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Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine

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Abstract—Springtime aggregations of the planktivorous right whale (*Eubalaena glacialis*) occur in the northern Great South Channel region of the southwestern Gulf of Maine, where they feed upon dense concentrations of the copepod *Calanus finmarchicus*. This association was studied during the multidisciplinary South Channel Ocean Productivity Experiment (SCOPEX) in 1988 and 1989. The spatial and temporal variability of the abundance, geographic distribution, and population structure of these copepods were analyzed using data from 99 vertically-stratified or horizontally-sequenced MOCNESS plankton tows.

Higher water column abundances and higher relative proportions of older copepod lifestages occurred near feeding whales compared to sites without whales, but total water column copepod biomass and *Calanus* abundance did not always differ between these types of locations. This suggests that the whales seek out aggregations of older copepod lifestages rather than simply the most dense aggregations. Other factors (and perhaps an element of chance) may influence which specific patches, among all patches potentially suitable in terms of copepod abundance and age composition, the whales utilize at a particular time.

The times and locations of the highest *Calanus* water column abundances varied between years, as did the presence of feeding whales, probably because of year-to-year differences in the springtime temperature cycle and current strength. A temporal progression of lifestages occurred within the region in both years during the roughly 3-week duration of each survey, indicative of a growing rather than a diapausing population, at least up to the copepodite 4 (C4) stage. Due in part to a delay in the springtime warming in 1989 compared to 1988, the copepod development cycle, which is largely driven by *in situ* temperature, was delayed about 1–2 weeks in 1989. Peak abundances of younger *Calanus* were found in the northwestern part of the region each year, whereas peak abundances of older *Calanus* were found in the southwestern and northeastern part. This was probably due to the advection of maturing copepods by the regional circulation, especially the near-surface current associated with the movement of the low-salinity surface plume which forms each spring off Cape Cod. The copepod development cycle occurs within a moving frame of reference (i.e. the water itself); thus, peak abundances of the older copepods (those fed on by the whales) occurred later in the spring and further downstream in 1989 (when there were colder springtime temperatures and faster currents) than in 1988 (when the springtime temperatures were warmer and currents slower).

Maximum *Calanus* abundances and biomass and water-column abundances of older copepodite stages were significantly higher (about double) in 1989 than in 1988, both in the region as a whole and at sites where whales were feeding. Maximum concentrations from the MOCNESS tows

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were 13,300 m^{-3} in 1988 and 30,800 m^{-3} in 1989; however, a thin, visibly-red surface patch of *Calanus*, sampled in 1989 by a bucket, had a concentration of 331,000 m^{-3}. Copepods were also more aggregated in the vertical (i.e. more highly concentrated at the depth of maximum abundance) in 1989 than in 1988, and samples from whale-feeding areas were more homogeneous in composition (higher proportion of *Calanus* relative to all zooplankton) in 1989. At smaller spatial and temporal scales, abundances varied by a factor of 1–890*X* in samples from horizontal tows spanning about 0.5–1.5 km and by a factor of 1–50*X* over 24 h in the same geographic location in whale-feeding areas. Some of this variability was probably due to advection by the semidiurnal tidal currents. Near feeding whales, the copepod spatial distribution was patchy on small scales (with an estimated mean patch "size" of about 500 m), but the patchiness varied in texture interannually. Copepod abundances were much lower in early spring (March 1988) than in later spring (May 1988), with the March population structure dominated by adult females and the May population dominated by copepodite 4 and 5 stages (C4 and C5).

INTRODUCTION

EACH spring from late May to early June, most of the North Atlantic population of the right whale (*Eubalaena glacialis*) is found within a small region in the southwestern Gulf of Maine off Cape Cod just north of the Great South Channel (CETAP, 1982; KENNEY and WINN, 1986; WINN *et al.*, 1986; KENNEY *et al.*, 1995). These planktivorous whales feed primarily on copepods, especially *Calanus finmarchicus* (Gaskin, 1982). Past studies have suggested that the whales come to this region in the spring primarily to feed, and very high abundances of *C. finmarchicus* have sometimes been collected in this area, especially in proximity to feeding right whales (CETAP, 1982; SCOTT *et al.*, 1985; WISHNER *et al.*, 1988). The whales tend to concentrate in different parts of this region in different years (KENNEY *et al.*, 1995), and previous springtime collections of zooplankton have also suggested much spatial variability in the abundance and distribution of the copepods (BIGELOW, 1924; FISH, 1936; CLARKE and ZINN, 1937; DAVIS, 1987a; SHERMAN *et al.*, 1987; MEISE-MUNNS *et al.*, 1990). Understanding the structure and variability of the copepod aggregations is necessary for understanding both the behavior and energetics of this endangered whale species, and, more generally, the nature of interactions between zooplankton and their environment in a dynamic coastal ecosystem.

The multidisciplinary South Channel Ocean Productivity Experiment (SCOPEX) was undertaken in 1988–1991 (field years 1988–1989, pilot program 1986) to study the association of right whales with their copepod prey in the northern Great South Channel (GSC) region. Observations by the ten principal investigators and co-workers included studies of the distributions and biology of whales and plankton, and of the physical and environmental factors that affect these species. The present paper analyzes the spatial and temporal variability of the abundance, geographic distribution, and population structure of the copepod *C. finmarchicus* during SCOPEX. Analyses of vertical migration and vertical distribution patterns from these samples will be presented elsewhere (WISHNER *et al.*, 1990; in preparation). KANN and WISHNER (submitted a) describe the distribution of the other zooplankton taxa from these samples.

METHODS

Sampling scheme

Data were obtained from three SCOPEX cruises on the R.V. *Endeavor* to the southwestern Gulf of Maine (Great South Channel) region (Fig. 1), centered at 41°20′N,

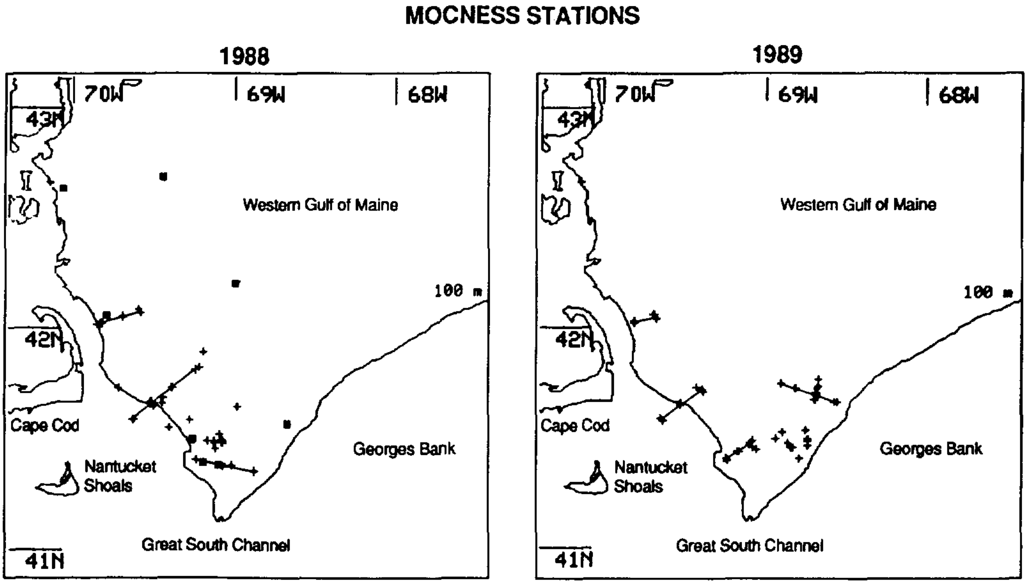


Fig. 1. MOCNESS station locations in 1988 (left) and 1989 (right) relative to geographic features and the 100-m isobath. The 1988 stations marked by squares are from the early spring (March) cruise. Lines join stations along transects.

Table 1. Summary of tow information. Tow locations are plotted in Fig. 1. "Multi" tows are ones that include both a horizontal portion and a vertical portion. Latitude and longitude, sampling times, the depths of each net and water volumes filtered for each of the nets in each of the 99 SCOPEX tows are available from the authors

Cruise	Year	Dates	Total tows	Total samples	Regional Vert. tows	Regional Horiz. tows	"Whale Area" Vert. tows	"Whale Area" Horiz. tows	Multi tows
EN-174	1988	13–17 Mar	9	74	9	0	0	0	0
EN-176	1988	26 Apr–16 May	44	346	27	0	11	1	5
EN-196	1989	18 May–12 Jun	46	367	27	1	12	6	0

69°00′W off Cape Cod and the New England coast (Table 1). The zooplankton abundances reported here were obtained primarily from MOCNESS plankton net tows (1 m^2 mouth opening, 335 μm mesh nets, nine samples per tow) (Wiebe *et al.*, 1976) using the University of Rhode Island MOCNESS system. Most opening–closing nets filtered from 150 to 300 m^3 (range 77–495 m^3) of water. Tow speeds were about 1.5 kt (83 cm s^{-1}) to maintain the optimal 45° net angle. The MOCNESS was equipped with a flowmeter and sensors for pressure (SeaBird), temperature (SeaBird), salinity (SeaBird), fluorescence (SeaTech *in situ* fluorometer), and light transmission (SeaTech 25 cm beam transmissometer). Physical measurements were recorded every 4 s.

Most tows were vertically stratified (Table 1) with depth intervals as follows: surface to near-bottom (usually about 10 m above the bottom), near-bottom up to 90 m, 90–50 m, 50–25 m, and the remaining five nets in 5-m intervals up to the surface. Water column depths at the tow locations (from the shipboard 12 kHz echosounder) varied from 45 to 235 m; the maximum depths of the vertically-stratified tows varied from 32 to 214 m. Where the water column was shallower than the full sampling scheme, additional samples were taken from some of the upper depth intervals or fewer nets were deployed. These depth intervals were originally selected during a pilot program in 1986 because they corresponded to distinct features in the hydrography and acoustic backscatter from the water column (WISHNER *et al.*, 1988; MACAULAY *et al.*, 1995). One deep, vertically-stratified tow was also taken each year, with narrow (5–10 m) depth intervals near the bottom.

Thirteen horizontally-sequenced tows were also taken during the 1988–1989 sampling years (Table 1). In these tows, sequential replicate samples were taken from the same depth interval to look at smaller scale variability within a single depth zone. Depths for these tows were chosen primarily to correspond to either the daytime or the nighttime depths of maximum copepod abundance and hypothesized whale feeding. When possible, the same depths were targeted day and night at the same location to ascertain differences associated with any vertical migration of the copepods. In addition to the depths of maximum copepod abundance, some depths where copepods were scarce were also sampled with horizontal tows for comparison.

In 1989, a surface patch was observed where the water was visibly red with copepods; this patch was sampled by surface bucket.

The geographic sampling scheme consisted of both regional and whale-targeted sampling (Fig. 1). Regional sampling during EN-176 and EN-196 was done primarily along transects and also in conjunction with 24-h studies of copepod feeding patterns conducted at fixed locations ("diel feeding stations", DURBIN *et al.*, 1995b). Transects consisted of three stations spaced about 12 km apart and oriented perpendicular to the expected south and southeastward flow along the western flank of the northern GSC. A vertically stratified tow was taken at each station during the day, and then repeated at night, so that the entire transect was sampled day and night within 24 h. On some transects, additional stations sampled immediately after the regular transect (for example, the diel feeding stations) were added at the ends. In 1988, three transects were done on the western side of the basin (north, middle and south); in 1989 these three transects were repeated and an additional transect in the northeast was also done. The western middle and southern transects included locations (usually the center station) of many previous right whale aggregations (CETAP, 1982; KENNEY *et al.*, 1995), the northwest transect was done to obtain plankton from the "upstream" inflowing water, and the northeast transect was added in 1989 because the whales were concentrated in that region during that year (KENNEY *et al.*, 1995). Transects were designed to cross or come close to the 100-m isobath in the northern GSC (Fig. 1), because right whales have most often been found near this feature (BROWN and WINN, 1989; KENNEY *et al.*, 1995).

A second type of regional sampling occurred at the 24-h diel feeding stations. Vertically-stratified tows were taken day and night at each of five stations each year (except for two missing tows). The five stations spanned a range of habitats including past and present whale locations, a northwestern site and a deeper offshore site. Several tows were also done in the shallow water northeast of Nantucket Shoals (two tows, 1988), at the deployment and position 11 days later of a satellite-tracked drifter (two tows, 1988), and at locations of prior sampling and prior whale aggregations (previously sampled during the same cruise or several years earlier during the 1986 pilot cruise) (three tows, 1988; three tows, 1989).

During the short EN-174 cruise, in early spring 1988 when the water column was still isothermal and before most of the right whales had arrived, nine vertically stratified tows scattered throughout the region were taken in conjunction with a CTD and acoustic backscatter survey made by other investigators (Fig. 1).

Targeted MOCNESS sampling was done near right whales. Whales were located most easily by aerial surveys (Kenney *et al.*, 1995), with positions of the whales radioed to the ship; when flying conditions were poor, ship surveys were used. Vertically-stratified and horizontal MOCNESS tows were done in these "whale areas" both day and night (Table 1). Observations of whale behavior and dive times in these areas are reported elsewhere (Winn *et al.*, 1995).

Sample processing

Plankton samples were preserved in 4% borate-buffered formalin at sea. For some extremely large samples (for example, within a copepod patch), samples were split at sea with a plankton splitter, and only a portion of the sample was preserved. Small measured portions of some samples were also taken for analyses by other investigators prior to preservation. Samples from the first net (open from the surface to near-bottom) were usually not preserved; thus most MOCNESS tows provided eight usable samples.

Biomasses were determined as wet weight per unit volume filtered, taking account of all splits and sample portions. Both the entire sample and the copepod-sized fraction were weighed in the lab after the sample was drained in a sieve. The copepod-sized fraction was separated from the large-sized fraction by picking out by hand all obvious larger non-copepods (fish, euphausiids, amphipods, etc.). Nine nets from two early spring tows (MOC8 and 13) during EN176 contained large amounts of a big diatom, similar in size to the copepods, which resulted in copious green slime after preservation. Wet weight measurements of these samples would have been biased by the large phytoplankton and slime contribution and consequently were not determined; therefore water column biomasses could not be calculated for these tows. Zooplankton counts of these samples were feasible by microscopy, however, and abundances were obtained as described below. Nineteen other nets from five other tows contained minor amounts of the phytoplankton but were considered usable for both biomass and abundance measurements.

For small samples (<10 g copepods), the entire copepod-sized fraction of the sample was split in a Folsom plankton splitter until a suitable number of animals for counting was obtained (usually 200–700 per sample). For the large relatively homogeneous samples from the copepod patches, a measured portion (by wet weight, usually about 5 g) of the copepod-sized fraction was resuspended in seawater and then split in the splitter for counting. Only the split was counted for the small-sized fraction; the entire large-sized fraction (described above) was counted. Copepods were identified to species and life stage; other animals were identified to species when possible. Wild M5 and M3 stereo-microscopes were used for counting and identification.

Abundances were calculated as number m^{-3}, after all splits and portions were accounted for. Integrated water column abundances (number m^{-2}) from tows spanning the whole water column were calculated for each life stage and total *Calanus* by summing the abundances through each depth interval (number m^{-3} within a depth interval times the range in m of the depth interval, summed for all intervals through the water column sampled by a vertically stratified tow). The total depth included varied with the tow. Mean abundance (number m^{-3}), useful for comparison to prior data from bongo and other open oblique net tows, was calculated as the integrated water column abundance divided by the depth of the tow. The layer of maximum *Calanus* abundance (presumably the most likely feeding target of the whales) was defined as the one net within each tow that yielded the highest concentration of "total *Calanus*". "Total *Calanus*" was defined as the abundance of all the *Calanus* lifestages from the copepodite 3 stage and older (i.e. copepodite 3–5, males, females). The younger copepodite stages were counted but may not have been collected quantitatively by the 335 μm mesh nets. Statistics involving these younger stages should be considered exploratory; however, the presence of younger stages was useful as an indicator of population development. Two horizontally-sequenced tows (one from each year), which targeted depth zones of the water column known to have low *Calanus* abundances, were not included in statistical tests involving maximum abundances.

A concentration index was developed to provide an indicator of the degree to which the copepod population was concentrated in the layer of maximum abundance relative to its distribution throughout the water column. The concentration index was defined as the maximum abundance or biomass divided by the mean abundance or biomass for each vertically-stratified tow. This non-dimensional parameter is thus independent of the depth of the tow.

Data analyses

Statistical tests were done using the Statview II program (Abacus Concepts) on Macintosh IIcx and Powerbook 170 computers. A probability of 0.05 was considered the level of significance.

Differences between day and night samples were tested with the Wilcoxon test for paired samples. Paired samples were considered to be those from the same geographic location taken on a sequential day and night. Eighteen day–night pairs were identified from the 1988 sampling ($n = 17$ suitable for maximum net comparisons) and 19 from 1989. Each year was tested separately because the copepod diel migration behavior changed between years.

Interannual differences and differences between locations with and without whales were tested with Mann–Whitney U tests. Only data from the two late spring cruises (EN-176 and EN-196) were included in statistical tests, except when specifically comparing early and late spring in 1988 (EN-174 and EN-176). For interannual comparisons, whale and regional (non-whale) areas were treated separately to reduce bias from differences in sampling intensity. As described above, locations near feeding right whales were specifically targeted for sampling, and we expected that copepod abundances might be highest near feeding whales. For whale versus non-whale location comparisons, each year was treated separately because copepod abundances and vertical migration patterns differed between years. "Whale present" tows were considered to be those taken when right whales were seen at the time of sampling within 1 nautical mile of the ship (daytime only). Seven tows, including both vertically stratified and horizontal tows, fit these criteria in each year. A larger group of tows was included in the broader "whale area" designation: these included tows taken at a location within 24 h of a whale sighting to allow for nighttime comparisons and samples taken in fog (when the whales could not be seen). Seventeen tows from 1988 and 18 from 1989 satisfied this broader definition. See Table 2 for the number of tows (N) appropriate for the different statistical comparisons. Information on whales came from notes taken by trained observers onboard the Endeavor (KENNEY *et al.*, 1995; WINN *et al.*, 1995).

Associations of physical parameters (from the MOCNESS sensors) with abundance and biomass (both integrated water column and in the maximum net) were examined using Spearman correlations. Physical variables used were temperature, temperature range, salinity, relative fluorescence, and percentage light transmission. The values used for the physical parameters were the means of the variable for the surface water net (uppermost net, depth range usually 0–5 m, but the lower boundary for some nets ranged from 3 to 9 m) and for the net with maximum abundance (variable depth range).

RESULTS

A total of 99 successful MOCNESS tows was completed during the three cruises. Tow information is summarized in Table 1, and tow locations are plotted in Fig. 1. A complete list of all tows, locations, and tow parameters is given by SCHOENHERR and WISHNER (1990). A total of 787 MOCNESS samples was processed from the two field years: 777 for biomasses and 737 for counts (Table 1). Approximately 221,000 individual *Calanus* were identified to life stage.

Abundance and biomass

Wet weight copepod biomass and abundance of total *Calanus* (copepodite 3 and older) were significantly correlated (Spearman tests) within the water column and within the maximum nets in both years. In other words, although the copepod age structure matured through the time of the cruises (discussed later) and individual biomass increases with increasing size (MCLAREN *et al.*, 1989), total copepod biomass and numerical abundance co-varied, and trends in wet weight biomass strongly reflected abundance trends.

Overall, day and night water column values were similar for abundances of all lifestages (copepodites 1–5, females, males), total *Calanus* and copepod-sized biomass in both 1988 and 1989, with only two exceptions (1989 female abundance and copepod biomass, night > day). Maximum total *Calanus* and maximum copepod biomass (largest sample in each tow) were also similar day and night in both years. In a few repeatedly sampled locations, day and night abundances appeared consistently offset, but the direction of the offset varied among locations, and no statistically significant pattern emerged (see later discussion on temporal changes). Because of the high degree of statistical similarity between day and night abundances, day and night samples were treated together in the regional and interannual comparisons.

Comparisons between areas for each year showed that in both 1988 and 1989, water column abundances of copepodite 5s were significantly higher in the "whale areas" than in the non-whale regional samples, and water column abundances of copepodite 1s were significantly lower (Table 2). Females and mean biomass in 1988 were also significantly greater in "whale areas" than in the overall region, and mean abundance showed a similar trend ($P = 0.07$). Copepodite 2s in 1989 were significantly less abundant in "whale areas" than regionally. Total water column biomass, total and mean *Calanus* abundances, and abundances of other lifestages were not significantly different between the two regions

Table 2. Summary of abundances and biomasses of C. finmarchicus *during* 1988 *(left section) and* 1989 *(right section). Water column abundances for each life stage and total abundance are in units of* numbers m^{-2}*; the mean water column abundance is in units of* numbers m^{-3}*; and maximum net abundances are in units of* numbers m^{-3}. *The total abundance is the summed abundance of all life stages from the copepodite* 3 *stage and older. Biomasses are in units of* mg m^{-2} *for the water column and* mg m^{-3} *for the maximum net.* "Wh" *are* "whale area" *samples;* "reg" *are regional samples (see text for definitions). The significance column shows comparisons for which* $P < 0.05$ *with Mann–Whitney U tests.* "Y" *indicates significant differences between years.* "A" *indicates significant differences between* "whale area" *and regional samples in the indicated year. The* "wp" *after the year shows significant comparisons between areas using the* "whale present" *definition*

		1988						1989					1989/1988	1989/1988	Significance
	N	Mean	S.D.	Min	Median	Max	*N*	Mean	S.D.	Min	Median	Max	(with means)	(with medians)	(Y = yr, A = area)
Water col: wh															
C1	16	0	1	0	0	3	12	0	1	0	0	2	0.7		A88,A89
C2	16	2452	3544	0	437	9664	12	1026	1537	0	245	4798	0.4	0.6	A89
C3	16	22,861	26,238	971	11,389	70,294	12	23,040	30,483	1140	11,979	97,827	1.0	1.1	
C4	16	51,194	60,121	1261	36,329	243,299	12	117,101	112,892	3966	86,574	409,450	2.3	2.4	Y
C5	16	41,775	44,403	243	20,292	128,755	12	106,483	124,190	16,505	68,787	469,900	2.5	3.4	Y,A88,A89,A88wp
F	16	5723	8480	6	2724	32,235	12	6650	6283	2293	4283	20,809	1.2	1.6	A88,A88wp
M	16	865	1111	0	213	3304	12	1915	944	737	1787	3930	2.2	8.4	Y
Tot abun (C3pl)	16	122,418	110,240	2625	101,303	427,618	12	255,188	249,800	25,030	183,628	954,283	2.1	1.8	
Biomass	16	78,596	69,327	1389	60,917	241,261	12	149,985	139,661	28,332	122,538	550,459	1.9	2.0	A88wp
Mean abun	16	1136	1189	30	748	4805	12	1788	1666	166	1389	6320	1.6	1.9	
Water col: reg															
C1	27	148	351	0	2	1390	27	34	89	0	0	406	0.2	0.0	
C2	27	9871	17,608	4	1100	64,094	27	5139	11,070	0	1119	49,286	0.5	1.0	
C3	27	30,594	34,712	3	14,723	110,430	27	35,152	39,096	2,011	23,856	179,738	1.1	1.6	
C4	27	24,174	28,283	16	17,857	123,814	27	91,119	52,744	24,946	82,137	207,903	3.8	4.6	Y
C5	27	8909	8965	8	7774	31,585	27	43,183	25,135	10,383	34,185	94,282	4.8	4.4	Y
F	27	1731	2026	0	973	9383	27	4064	2695	356	3497	9700	2.3	3.6	Y
M	27	372	676	0	181	3510	27	1376	1351	74	909	5484	3.7	5.0	Y
Tot abun (C3pl)	27	65,780	61,412	509	47,000	217,292	27	174,894	88,343	59,578	152,500	351,948	2.7	3.2	Y
Biomass	24	38,205	28,023	372	40,117	101,203	27	86,677	34,028	33,408	78,887	169,964	2.3	2.0	Y
Mean abun	27	585	581	7	356	1984	27	1513	1080	449	1187	5357	2.6	3.3	Y
Max net: wh															
Tot abun (C3pl)	16	5154	3900	119	5093	13,317	18	13,844	9583	855	12,454	30,789	2.7	2.4	Y,A88,A89wp
Biomass	16	3151	2502	54	2174	7553	18	5908	3964	499	5474	13,488	1.9	2.5	Y,A88,A88wp,A89wp
Max net: reg															
Tot abun (C3pl)	27	2730	3250	20	1693	13,751	27	9535	5696	1220	7914	25,758	3.5	4.7	Y
Biomass	27	1072	1028	12	840	3938	27	3634	1905	172	3628	8,253	3.4	4.3	Y

when the broad definition of whale areas was used. However, when the narrower definition of "whale present" areas was used (whales actually visible at the time of sampling; n = seven tows in 1988 and two in 1989 usable for water column totals), the abundances of copepodite 5s and females, as well as mean biomass and water column biomass, were significantly higher in "whale present" locations than regionally in 1988 (Table 2); abundances of copepodite 4s and total *Calanus* showed similar nearly significant trends ($P = 0.07$ and 0.08, respectively). No significant differences in abundances between tows from "whale present" locations and the overall region were found in 1989, probably because of the small number (two) of tows spanning the entire water column (and thus usable for water column comparisons) from the "whale present" locations.

Differences in the abundance and proportion of larger copepods (total of copepodite 4 and older) between "whale area" and regional samples were also investigated (Mann–Whitney U tests) because we suspected that the whales were feeding primarily on these larger lifestages. Proportions of these "whale food size" *Calanus* relative to total *Calanus* (copepodite 3 and older) were significantly higher in "whale areas" than elsewhere in both 1988 and 1989 in the total water column and in the maximum nets. However, abundances of "whale food size" copepods in the water column and maximum nets were significantly higher in "whale areas" vs regionally only in 1988.

Interannual comparisons (with regional and "whale area" samples tested separately) showed that water column copepod abundances were generally higher in 1989 than in 1988. In the regional samples, water column copepod-sized biomass, total *Calanus* abundance, and abundances of all life stages from copepodite 4 and older were significantly higher in 1989 than in 1988 (Table 2). However, in the "whale area" tows, only copepodite 4s, 5s and males were significantly more abundant in 1989 (Table 2), although biomass and total *Calanus* abundance showed similar, nearly significant trends ($P = 0.08$ and 0.07, respectively).

Calanus was about twice as abundant in 1989 as in 1988. Ratios of the means of the water column abundances between years (1989/1988) for each of the different older lifestages (copepodite 4s and older) and total *Calanus* ranged from 2.3 to 4.8 in the overall region and 1.2–2.5 in the "whale areas" (Table 2). Similar ratios using median abundances were 3.2–5.0 regionally and 1.6–8.4 in "whale areas". Interannual biomass ratios (using means) were 2.3 regionally and 1.9 in "whale areas".

The highest *Calanus* concentrations (number m^{-3}) found in SCOPEX MOCNESS tows were 41,600 (1986 pilot program) (Wishner *et al.*, 1988), 13,300 (1988), and 30,800 (1989). The bucket sample (1989), taken in a visibly red surface patch, gave an abundance of 331,000 m^{-3}. Maximum total *Calanus* abundances and copepod biomass (largest sample in each tow) were significantly higher in 1989 compared to 1988 in both regional and "whale area" samples (Table 2; Fig. 2). Also, since the copepods in most of the region were vertically migrating in 1988 but not in 1989, the median middepth of the net with maximum abundance differed between years. In 1988, this depth was 75 m in the day and 9.8 m at night, while in 1989, it was 12 m in the day and 12.5 m at night.

"Whale area" samples were significantly more homogeneous in their composition in 1989 vs 1988 (Table 3). "Whale area" maximum abundance samples were composed of a mean of 91.7% *C. finmarchicus* of total copepods and a mean of 91.4% *C. finmarchicus* of total zooplankton in 1988; 1989 composition was 97.9% and 97.3%, respectively (Table 3). There were no significant interannual differences in percent composition in the regional comparison.

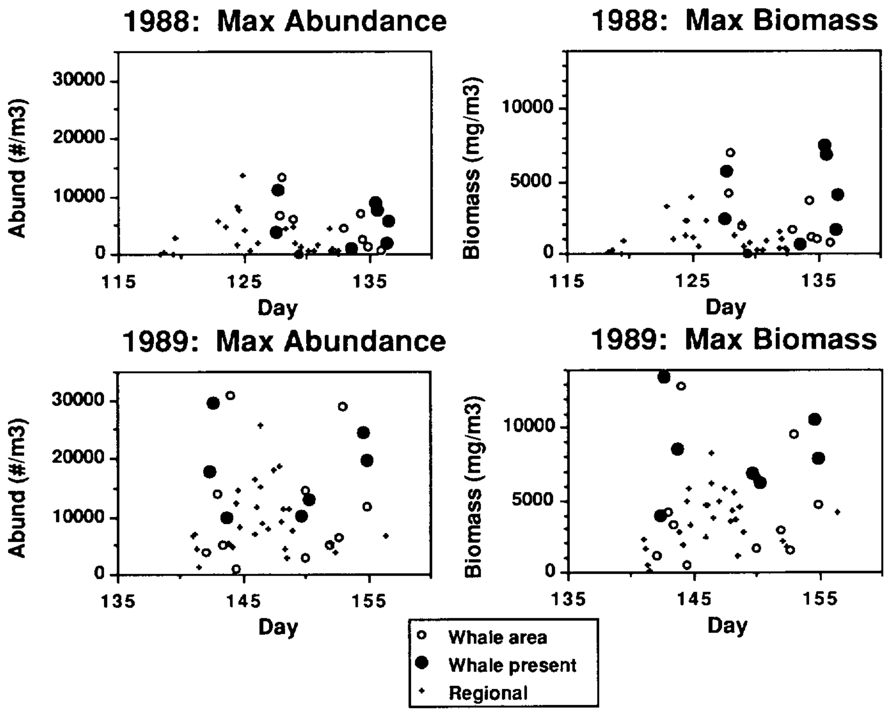


Fig. 2. Maximum *Calanus* abundance (total of copepodite 3 and older) and maximum copepod biomass from the largest sample in each net tow relative to the sampling day in right whale feeding areas (round symbols) and regionally (plus symbols) during 1988 (top) and 1989 (bottom). For whale areas, solid symbols are samples taken when feeding whales were present at the time, open circles are samples from locations where whales were present within 24 h of the tow.

Table 3. Percentage composition of the maximum net samples by year and region. See Table 2 for an explanation of the significance column

	1988						1989						Significance
	N	Mean	S.D.	Min	Median	Max	*N*	Mean	S.D.	Min	Median	Max	(Year, Area)
Max net: wh													
% C.f. of cop	16	91.7	9.3	73	94.5	100	18	97.9	3.6	85	99	100	Y,A89
% cop of total	16	99.6	0.7	98	100	100	18	99.5	1.2	95	100	100	A88
% C.f. of total	16	91.4	9.5	72	94.5	100	18	97.3	4	85	99	100	Y,A89
Max net: reg													
% C.f. of cop	27	92.9	8.7	68	96	100	27	93.3	8.9	61	96	100	
% cop of total	27	96.4	8.3	60	99	100	27	97.8	5	77	100	100	
% C.f. of total	27	89.4	11.7	54	94	99	27	91.4	11.3	55	95	100	

Table 4. Values of the concentration index for biomass and Calanus *abundance by year and region*

	Biomass			Abundance		
	N	Mean Conc. Index	S.D.	*N*	Mean Conc. Index	S.D.
1988						
Whale area	15	4.48	2.06	15	4.63	2
Regional	24	3.36	2.5	27	4.6	3.46
Combined	39	3.79	2.38	42	4.61	2.99
1989						
Whale area	12	4.79	1.89	12	7.51	2.47
Regional	27	5.44	2.81	27	7.63	3.82
Combined	39	5.24	2.56	39	7.59	3.43
EN 174	9	3.49	2.3	3	5.51	3.46

The nature of differences in maximum concentrations between "whale area" and regional samples varied between years. In 1988, total *Calanus* abundances and copepod biomass were significantly higher in the broadly defined "whale areas" compared to regional locations (Table 2), and copepods composed a significantly higher proportion of the total plankton in "whale areas" (Table 3) (99.6% in "whale areas"; 96.4% in regional samples). However, only copepod biomass was significantly different between regions in 1988 when the narrower "whale present" definition was used. In 1989, maximum abundances and biomass were not significantly different between locations with the broad "whale area" definition, but were significantly higher in "whale present" areas than regionally (Table 2). In 1989, *C. finmarchicus* also composed a significantly higher proportion of the total copepods and total plankton in both "whale areas" and "whale present" areas than regionally (Table 3).

Analysis of the concentration index (Table 4) suggested that the copepods were more aggregated in the vertical in 1989 than in 1988. The concentration indices for both total *Calanus* abundance and copepod biomass were significantly higher in 1989 compared to 1988 overall (Mann–Whitney U tests), in the regional samples, and for abundance but not biomass in the "whale areas".

Geographic and spatial distribution

The locations of the highest *Calanus* water column abundance varied between years. In both years, maxima occurred in a band north of and slightly deeper than the 100-m isobath (Fig. 3). Patches of exceptionally high abundance, often in association with feeding whales (Winn *et al.*, 1995), occurred in both years within this band of elevated abundance. In 1988, patches of highest total *Calanus* abundance were in the southwest of the region. In 1989, maxima occurred in the northeast. Peak abundances in 1988 occurred where the water column was about 100–180 m deep and in 1989 where the water column was about 140–180 m deep. However, there were no significant correlations using the entire sample set between water column depth and either abundance or biomass in the integrated water column or maximum nets (Spearman correlations).

The geographic distributions of the different lifestages varied (Fig. 4). The youngest

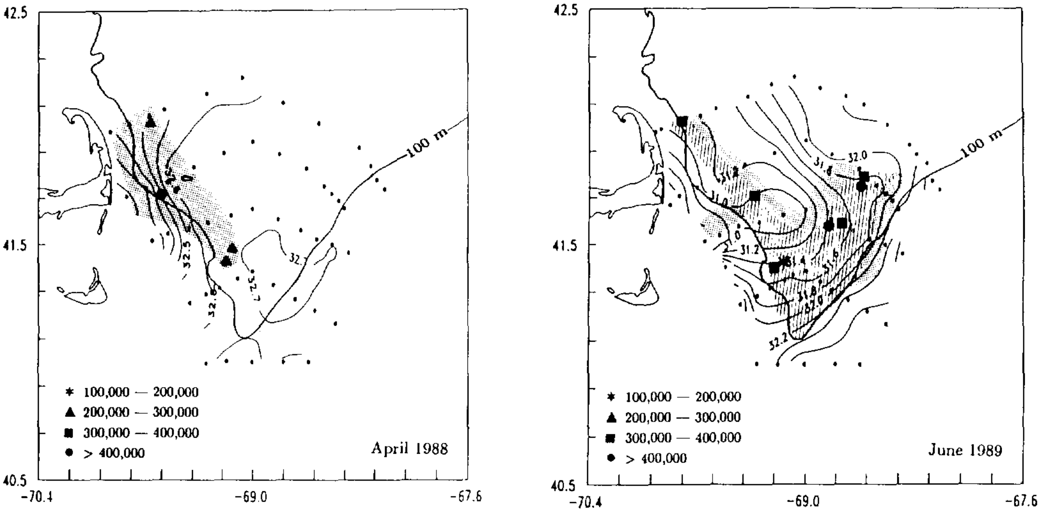


Fig. 3. Distributions of *Calanus* and surface (2 m) salinity in 1988 (left) and 1989 (right) relative to the 100 m isobath. Water column abundances (number m^{-2}) of total *Calanus* (copepodite 3 and older stages) are shown as shaded areas, with symbols (see key on figure) showing locations of peak abundances. The dotted shading represents water column *Calanus* abundances from 100,000–200,000 m^{-2}; the line shading represents abundances from 200,000–300,000 m^{-2}. The maximum value in a day–night pair (same site) was used for contouring abundances. The small dots show the hydrographic station locations used to contour the surface (2 m) salinity fields. The CTD data were obtained during surveys on 26–29 April 1988 and 6–12 June 1989 (see Chen (1992) and Chen *et al.* (1995a,b) for details).

stages occurred in the northwest part of the region in both years. Older stages were located progressively towards the center and finally the northeast. The maximum abundance of the different lifestages progressed in time as well as in space (see below).

Information on small-scale variability and patchiness within the layer of maximum abundance in the whale areas was obtained from the horizontally sequenced tows, which traversed total distances of about 440–1860 m (Fig. 5). Distance in meters was assumed to be numerically approximate to cumulative volume filtered because the net mouth area was 1 m^2. Patch "sizes", estimated by measuring the distance between abundance minima on either side of an abundance peak within the horizontal tows that included both peaks and minima, ranged from about 230 to 840 m, with a mean of 530 ± 280 ($n = 5$; one value from 1988 and four values from 1989). The maximum coefficient of variation for the samples within each tow (standard deviation / mean × 100), an indicator of abundance variability along the tow path, occurred in tows of about 1–1.5 km, i.e. about 2–3 patch lengths (Fig. 5). One explanation is that variability within a tow peaked when the tow length was at the spatial scale of a few patches (such that the individual samples within the tow came from either a patch or inter-patch zone) compared to shorter tows located entirely within a single patch or longer tows in which individual samples probably integrated patch and inter-patch areas. The coefficient of variation (abundance variability for the entire tow) did not differ significantly between years or between day and night tows (Mann–Whitney U tests), but the texture of the patchiness appeared different in the two years. Horizontal

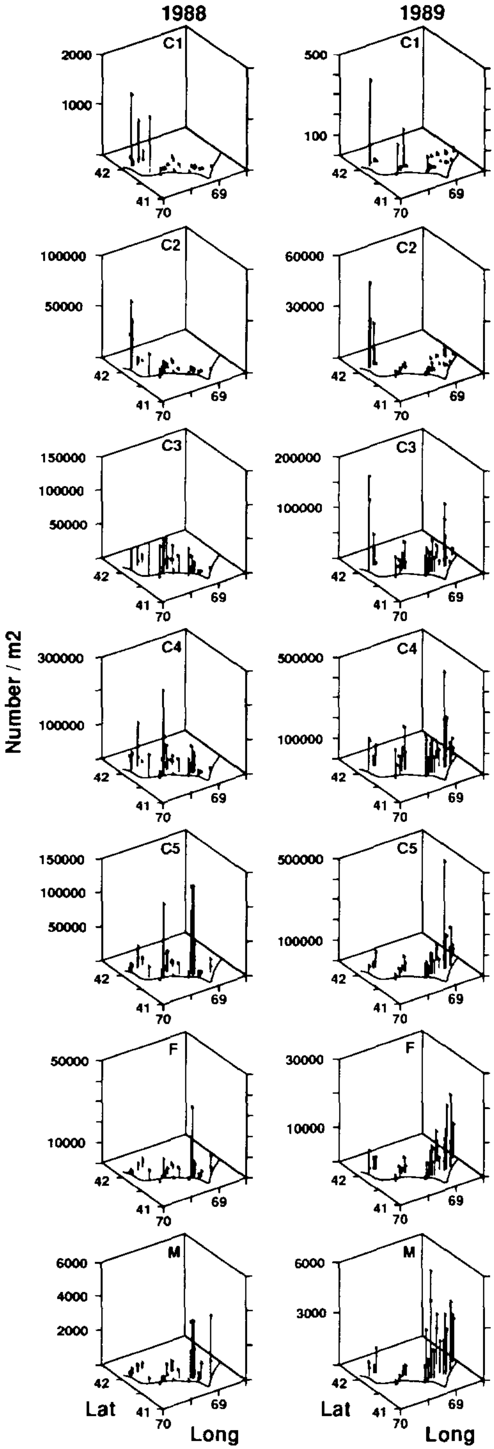


Fig. 4. Three-dimensional view of the geographic distribution of each lifestage of *Calanus* during 1988 (left) and 1989 (right). The height of the lines shows the water column abundance (number m^{-2}). Abundance axes vary. The other two axes show latitude and longitude. The V-shaped feature represents the 100-m isobath.

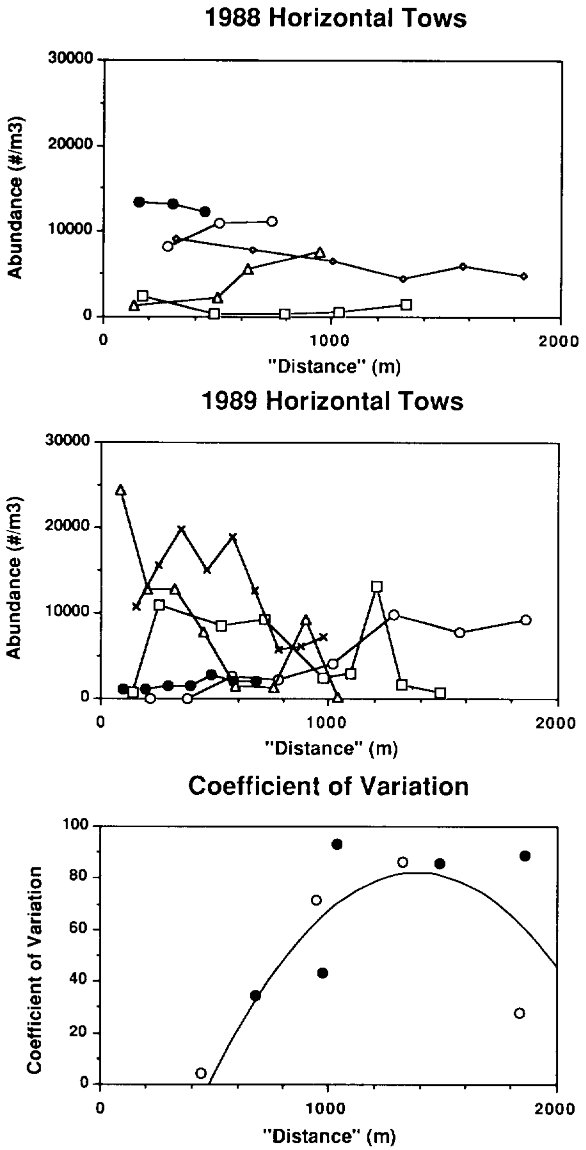


Fig. 5. Small-scale variability in *Calanus* abundance as shown in the horizontal MOCNESS tows. All tows included in these graphs were taken within the layer of maximum *Calanus* abundance (total of copepodite 3 and older) in whale areas. The graph for each year shows abundances in the sequential nets of each tow as a function of approximate distance, numerically equivalent to cumulative volume filtered since the net had a mouth opening of 1 m^2. Lines connect sequential nets from the same tow (different symbol type for each tow). Open symbols are from day tows, closed symbols are from night tows, and the Xs are from a dusk tow. Middle path of horizontal tows, 1988 and 1989, respectively. Open circle: 1 m, 16 m; closed circle: 1 m, 19 m; square: 99 m, 1 m; triangle: 120 m, 10 m; diamond: 126 m; ×: 3 m. The bottom graph shows the coefficient of variation as a function of approximate distance. The curve fits a second order polynomial function ($P = 0.03$, adjusted $r^2 = 0.518$). In this graph, symbols are differentiated by year (open circle: 1988; closed circle: 1989) and each coefficient of variation comes from one tow. See the text for further explanation.

tows in 1989 showed more peaks and small-scale variation between adjacent nets, while 1988 tows showed longer-scale trends in abundance (Fig. 5). Abundances within the horizontal tows varied by a median factor (maximum abundance / minimum abundance) of 2.1 (range 1.1–6.4, $n = 5$) in 1988 and 18.3 (range 2.6–886.3, $n = 5$) in 1989.

Temporal changes

The 3-week cruises in each year spanned a period of time of rapid development of a *Calanus* cohort, with the youngest lifestages showing maxima early in the cruises and older lifestages peaking successively later (Fig. 6). Water column abundances of copepodites 1, 2, 3 and 5 in 1988 and copepodites 2 and 3 in 1989 were significantly correlated with Julian day (Spearman correlations, $n = 43$ in 1988 and 39 in 1989). There was no significant trend over time within each cruise of total *Calanus* abundance (copepodite 3 and older), the abundance of the large "whale food size" stages (total of copepodite 4 and older), or copepod biomass in either the integrated water column or in the maximum nets (Figs 2, 7 and 8). However, the proportion of the large "whale food size" stages relative to total *Calanus* (copepodite 3 and older) was significantly correlated with Julan day in both years in both the water column and maximum nets (Fig. 8).

Locations that were resampled at multiple-day intervals during the cruises provided another view of temporal change (Fig. 9). Two non-whale sites were resampled during the cruises: the location of the 1986 whale aggregation (41°22.6′N, 69°01.4′W) (1988 cruises, 14 and 55-day intervals) and the eastern station on the northwest transect (42°03.5′N, 69°41.2′W) (1989 cruise, 15-day interval). In 1988, the water parcel associated with a satellite-tracked drifter was also sampled twice as the drifter moved south from 41°53.5′N, 69°11.4′W to 41°35.1′N, 69°16.8′W (11-day interval). Water column and maximum net abundances at these three stations were initially below median regional abundances (Fig. 9) (Table 2). The transect and drifter stations showed abundance increases over the stated time intervals to the median or above; abundances at the former whale site decreased over time (Fig. 9). The temporal pattern at repeatedly sampled 1988 and 1989 whale locations was different than at the non-whale regional areas. Initial values at the "whale area" stations were sometimes very high, but abundances at these same geographic locations typically showed large fluctuations over short time intervals (one to several days), especially at night (Fig. 9). Within a 24-h interval, maximum abundances and water column abundances in "whale areas" varied by median factors (highest value/lowest value) of 6.6 (range 2.2–50.4, $n = 9$) and 9.2 (range 4.1–43.4, $n = 8$) respectively in 1988 and 4.9 (range 1.2–36.0, $n = 10$) and 3.1 (range 1.8–10.4, $n = 8$) respectively in 1989. However, since day and night abundances from some sites showed a consistent offset (Fig. 9) which might bias these factors, an additional comparison was made between either days or nights and using estimates only from the vertically stratified tows. When this was done, maximum abundances and water column abundances between sequential days or sequential nights in whale areas varied by median factors (higher value/lower value) of 3.6 (range 1.1–5.8, $n = 7$) and 3.7 (range 1.6–3.8, $n = 7$), respectively.

During the EN-174 cruise in early spring (March) 1988, water column and maximum copepod abundances and water column copepod biomass were significantly lower than during the EN-176 cruise later that spring in May (Table 5) (Mann–Whitney U tests). Spatially, the highest water column biomasses in the early spring were clustered in the southwest near where peak abundances occurred later during EN-176, but one high value

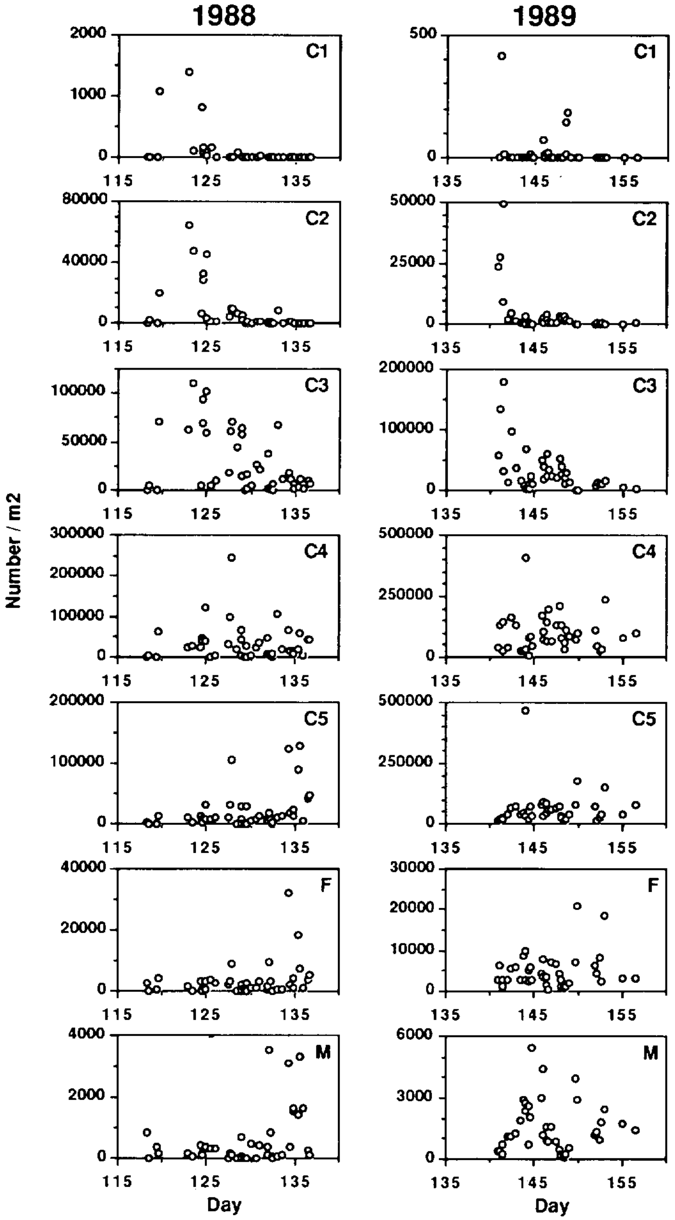


Fig. 6. Water column abundances (number m^{-2}) of each *Calanus* lifestage relative to sampling day (in Julian days) during the two major sampling cruises. 1988 abundances are in the left column, and 1989 abundances are in the right column. Abundance axes vary.

also occurred at the northernmost station located east of Wilkinson Divide (see Fig. 1 for station locations). The degree of vertical concentration of the copepods, as represented by the concentration index, was not significantly different between the two 1988 cruises (Table 4), although the water column was nearly isothermal (unstratified) in March and

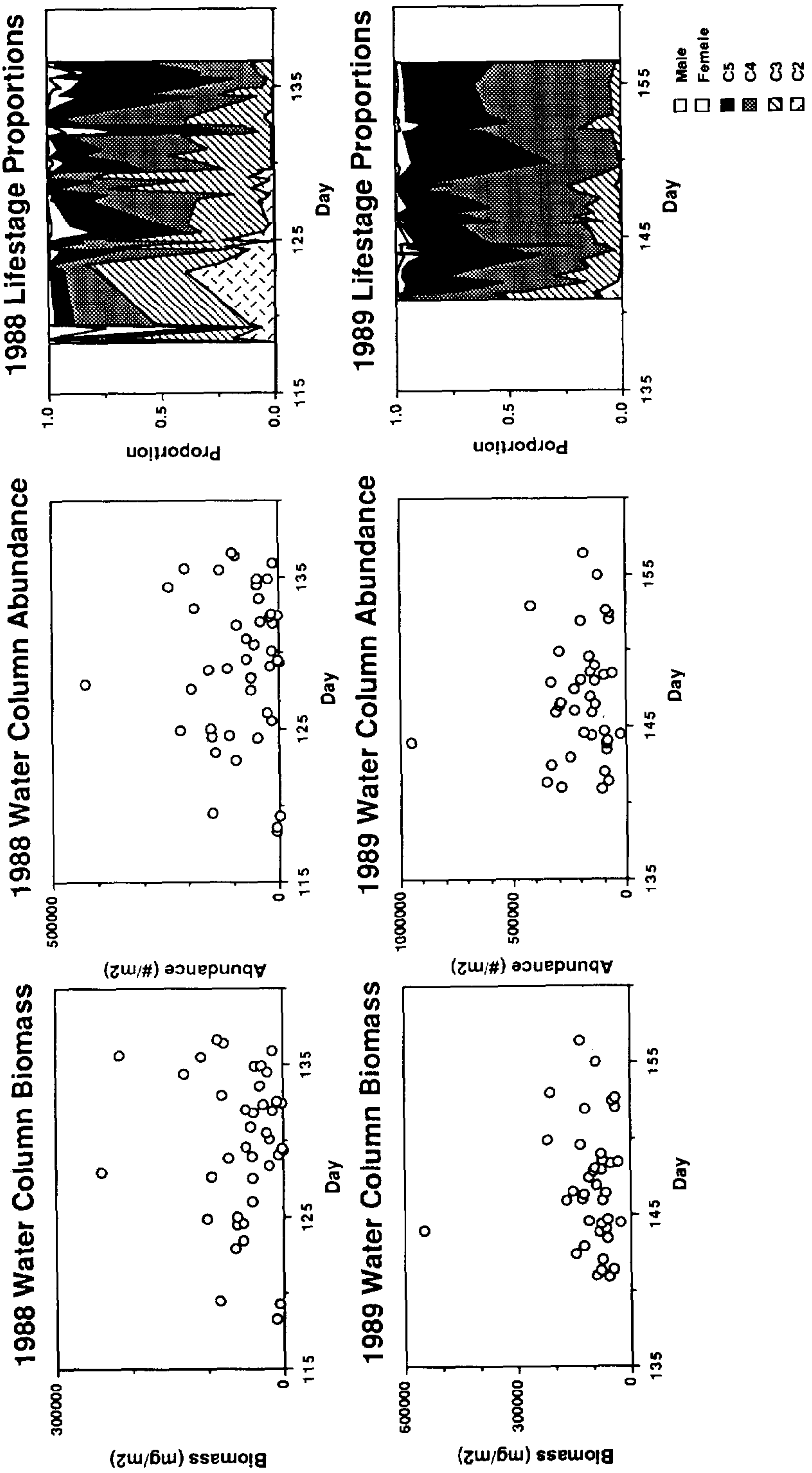
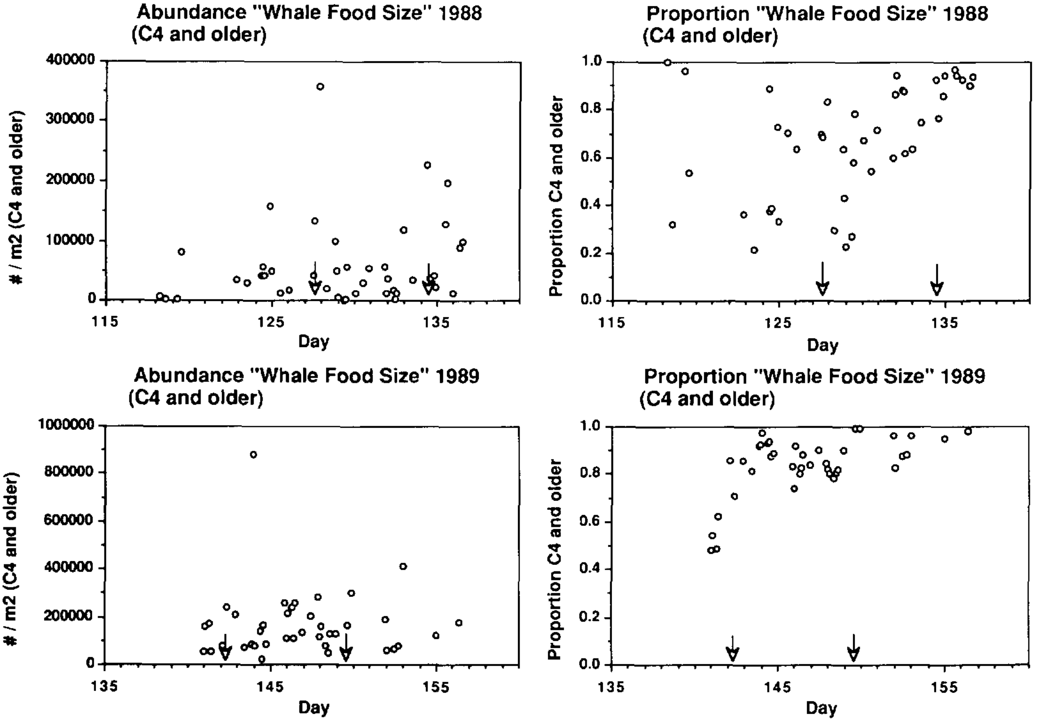


Fig. 7. Water column copepod biomass (left column), total *Calanus* water column abundance (copepodite 3 and older) (center), and the proportions of each lifestage in the water column (right) relative to Julian day for 1988 (top row) and 1989 (bottom row). Biomass and abundance axes differ between years.


Abundance "Whale Food Size" 1988 (C4 and older)

Proportion "Whale Food Size" 1988 (C4 and older)

Abundance "Whale Food Size" 1989 (C4 and older)

Proportion "Whale Food Size" 1989 (C4 and older)

Fig. 8. Water column abundance (left) and proportion (right) of older "whale food size" life stages (total of copepodite 4 stage and older) relative to Julian day in 1988 (top) and 1989 (bottom). Times when whales were first seen at each of the two major feeding areas are indicated by the arrows. Abundance axes differ between years.

stratified in May. Similar to the later spring, *C. finmarchicus* in March was the dominant zooplankter numerically (80–99% of zooplankton; 81–99% of copepods; $n = 3$).

Population structure

The proportions of the different lifestages over time also reflected the development and aging of the population (Fig. 7). During the late spring cruises, younger stages represented a diminishing proportion of the population over time. Older stages, however, showed substantial variability (especially in 1988) when all tows were plotted together as in Figs 7 and 8. At least part of this apparent temporal variability, however, was actually due to spatial variability. For example, Fig. 10(A) shows the distribution by lifestage and depth of the *Calanus* on the same geographical transect from each of the 2 years. Each of these transects was completed in a single night and covered a horizontal distance of about 25 km. In 1988, the population was distinctly skewed towards older stages at the east end of the transect; in 1989 the population structure remained substantially the same at all three locations.

Although the 1988 and 1989 cruises did not overlap Julian days, they spanned approximately the same *Calanus* developmental phases because the Julian dates of this development were different between the 2 years. Temporal benchmarks of population

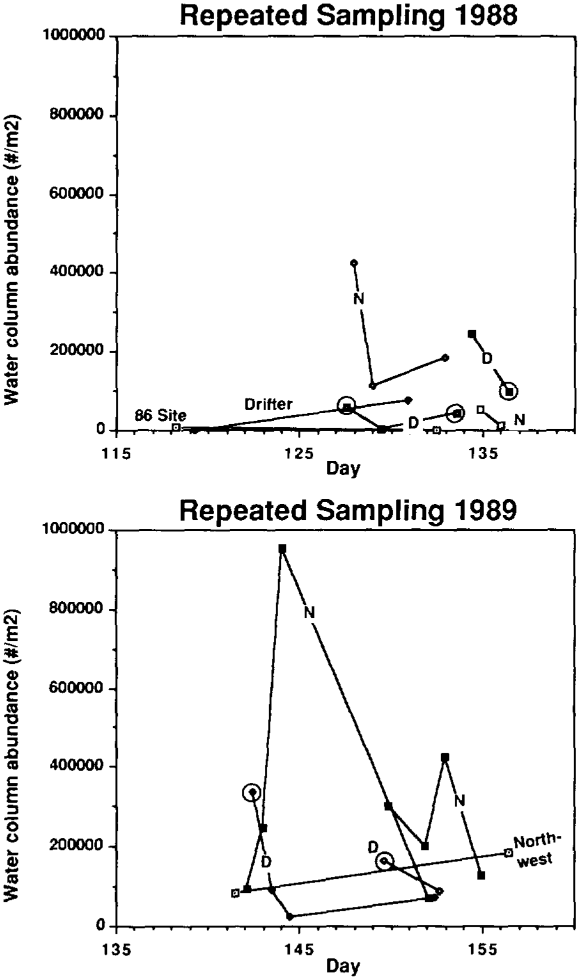


Fig. 9. Changes in total *Calanus* water column abundance over time in repeatedly sampled fixed geographic locations or drifter-tagged water parcels in 1988 (top) and 1989 (bottom). Each symbol represents a different series. For whale areas, day (D) and night (N) series are plotted separately because of apparent offsets at some locations. Samples from locations with feeding whales present are circled. See text for locations of other labelled sites.

structure (Table 6) suggest that similar population structures, especially the occurrence of the copepodite 4s and 5s that the whales apparently feed upon, occurred 1–2 weeks later in 1989 than in 1988. Copepodite 4 and 5 abundances peaked during days 124–136 in 1988 and 143–153 in 1989. Additional analyses of cohort development time, based on a subset of five of these stations each year, have been done by Durbin *et al.* (1995a).

The population structure of the copepods during the March EN-174 cruise was markedly different from that of the later May–June cruises, with a mean of 85.3 ± 4.7% ($n = 3$) of the individuals being adult females. None of the other lifestages (copepodite 3 and older) was represented by more than 6.6% of the individuals. A few copepodite 1 and 2 stages

Table 5. Values of water column abundance and biomass, mean abundance and maximum net abundances and biomass in the EN-174 (March 1988) samples. Units are explained in Table 2

	N	Mean	S.D.	Min	Median	Max
En-174 Water Col						
Tot abun (C3pl)	3	6961	1380	5528	7080	8279
Biomass	9	10,878	3536	4914	11,421	15,384
Mean abun	3	48	12	34	52	57
En-174 Max Net						
Tot abun (C3pl)	3	237	109	111	298	301
Biomass	9	244	122	65	282	403

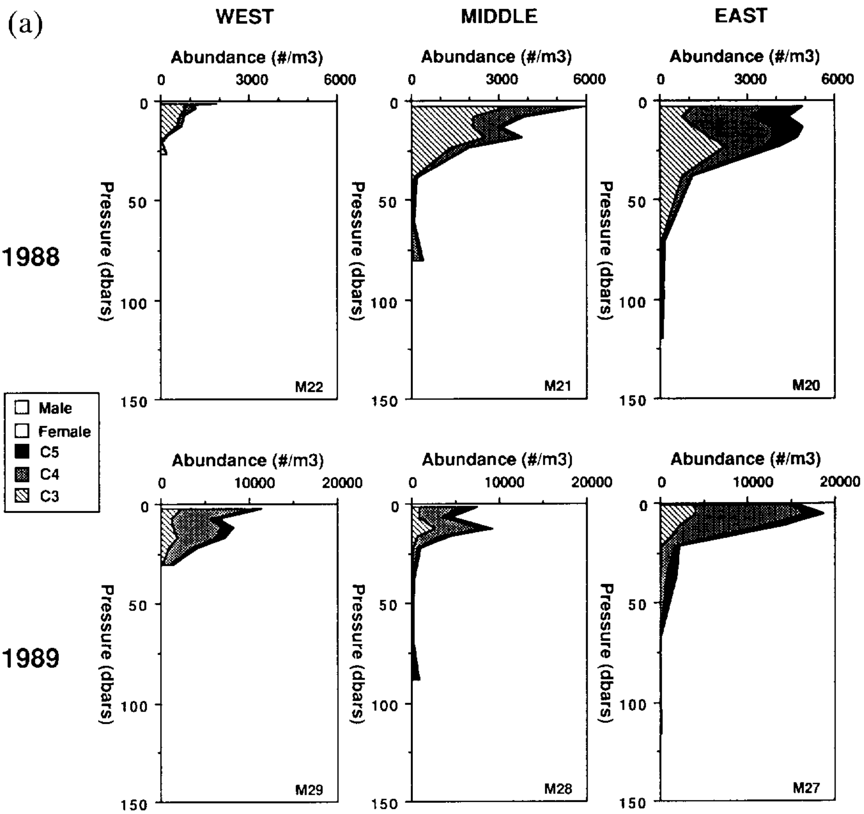


Fig. 10. (a) Vertical profiles of *Calanus* abundance by lifestage on the middle western transect at night during 1988 (7–8 May) (top) and on the same transect during 1989 (27–28 May) (bottom). Abundance axes differ between years. (b) (Next page) profiles of temperature (solid line) and salinity (dashed line) from CTD casts adjacent to the MOCNESS tows. See Fig. 1 for the geographic location of the transect and Fig. 3 for the regional surface salinity.

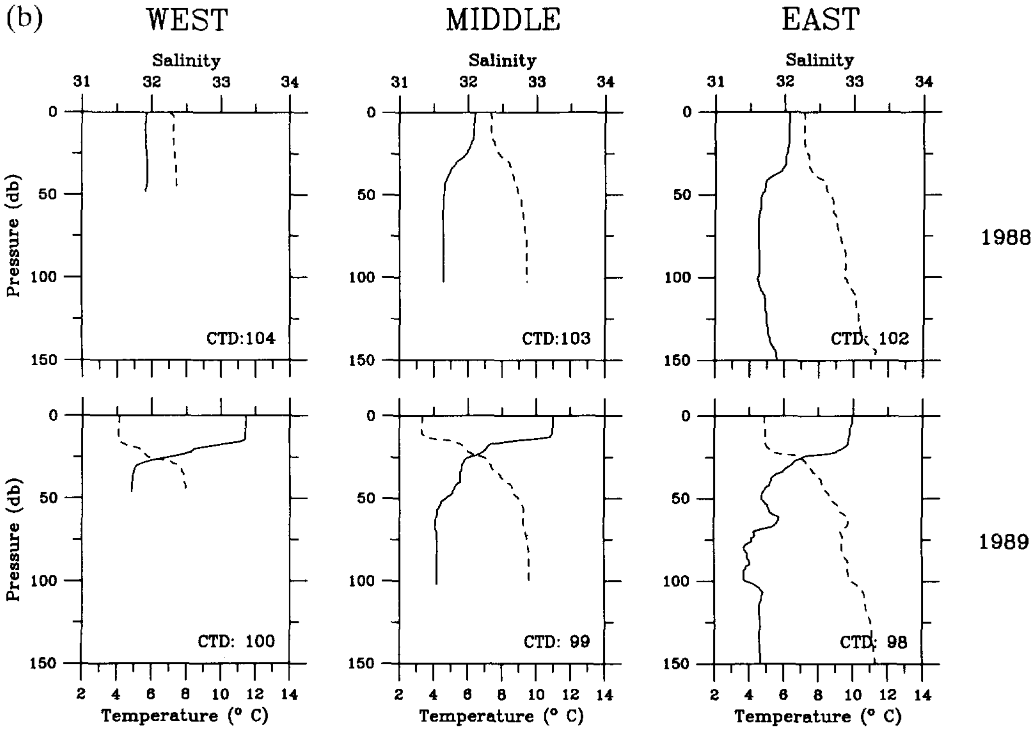


Fig. 10. (*Continued*)

Table 6. Interannual variability in the time of population development benchmarks. Particular benchmarks of plankton composition by lifestage proportion are shown in the left column. The second two columns show the Julian day in each year when the composition of the plankton samples consistently fit the level in the left column. Multiple Julian days are given for some benchmarks because of geographic variability. The right column shows the approximate number of days difference between 1989 *and* 1988 *in the attainment of these benchmarks*

Population devel. benchmark (Lifestage percentage)	1988 Day	1989 Day	Interannual difference (No. of days)
C3 < 40%	132	141	9
C3 < 20%	132,135	143	11,8
C5 > 30%	132	143–145,150	11–13,18

were present (means of 4 m^{-2} and 53 m^{-2}, respectively), but these and the even smaller naupliar stages would not have been collected quantitatively by the coarse mesh nets.

Physical associations

High total *Calanus* abundances in the water column and in the maximum nets were significantly correlated with low mean surface (0–5 m) salinity in 1988 (see Fig. 3 for surface salinity values). Day and night samples were also considered separately for associations with physical parameters because of the pronounced vertical migration behavior of the copepods in 1988; when this was done, only the night correlations with surface salinity (when the copepods were in the upper water column) were significant. High nighttime total abundance in the maximum net samples was also significantly correlated with low mean salinity of the water traversed by these nets in 1988. Significant relationships between total *Calanus* abundance and salinities were not apparent in the 1989 data set. In both years, however, high water column abundances of younger lifestages (copepodites 2–4 in 1988 and copepodites 1–3 in 1989) were significantly correlated with low surface salinities, while high abundances of older lifestages [copepodites 5 (1988 only), males, and females] and high proportions of total copepodite 4 and older individuals were significantly correlated with high salinities at the surface or in the net with maximum abundance. In 1988 when the copepods were vertically migrating, most of these relationships were evident only at night, while in 1989, a year with limited vertical migration, most of these correlations occurred both day and night.

There were also some significant relationships to light transmission and *in situ* fluorescence. In 1988, high maximum biomass and low light transmission at the depth range of the net with maximum biomass were significantly correlated. In 1989, high nighttime *in situ* fluorescence at the depth of the maximum nets and high *Calanus* abundance or biomass in these nets and in the total water column were significantly correlated, while during the day, low fluorescence at the maximum net depth was significantly associated with high *Calanus* abundance and biomass in these nets.

DISCUSSION

Quantifying abundances

Accurate copepod abundance estimates are essential for energetic models being developed for right whales and for population dynamics models of the overall Gulf of Maine–Great South Channel ecosystem. In a bioenergetic model for the right whale, Kenney *et al.* (1986) estimated that a whale needed zooplankton concentrations between 4.6×10^3–1.1×10^7 m^{-3} in order to meet daily energy requirements, and similar observations of the utilization of dense plankton aggregations have been made for other whales as well (e.g. Kawamura, 1974; Brodie *et al.*, 1978; Sameoto, 1983; Schoenherr, 1991). Many of the copepod abundance estimates from right whale feeding areas in the Great South Channel are at the base of or below these estimated whale energetic requirements.

It is likely that net tows are undersampling the plankton. Bongo nets and other small conical nets, usually towed obliquely through the water column, have yielded maximum *Calanus* abundances in this region of only about 1000–6500 m^{-3} (Bigelow, 1924; Fish, 1936; Clarke and Zinn, 1937; Kenney *et al.*, 1986; Sherman *et al.*, 1987; Wishner *et al.*, 1988; Mayo and Marx, 1990; Meise-Munns *et al.*, 1990). This is similar to the mean abundances (total water column abundance/depth) calculated here (Table 2), which in essence homogenize the water column and ignore depth zones of high concentration. Abundance estimates from continuous plankton recorders, towed at 10 m depth, are often even lower by 1–2 orders of magnitude (Jossi and Goulet, 1990), but *Calanus* abundances over shallow Stellwagen Bank (bottom depths from 18–40 m), measured by continuous plankton recorders, reached nearly 10^5 m^{-3} in 1986 when right whales were common there in the summer (Payne *et al.*, 1990). The highest abundance from a MOCNESS tow in the Great South Channel area, 41,600 m^{-3}, also occurred in 1986 (May) (Wishner *et al.*, 1988). Vertically-stratified BIONESS tows in Emerald Basin, one of the deep basins farther north where *Calanus* overwinter, gave a maximum *Calanus* spp. abundance of 19,726 m^{-3} in September 1985 at about 270 m depth (Sameoto and Herman, 1990). However, the bucket sample from the 1989 SCOPEX cruise yielded an abundance of 331,200 m^{-3}. Crude nearest neighbor estimates, obtained by photographing plankton near a ruler outside the porthole of the Delta submersible near feeding right whales in the Great South Channel region in June 1987, indicated patch densities of up to 1.6×10^6 m^{-3} at depths of 16 m (Wishner and Winn, 1987a,b; Martin and Wishner, unpublished results). Mayo has recently observed copepod abundances of $1–3 \times 10^6$ m^{-3} in surface micropatches in Cape Cod Bay near feeding right whales (personal communication), and Alldredge *et al.* (1984) reported densities of up to 26×10^6 m^{-3} for deep-living diapausing *Calanus pacificus* off California observed *in situ* with WASP. Thus, although 1986 may have been a peak year for *Calanus* in the southwestern Gulf of Maine, it is also clear that abundance estimates remain uncertain and that the methodology for determining copepod abundances, especially at the small scales directly involved in whale feeding, needs to be refined.

It is possible that the copepods are aggregated more densely into thinner layers or in smaller portions of a larger patch than are separately sampled by the net tows, and that the whales feed mostly in these particularly dense zones. There is some evidence from the SCOPEX program for such smaller scale features, such as the enhancement of plankton abundances in slicks in which right whales were feeding (Beardsley *et al.*, 1990; in preparation), the small-scale horizontal patchiness observed in MOCNESS tows (Fig. 5), and the small-scale layering and horizontal patchiness seen in the continuous acoustic backscatter data (Macaulay *et al.*, 1990, 1995). Macaulay *et al.* (1995) found that right whales altered their swimming behavior in areas containing copepod patches (detected at 200 kHz) with a scale size of 0.3–0.5 km, approximately the same size as the patch structure observed with the horizontal MOCNESS tows. However, we do not know how abrupt the edges of copepod layers and patches are, nor how individuals or size groups within a patch are arrayed. These could be important features to a feeding whale and help in interpreting their swimming and dive patterns (Winn *et al.*, 1995).

Neither net tows nor acoustics adequately sampled copepods in the near-bottom region. When diel vertical migration was pronounced as in 1988, the copepods seemed to form a dense near-bottom layer during the day, which was poorly delineated with our shipboard sampling gear. Feeding by right whales on near-bottom copepod aggregations in the Great South Channel was suggested by whale dive characteristics (Winn *et al.*, 1990; 1995; Goodyear, 1993; Kraus, personal communication). Whales in 1988 made longer dives during the day, when migrating copepods were deep, and shorter dives at night, when the migrating copepods were near the surface. In 1989 when the copepods did not migrate but remained shallow both day and night, the longest dives were at night (Winn *et al.*, 1995).

Temporal variability

The overall similarity between day and night water column abundances for almost all copepod categories indicated that differential net avoidance between day and night was not a general characteristic of *Calanus* behavior, with the possible exception of females in

1989 and total abundance in some of the whale-feeding locations (Fig. 9). Regardless of the different vertical migration patterns in 1988 and 1989 (Wishner *et al.*, 1990; in preparation; Durbin *et al.*, 1995a), most (or at least an equivalent proportion) of the population was sampled similarly both day and night in most areas.

Several significant interannual differences in the abundance and distribution of the copepods were observed (Table 2). Maximum *Calanus* abundances and biomass and water column abundances of older copepodite stages were significantly higher in 1989 than in 1988, both regionally and where whales were feeding, although the magnitude of the difference was usually greater in the regional samples than in whale areas. Based on the concentration index, copepods were also more vertically concentrated in 1989 than in 1988, and 1989 copepod samples from whale areas were more homogeneous in composition. Copepod population development (i.e. the appearance of older lifestages) was delayed in 1989 relative to 1988, although in both years there was a progression over time from younger to older stages, indicative of a maturing rather than a diapausing population (at least up to the copepodite 4 stage). The behavior of the copepods also differed markedly between years, with strong vertical migration in 1988 and limited or no migration in most areas in 1989 and also in 1986.

Possible causes of these interannual differences include differences in the physical environment (especially those associated with the spring freshwater plume) (Chen *et al.*, 1995a,b), food levels (Durbin *et al.*, 1995b), and non-whale predator abundance (fish and euphausiids) (Macaulay *et al.*, 1995), and the history of the overwintering population that produced the cohort that grew during the SCOPEX study. Regardless of this interannual variability, however, the whales are apparently able to find and feed on the copepods in this region every year.

Contrasts between "whale areas" and the general region

Higher water column abundances and proportions of older lifestages (especially copepodite 5s) and lower water column abundances of younger lifestages characterized the whale areas compared to the general region. Samples from the densest layer in each tow (the maximum nets) also tended to have a higher proportion of copepods relative to all zooplankton and a higher proportion of *C. finmarchicus* in the whale areas than regionally. However, copepod biomasses and total *Calanus* abundances, both in the water column and in the maximum nets, were sometimes, but not always, significantly higher in whale locations than regionally in the GSC, depending on the year and whale location definition used (Table 2). The degree of vertical concentration of the copepods, described by the concentration index, also did not vary significantly between whale and non-whale areas in either year (except for water column biomass in 1988).

These results suggest that the whales seek out aggregations of older copepod lifestages rather than simply the most dense aggregations. An indicator of the importance of lifestage to the potential food value of the copepods is suggested by the relative dry weights of *C. finmarchicus* lifestages; dry weight ratios of copepodite 1–5 and females were 1:2:6:13:53:94 in May 1980 on the Scotian Shelf (McLaren *et al.*, 1989). Carbon contents of copepod lifestages are reported in Durbin *et al.* (1995a,b). The right whales in the GSC apparently target larger energetically rich (Comita *et al.*, 1966; Durbin *et al.*, 1995a,b) lifestages that occur in dense monospecific layers, as previously hypothesized from the 1986 pilot program (Wishner *et al.*, 1988).

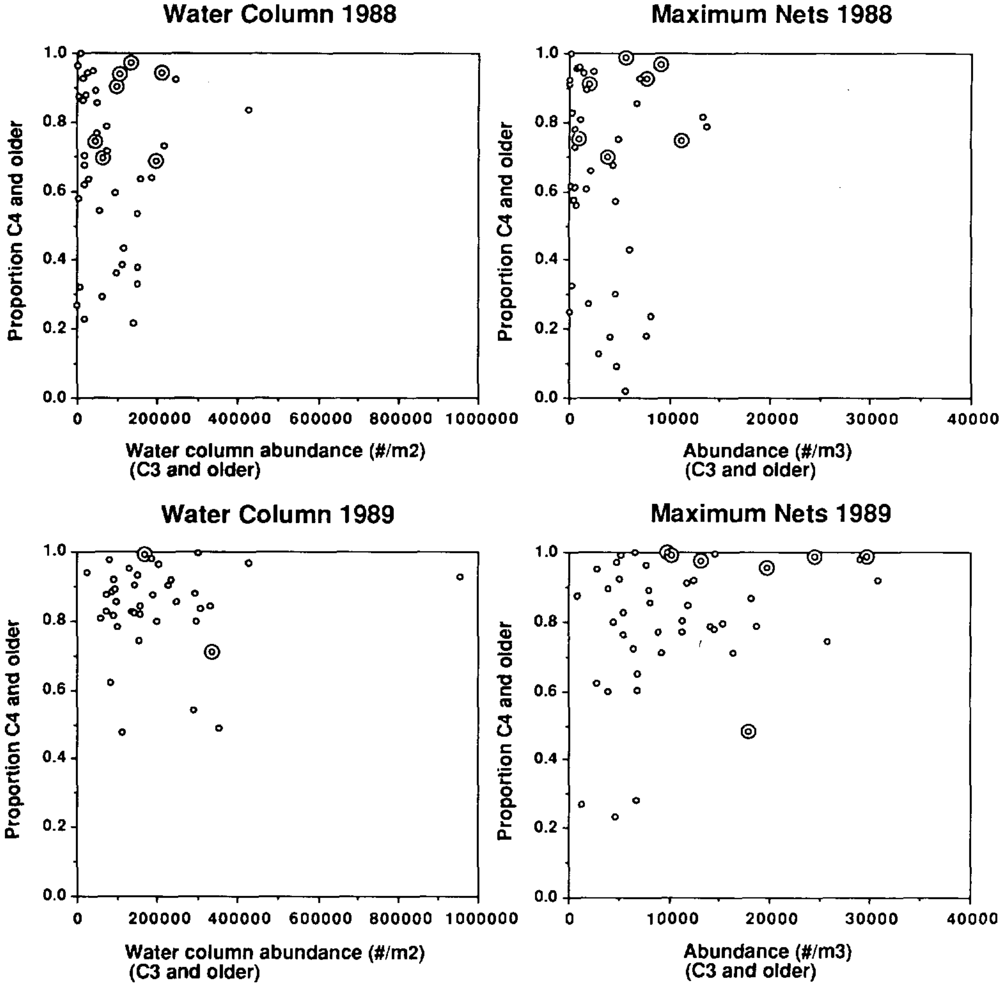


Fig. 11. Total *Calanus* abundance (copepodite 3 stage and older) vs the proportion of the larger "whale food size" stages (copepodite 4 stage and older) in the water column (left) and maximum nets (right) from 1988 (top) and 1989 (bottom). Samples from locations with feeding whales present are double circled.

Associations between copepods and right whales have been documented in other locations, especially at small spatial scales. Murison and Gaskin (1989), sampling mostly during daytime at 5-km intervals on a 20 × 25 km grid in the Bay of Fundy, found significantly higher copepod biomasses near feeding right whales than at locations where whales were absent. Mayo and Marx (1990), sampling in Cape Cod Bay, found significantly higher densities of copepods in surface tows within 5 m of feeding right whales compared to farther away.

How the whales find and select particular patches in which to feed remains an open question. Figure 11, showing some of the characteristics of the patches in the GSC in which whales were feeding, uses parameters (abundance and a size class indicator) that could be within the visual capabilities of the right whale. The most obvious feature is that the percentage of these larger "whale food size" lifestages at locations with feeding right whales was at least 70% (with one exception) and often over 90%. Measured total *Calanus* abundances at the "whale present" locations spanned a wide range, however, with minimum concentrations (in the depth zone of maximum abundance) of 1023 m^{-3} in 1988 and 9749 m^{-3} in 1989. Although the low 1988 value may be due in part to sampling artifacts described later, it is also possible that in years of low overall copepod abundance, as 1988 appeared to be, whales may feed on suboptimal copepod concentrations. A threshold for right whale feeding of about 800–1000 organisms m^{-3} was also found by Murison and Gaskin (1989) in the Bay of Fundy and by Mayo and Marx (1990) in Cape Cod Bay.

Many SCOPEX samples, from locations where whales were absent or could not be seen even if present, fell within the utilized range of abundance and size class proportion and would appear to be potential targets for whales (Fig. 11). Similar occurrences of high copepod densities away from whales were also observed by Murison and Gaskin (1989) and Mayo and Marx (1990). This suggests that other factors (for example, the chance of encounter) may influence which specific patches, among all patches potentially suitable in terms of copepod abundance and age composition, the whales utilize at a particular time.

Several phenomena may account for the variable association between copepod abundances and right whales. First, there are several possible sampling artifacts. In 1988, the MOCNESS sampling may have missed a portion of the daytime copepod population as previously described ("whale present" samples were all taken during the day), which was aggregated near the seafloor below the lower sampling limit of about 7–10 m altitude. (However, water column and maximum net abundances overall were not significantly different between day and night in either year.) Also, the copepods may have been highly concentrated in very thin layers such that high localized abundances were diluted by nets that covered broader depth intervals. For example, the daytime tow in 1988 with 5 m depth intervals near the bottom (where the copepods were aggregated) gave a maximum abundance of 5585 m^{-3} while the immediately proceeding tow with the standard more broadly spaced depth intervals had a maximum concentration of only 1993 m^{-3}. On the other hand, a similar comparison in 1989 showed more similar concentrations at depth (maxima of 2030 m^{-3} for the narrow depth intervals vs 1618 m^{-3} for the broad interval), probably because most copepods remained near the surface in the day in 1989.

Second, the copepod concentrations in the GSC seemed to be spatially and temporally patchy. They may have been missed by some net tows even in the vicinity of whales or they may have disintegrated or been advected elsewhere over time. In the 1986 pilot program, for example, one net tow near whales apparently crossed a patch edge, and the 1989 samples across a slick with a feeding whale in it also provided evidence for sharp patch edges. The fluctuations in abundances with time in repeatedly sampled whale areas and the narrow spatial peaks of abundance in the horizontally sequenced tows suggest that the copepod patches were small and localized, temporally ephemeral, and subject to differential advection by the semidiurnal tidal flow and mesoscale currents. Patch characteristics may change between years (Fig. 5) because of differences in copepod behavior and the physical factors influencing aggregation.

Interactions with physical phenomena

A schematic of the regional circulation in springtime, based on drifter and Acoustic Doppler Current Profiler (ADCP) measurements made in SCOPEX, is shown in Fig. 12

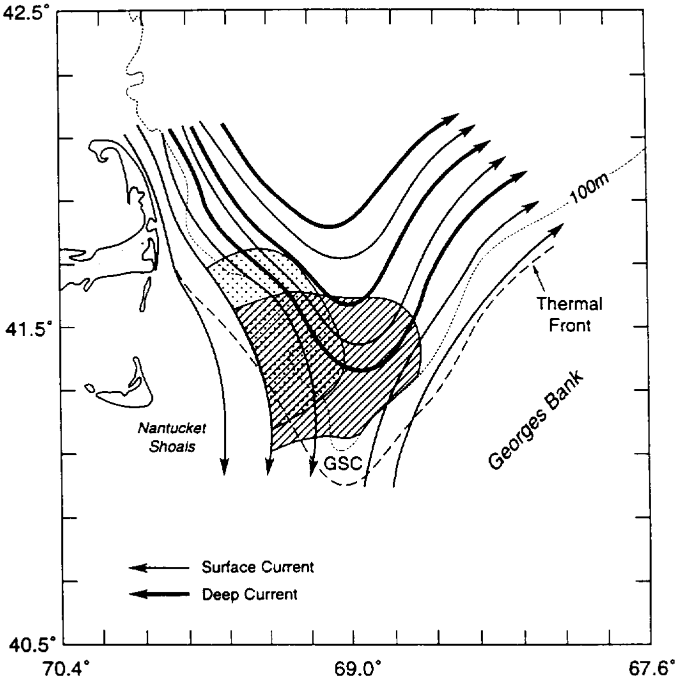


Fig. 12. Schematic of near-surface and deep currents during springtime in the northern Great South Channel region. The two main near-surface currents are shown by narrow arrows, while the broad cyclonic flow at depths greater than 50 m is shown by broad arrows. This schematic was developed from drifter and ADCP measurements made during the two main regional CTD surveys (April 1988; June 1989). The shading shows areas of surface current convergence for each year (dotted for 1988; lined for 1989) computed from the ADCP data. Also shown is the mean position of the surface thermal front caused by tidal mixing over the shallower sides of the Great South Channel. There is a distinct change in faunal composition across this front, with both *Calanus* and sightings of feeding right whales occurring primarily to the north of the front (WISHNER *et al.*, 1988; BROWN and WINN, 1989). Note that the thermal front is always shallower than 100 m. See CHEN (1992) and CHEN *et al.* (1995a,b) for a more detailed description of the SCOPEX physical measurements. See Fig. 3 for geographical plots of *Calanus* abundances and surface salinities to compare with the currents.

(see CHEN, 1992 and CHEN *et al.*, 1995a and b for a more detailed discussion of these physical measurements). Figure 12 shows two main near-surface currents in the northern GSC region. The first is a broad coastal current which flows generally south- and southeastward along the western flank of the GSC. As this current progresses southward, it splits into one branch which continues to flow southward along the western flank of the GSC and over and around Nantucket Shoals. The second branch turns east and northeast in a broad cyclonic flow, where it forms the second main current which flows north- and northeast through the GSC and around the northwest flank of Georges Bank. Beneath this near-surface flow at depths greater than 50 m, there is generally a cyclonic current roughly following the 100-m isobath from the east coast of Cape Cod to the northwestern flank of Georges Bank. The southward-flowing coastal current carries relatively fresh water from spring river runoff further upstream into the western Gulf of Maine, which can appear as a surface plume of low-salinity water off Cape Cod in late spring. The volume transport of this southward flowing coastal current was about twice as large in June 1989 (0.12 ± 0.06 Sv) compared to April 1988 (0.07 ± 0.03 Sv), and fresher surface water occupied a large area of the northern GSC in 1989. The southeastward transport of Maine Intermediate Water between 40 and 120 m depth was also about twice as large in 1989 as in 1988 (0.66 ± 0.14 and 0.31 ± 0.38 Sv, respectively). Part of this increase in transport in 1989 vs 1988 is due to increased river runoff in 1989 and the occurrence of the 1989 cruise later in the seasonal cycle than the 1988 cruises.

The highest total copepod abundances and biomasses (especially in 1988), and high abundances of younger stages, were associated with the presence of the low-salinity surface water (Fig. 3). Younger copepod lifestages appeared to be advected into the northern GSC region early in the spring in this low-salinity water and developed over time as the water flowed south and then east (Fig. 12). Older lifestages were associated with relatively high salinities, suggesting that they occurred mostly outside or at the edge of the low-salinity plume. Peak copepod abundances often seemed to be associated with the leading edge of the low-salinity water (Fig. 3), which also corresponded to a zone of fluid convergence as determined from calculations of residual current fields from ADCP data (Fig. 12) (CHEN, 1992). Correlations between high total copepod abundance and low surface salinity were strongest in 1988, and the convergence area was confined to the western flank of the GSC, because the edge of the plume crossed through the sampling area at that time. In 1989, most of the sampling area was already covered by the low salinity plume, and the convergence area spread eastward to the western flank of Georges Bank (Figs 3 and 12). A similar salinity-associated aggregation of a related copepod species was described in the Fraser River plume (MACKAS and LOUTTIT, 1988), and the role of fluid convergence in the concentration of fish in a frontal zone of a warm-core ring was modelled by OLSON and BACKUS (1985).

Calanus was present and numerically dominant in the early spring in 1988 in this area (during the EN-174 cruise) and later in the central part of the region outside the low salinity water, but abundances were typically low. Although the adult females present during the early spring 1988 cruise probably were the parents of some of the copepods that were present and growing during the whale feeding period, it seems unlikely that this small resident population alone could produce the massive numbers of young found in the patches. The dense copepod aggregations were probably a combination of both advected and locally spawned individuals. The primary source of the advected animals would appear to be the northwestern Gulf of Maine (rather than Georges Bank or the North Atlantic Slope Water), given the apparent association of the zooplankton with the low-salinity surface plume in 1988. Genetic studies of *Calanus* also support this (KANN and WISHNER, submitted b).

The specific location within the general region each year of peak abundances of the older copepod lifestages (and the whales that feed upon them) is probably a function of both the strength of the currents (Fig. 12) and the water temperature. While the seasonal cycle of development of *Calanus* is largely driven by temperature (CORKETT *et al.*, 1986; DAVIS, 1987b), its development occurs within a moving frame of reference. The time scale for zooplankton to be advected from the western flank of the northern GSC to the western flank of Georges Bank can be estimated from the transport values given above and the trajectories of the satellite-tracked drifters drogued at 5 m deployed during April–May 1988 and June 1989. In 1988, one drifter started 28 April on the western flank of the GSC at 41.44°N, 69.07°W, moved southeastward then northeastward making several cyclonic turns in the GSC, and finally arrived 27 days later (25 May) at 41.41°N, 68.75°W on the western flank of Georges Bank. In contrast, in 1989, a drifter went from the western flank of the GSC at 41.56°N, 69.34°W to the western flank of Georges Bank (41.31°N, 68.95°W) in about 10 days. These drifter results and the ADCP-derived currents both suggest that the time scale for passive particles to cross the northern GSC was greater in 1988 (about one month) than in 1989 (about one-half month).

In 1989, the water in the GSC region remained colder later into the spring than in 1988, and older copepod developmental stages occurred about 1–2 weeks later (Table 6). This delay in development was probably due, at least in part, to the lower temperatures. Satellite images (Cornillon, personal communication) showed that the surface water temperature in the region on 28–29 May was 10–11°C in 1988 and 9°C in 1989. The estimated development time of *C. finmarchicus* from hatching to the copepodite 5 stage is 24.9 days at 11°C and 30.3 days at 9°C (a difference of 5.4 days), using CORKETT *et al.*'s (1986) equations derived from laboratory studies. However, in reality, copepods are exposed to a range of temperatures during development because of their vertical migration, the warming of the water over time, and the spatial distribution of temperature within the region. Differences between years in these factors and also the time of hatching would affect the temperature exposure of the copepods, and thus their rate of development, and could account for much of the interannual variability observed in their development time. Additionally, DURBIN *et al.* (1995a,b) show that food levels and copepod grazing rates were lower in 1989 than in 1988, suggesting that food limitation may have also slowed the copepod development rates. The presumed longer time needed for development in 1989, as well as the higher southeastward and cross-channel transport, meant that the copepods were carried farther in 1989 in association with the low-salinity plume before reaching the copepodite 4 and 5 stages. Thus the peak abundances of older copepods in 1989 occurred later in the spring and farther downstream in the northeast part of the region, while 1988 peak abundances of these stages occurred earlier and in the southwest (Figs 3 and 4). Aggregations of feeding right whales in the two years followed the same geographic and temporal pattern (KENNEY *et al.*, 1995). Similar patterns of copepod development within a regional advective system have been studied by PETERSON *et al.* (1979) in the California Current and DAVIS (1984) on Georges Bank. PERRY *et al.* (1993) have analyzed zooplankton distributions in relation to currents at the Georges Bank front.

The north–south trending salinity front that marked the leading edge of the low-salinity water was also associated with small-scale changes in copepod population structure. In 1988, this feature crossed through the location of an east–west MOCNESS transect shortly before sampling (Figs 3 and 10). At the time of sampling, the water column at the western station was colder and unstratified compared to the stratified middle and eastern stations, which may explain why the copepod population structure differed along the 25 km transect in that year (Fig. 10). In 1989, however, the copepod population structure was similar at all three stations on this same transect, probably because the front was located to the east of the transect, and all stations were in stratified water on the lower salinity side of the front.

Variability in percent light transmission appears to be an indicator of extremely high concentrations of copepods in this area, probably from direct obstruction of part of the light beam by individual copepods (BEARDSLEY *et al.*, 1990). However, correlations of high biomasses and abundances with low mean percentage light transmission values were significant only for some comparisons in 1988. For 1988, there was also no apparent correlation of copepod abundances or biomasses with ambient potential food levels as indicated by *in situ* fluorescence. In 1989, however, correlations between fluorescence and abundance were significant but reversed in sign from day to night, suggestive of a feeding effect, especially since the copepods were not vertically migrating and remained at about the same depth day and night. Regional and interannual associations of food levels with copepod feeding rates were observed by other SCOPEX investigators (Durbin *et al.*, 1995b).

CONCLUSIONS

(1) Springtime aggregations of the planktivorous right whale (*Eubalaena glacialis*) occur in the northern Great South Channel region of the western Gulf of Maine where they feed upon dense concentrations of the copepod *Calanus finmarchicus*. This association was studied during the multidisciplinary South Channel Ocean Productivity Experiment (SCOPEX) in 1988 and 1989. Regional comparisons for each year showed higher water column abundances, and higher relative proportions, of older copepod lifestages near feeding whales than in areas without whales, but total water column copepod biomass and *Calanus* abundance did not always differ between these types of locations. This suggests that the whales seek out aggregations of older copepod lifestages rather than simply the most dense aggregations. Other factors (such as the chance of encounter) may also influence which specific patches, among all patches potentially suitable in terms of copepod abundance and age composition, the whales utilize at a particular time.

(2) The times and locations of the highest *Calanus* water column abundances varied between years, as did the presence of feeding whales, probably because of year-to-year differences in the springtime temperature cycle and current strength. A temporal progression of lifestages occurred within the region in both years during the roughly 3-week duration of each survey, indicative of a growing rather than a diapausing population, at least up to the copepodite 4 stage. Due in part to a delay in the springtime warming in 1989 compared to 1988, the copepod development cycle, which is largely driven by *in situ* temperature, was delayed about 1–2 weeks in 1989. Peak abundances of younger *Calanus* were found in the northwestern part of the region each year, whereas peak abundances of older *Calanus* were found in the southwestern and northeastern areas. This was probably due to the advection of maturing copepods by the regional circulation, especially the near-surface current associated with the movement of the low-salinity surface plume which forms each spring off Cape Cod. The copepod development cycle occurs with a moving frame of reference (i.e. the water itself); thus, peak abundances of the older copepods (those fed on by the whales) occurred later in the spring and further downstream in 1989 (when there were colder springtime temperatures and faster currents) than in 1988 (when the springtime temperatures were warmer and currents slower).

(3) Maximum *Calanus* abundances and biomass and water-column abundances of older copepodite stages were significantly higher (about double) in 1989 than in 1988, both in the region as a whole and at sites where whales were feeding. Copepods were also more aggregated in the vertical (i.e. more highly concentrated at the depth of maximum abundance) in 1989 than in 1988, and samples from whale-feeding areas were more homogeneous in composition (higher proportion of *Calanus* relative to all zooplankton) in 1989.

(4) At smaller spatial and temporal scales, abundances varied by a factor of 1–890X in samples from horizontal tows spanning about 0.5–1.5 km and by a factor of 1–50X over

24 h in the same geographic location in whale-feeding areas. Some of this variability was probably due to advection by the semidiurnal tidal currents. Near feeding whales, the copepod spatial distribution was patchy on small scales (with an estimated mean patch "size" of about 500 m), but the patchiness varied in texture interannually.

(5) Copepod abundances were much lower in early spring (March 1988) than in later spring (May 1988), with the March population structure dominated by adult females and the May population dominated by copepodite 4 and 5 stages.

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