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Spatial and seasonal patterns in abundance and age-composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank: 1977–1987

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Abstract—The mean seasonal cycle and distribution of various life history stages of *C. finmarchicus* throughout the Georges Bank (GB)–Gulf of Maine (GOM) region were characterized based on 5966 MARMAP zooplankton samples collected during 106 surveys over a 10-year period (autumn 1977–autumn 1987). A high degree of seasonal and spatial variability in *C. finmarchicus* abundance throughout the region was evident in contoured portrayals of data, grouped into standard stations and 2-month "seasons".

Eight subareas of the Gulf of Maine–Georges Bank region were identified through cluster analysis of standard stations having similar seasonal patterns in mean abundance of *C. finmarchicus* stages C3, C4, C5 and adults. These were the northern Gulf of Maine (Northern GOM); southern Gulf of Maine (Southern GOM); Scotian Shelf–coastal Gulf of Maine (Scotian–Coastal GOM); Mass Bay; tidally mixed Georges Bank (Mixed GB); tidal front on the Bank separating mixed from seasonally stratified water (Tidal Front GB); seasonally stratified water on the Bank (Stratified GB) and the Continental Slope adjacent to Georges Bank (SLOPE).

A distinct seasonal abundance cycle was present in all subareas, but, the magnitude and timing of annual maxima varied greatly among subareas. Peak abundance was reached early (March–April) in Mixed GB, Tidal Front GB and Mass Bay, and late (July–August) in Northern GOM and Scotian–Coastal GOM. Remaining subareas had maxima in May–June. Abundance increased 10-fold from January–February to March–April and decreased sharply from July–August to September–October in all areas except southern GOM and northern GOM. The amplitude of the annual cycle was weakest in northern GOM and southern GOM, where high concentrations of *C. finmarchicus* persisted year-round, and strongest in the tidally mixed shallow water on GB, where the sparsest densities of *C. finmarchicus* occurred most of the year. Abundance curves for the various areas converged in March–April, when *C. finmarchicus* was ubiquitously very abundant ($> 10^4/10\ \mathrm{m}^2$), and diverged from September to December.

C. finmarchicus stage distribution in the GB–GOM area was highly negatively correlated with mean water column temperature during the stratified season. This seemed more related to the hydrography of the region, which isolates warmer well mixed Georges Bank from the Gulf of Maine and the stratified areas on the Bank, than to temperature, because *Calanus* abundances decline on the Bank before water temperatures exceed their preferences.

A large part of the spatial and seasonal variation in *C. finmarchicus* abundance and age structure appears to be tightly coupled to major hydrographic regimes and to major circulation patterns in the region. There was a sharp ecotone between well-mixed Georges Bank and the Gulf of Maine as defined by *C. finmarchicus* abundance patterns and life history distributions. The ecotone is present year-round but is most apparent during the stratified season (May–October), when thermohaline density gradients and the near-surface current jet along the northern flank are generally strongest. The Gulf of Maine had the highest abundances of *C. finmarchicus*, and lowest spatial and seasonal variation in the region, while tidally mixed Georges Banks displayed the opposite pattern. This

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indication of stable population centers in the Gulf of Maine would make it a major source of *Calanus* in the region, particularly during March–April. Distributional patterns also suggest a strong *Calanus* influence from Scotian Shelf water in northern Gulf of Maine and on the southern flank of Georges Bank. Published by Elsevier Science Ltd

INTRODUCTION

There is continuing evidence that Earth's climate is changing (Manabe and Stouffer, 1994). One of the strongest signals of these changes will likely be variations in oceanic current systems, wind patterns and seasonal density stratification. Georges Bank (Fig. 1) is considered to be a transitional zoogeographic zone, with a wide seasonal range in water temperature and strong seasonality in fish species composition (Grosslein and Azarovitz, 1982). The hydrography on Georges Bank (GB) is also spatially and seasonally variable (Flagg, 1987). Much of this hydrographic variability is due to strong tidal currents interacting with the shallow bathymetry of the Bank. Additionally, several distinct water mass types from the surrounding region converge on GB, establishing seasonally and annually varying hydrographic conditions and fronts (Flagg, 1987). This environmental variablility, in addition to advective events, influences the distribution and annual variability of biological communities on the Bank (Flierl and Wroblewski, 1985; Cohen *et al.*, 1988; Meise-Munns *et al.*, 1990; Kane, 1994; Werner *et al.*, 1993; Lough *et al.*, 1994). Global Ocean Ecosystems Dynamics (GLOBEC) Northwest Atlantic field program (GLOBEC, 1988) was established to understand key trophodynamic processes and how the anticipated environmental changes in oceanic currents, hydrographic conditions and wind events might influence the fishery productivity on GB.

The abundance and distribution of cod and haddock, two of the principal fish species of interest, have varied widely over the past three decades. Most of this variation is believed to result from high fishing mortality (Hunt, 1988; NEFC, 1989). However, natural environmental variability also appears important (Flierl and Wroblewski, 1985; Smith and Morse, 1985; Cohen *et al.*, 1988). Eggs, nauplii and early stages of *C. finmarchicus* are important food items of larval cod and haddock (Kane, 1984). Consequently, perturbations in the abundance and distribution of *Calanus finmarchicus* may influence their abundance throughout the region.

A number of earlier studies, beginning with Bigelow (1926), have resolved some aspects of the distribution and population dynamics of *C. finmarchicus*. It is a large boreal copepod ranging from the Arctic to Chesapeake Bay (Davis, 1987a) and is among the dominant zooplankton species (including *Pseudocalanus* spp., *Paracalanus parvus*, *Centropages typicus*, *Centropages hamatus*, *Metridia lucens* and *Oithona similis*) in the GB–GOM region. On GB, *Calanus finmarchicus* dominates the annual zooplankton biomass (Davis, 1987a) and biovolume (Sherman *et al.*, 1987). When *C. finmarchicus* abundance is at its maximum (April–June), it is responsible for over 90% of the zooplankton biomass, even though it is subordinate in numbers to *Pseudocalanus* spp. (Davis, 1987a).

With seasonal increases in water temperature, *C. finmarchicus* enters diapause in the fourth and fifth copepodite stages in mid-summer and spends the remainder of the year at depths of 50–300 m in the Gulf of Maine (GOM) (Bigelow, 1926; Clarke, 1933; Mullin, 1963) and in Slope Water (200–500 m bottom depth) seaward of the Bank (Miller *et al.*, 1991). Davis (1987a) indicates that *C. finmarchicus* spawns on GB in February, producing two generations between March and July. During this time it is more abundant over the

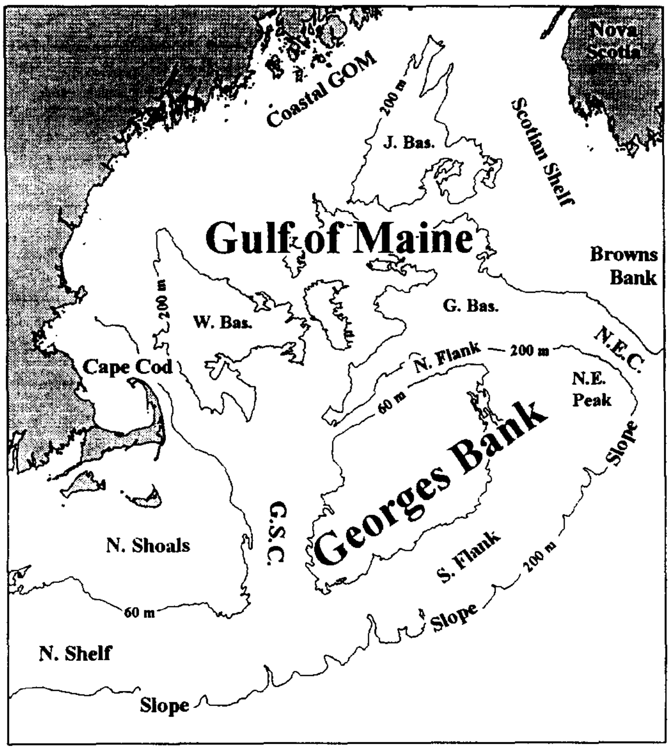

Fig. 1. Major bathymetric features and landmarks in the Georges Bank–Gulf of Maine region. Landmarks: Nova Scotia, Cape Cod; Banks and Shoals: Georges Bank, Browns Bank, Nantucket Shoals (N. Shoals); Channels: Northeast Channel (N.E.C.), Great South Channel (G.S.C.); Major Basins: Georges Basin (G. Bas.), Jordan Basin (J. Bas.), Wilkinson Basin (W. Bas.); Continental Slope (Slope); Other: Southern Flank of Georges Bank (S. Flank), Northern Flank of Georges Bank (N. Flank), Coastal Gulf of Maine (Coastal GOM), Scotian Shelf, Nantucket Shelf (N. Shelf).

deeper regions of the Bank (60–100 m) than in the shallow tidally-mixed area, GOM, or Slope Water (GLOBEC, 1992).

Although some broad aspects of the population dynamics of *C. finmarchicus* have been described, many details remain vague, particularly the locations of overwintering populations, the influence of physical factors such as circulation and temperature on its distribution, abundance, and development, and the relative contribution of GB, GOM, and the Scotian Shelf to population dynamics of *C. finmarchicus* throughout the region. Bigelow's pioneering surveys of the entire region did not adequately sample the shallow water on GB. More recent surveys summarized by Davis (1987a) encompassed only a few years. Sherman *et al.* (1987) characterized the zooplankton community in the immediate vicinity of GB using the first 5 years (1977–1981) of data collected by the National Marine Fisheries Service, Marine Monitoring Assessment and Prediction (MARMAP) program (Sherman, 1980).

Our purpose here is to characterize the distribution and seasonal cycle of various life history stages of *C. finmarchicus* throughout the GB–GOM region based on MARMAP zooplankton collections made over a 10-year period (autumn 1977–autumn 1987). We also examine relationships between seasonal and spatial patterns in the life history stages of *C.*

finmarchicus and water column temperature. This work establishes a "climatology" for *C. finmarchicus* and forms a benchmark for comparisons with current GLOBEC investigations.

METHODS

Field collection

Zooplankton samples were collected during 106 surveys aboard vessels from the U.S.A., Poland, the Soviet Union, and the German Democratic Republic during 1977–1987 as part of the National Marine Fisheries Service (NMFS) MARMAP program (Sherman, 1980). Approximately 6–12 surveys of the Northeastern U.S. continental shelf were conducted each year. Most surveys occupied standard MARMAP stations which are *ca* 25–35 km apart (Fig. 2). Approximately one-third of the collections were made during surveys (e.g. NMFS groundfish trawl surveys and scallop surveys, etc.) on which sampling density and station distribution differed from the pattern shown in Fig. 2.

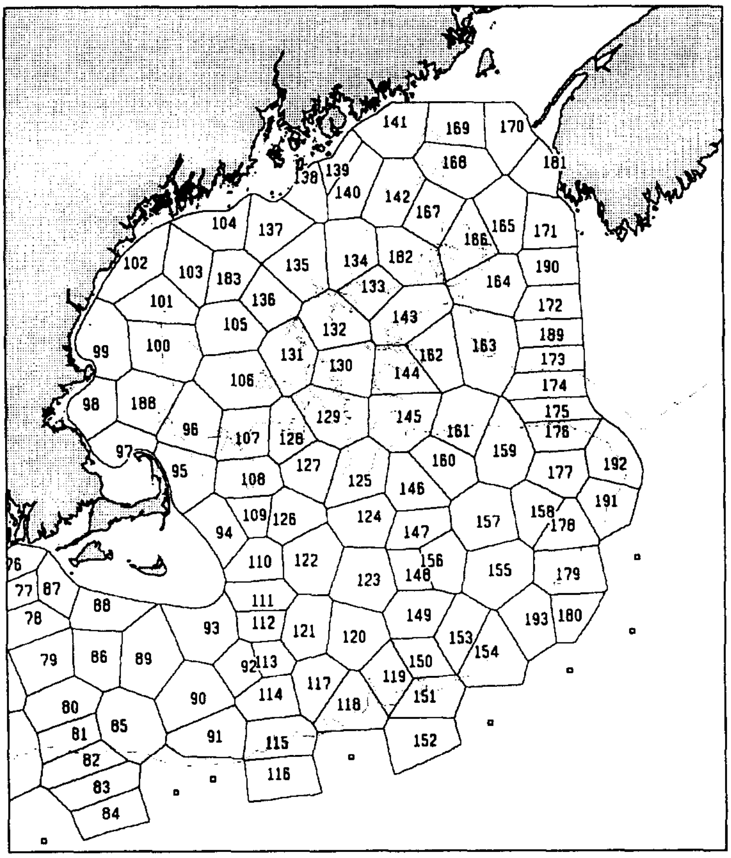

Fig. 2. Locations of standard MARMAP stations and tiles (polygons). The station/tile number is centered over the standard coordinate. Standard MARMAP stations/tiles 93–193 (excluding 184–187) were used in this study.

Zooplankton were collected with a 61 cm diameter, 0.333 mm mesh net attached to a bongo sampler (Posgay and Marak, 1980). Oblique tows were made from the surface to a depth of 5 m above the bottom and back to the surface. Tows were confined to the upper 200 m of the water column when bottom depth exceeded 200 m. The nets were towed at speeds ranging from 1.5 to 3.5 knots (2.8–6.5 km h^{-1}), lowered at a wire speed of 50 m min^{-1} and retrieved at 20 m min^{-1}. The volume of water filtered was measured with a General Oceanics* digital flowmeter, and a Bendix Model T-1 time-depth recorder was used to record the towing profile and maximum sampling depth. Flowmeters were routinely calibrated before and after each survey (Potter, 1978). Additional details of sampling procedures as well as maps of individual cruise tracks are given in Sibunka and Silverman (1984, 1989). Zooplankton samples from the 0.333 mm nets were sorted, identified, staged and counted at the Plankton Sorting Center, Szczecin, Poland. This mesh size quantitatively catches copepodite C_3 and above of *C. finmarchicus*. This portion of the population was analyzed for this paper.

Statistical analyses

The compiled data set consists of 5966 samples. To unify data from several field programs, each with different spatial sampling patterns, data were grouped into tiles (Green and Sibson, 1978; Ripley, 1981) shown in Fig. 2. The tiles were defined by the standard coordinates of the MARMAP stations (Fig. 2) where samples were repeatedly collected during MARMAP surveys. In this partitioning scheme, all samples located within a tile are closer to the standard MARMAP station used to define the tile than to any other standard MARMAP station.

We judged the sampling frequency to be insufficient for the construction of representative mean monthly portrayals of the seasonal distribution and annual cycle of copepod abundance, but sufficient for constructing 2-month mean portrayals. Cumulative frequency plots of the number of observations per tile show that 50% of the tiles were sampled approximately five times in January–February and up to 11 times in September–October during the MARMAP decade (Fig. 3). Consequently, data over the entire 10 year period, irrespective of year, were grouped into six 2-month intervals or "seasons" (January–February, March–April, May–June, July–August, September–October, and November–December).

Abundance estimates (no. per 10 m^2) of *C. finmarchicus* were log-transformed [$\log_{10}$(abundance + 1)] prior to statistical compositing and analyses. Contoured distributional maps for each 2-month period were generated using means of log-transformed abundances grouped by tile (Appendix A), standard tile coordinates transformed to map coordinates using Lambert's conic conformal map projection (Snyder, 1987), and Surface III contouring software (Sampson, 1988). FASTCLUS (SAS Inst., 1990), a statistical clustering program, was used to identify and demarcate ecologically distinct subareas of the GB–GOM region. Tiles having similar 2-month mean abundances of *C. finmarchicus* stages C_3, C_4, C_5 and adults throughout the annual cycle were clustered (grouped) into subareas using the nearest centroid sorting method with allowance for cluster seed updates.

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*The use of trade names does not imply endorsement by NOAA/National Marine Fisheries Service.

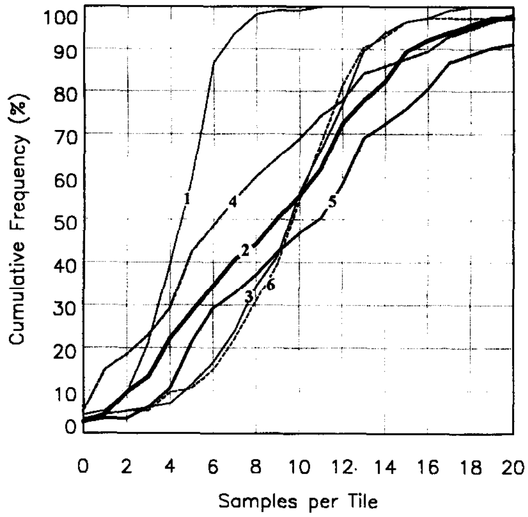


Fig. 3. Cumulative sampling frequency by two month season during 1977–1987 MARMAP period. January–February (1), March–April (2), May–June (3), July–August (4), September–October (5), November–December (6).

RESULTS

January–February

Total abundance of *C. finmarchicus* is high (10^4–10^5/10 m^2) throughout most of GOM, while lower abundances occur in the nearshore western Gulf (Mass Bay–Cape Cod) and on the Scotian Shelf (Fig. 4). Highest mean abundances (1.2–1.7×10^5/10 m^2) are present over the Wilkinson and Jordan Basins (Fig. 4). The area of GOM with *Calanus* abundance $> 10^5$/10 m^2 is minimal during January–February relative to other periods.

There is a sharp contrast between GOM and GB. On GB, mean abundances are at least an order-of-magnitude lower (10^3–10^4/10 m^2) than in GOM, except for the Northeast Peak. Though abundances are low on GB in January–February, they do represent an increase, particularly in adults and C_5, over levels during November–December (Fig. 4). Adults, and to a lesser extent C_5 copepodites, are beginning to be numerous in shallow water along the northern flank, Great South Channel, Northeast Peak and adjacent areas of the southern flank. Throughout the region, a progression is evident in age-composition of the population, with adults $> C_5 > C_4 > C_3$. Copepodites C_4 are relatively abundant along a broad swath stretching between Wilkinson and Jordan basins, but less abundant than C_5 and adults. C_3 is generally sparse during January–February (Fig. 4). Also note that its distributional pattern is opposite that for C_4, C_5, and adults: C_3 is less abundant in the central GOM than on GB, and areas in northern GOM, with lowest C_3 abundances generally aligned with areas having greatest abundances of older stages. C_3 copepodites are most abundant along the southeastern flank of GB (Fig. 4).

March–April

C. finmarchicus is ubiquitously very abundant ($> 10^4$/10 m^2) during March–April, approximately 10-fold higher than during the preceding January–February period (Fig. 4). Greatest abundances ($> 10^5/10\,m^2$) appear along a band from western GOM across central GOM, over Jordan Basin, and in patches along the southern flank of GB.

As in January–February, adults and C_5 copepodites are most abundant in northern GOM. Note, however, that in nearshore western GOM, copepodites rather than adults are responsible for the elevated *Calanus* abundance. C_3 and C_4 copepodites are more uniformly distributed during March–April than during January–February. Lowest abundances of these stages occur between the southern edge of Wilkinson Basin and the northern edge of the Great South Channel (Fig. 4). On GB, C_3 and C_4 copepodites increase sharply from January–February to March–April, particularly along the southern flank. High total abundance in this area is mostly from C_3 and C_4 copepodites, and not adults and C_5 as in central GOM.

May–June

C. finmarchicus abundance is high ($> 10^5/10\,m^2$) throughout the central and western GOM and along nearly the entire length of the southern flank of GB (Fig. 4). These areas of elevated abundances reach maximal size during May–June. A band of lower total abundance ($> 10^4/10\,m^2$) extends from the Scotian Shelf across the Northeast Channel, through the shallow water on GB, and onto the shallow water flanking Nantucket Shoals.

The most striking feature in stage distribution for this 2-month period is the paucity of all life history stages of *C. finmarchicus* in the shallow (< 60 m) water on GB. Areas of greatest abundance of C_4, C_5 and adults are in the vicinity of Wilkinson and Jordan Basins, and in a band covering the southern flank, Great South Channel (GSC) and Slope. C_3 is more patchy with highest abundance found inshore in the western GOM through the GSC and onto the southern flank of GB. In May–June C_5 predominates over other stages in the central GOM and is principally responsible for the high total abundances. This age-structure varies from that observed from January to April, when adults are more numerous than C_5 copepodites.

July–August

The largest numbers of *C. finmarchicus* ($> 10^5/10\,m^2$) still reside in the GOM over an area comparable in size to that during May–June (Fig. 4). Patches of high abundance along the southern flank of GB, Slope and Nantucket shelf are less coherent than during May–June as a result of declining adult abundance. Similar decreases in adults and total abundance are evident in the nearshore western GOM.

The shallow water on GB is nearly depleted of *C. finmarchicus*. The annular abundance gradient established in May–June is more pronounced with total abundance and adults increasing three and four orders-of-magnitude, respectively, from the shallow water on the Bank to the nearby deep GOM water. Though lowest numbers of C_3 are also present in the shallow water, the delineation between GB and GOM is less sharp than that for older stages of *Calanus*.

September–October

Total abundance still exceeds $10^5/10\,m^2$ throughout a large portion of GOM (Fig. 4). As in the previous two periods, abundance on the Scotian Shelf is lower than central GOM. On

GB *Calanus* abundance is low, approximately 1/10th the levels observed during July–August. Relatively high abundances ($> 10^4/10\,m^2$) on the Bank are restricted to the deeper water over the GSC and adjacent areas on the southern flank.

C. finmarchicus is exceptionally scarce in the shallow water on the Bank. The abundance gradient, radiating from shallow to deep water on the Bank, is much steeper than during the preceding two periods. For example, total abundance increases five orders-of-magnitude proceeding from the shoals across the northern flank and into Georges Basin (Fig. 4). *C. finmarchicus* also is not abundant in the shallow water flanking Nantucket Shoals and isolated patches over the continental slope.

C. finmarchicus adults are moderately abundant ($> 10^3/10\,m^2$) only in central (offshore) GOM and very abundant ($> 10^4/10\,m^2$) only in isolated patches. These patches appear as remnants of the large coherent area of adult abundance established in January–February and persisting through July–August. The area of low adult abundance on GB coincides approximately with water less than 60 m deep. Throughout the region, copepodites C_5, and to a lesser extent C_4, generally predominate over adults, continuing the trend observed during May–June and July–August. C_5 is relatively abundant ($> 10^3/10\,m^2$) throughout most of the deep water on GB but scarce in the shallow water on the Bank, water flanking Nantucket Shoals, and along the Slope. On GB copepodite C_4 is abundant only on the southern flank near the GSC. This area had high densities of C_4 during the preceding period (Fig. 4). In GOM C_4 is ubiquitously abundant ($> 10^4/10\,m^2$), and is particularly abundant along a swath between Wilkinson and Jordan Basins. Abundance of copepodite C_3 is low throughout the region, except in northern GOM and a small section of the southern flank of GB, where high concentrations of C_3 occurred during the preceding July–August period.

November–December

The distributional pattern of *C. finmarchicus* during November–December is similar to September–October. Highest abundance still occurs in GOM, but the area with total abundance greater than $10^5/10\,m^2$ is greatly diminished (Fig. 4). Similarly, the patch of high total abundance ($> 10^4/10\,m^2$) present in the GSC and adjacent southern flank in September–October is not present in November–December. *C. finmarchicus* continues to be scarce in the shallow water on the Bank, near Nantucket Shoals, and along the Slope.

Adults are found mainly in offshore areas of the GOM. In central GOM, the area of high adult abundance ($> 10^4/10\,m^2$) extant in July–August has receded to several small patches in the vicinity of Wilkinson and Jordan Basins. On the Northeast Peak of GB, moderate numbers of adults are present; elsewhere on the Bank adults are rare.

C_5 generally dominates over other life history stages throughout the region. C_5 is very abundant ($> 10^4/10\,m^2$) throughout GOM, but, the area in central GOM with concentrations of $C_5 > 10^5/10\,m^2$ is diminished relative to September–October. C_5 is much less abundant on GB than in the GOM. On the Northeast Peak, the southern flank and GSC values exceed $10^3/10\,m^2$. The overall distribution pattern for C_4 is similar to that of adults, except C_4 are relatively more numerous in GSC, and adjacent areas along the southern flank of GB. These areas of the Bank had relatively high concentrations of C_4 during September–October. There are very few C_3 found anywhere (Fig. 4). C_3 reaches its annual minimum abundance on GB during November–December, whereas the minimum in GOM is during January–February.

Regional and seasonal differences in abundance and age-composition

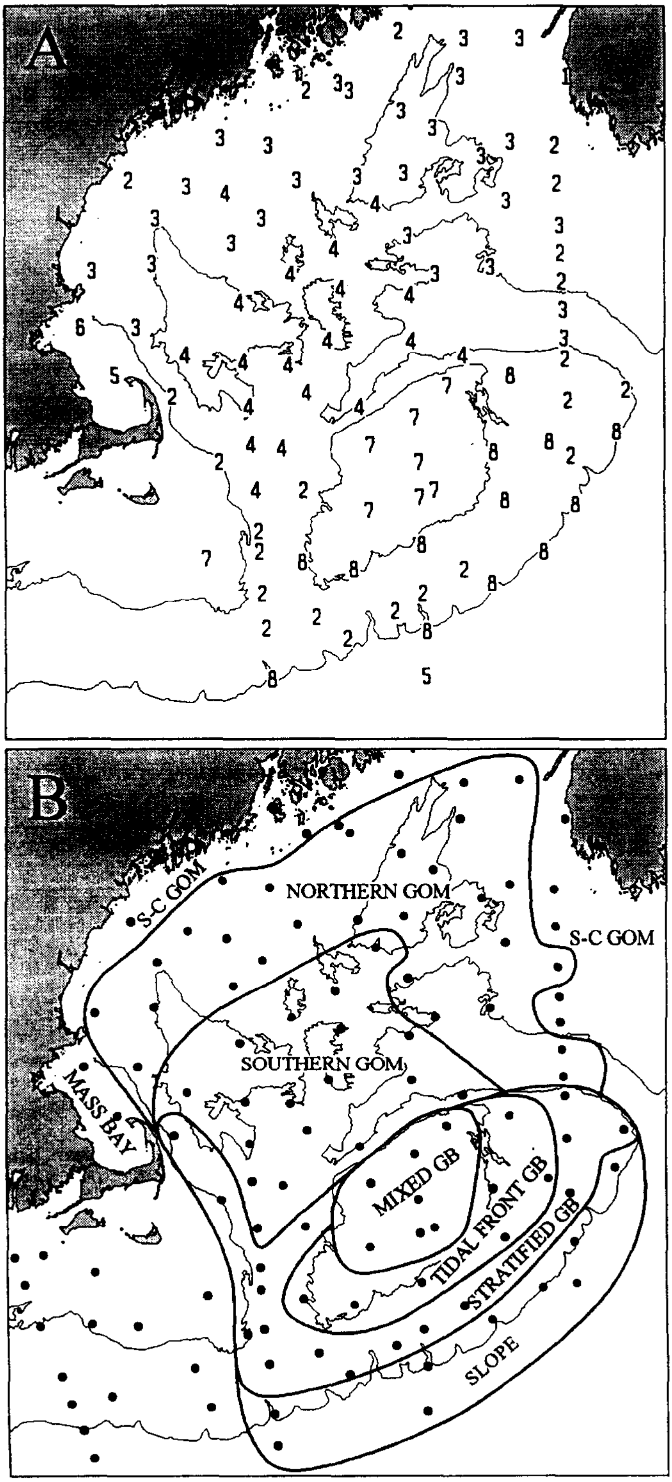
Further identification and generalization of the spatial and temporal patterns was accomplished by grouping tiles (Fig. 2) having similar annual cycles of *C. finmarchicus* abundance and age-composition into subareas of the GB–GOM region. The clustering procedure (described earlier) identified eight groups or statistical clusters (Fig. 5A). From this and consideration of distributional patterns (Fig. 4) we defined eight subareas (Fig. 5B): northern Gulf of Maine (Northern GOM); southern Gulf of Maine (Southern GOM); Scotian shelf–Coastal Gulf of Maine (Scotian–Coastal GOM); Mass Bay; tidally mixed Georges Bank (Mixed GB); tidal front on the Bank separating mixed from seasonally stratified water (Tidal Front GB); seasonally stratified water on the Bank (Stratified GB); and Continental Slope adjacent to GB (SLOPE). Subareas Scotian–Coastal GOM and Stratified GB belong to the same statistical group (cluster no. 2) but are separated by the Northeast Channel. Cluster no. 8 was also split into two subareas (Tidal Front GB and SLOPE) by a band of tiles in cluster no. 2 (Stratified GB subarea). Tiles in Mass Bay (cluster nos 5 and 6) were grouped into one subarea (Mass Bay) because of their proximity to each other and the mouth of the bay. Cluster no. 1, occurring on the coast of Nova Scotia (tile 181, Fig. 2) always appeared as a statistical outlier and was joined with the adjacent stations in Scotian–Coastal GOM for further analyses.

A distinct seasonal abundance cycle is present in all subareas, however, the magnitude and timing of annual maxima varies greatly among subareas (Fig. 6). Peak abundance is reached early (March–April) in Mixed GB, Tidal Front GB and Mass Bay, and late (July–August) in Northern GOM and Scotian–Coastal GOM. Remaining subareas have maxima in May–June. Abundance increases 10-fold from January–February to March–April and decreases sharply from July–August to September–October in all areas except Southern GOM and Northern GOM. More gradual declines occur after September–October until the annual minimum is reached in January–February, except in Tidal Front GB and SLOPE (November–December), and Mixed GB (September–October).

Abundance curves for the various areas converge in March–April and diverge from September to December. This spatial homogeneity/heterogeneity is also apparent in Fig. 4. The amplitude of the annual cycle is weakest in Northern GOM and Southern GOM, where high concentrations of *C. finmarchicus* persist year-round, and strongest in the tidally mixed shallow water on GB, where the sparsest densities of *C. finmarchicus* occur most of the year.

Overall, variance in *C. finmarchicus* abundance (interannual, seasonal, and spatial) is related inversely to abundance. Areas with greatest mean abundance (i.e. Southern GOM) have the lowest inter-intraseasonal variation (Fig. 6, Table 1, Appendix A and Appendix B), and highest spatial coherence (lower coefficients of variation in mean abundance among tiles (Fig. 7, Appendix A), while the reverse is true for areas of low abundance (i.e. Mixed GB).

There are also some noteworthy similarities and differences in the age-composition of *C. finmarchicus* among the eight subareas (Fig. 8). In January–February adults dominate (60–80%) the population in all subareas (except Mass Bay). The remainder of the population is primarily C_5 copepodites. C_4 and C_3 collectively account for only trace proportions (not apparent in Fig. 8) except in SLOPE (17%), Mass Bay (10%), and Tidal Front GB ($\sim$5%). This represents a normal transition in age structure from the preceding November–December period, when C_5 copepodites predominate (70–90%) in all subareas (Fig. 8).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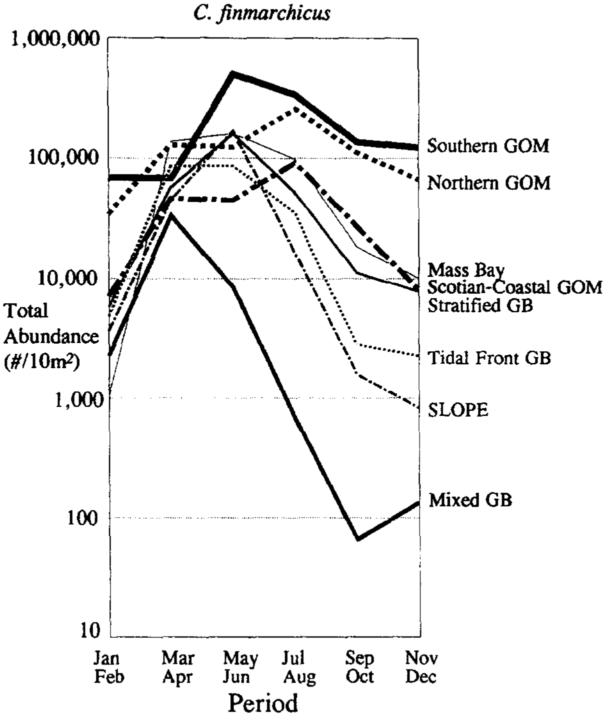


Fig. 6. Annual cycle of *C. finmarchicus* abundance in each subarea. (See Fig. 5B for subarea locations.)

Relationship between abundance and water temperature

The relationship between abundances of copepodites C_3, C_4, C_5 and adults and mean water column temperature was examined for each 2-month period (Fig. 9). From January–April there was no statistically significant relationship between abundance and water column temperature ($P > 0.05$). A negative association between abundance and temperature emerged in May–June, intensified during July–August and September–October (highest correlation coefficients), and remained high through November–December (all correlations significant at $P < 0.05$). During the May–October stratified season the relationship of abundance to temperature was usually weakest for C_3 (i.e. lowest correlation coefficient, although $P < 0.05$). From July to October the correlation coefficients and regression slopes increased with stage ($C_3 < C_4 < C_5$). The slope for adults was highest in November–December.

Fig. 5. Locations of subareas identified by cluster analysis of seasonal abundance of life history stages of *C. finmarchicus*. (A) Cluster number (1–8) assigned to each tile by clustering algorithm. (B) Subareas: Scotian Shelf–coastal Gulf of Maine (S–C GOM); northern Gulf of Maine (Northern GOM); southern Gulf of Maine (Southern GOM); tidal-mixed Georges Bank (Mixed GB); tidal front Georges Bank (Tidal Front GB); stratified Georges Bank (Stratified GB); Continental Slope (SLOPE); and Mass Bay (Mass Bay tile 97,98: cluster 5 and 6). Additional details are provided in Methods.

Table 1. *Mean* Calanus finmarchicus *abundance* ($\log_{10} + 1$), *variance, and number of observations by season and subarea*

Subarea	January–February mean (var.) *N*	March–April mean (var.) *N*	May–June mean (var.) *N*	July–August mean (var.) *N*	September–October mean (var.) *N*	November–December mean (var.) *N*
Southern GOM	4.84 (0.21) 100	4.83 (0.45) 167	5.70 (0.73) 216	5.53 (0.42) 114	5.14 (0.46) 214	5.09 (1.17) 181
Northern GOM	4.54 (0.61) 141	5.11 (1.43) 133	5.10 (2.75) 250	5.41 (1.63) 118	5.05 (0.71) 207	4.82 (1.29) 276
Scotian–Coastal GOM	3.85 (0.22) 34	4.66 (2.15) 30	4.65 (2.72) 44	4.96 (2.25) 14	4.43 (0.99) 42	3.91 (1.25) 56
Mixed GB	3.36 (0.35) 34	4.52 (0.91) 82	3.93 (1.63) 74	2.83 (2.95) 103	1.81 (3.14) 103	2.13 (2.47) 78
Tidal Front GB	3.68 (0.30) 49	4.93 (0.68) 114	4.93 (0.82) 81	4.54 (1.44) 112	3.45 (1.88) 134	3.35 (2.25) 108
Stratified GB	3.77 (1.02) 80	4.76 (1.02) 198	5.21 (1.46) 172	4.71 (0.98)169	4.05 (0.85) 268	3.89 (0.93) 225
SLOPE	3.56 (0.49) 21	4.65 (1.86) 71	5.23 (0.54) 47	4.21 (1.48) 41	3.19 (1.44) 72	2.92 (1.67) 48
Mass Bay	3.03 (2.15) 12	5.14 (0.40) 13	5.21 (2.13) 15	4.99 (0.25) 9	4.26 (1.36) 19	4.01 (0.44) 23

During May–June, *C. finmarchicus* of all stages have an apparent split in abundance numbers at or about 8°C (Fig. 9). By July–August, this dichotomy about the regression line is no longer apparent.

DISCUSSION

Mass Bay

Our results support those of Bigelow (1926) who identified Mass Bay as an area separate from the rest of the GOM *C. finmarchicus* community. *C. finmarchicus* abundance and age-composition at the two stations (tiles) in Mass Bay were consistently different from other subareas in GOM (Figs 6 and 8). Seasonal mean phytoplankton biomass (Chl *a*) levels in Mass Bay are among the highest in the study area (Fig. 10). The particularly high phytoplankton biomass levels during spring bloom (January–February) and ensuing two orders-of-magnitude increase in *C. finmarchicus* mean abundance (Fig. 6), and strong dominance by C_3 during March–April (Fig. 8) suggest that Mass Bay may be acting as a small scale "*C. finmarchicus* pump" (Plourde and Runge, 1993) supplying *Calanus* into the GOM.

Gulf of Maine

When patterns of *C. finmarchicus* abundance and stage composition in the GOM are examined the influence of water mass and circulation in the GOM becomes apparent. It is well recognized that one of the major inputs of water to the GOM is from Scotian Shelf water (Hopkins and Garfield, 1979), which enters the Gulf through the Northeast Channel and passages between Cape Sable and Browns Bank (Brown and Irish, 1993). There is increasing evidence that Scotian Shelf water also flows onto GB. Bigelow (1927) provides some evidence of this from surveys in February and April, 1920. Further evidence from recent hydrographic and satellite data is provided by Hopkins and Garfield (1981), EG and G (1980), Flagg (1987) and Bisagni *et al.* (1996). Analyses of MARMAP hydrographic data show an early winter maxima of shelf water volume occurring at nearly the same time as the January salinity minima reported by Smith (1983,1989a, 1989b) south of Cape Sable, suggesting a regular occurrence of Scotian Shelf water crossing the Northeast Channel onto

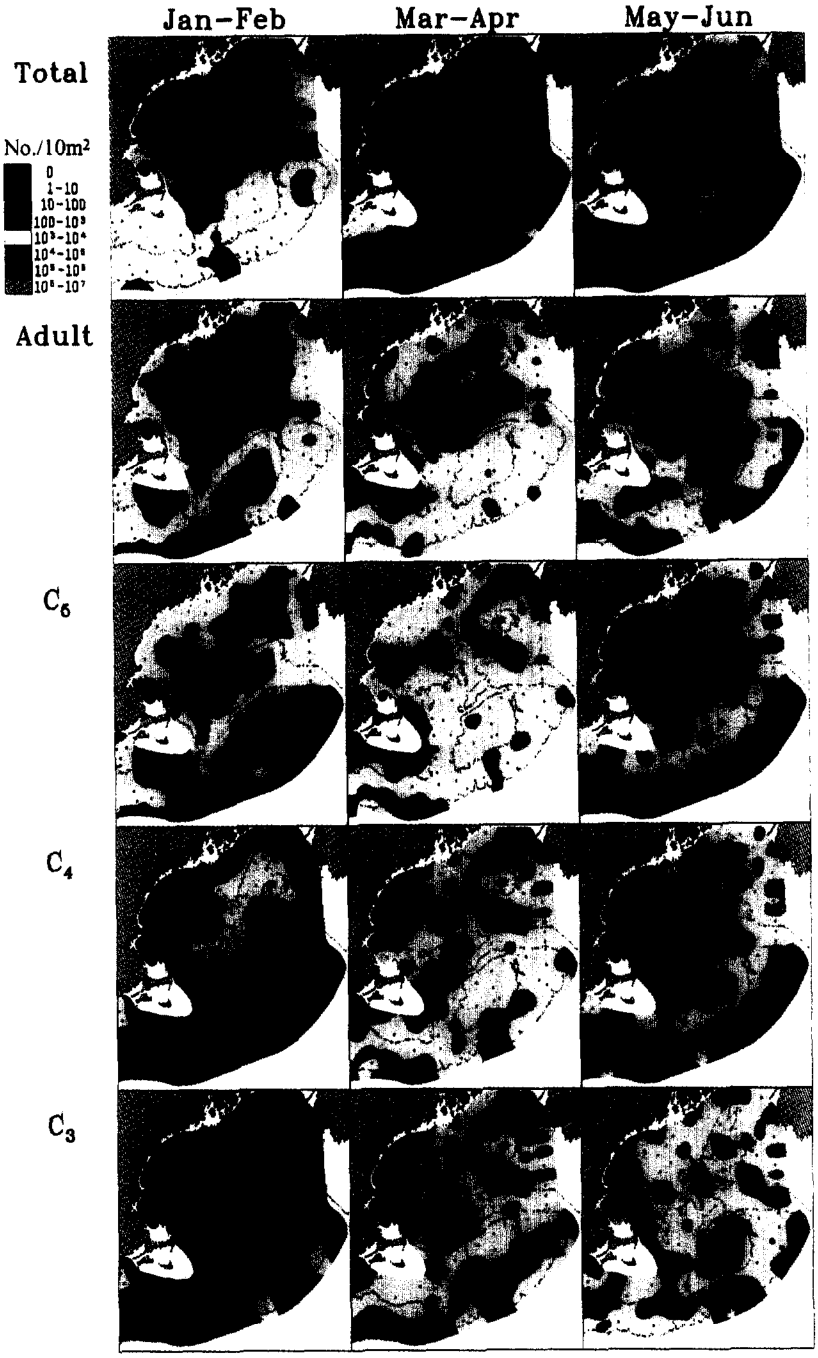


Fig. 4. Seasonal distribution of *Calanus finmarchicus*. Seasons: January–February, March–April, May–June, July–August, September–October, November–December. Top to bottom row: total abundance, adults, C_5, C_4, and C_3 copepodites. Additional details are provided in Method section. (*Continued overleaf.*)

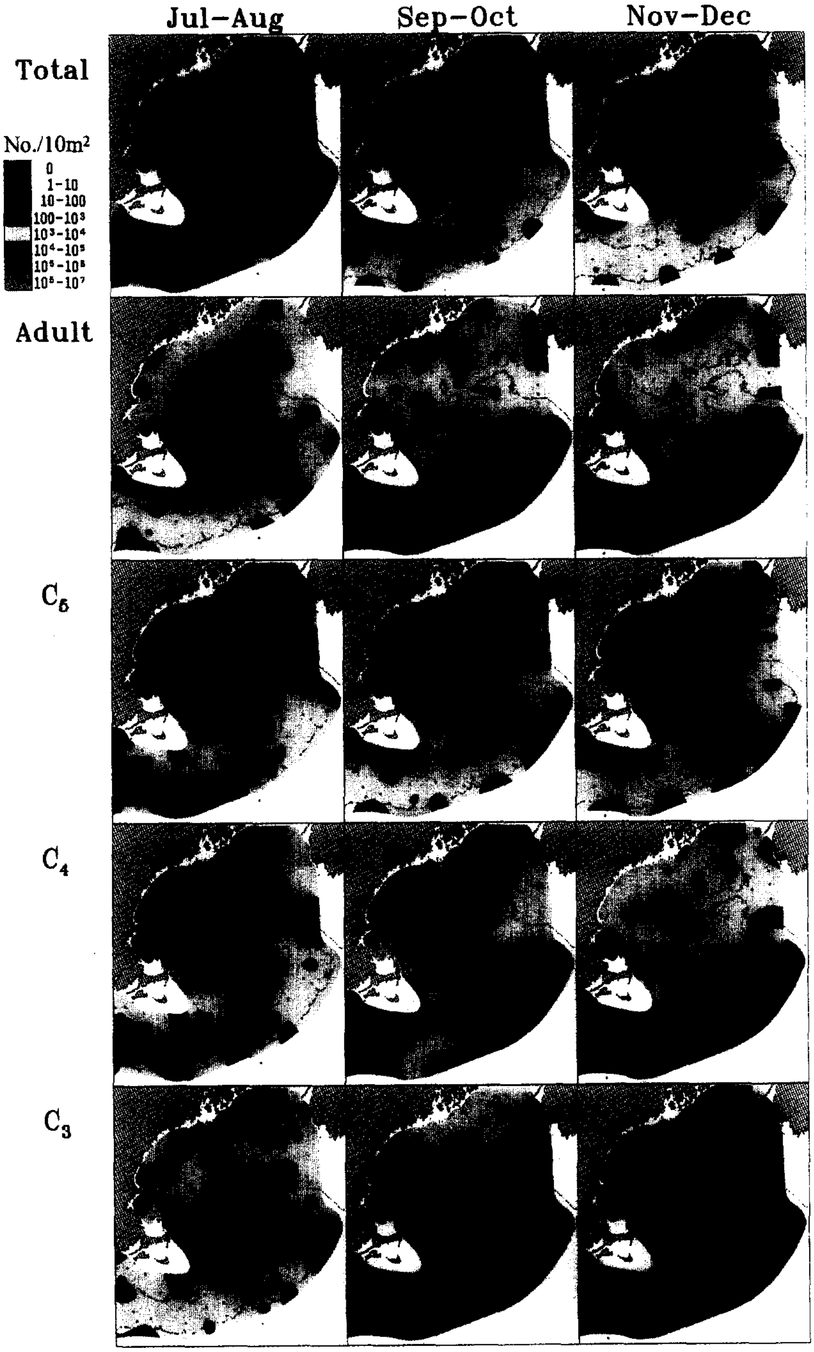


Fig. 4. *Continued.*

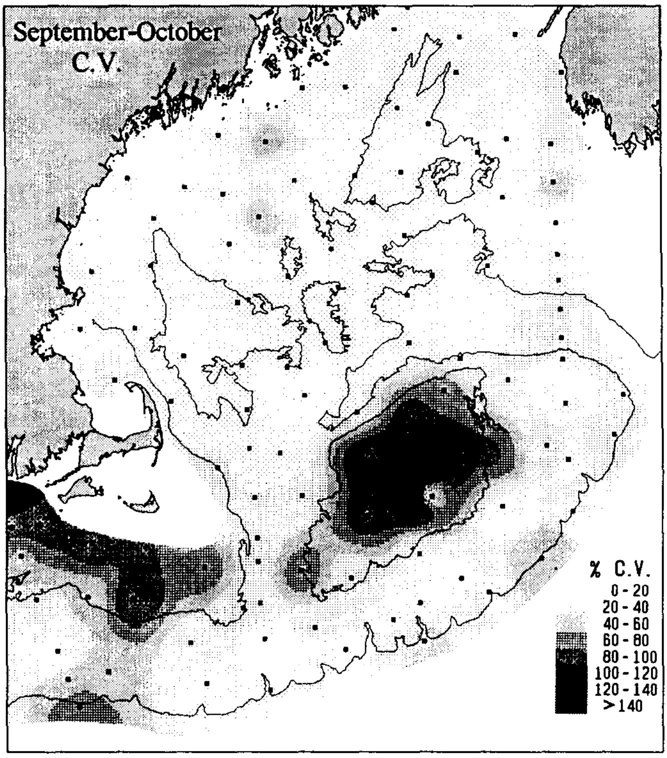


Fig. 7. Distribution of coefficients of variation of total abundance for *Calanus finmarchicus* during September–October based on $\log_{10}$-transformed means generated for Fig. 4. See Appendix B for additional months.

GB (Mountain, 1991). However, differences in the near-surface water properties on Southern GB between late winter–spring 1992 and 1993 indicate that there can be significant interannual variability in the timing of and/or hydrographic properties of Scotian Shelf water present on GB (Bisagni *et al.*, 1996).

Several authors have shown how zooplankton distributional patterns in GOM are influenced by Scotian Shelf currents (Sameoto and Herman, 1992; Corey and Milne, 1987). Sameoto and Herman (1992) present evidence for at least two other *Calanus* spp. movements southward from the Scotian Shelf into shelf-slope waters. This southward movement is obscured for *C. finmarchicus* by a heavy concentration of a resident population in the basins of the southern Scotian Shelf and on the shelf-water/slope-water front. Corey and Milne (1987) suggest that the strong connection in timing between southwest Nova Scotia and the Bay of Fundy *C. finmarchicus* populations results from movement of Scotian Shelf waters into GOM and the Bay of Fundy. This, in combination with the Maine Coastal Current would explain the formation of the *C. finmarchicus* Scotian–Coastal GOM subarea. Brooks and Townsend (1989) and Bisagni *et al.*, 1996 have shown that the Maine Coastal Current can influence planktonic distributions over Jordan Basin. Our results also support this. Higher percentages of younger copepodites in Northern GOM (Fig. 8) appear in the same temporal pattern as in the Scotian–Coastal GOM. Seasonal abundance patterns are also similar, although the Northern GOM has greater abundances (Fig. 6).

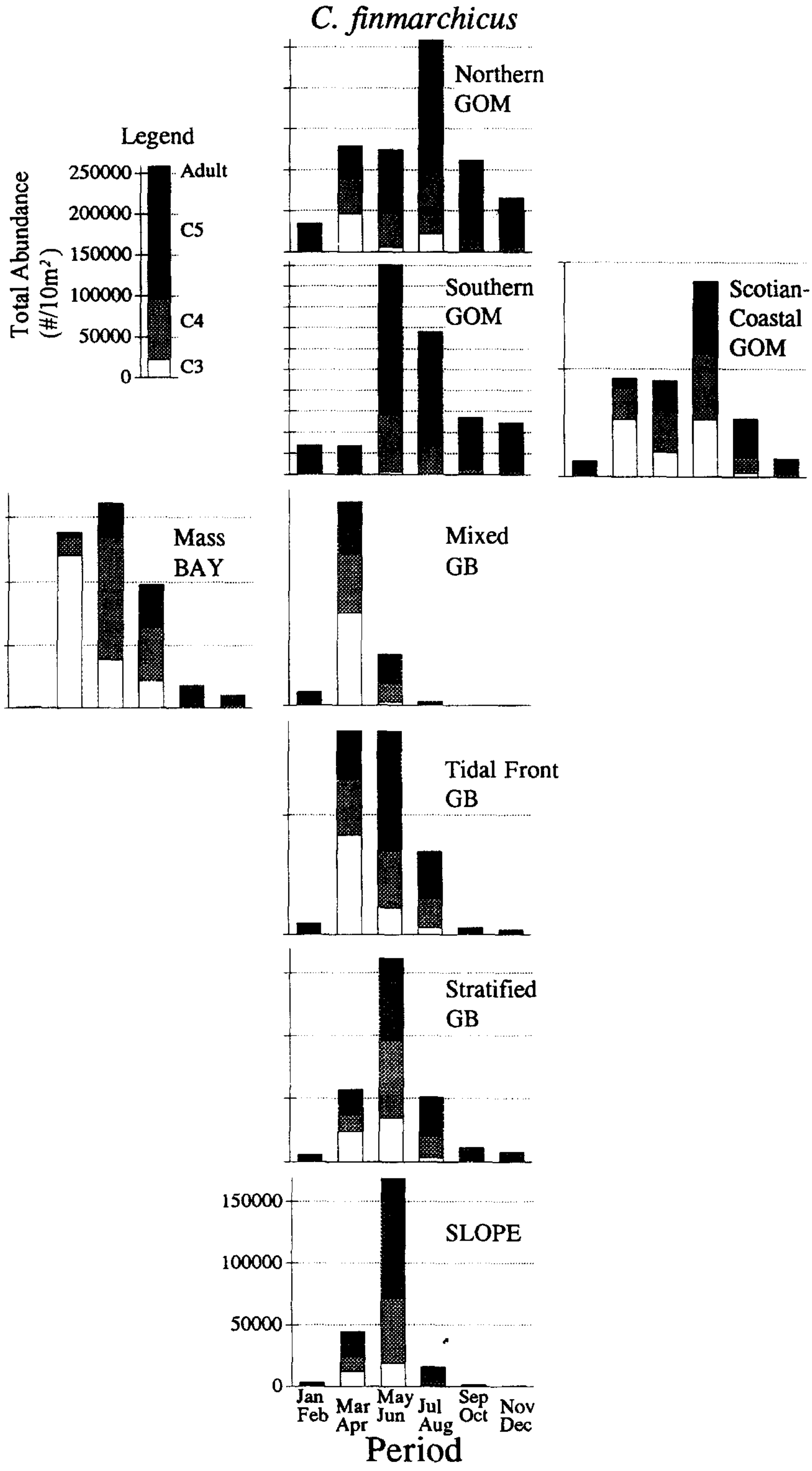
Southern GOM is the area of highest overall *C. finmarchicus* abundance (Fig. 6) and lowest seasonal, spatial and interannual variance (Table 1, Appendix A and Appendix B). The population is dominated by adults from January–April and C_5 copepodites the remainder of the year. Wilkenson Basin resides largely in this subarea and has long been thought to be a haven for *C. finmarchicus* (see Davis, 1987a). Our analyses support this hypothesis and suggest that this area of the GOM may be an important source of *C. finmarchicus* for the rest of the region (Fig. 4, see discussion below), particularly for the adjacent shallow waters on GB during winter and early spring.

Adult and younger copepodites of *C. finmarchicus* are present throughout the year in the Northern GOM and in Scotian–Coastal GOM (Fig. 8). Sameoto and Herman (1992) have found younger stages in the Gulf of St Lawrence late in the autumn, suggesting late season reproduction. *C. finmarchicus* copepodites 1–3 were present in about 5% of the small mesh (165 and 53 μm) samples taken in the GOM–GB region during MARMAP surveys in October–December, 1978–1980 (Meise *et al.*, 1995). Durbin *et al.* (1995) have found *C. finmarchicus* nauplii on GB as early as January. Together these results suggests that a portion of the *C. finmarchicus* population continues to reproduce throughout the year. Perhaps this helps to explain the continuously elevated populations of *C. finmarchicus* and relatively low seasonal variability in Northern GOM and Southern GOM (Fig. 6).

Georges Bank

Steep bathymetric gradients, strong tidal currents, and hydrographic fronts distinguish GB from surrounding water and establish several distinct water masses on the Bank (Butman and Beardsley, 1987; Flagg, 1987). A large part of the spatial and seasonal variation in *C. finmarchicus* abundance and age-structure appears related to these hydrographic regimes and to major circulation patterns in the region. There are several oceanographic features on the Bank relevant to the distribution of *Calanus finmarchicus*.

Diurnal and semidiurnal tides, interacting with the shallow bottom topography of the


C. finmarchicus
Legend
Total Abundance (#/10m²)
250000
200000
150000
100000
50000
0
Adult
C5
C4
C3
Northern GOM
Southern GOM
Scotian-Coastal GOM
Mass BAY
Mixed GB
Tidal Front GB
Stratified GB
SLOPE
150000
100000
50000
0
Jan Feb
Mar Apr
May Jun
Jul Aug
Sep Oct
Nov Dec
Period

Bank, generate exceptionally strong tidal currents (Brown and Moody, 1987) that maintain a vertically well-mixed water column inside the 60 m isobath throughout the year (Yentsch and Garfield, 1981; Loder and Greenberg, 1986; Bisagni, 1992). In the deeper areas of the Bank, the water column is vertically mixed during winter but thermally stratified during summer. A tidal front separates the vertically mixed shallow water from the surrounding stratified water and often extends across the Great South Channel to Nantucket Shoals (Butman and Beardsley, 1987). Additionally, along the northern edge of the Bank, where the water column deepens rapidly from 60 m to 200 m within a relatively short distance ($\sim <30$ km), a strong west–east current jet enhances the separation of GB from GOM (Flagg, 1987). From spring through autumn, cold, winter-residual water known as the "cold band" occurs beneath the seasonal thermocline within the 60–100 m isobaths from the Northeast Peak of GB south to near Cape Hatteras (Butman and Beardsley, 1987; Flagg, 1987). The axis of the cold band is along the 80 m isobath on GB (Flagg, 1987). Along the southern flank, at approximately the 80–200 m isobath, a salinity gradient identifies the shelf-water/slope-water front, which persists throughout the year (Flagg, 1987).

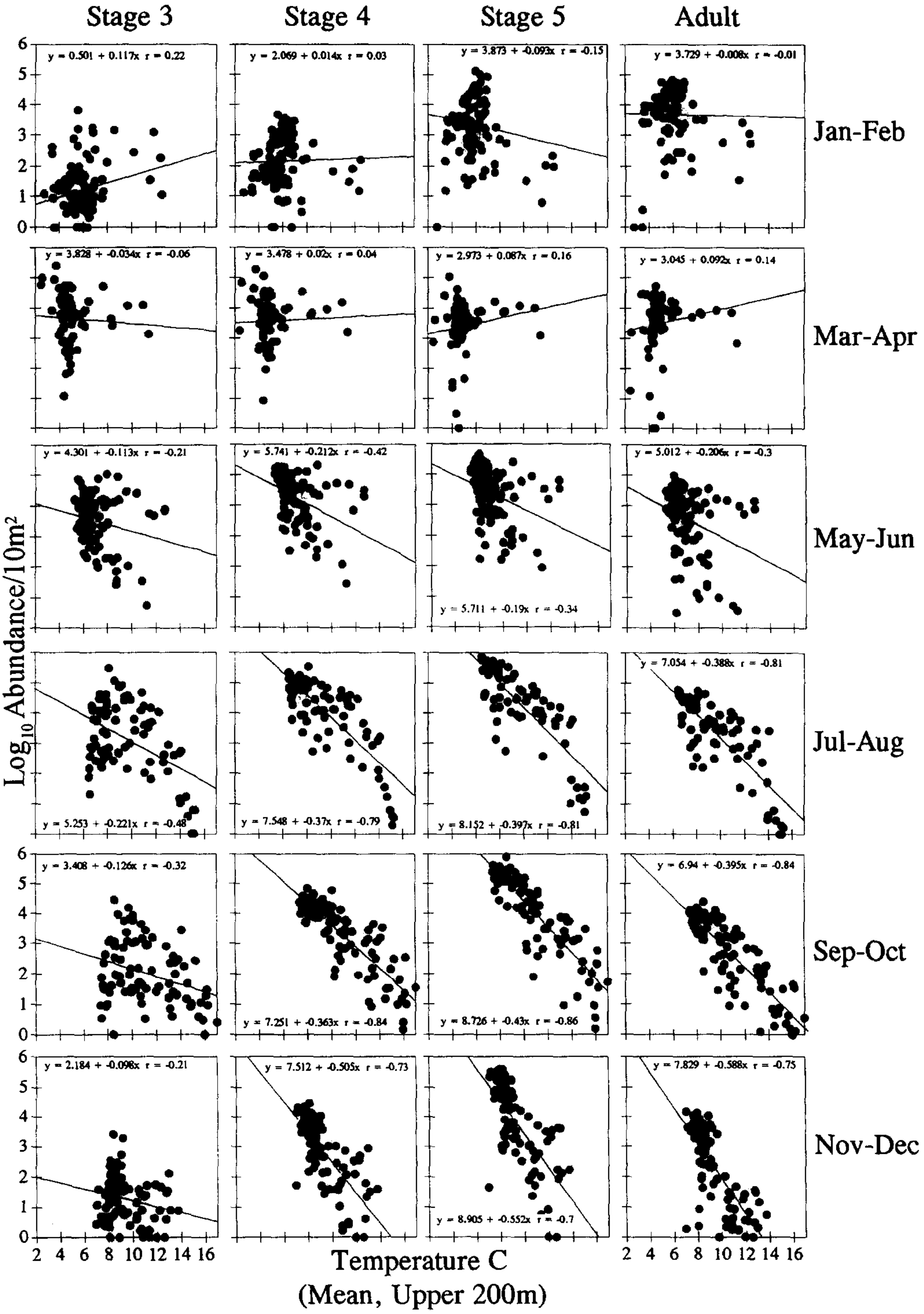
During spring and summer, a clockwise recirculation pattern sets up around the shallow water on the Bank, prolonging mean residence time (~ 60 days) of the shallow water and reducing horizontal exchange (Colton and Anderson, 1983; Butman *et al.*, 1987). In winter, recirculation is minimal, the prevailing northwest winds drive surface water offshore (Bumpus, 1976), and there is greater exchange with GOM and Scotian Shelf water (Flagg, 1987).

The four *C. finmarchicus* subareas identified on GB (Fig. 5a) reflect the seasonally integrated influence these frontal systems have on population dynamics. Subarea Mixed GB coincides with the tidally mixed unstratified shallow water; subarea Stratified GB with the seasonally stratified surrounding water; and subarea Tidal Front GB identifies the influence of the tidal mixing front separating these two water masses. (Note that the Tidal Front GB subarea does not circumscribe Mixed GB probably because our station spacing along the northern flank of GB is too coarse.) Finally, subarea SLOPE encompasses the slope water mass seaward of the shelf break (> 100–150 m depth).

From July–December, *C. finmarchicus* is relatively scarce in the shallow water on the Bank. A sharp delineation between the shallow and surrounding deeper water is also present in age-composition. Our portrayals of mean conditions support the work of Perry *et al.* (1993) who reported sharp gradients in the composition and abundance of the zooplankton community along the northern flank of GB in July 1988. Their study revealed adults and late stage copepodites of *C. finmarchicus* were much less abundant on the GB (unstratified) side of the tidal mixing front than on the GOM (stratified) side. Thus, a sharp ecotone separates the northern flank of GB from the adjacent Georges and Wilkinson basins. The ecotone is present year-round (Fig. 4) but is most apparent during the stratified season (May–October), when thermohaline density gradients and the near-surface current jet along the northern flank are generally strongest (Flagg, 1987).

The paucity of *C. finmarchicus* in Mixed GB begins in May–June and persists through December (Fig. 4). The temperature–copepodite relationship for May–June shows a bifurcation in abundance between 8–12°C, with lower abundance generally attributable to

Fig. 8. Annual cycle of age-composition of *C. finmarchicus* populations in each subarea. (See Fig. 5B for subarea locations.)


Stage 3
Stage 4
Stage 5
Adult
Jan-Feb
Mar-Apr
May-Jun
Jul-Aug
Sep-Oct
Nov-Dec
y = 0.501 + 0.117x r = 0.22
y = 2.069 + 0.014x r = 0.03
y = 3.873 + -0.093x r = -0.15
y = 3.729 + -0.008x r = -0.01
y = 3.828 + -0.034x r = -0.06
y = 3.478 + 0.02x r = 0.04
y = 2.973 + 0.087x r = 0.16
y = 3.045 + 0.092x r = 0.14
y = 4.301 + -0.113x r = -0.21
y = 5.741 + -0.212x r = -0.42
y = 5.711 + -0.19x r = -0.34
y = 5.012 + -0.206x r = -0.3
y = 5.253 + -0.221x r = -0.48
y = 7.548 + -0.37x r = -0.79
y = 8.152 + -0.397x r = -0.81
y = 7.054 + -0.388x r = -0.81
y = 3.408 + -0.126x r = -0.32
y = 7.251 + -0.363x r = -0.84
y = 8.726 + -0.43x r = -0.86
y = 6.94 + -0.395x r = -0.84
y = 2.184 + -0.098x r = -0.21
y = 7.512 + -0.505x r = -0.73
y = 8.905 + -0.552x r = -0.7
y = 7.829 + -0.588x r = -0.75
Log10 Abundance/10m2
0 1 2 3 4 5 6
2 4 6 8 10 12 14 16
Temperature C
(Mean, Upper 200m)

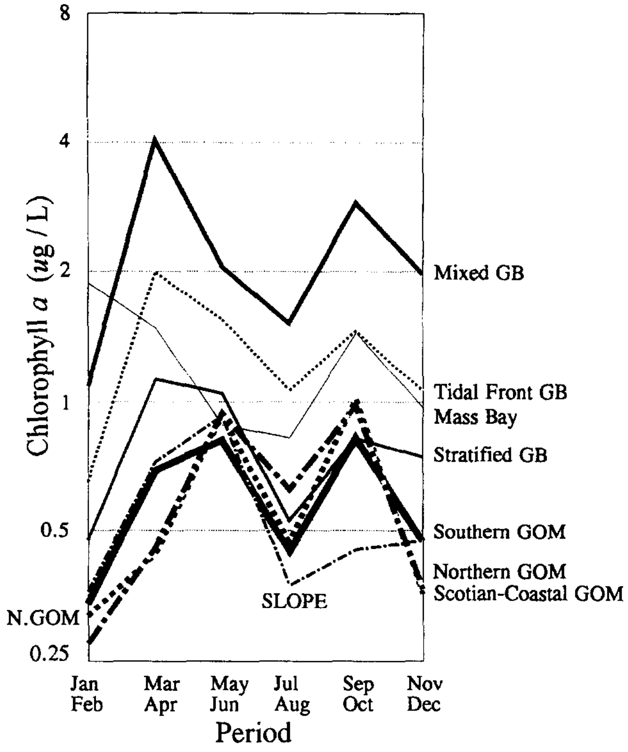


Fig. 10. Annual cycle of chlorophyll *a* abundance in each subarea. (See Fig. 5B for subarea locations.)

Mixed GB (Fig. 9). Temperature in this range is not detrimental to *C. finmarchicus* (Marshall and Orr, 1955), and so would not (by itself) explain the distributional pattern on GB in May–June. However, the decline in the population from March–April to May–June is concurrent with the arrival of high numbers of *Sagitta* spp. (Davis, 1987a; Sullivan and Meise, 1996). Moreover, the pattern of relatively lower abundances of *C. finmarchicus* in Mixed GB than Stratified GB is consistent (inverse) with the pattern reported by Sullivan and Meise (1996) of highest mean densities of immature *Sagitta elegans* and other chaetognaths in the shallow water on the Bank. *Sagitta elegans*, found in the Irish Sea, prey mainly on copepods at a rate of 0.75–3.55 prey items/day/animal (Alvarez-Cadena, 1993). On GB, *Sagitta* spp. abundance levels can be as high as 10^6/ 10 m^2 during the April–June time period (Meise *et al.*, 1995; Sullivan and Meise, 1996). Therefore, even at the lower feeding rates of the above study, *Sagitta* has the potential to significantly impact the *Calanus* population on GB. Spring migrating Atlantic mackerel, *Scomber scombrus* and sand lance, *Ammodytes ammericanus*, also form dense aggregations on GB in May–June (Grosslein and Azarovitz, 1982) and are potentially significant grazers of *C. finmarchicus*, but the quantitative extent of their influence on the Bank is also uncertain.

Fig. 9. Relationship between depth-weighted mean water column temperature and mean abundance of *Calanus finmarchicus* adults and copepodites C_3–C_5 for each 2-month period. Each point represents means computed for a standard tile (Fig. 2) using all (1977–1988) data. Also shown are regression and correlation coefficients.

In addition to possible predation by *Sagitta* and others, there are several physical features that help maintain the pattern of low abundance through December in Mixed GB and relatively higher abundance in Stratified GB. In Mixed GB, water temperatures exceed 12°C from July to October (Fig. 9) and are in the range avoided by *C. finmarchicus* (Davis, 1987b). In Stratified GB, mean water column temperature is more suitable ($\leq 10°C$) for late stage copepodites and adults due to the presence of the cold band beneath the seasonal thermocline. During summer and autumn, Mixed GB is semi-closed, having limited horizontal exchange with surrounding water (Flagg, 1987). These features, combined with the relatively long generation times of *C. finmarchicus* and its seasonal migration into deeper waters, make replenishment of Mixed GB unlikely until winter, when the GB–GOM frontal zone is less distinct and there is more movement of GOM water onto GB (Hopkins and Garfield, 1979). Seasonal distribution maps support this idea (Fig. 4). Repopulation of Mixed GB by adults begins in January–February along the northern flank, Northeast Peak, and the eastern side of Mixed GB and continues through March–April, when annual peak abundance is achieved in the Mixed GB and Tidal Front GB areas.

As the seasons progress, the same limited horizontal exchange that isolates mixed GB starting in May–June would result in an increase of later copepodite stages in Stratified GB, as the spring time cohort matures here or is advected in from the GOM or Scotian Self and remains in this area. Advection of GOM *Calanus* through the northeast peak onto the Southern GB has been suggested by Davis (1987a) and by our results in the lack of a sharp abundance gradient. However influence from the Scotian Shelf is suggested by the overflow of cluster group 2 on the Northeast Peak of GB (Figs 4 and 5). The cold band, which is present between the 60–100 m isobath (Butman and Beardsley, 1987; Flagg, 1987), and the influx of Scotian Shelf water (Bisagni *et al.*, 1996) result in lower average water column temperature in Stratified GB. Advection of both colder water and of *Calanus* copepodites into Stratified GB continues to occur while Mixed GB remains isolated. This may explain, in part, the negative relationship between water column temperature and copepodite abundance reported here (Fig. 9). Isolated Mixed GB warms seasonally and is not replenished with *Calanus* while Stratified GB continues to have cold water and *Calanus* input from the GOM–Scotian Shelf.

Annual peaks in the *C. finmarchicus* population and younger copepodite stages coincide with annual phytoplankton biomass maxima (Figs 8 and 10). Plourde and Runge (1993) show *C. finmarchicus* egg production to be tied closely to phytoplankton biomass (Chl *a*) and primary production. The higher percentage of C_3 and C_4 copepodites in the Mixed and Tidal Front areas of the Bank, suggests higher *C. finmarchicus* productivity in the shallow water (Davis, 1987b). Highest seasonal abundance levels co-occur with Chl *a* and primary production (O'Reilly *et al.*, 1987) maxima until predation levels become too high (May–June) or *C. finmarchicus* begins its seasonal retreat to deeper waters in the GOM. The hydrographic and temperature regimes and Chl *a* (Fig. 10) differences between subareas may explain the higher abundance and stage differences in our study (total abundance: Tidal Front GB < Stratified GB) (C_3 percentage: Stratified GB < Tidal Front GB). A knowledge of stage distribution by depth would permit a better index of the effects of temperature and mean advection on the GB's *Calanus* population (Werner *et al.*, 1993). We believe the existence of the cold band and the influx of GOM–Scotian Shelf water (see below) offer environmental conditions favorable to *C. finmarchicus*, allowing it to maintain relatively higher abundances in Stratified GB compared with the rest of GB.

CONCLUSIONS

One of the more interesting results from this work is the low variances associated with the high 10-year mean abundance of *Calanus finmarchicus* in the GOM, and to a lesser extent, over the stratified areas of GB, during all 2-month periods (Fig. 7, Appendix A and Appendix B). This suggests there are stable population centers and pathways onto GB. This is particularly evident during the March–April period when *Calanus* appears to "wash-over" the bank from its high population centers in the GOM. The work of Perry *et al.* (1993) and our analyses indicate a sharp gradient, after this period, in the abundance of *Calanus finmarchicus* along the northern flank of GB. This ecotone is associated with strong gradients in density stratification, and the along-bank current jet, which limit exchange between GOM and GB. During the stratified season, *C. finmarchicus* abundance gradients are less sharp between the Northeast Peak and adjacent water in the GOM, suggesting that the Northeast Peak may be a major pathway for movement of *Calanus* from GOM onto the southern flank of GB. However, resolution of the relative influence of GOM (via the Northeast Peak) and Scotian Shelf water (via Northeast Channel) on the dynamics of the *C. finmarchicus* population on the southern flank of GB during the stratified season remains to be clarified.

Spatial and seasonal variability in mean *C. finmarchicus* abundance is particularly high on GB and appears closely coupled to the spatially and seasonally complex hydrography of the Bank. The four *C. finmarchicus* subareas identified on GB reflect this heterogeneity and the seasonally integrated influence which several frontal systems have on population dynamics. The congruence among the four *C. finmarchicus* subareas and major hydrographic regimes on GB suggest that *C. finmarchicus* distributional patterns would be very sensitive to long-term trends in stratification and circulation patterns. In coastal waters off southern California, long-term decreases (70%) in zooplankton biomass accompanied increases in vertical density stratification (Roemmich and McGowan, 1995a, 1995b). While it is not certain at present how long-term climate change would affect the GB ecosystem, our analyses of mean conditions during 1977–1987 forms a baseline for detection of such change. Additionally, there is a need for longer-term studies with more complete vertical distribution and life history information, which would provide a better understanding of the influence of stratification, circulation, and immigrant *Calanus* populations to the GB–GOM region.

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APPENDIX A

Sample frequency, mean abundance ($\log_{10}+1$) *and coefficient of variation for* Calanus finmarchicus *by season*

	January–February				March–April				May–June				July–August				September–October				November–December			
Tile no.	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV
Scotian–Coastal GOM																								
102	6	6	3.99	12	4	4	5.28	12	6	7	5.34	13	5	5	4.54	52	7	12	4.81	11	6	8	4.96	9
138	3	3	4.13	9	2	2	5.33	12	6	7	5.09	10	3	3	5.2	12	3	3	5.07	5	7	12	3.55	46
141	5	5	3.99	18	6	7	4.48	25	6	8	3.91	41	3	5	5.29	10	3	3	4.86	1	6	7	4.06	13
171	6	6	3.54	7	5	5	4.89	6	7	8	4.46	43					5	7	4.06	22	7	8	3.6	16
173	6	6	3.96	7	5	6	3.54	72	5	5	3.45	82	1	1	4.7		5	5	4.77	14	8	9	3.62	37
189	4	4	3.81	10	4	5	5.37	9	6	6	5.4	10					6	6	4.32	13	4	6	4.01	10
190	4	4	3.63	9	1	1	4.16		3	3	5.01	19					4	6	3.41	49	4	6	3.83	15
Northern GOM																								
99	6	6	4.25	12	5	6	5.24	9	5	6	5.29	13	3	3	5.57	6	6	10	5.17	5	7	12	4.59	14
100	7	7	4.91	10	7	9	5.63	10	9	15	5.6	10	7	7	4.94	41	8	17	5.31	10	9	15	5.43	7
101	7	8	4.63	11	6	6	5.38	12	9	10	5.66	7	7	8	5.12	40	8	16	5.28	6	9	15	4.96	28
103	4	4	4.39	12	6	9	5.52	11	9	10	5.71	10	6	8	5.17	38	7	9	5.51	7	8	12	5.26	12
104	6	6	4.18	15	1	1	5.28		10	10	5.55	7	5	5	5.87	6	5	6	5.39	5	9	12	4.7	10
105	6	6	4.95	10	5	6	5.18	9	10	10	5.74	7	7	9	5.71	7	7	8	5.42	4	7	10	5.33	11
134	4	4	4.84	12	5	5	5.39	11	9	11	5.29	32	4	5	5.86	4	4	5	5.86	4	6	8	5.61	8
135	5	5	4.94	4	1	2	4.37	10	10	12	5.38	7	6	9	5.69	8	5	6	5.39	6	8	13	5.06	12
136	6	6	4.08	45	4	4	5.43	13	8	8	5.69	6	4	5	5.86	9	5	5	4.39	50	7	10	5.33	8
137	5	5	4.38	7	6	6	4.45	48	8	9	4.17	55	6	6	5.87	8	5	6	4.29	46	9	15	4.84	12
139					3	3	3.82	72	1	1	5.68		1	1	5.37		1	1	4.79					
140	5	5	4.55	6	3	3	5.22	14	6	7	5.43	11	6	10	4.9	34	4	5	5.15	9	9	16	4.59	28
142	6	6	5.01	11	4	5	5.5	12	8	8	5.85	6	4	4	5.93	4	4	4	5.69	6	7	8	5.45	9
143	6	6	4	47	2	2	5.61	3	10	13	5.28	30	4	5	5.89	5	5	7	5.28	7	7	10	4.72	34
162	2	2	4.88	12	6	7	5.21	8	7	10	4.91	34	2	2	5.75	2	4	4	5.22	4	7	8	4.58	38
163	5	5	4.15	16	4	4	5.79	12	8	10	4.95	34	1	1	4.92		6	9	4.68	13	7	10	4.3	36
164	3	3	4.46	3	3	4	3.63	59	7	10	4.52	51	1	1	4.71		7	8	4.95	6	5	7	4.56	7
165	3	3	4.54	7	2	3	5.37	6	5	6	3.57	72	1	1	4.22		5	5	4.95	8	5	5	4.52	9
166	2	2	4.82	7	5	5	4.36	51	6	8	5.03	39	1	1	5.63		5	5	5.36	7	4	4	5.3	2
167	4	4	5.18	6	3	4	5.24	14	5	5	5.63	9					3	5	5.65	5	3	4	5.66	9
168	4	4	4.76	8	2	2	5.32	5	6	8	4.82	39	2	2	5.29	3	3	3	5.53	7	4	7	4.86	14
169	3	3	4.41	18	3	4	5.36	8	5	7	3.77	64	2	2	6.06	1	3	5	4.96	4	4	6	3.82	47
170	3	3	4.48	6	2	2	5.61	10	6	7	4.83	42	1	1	4.68		3	4	5.33	6	4	7	5.18	12
172	6	6	4.2	6	5	5	4.35	50	5	5	4.42	51	1	1	5.26		6	6	4.78	7	8	9	4.35	6
174	6	6	4.42	7	7	9	4.93	11	7	7	4.06	64	1	1	4.74		5	6	4.38	26	9	11	4.01	36
175	7	7	4.38	13	3	4	4.54	13	6	6	3.79	71	2	2	5.35	4	6	17	3.81	26	10	11	3.99	36
182	5	5	5.02	11	3	4	4.97	11	7	8	4.18	58	4	4	5.98	7	4	5	5.56	4	8	10	4.86	34

Continued

	January–February				March–April				May–June				July–August				September–October				November–December			
Tile no.	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV
183	6	6	4.78	6	3	3	4.96	17	8	12	5.81	6	7	10	5.05	36	5	5	5.34	2	7	9	4.91	36
188	7	8	4.17	12	6	6	5.68	11	9	11	5.23	19	3	4	4.59	24	8	15	4.97	7	7	12	4.51	9
Southern GOM																								
96	7	7	5.03	10	8	11	4.67	9	10	11	5.45	32	5	5	5.85	4	8	12	5.49	8	10	12	4.65	45
106	7	7	5.01	7	8	9	5.1	8	9	13	5.91	6	8	9	5.84	10	7	13	5.67	4	7	11	5	33
107	4	4	5.23	10	8	11	5.08	13	10	14	5.63	16	4	5	5.89	2	6	9	5.66	4	8	11	4.99	33
108	6	6	4.83	9	10	12	4.8	8	11	17	5.87	9	3	4	5.95	3	8	14	5.43	8	9	12	5.59	7
109	4	4	5.16	9	6	8	4.68	8	10	13	5.32	30	4	5	5.97	4	7	11	5.27	7	8	9	5.4	6
110	6	6	4.8	8	7	8	4.83	13	10	16	5.75	11	6	8	5	15	10	23	4.64	27	11	13	5.09	7
125	6	8	4.51	10	10	17	4.74	10	11	17	6.05	9	11	17	4.8	15	8	17	4.5	16	11	13	5.15	8
126	5	6	4.61	7	8	12	4.67	11	8	11	5.43	15	3	4	5.8	3	8	15	5.13	6	8	9	4.93	8
127	4	4	4.7	10	6	7	4.38	5	11	13	5.61	7	3	5	5.5	4	7	12	5.08	8	6	7	5.31	7
128	3	3	5.01	9	6	7	4.69	9	8	10	5.93	6	3	5	5.66	5	5	6	5.04	6	6	6	5.44	7
129	5	5	5.02	12	8	13	4.97	12	9	9	5.75	8	4	6	5.57	5	8	13	5.37	3	10	14	5	29
130	4	4	4.84	6	4	4	5.01	10	9	9	5.82	5	4	5	5.85	8	5	5	5.5	4	6	7	5.5	11
131	5	5	5.02	4	7	7	5.32	13	9	10	5.82	5	5	7	5.93	5	6	7	5.5	5	6	8	5.66	7
132	5	5	4.85	7	6	7	5.01	8	9	10	5.69	7	4	5	5.95	8	7	8	5.4	5	7	10	4.81	34
133	4	4	5.03	10	3	4	4.83	11	6	7	5.05	41	4	4	5.95	3	4	4	5.37	2	5	6	5.42	6
144	8	9	4.66	6	4	5	4.97	9	9	10	5.66	7	5	5	5.8	3	6	8	5.14	6	7	8	5.15	5
145	6	7	4.72	5	7	10	4.91	16	10	13	5.74	8	5	6	5.65	5	9	23	5.13	7	9	11	5	17
161	6	6	4.67	10	10	15	4.61	29	10	13	5.7	5	6	9	4.96	12	9	14	4.53	15	11	14	4.45	10
Mixed GB																								
123	6	6	3.14	16	7	12	4.99	10	10	12	3.85	38	8	13	2.47	58	10	17	2.04	85	11	13	0.95	152
124	6	6	3.57	7	9	12	4.35	9	10	13	3.75	46	8	13	2.78	58	10	20	1.88	94	11	12	2.94	48
146	5	5	3.41	20	7	12	4.61	13	11	12	4.04	20	10	22	2.52	73	10	17	2	87	11	15	2.71	44
147	5	5	3.45	19	8	12	4.49	11	11	13	3.69	33	11	18	2.25	72	9	16	0.37	266	11	13	1.86	94
148	6	6	3.01	19	7	11	4.35	33	11	12	4.31	20	5	7	3.15	44	6	8	1.25	131	11	11	1.72	93
156	1	1	3.19		6	9	4.61	38	1	1	5.28		8	14	3.95	44	6	7	2.9	42	2	2	1.47	100
160	5	5	3.66	15	9	14	4.27	16	10	11	3.83	30	8	16	3.1	50	10	18	2.46	73	11	12	2.63	37
Tidal Front GB																								
120	6	8	3.31	12	9	14	4.64	31	10	13	4.96	22	11	20	5.05	14	10	19	4.13	27	10	11	2.05	79
121	4	4	2.92	22	11	17	4.76	13	11	14	4.48	13	9	14	4	44	8	13	2.74	70	10	11	3.45	34
149	5	5	3.4	9	9	19	5.17	11	11	13	5.51	13	10	15	4.82	30	10	16	4.3	16	11	12	3.16	47
155	8	11	3.88	12	10	18	5.36	10	10	12	5.56	10	8	15	4.69	29	10	16	3.94	16	10	11	3.47	35
157	5	8	3.74	10	9	16	4.83	14	10	12	4.65	15	8	19	4.34	28	10	21	2.12	82	11	13	2.19	69
158	6	7	4.16	6	9	12	5.03	9	7	8	4.96	18	8	13	4.43	11	8	18	3.31	30	8	8	3.64	16
159	6	6	3.93	10	10	18	4.67	18	9	9	4.26	20	8	16	4.29	14	9	31	3.61	21	11	42	4	32
Stratified GB																								
94	5	5	4.02	10	9	14	4.01	35	10	12	5	17	10	13	3.69	36	10	29	4.12	25	9	10	4.07	13
95	6	6	3.92	20	9	12	5.01	15	10	10	5.6	7	10	12	4.96	17	9	17	4.71	10	10	49	3.99	23
111	5	5	4.33	3	8	13	4.31	7	7	8	5	9	10	12	4.42	14	9	26	3.83	26	11	14	3.95	29
112	4	4	3.99	6	7	11	4.47	8	9	13	4.63	12	7	8	5.02	10	7	10	4.15	34	11	11	3.67	33
113	5	5	3.78	7	8	11	4.58	13	8	9	4.95	14	6	7	4.56	43	8	13	4.12	32	11	13	3.87	15
114	5	6	2.93	47	8	12	4.52	32	9	12	5.12	33	10	13	5.14	10	8	12	4.18	15	11	12	3.82	15
117	4	4	2.72	60	9	15	4.75	19	10	13	4.98	43	9	13	4.66	31	9	14	4.23	30	11	12	3.9	15
118	4	4	2.64	62	8	13	4.84	21	9	12	4.63	46	8	9	4.8	11	8	15	3.69	17	10	11	3.95	16
119	5	5	3.83	4	10	15	4.93	31	9	10	5.88	9	9	11	5.2	11	9	13	4.13	18	10	10	3.81	15
122	5	6	4.19	6	9	16	4.72	9	11	18	5.33	12	10	20	4.46	18	10	16	3.75	31	10	13	4.11	32
150	4	4	3.97	4	7	12	5.36	10	10	11	5.85	9	8	11	5.07	12	9	13	4.08	10	11	13	3.26	48
153	6	6	3.89	21	6	10	4.77	36	10	11	5.04	33	8	13	5.28	10	8	13	4.08	17	10	10	3.37	38
176	6	6	3.58	47	8	10	4.69	15	8	8	5.49	10	5	6	4.86	11	7	24	4.21	18	11	13	4.44	18
177	6	7	4.23	11	10	15	4.98	10	10	10	4.98	16	6	7	4.11	14	9	31	3.96	15	11	20	4.05	18
178	5	5	4.05	10	7	10	5.07	12	10	10	5.55	12	6	8	4.43	15	8	12	4.04	13	10	10	3.62	16
192	2	2	3.68	12	6	9	5.3	11	5	5	5.88	7	5	6	4.75	14	7	10	3.41	25	4	4	3.68	11

Continued

	January–February				March–April				May–June				July–August				September–October				November–December			
Tile no.	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV	*Y*	*N*	Mean	CV
Slope																								
115	3	3	3.21	14	8	15	4.9	15	8	10	5.14	14	3	5	4.59	14	8	13	3.48	19	10	12	2.64	64
151	3	3	3.85	4	8	14	4.7	22	8	9	4.67	22	2	3	3.24	76	7	11	2.66	52	9	9	2.64	51
152													1	1	4.91									
154	6	7	3.52	21	9	11	4.73	18	10	11	5.47	10	6	8	4.24	9	9	13	3.54	34	10	11	3.54	22
179	4	4	3.91	23	8	13	4.66	31	8	8	5.41	7	8	10	4.25	19	9	12	3.26	36	8	8	2.69	46
191	2	2	3.31	21	7	10	4.71	35	5	5	5.36	6	5	7	3.92	42	8	13	3.36	28	4	4	3.08	20
193	2	2	3.31	7	6	8	3.87	59	4	4	5.49	10	6	7	4.45	24	7	10	2.65	55	4	4	2.96	28
Mass Bay																								
97	6	6	2.25	75	6	6	4.87	15	6	6	4.7	46	5	6	4.82	5	7	9	4.13	38	7	12	3.98	19
98	6	6	3.81	12	6	7	5.38	7	7	9	5.55	8	3	3	5.34	12	7	10	4.37	14	6	11	4.04	14
Nantucket Shoals																								
93	5	5	3.3	12	9	19	4.1	27	10	12	4.03	41	10	17	3.72	33	11	28	2.19	70	9	9	3.04	39
Nova Scotia																								
181	6	6	1.98	46	2	2	1.12	100	6	6	3.12	56	1	1	4.67		4	4	3.74	21	5	7	2.21	49
Other																								
75	5	5	2.58	60	10	21	2.44	87	11	14	4.06	36	10	18	4.08	18	9	12	1.8	101	7	7	2.54	68
76	3	3	3.33	27	6	10	2.31	73	9	11	3.56	36	4	6	3.77	9	8	9	1.19	146	8	8	2.03	81
77	3	3	3.71	30	8	12	2.81	56	7	8	4.47	20	8	11	3.92	9	5	5	2.46	84	10	10	3.19	22
78	3	3	3.93	24	10	16	3.68	33	10	12	4.94	16	9	12	4.93	13	10	14	3.35	56	10	10	3.03	39
79	4	4	3.93	18	9	15	4.34	23	11	14	5.57	8	9	17	5.09	12	10	13	4.27	32	11	11	3.25	34
80	3	3	3.93	4	7	15	5.2	14	11	15	5.73	8	8	11	4.75	33	8	11	4.12	15	10	12	3.49	36
81	3	3	3.77	4	8	13	4.88	13	6	7	5.21	13	3	4	4.83	15	8	12	3.66	48	9	10	4.13	13
82	4	4	1.98	58	6	11	4.76	17	8	9	4.97	16	3	3	3.51	27	7	9	2.09	78	8	9	2.57	74
83																					1	1	2.92	
84																								
85	4	4	3.94	4	9	24	5.09	11	10	11	5.77	4	8	12	5.32	5	8	12	3.67	46	9	10	3.07	66
86	5	5	3.38	17	8	9	4.41	18	11	14	5.54	11	8	11	5.18	4	9	15	3.81	43	10	10	3.26	37
87	4	4	3.77	17	9	13	3.41	32	9	10	4.38	16	9	11	4.14	15	9	13	1.94	95	9	9	1.84	94
88	5	5	3.33	22	8	14	3.77	33	11	13	5.02	13	10	17	4.43	29	9	21	2.01	91	9	9	2.14	73
89	5	6	3.19	17	11	25	4.33	18	11	15	4.81	16	10	22	4.42	26	10	19	2.42	93	10	10	3.3	17
90	6	6	3.85	19	9	15	5.03	11	11	13	5.24	30	10	19	5.27	10	11	17	3.93	33	9	11	3.71	35
91	5	5	3.03	51	9	12	5.16	14	9	11	5.15	32	7	10	5.13	8	9	11	4.33	14	10	10	3.93	17
92					7	8	4.8	10	2	2	5.6	0	7	10	4.95	17	5	6	4.25	20				

Y is the number of years sampled; *N* is the number of observations during season; CV is the coefficient of variation.

APPENDIX B

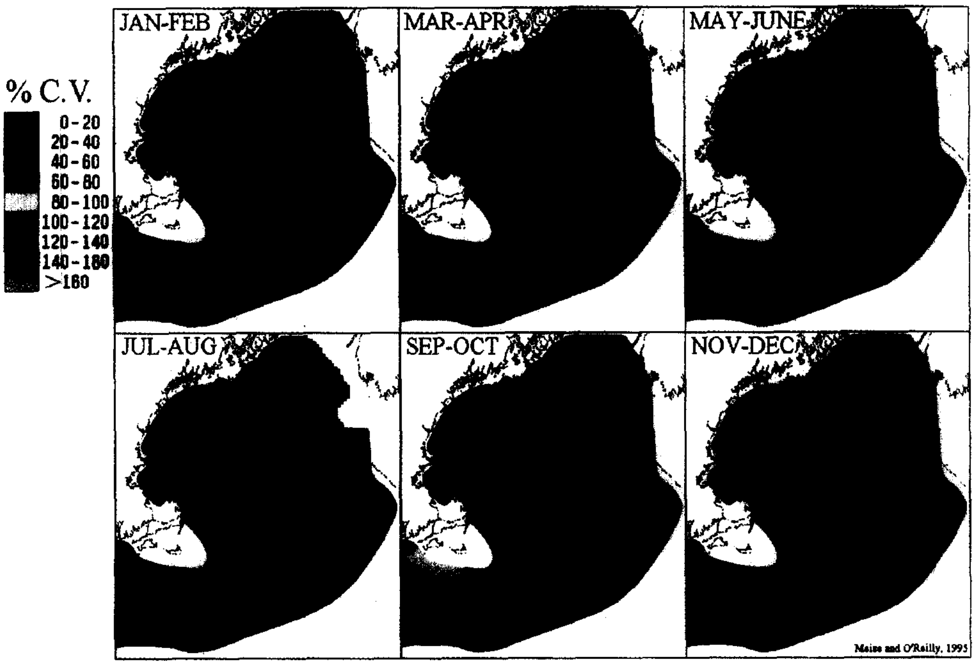

Fig. B1. (CDROM) Seasonal distribution of coefficients of variation for *Calanus finmarchicus* (total abundance). Seasons: January–February, March–April, May–June, July–August, September–October, November–December. Additional details are provided in Methods.