Acartia* spp. may have been transported across the transect in a spring low-salinity surface plume; seasonal vertical migration of *Calanus finmarchicus* is likely to have caused the observed switch between the deep distribution through much of the year and surface distribution in spring. Several species showed different vertical distributions during stratified and mixed periods (e.g. *Oithona similis*, Fig. 6a; *Centropages typicus*, Fig. 9b), with strong vertical gradients in abundance in stratified waters in summer, and more uniform distributions with mixing in the fall. Whether the seasonal shift was due to the inability of these species to maintain their vertical positions in the water column or the lack of strong physical gradients to cue active swimming behaviors is unknown. Strong diel vertical migration

Table 2. ANOSIM2 tests for significance of Sample date, Depth, and Station. Statistical significance is determined for Bonferroni-corrected p values (Station, n = 8; Depth, n = 6). *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001. See text for explanation of ρ value

	Sample date	Depth	Station
Station			
A	ρ = 0.682****	ρ = 0.053	—
B	ρ = 0.609****	ρ = 0.417*	—
C	ρ = 0.526****	ρ = 0.485**	—
D	ρ = 0.369***	ρ = 0.462*	—
Depth			
Surface	ρ = 0.628****	—	ρ = 0.067
Midwater	ρ = 0.53****	—	ρ = 0.039
Deep	ρ = 0.543****	—	ρ = 0.603****

behavior likely explained the concentration of *Metridia lucens* (Fig. 6b) in deeper water in a fully mixed water column, although the causes of the deep concentration of *Microcalanus pusillus* (Fig. 6c) are less clear.

Comparisons among congeneric species

Three pairs of congeners were sufficiently abundant to allow comparisons of their spatial and temporal patterns. *Acartia longiremis* and *A. hudsonica* showed considerable overlap, with both species appearing in the surface waters by late May, and extending throughout the water column in June and July, although *A. hudsonica* was distributed evenly, while *A. longiremis* reached highest abundances in the deep samples (Fig. 12a). In contrast, overlap between *Centropages typicus* and *C. hamatus* was minimal. Although both species were present in slightly greater densities in the surface samples, they

only co-occurred in 1 mo (Fig. 12b). *C. hamatus* and *C. typicus* are not temporally separated throughout much of their range (Kane 1997, 1999). *Pseudocalanus moultoni* and *P. newmani* were present throughout the year but, during stratification, *P. moultoni* was more abundant in deep samples, while *P. newmani* was much more concentrated at the surface (Fig. 12c). This pattern was most clearly seen by comparing only the surface and deep samples, since the midwater net necessarily samples from both above and below the pycnocline (Fig. 13). With the start of vertical mixing, this pattern of vertical segregation was erased.

Sources of error in the analysis of temporal and spatial patterns

This description of the WMCR copepod community in this study is incomplete due to the nature of the sampling program. Vertical abundance patterns of species

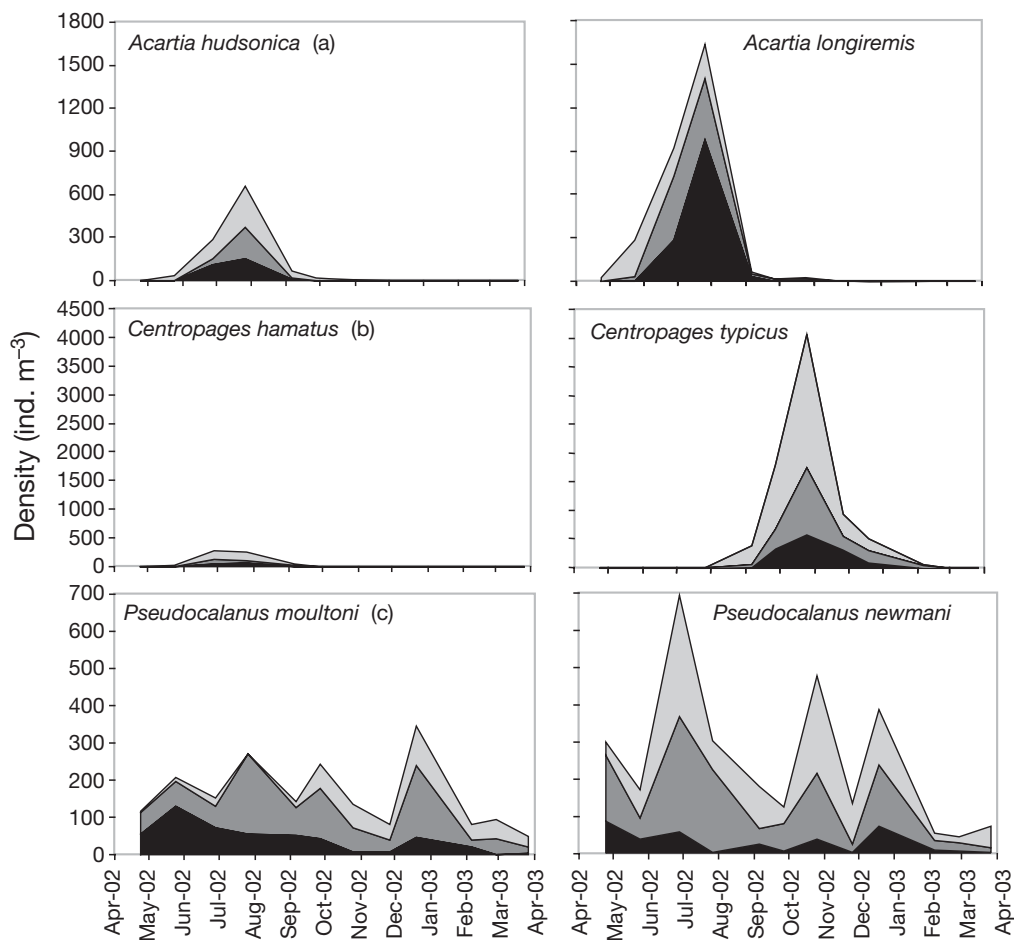


Fig. 12. Abundance patterns of congeneric species, averaged across stations. Shading indicates depth: surface (light gray), midwater (dark gray), and deep (black). Each pair of congeners is plotted on the same scale; scales differ among pairs. (a) *Acartia hudsonica* and *A. longiremis*, (b) *Centropages hamatus* and *C. typicus*, (c) *Pseudocalanus moultoni* and *P. newmani*

are subject to short-term variation, with the occurrence of low-salinity plumes, changing thermocline depths, wind-induced turbulence (Incze et al. 2001), and presence of predators (Ohman 1990, Bollens & Frost 1990, Frost & Bollens 1992). Also, sampling was undertaken only during daylight hours, so the consequences of diel vertical migration were not detected. This is a topic that merits future study, since many of the species observed in this study exhibit diel vertical migration, including *Acartia* spp., *Metridia lucens*, *Temora longicornis*, and others (see e.g. Williams et al. 1994, Hays 1995). Spatial scales of sampling may have aliased the results (as discussed above) and the contour analysis may inaccurately portray some spatial patterns. These section plots (Figs. 6 to 9) are provided to allow visualization of the patterns; data points are indicated to allow accurate interpretation.

Comparisons among coastal regions

Many copepod species recorded in this study have also been documented on Georges Bank and in Massachusetts Bay (Bigelow 1924, Kane 1993, Turner 1994). However, there are notable differences in relative species' abundances, seasonal patterns, and peak timing from one region to another. In the WMCR, *Oithona similis*, *Temora longicornis*, and *Centropages typicus* predominated; the dominant species on Georges Bank were *C. hamatus*, *C. typicus*, and *Calanus finmarchicus* (Kane 1993); and in Massachusetts Bay were *O. similis*, *Paracalanus parvus*, and *Pseudocalanus newmani* (Turner 1994). Four WMCR species (*C. hamatus*, *C. typicus*, *P. parvus*, and *T. longicornis*) were highly seasonal, although they were abundant year-round in one or both of the other regions (Davis 1987, Turner 1994). Conversely, *Pseudocalanus* spp. had a strong summer peak on Georges Bank (Davis 1987), but neither *P. moultoni* nor *P. newmani* showed seasonal

peaks in abundance in the WMCR. Only 2 of the abundant species in Massachusetts Bay exhibited seasonal abundance trends (*Acartia hudsonica* and *A. tonsa*, Turner 1994).

The observed differences in temporal patterns of species abundance between the WMCR, Georges Bank, and Massachusetts Bay may be a result of varying physical characteristics. Georges Bank does not receive direct estuarine output and thus despite its shallow water, it differs from true coastal regions. Much of the Massachusetts Bay area sampled by Turner (1994) is shallower than water sampled in this research. Additionally, due to dissimilar circulation patterns (e.g. along-shore flow in the WMCR and the summer recirculation on Georges Bank) the retention time is likely quite different between these areas.

Another reason for differences among these communities may be variation in the type and abundance of predators. Predation has been argued to be the architect of zooplankton community structure (Hayward & McGowan 1979, McGowan & Walker 1979). The presence of an abundant predator on Georges Bank may suppress a copepod species that is dominant in regions where that predator is absent. Predation effects also include feeding on naupliar stages by other copepods, so the abundance of one species may directly affect the abundance of others. As more studies shed light on the feeding preferences of each species, the importance of interactions among species in determining community composition will become clearer.

Differences in seasonal patterns of species' abundances suggest that the population dynamics and community interactions may differ among these adjacent regions. These comparisons must be interpreted cautiously, since the studies were conducted in different years, using different sampling gears. However, studies in other regions have shown that seasonal patterns of zooplankton species' abundance may be consistent from year to year (e.g. Mazzocchi & Ribera d'Alcala

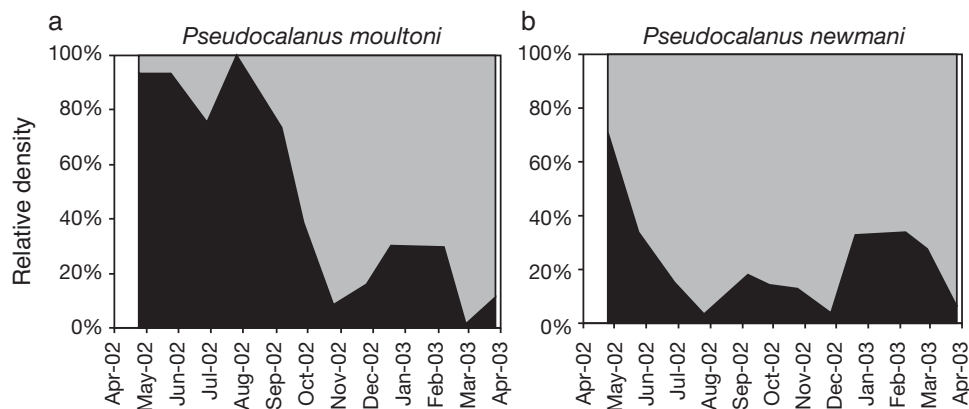


Fig. 13. Relative densities of (a) *Pseudocalanus moultoni* and (b) *P. newmani* as a function of depth. Shading indicates depths: surface (light gray), deep (black). Samples are averaged across stations

1995), suggesting that regional comparisons spanning different years may be of value.

This study of the WMCR indicates that adjacent coastal regions may exhibit notably different patterns and seasonal peaks in relative species' abundances. These may result from interactions with different prey, predator, and competitor species, and may in turn cause and maintain ecologically important dissimilarities between the zooplankton communities of each region. This study further demonstrates that accurate assessment of the population dynamics, ecological interactions, and community composition of zooplankton within a region requires sampling at appropriate time and space scales.

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