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# Late fall - early winter recruitment of *Calanus finmarchicus* on Georges Bank

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ABSTRACT: The development of *Calanus finmarchicus* in the Gulf of Maine (GOM), USA, and on Georges Bank (GB) was investigated during late fall, 1994, and winter, 1995, as part of the US-GLOBEC Georges Bank program. During November almost all of the *C. finmarchicus* population in both regions was present as C5, with a small proportion of C4 and females. There were very few animals on GB. In the southern GOM about a third of the *C. finmarchicus* population was in the upper 80 m and actively feeding; the remainder were below 120 m. On GB the *C. finmarchicus* population was also feeding; gut pigment content in both areas was between 3 and 13 ng copepod$^{-1}$. About one third of the adult females on GB were reproductively active while none in the GOM were reproductively active. By January *C. finmarchicus* C6 females formed a large proportion of the older stage animals on the Bank and in surface waters of the southern GOM. These were actively feeding and reproducing with a large cohort of young nauplii of *C. finmarchicus* present in the southern GOM and smaller numbers on the northeast peak of the Bank. There were very few *C. finmarchicus* nauplii on the crest of the Bank or on the southern flank. Based on abundances and stage composition, it appeared that spawning began in late December and that repopulation of the Bank took place in the region of the NE peak, with nauplii and reproductively active females being transported onto this region of the Bank from the GOM.

KEY WORDS: *Calanus* · Georges Bank · Population dynamics · Egg production · Diapause

## INTRODUCTION

*Calanus finmarchicus* is a dominant large copepod in sub-Arctic waters of the North Atlantic Ocean extending from the mid-Atlantic shelf off the U.S. east coast to the Barents Sea north of Norway (Conover 1988). It is abundant during spring on Georges Bank (GB) (Davis 1987), where its nauplii are important food for larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* (Kane 1984, Buckley & Lough 1987). In the traditional view of its life cycle, *C. finmarchicus* spends the late summer and fall in a resting or quiescent stage, usually as the fifth copepodite stage (C5). It is not clear whether this represents a true diapause (Miller et al. 1991). Molting to the adult stage takes place during winter and spawning begins when sufficient food levels are reached during the spring bloom (Conover 1988). However, there are also observations of a physiologically active fall-winter component of *C. finmarchicus* residing in the surface layer. For example, Hirche (1983) found evidence of actively feeding late copepodite stages in the surface layer of Korsfjord, Norway in late summer and fall. In the Clyde Sea area and in Loch Striven, spawning started in mid-February (Nicholls 1933, Marshall et al. 1934) and in Malangen fjord, northern Norway, spawning commenced in mid-March (Diel & Tande 1992), apparently in each case prior to the start of the spring diatom bloom.

On GB the biomass peak of *Calanus finmarchicus* occurs during May and June (Davis 1987, Sherman et al. 1987). In this region, *C. finmarchicus* is considered

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to be a late winter-spring species which begins spawning in late February (Davis 1984, 1987). However, these conclusions are based on abundances of late stage copepodites rather than on direct measurements of egg production rates or of the abundance of naupliar stages. Since GB and coastal waters in the southern Gulf of Maine (GOM) remain productive throughout the winter because of shallow depths (O'Reilly et al. 1987, Townsend et al. 1992), it is possible that in this region *C. finmarchicus* initiates spawning sooner than the late winter-spring bloom. Here we present evidence that part of the *C. finmarchicus* population in the southern GOM is actively feeding during the fall and that spawning in both the southern GOM and on the NE peak. the area where *C. finmarchicus* is first advected onto GB, begins in late fall-early winter.

## METHODS

Data were obtained from cruises carried out during 8 to 18 November 1994 (AL9410) and 10 to 22 January 1995 (EN259). Station locations are shown in Fig 1A, B. At each station a CTD cast was made to within a few meters of the bottom (Neil Brown Mark V on AL9410, and a Neil Brown Mark III on EN259). Both CTDs were equipped with a fluorometer and transmissometer but because of a fluorometer malfunction during January we only have fluorescence data for the November cruise. Zooplankton was collected with a 1 $m^2$ MOCNESS and a plankton pump system. The MOCNESS was equipped with 0.150 mm nets, which quantitatively sampled all of the *Calanus finmarchicus* copepodite stages. Usually, MOCNESS zooplankton samples were collected from 0 to 15 m, 15 to 40 m, 40 to 100 m or the bottom (if <100 m) and 100 m to the bottom (if >100 m). At Stns 7 and 9 on AL9410 samples were collected at 20 m intervals from the bottom to the surface. To avoid clogging, water volumes filtered by the nets were kept to a minimum by using slightly faster than normal retrieval rates (15 m $min^{-1}$) and a tow speed of approximately 1.5 knots (80 cm $s^{-1}$). The plankton pump system was used to collect naupliar stages. It consisted of a 2.5 inch (6.4 cm) diameter ribbed suction hose and an 8 hp gasoline pump which pumped water into a 0.050 mm mesh net suspended in a receiver tank on the deck of the ship. Flow rates (approximately 500 l $min^{-1}$) were measured with a Signet flow meter Samples were collected at 5 m intervals down to 60 m starting at 2.5 m below the surface. At each depth a volume of 0.5 $m^3$ was filtered. Samples collected within the 0 to 15, 15 to 40, and >40 m depth ranges were combined. Both MOCNESS and pump samples were preserved in 4% borate buffered formalin for later analysis.

Gut pigments (Mackas & Bohrer 1976) were measured on C5 and C6F *Calanus finmarchicus* to provide an index of feeding level. Samples were collected at selected sta-

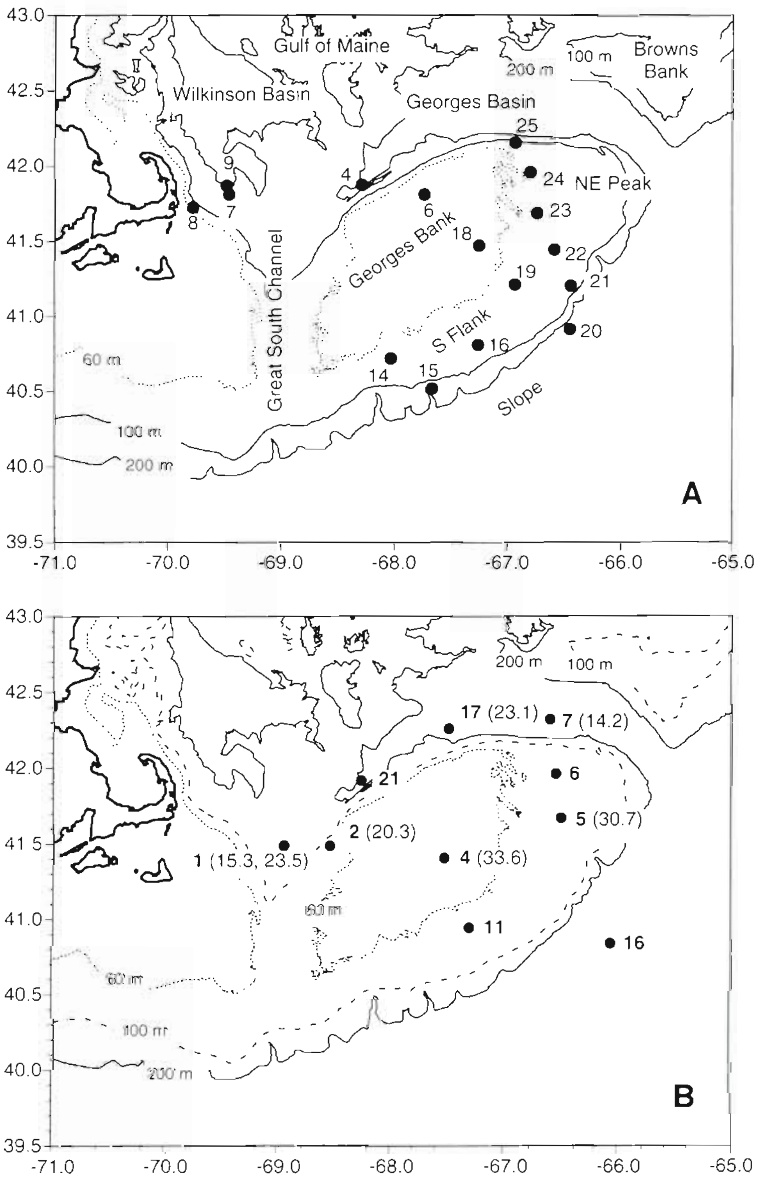



Fig. 1. Study area showing (A) stations during RV 'Albatross IV' cruise 9410, 8 to 18 November 1994, and (B) stations occupied during RV 'Endeavor' cruise 259, 10 to 22 January 1995. Egg laying rates (eggs $female^{-1}$ $d^{-1}$) of *Calanus finmarchicus* adult females are shown in parentheses

tions (shown in Fig. 1A, B), either from the 0 to 15 m depth MOCNESS net (AL9410), or from a separate oblique net haul from the surface to 40 m with a 0.75 m diameter 0.300 mm mesh net (EN259). The gut pigment analysis was conducted on board using live rather than frozen copepods. Samples for analysis were immediately anesthetized with MS-222 (0.58 g $l^{-1}$ filtered seawater; Durbin et al. 1990) and kept on crushed ice in a refrigerator until being sorted under a dissecting microscope at low light. During AL9410 10 groups of 5 from each station were analysed, while during EN259 30 animals were analysed individually. Pigment extraction was carried out in 10 ml glass tubes to which 5 ml of 90% aqueous acetone was added. These were then placed in a freezer, allowed to extract for 24 h, and read on a Turner Designs fluorometer before and after acidification. Chlorophyll *a* and phaeopigments (as chlorophyll *a* equivalents) were calculated and expressed as nanograms pigment per copepod (Parsons et al. 1984).

Groups of 5 of C5 and C6F animals from these same anesthetized samples were viewed under low power with a dissecting microscope and an image of each group recorded on videotape for later prosome length measurements (Image, version 1.47, National Institute of Health). Each group was then transferred to a CHN boat and placed in a desiccator for later carbon and nitrogen analysis (Carlo Erba NA 1500 Nitrogen Analyzer).

In the laboratory, the MOCNESS samples selected for analysis were split with a folsom splitter to provide a subsample of about 1000 to 1200 individuals for enumeration of *Calanus finmarchicus* life stages. Nauplii were not counted since, with the possible exception of the last 2 *C. finmarchicus* naupliar stages, they were not quantitatively sampled. Plankton pump samples were split using the same protocol to provide a subsample of about 1200 individuals. In these samples both the nauplii and copepodites of the target species were staged.

To measure egg laying rates, female *Calanus finmarchicus* were caught with a 1 m diameter, 0.333 mm mesh sized plankton net towed obliquely from depths ranging between 50 and 100 m to the surface. Forty females were quickly sorted out within 1 h after capture. Individual females were incubated in filtered seawater (FSW) in plastic petri dishes (50 ml capacity) for 24 h at 6 to 7°C under a 12 h light:12 h dark cycle. Eggs were counted and removed each 8 h to minimize cannibalism. At some stations, when time was limiting or weather too rough, females were individually incubated in 45 ml tissue culture flasks and then both eggs and animal preserved by adding formaldehyde to the container at the end of the incubation period. Comparisons of the various incubation methods, including incubation of groups of females in 2 l egg separators (as described in Runge 1985), have shown that during calm conditions egg production rates are estimated equally well by any of the 3 methods. In rough conditions, however, incubation of individual females in dishes or tissue culture flasks yielded higher egg laying rates, presumably because of a higher rate of cannibalism of suspended eggs before the eggs fall through the mesh barrier in the egg separation containers (Runge & Plourde 1996). The incubation of individuals, moreover, yields information on clutch size and spawning frequency. The incubation methods used here, therefore, provide the most accurate and informative estimates of egg laying rate.

A reproductive index (*RI*) was determined at selected stations. Between 19 and 61 females were sorted at random from preserved MOCNESS samples. The state of maturity of oocytes in each female was classified according to criteria described in Table 1 of Runge (1987).

## RESULTS

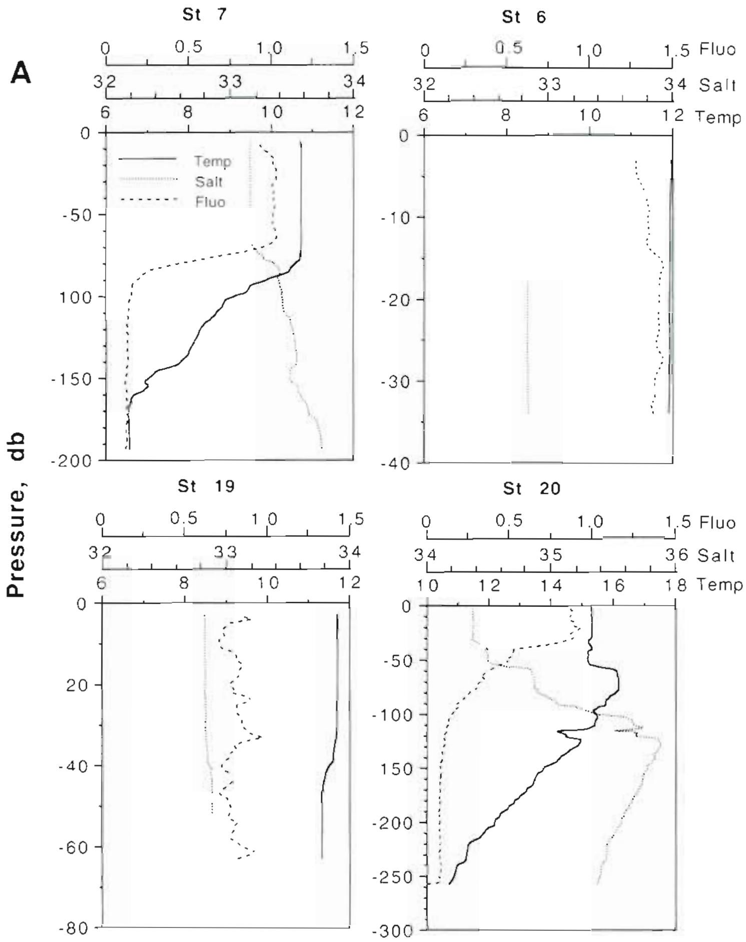
### Hydrography

During November the temperature of surface water in the southern GOM and on GB was between 10.5 and 12°C (Fig 2A). The water column on the shallow part of the Bank (Stn 6) was well mixed, weakly stratified in the deeper waters on the Bank (Stn 19), and more strongly stratified in the southern GOM (Stn 7) with a surface mixed layer extending down to 70 m. Chlorophyll fluorescence was high throughout the water column on the Bank and in the surface mixed layer in the southern GOM (Fig. 2A). Bottom temperature in the GOM was about 6.5°C. At the slope station (Stn 20) the surface mixed layer only extended down to 30 m, and surface temperature and salinity were considerably higher than in the GOM or on GB (Fig. 2A).

By January, while the surface water temperatures had cooled considerably from November, they were still relatively high, ranging between 6.9°C at Stn 4 on the shallow Bank crest and 8.2°C at Stn 11 on the southern flank (Fig 2B). At Stn 7 in the Northeast Channel a thin (~10 m) surface layer of low temperature and salinity water suggests an influx of Scotian Shelf water (Fig. 2B). There was no evidence of this colder, lower salinity water at Stn 5 on the NE peak.

### *Calanus finmarchicus* abundance

The abundance of *C. finmarchicus* on GB (Stns 6 and 19) was very low in November (AL9410). Total density was <1000 $m^{-2}$ (Table 1), with copepodite stages C4




and C5 dominating and some C6 also present. In contrast, abundance of *C. finmarchicus* in the Great South Channel (GSC) region of the southern GOM was much higher (27 800 and 37 300 m$^{-2}$ at Stns 7 and 9 respectively, Table 1). At these 2 stations, stage C5 was predominant, stage C4 was abundant, and younger copepodites (C1–C3) and adult females were present in low numbers (Table 1). At Stn 20 in the slope water *C. finmarchicus* copepodite stages were present in about equal numbers (Table 1). Low numbers of several stages of *C. finmarchicus* nauplii were observed at Stn 7 in the GSC region of the southern GOM and at Stn 20 in the slope waters (Table 1).

In the southern GOM (Stn 7), night-time vertical distribution of C4, C5 and C6F *Calanus finmarchicus* was bimodal in November. About one third of the population was located in the upper 80 m, the surface mixed layer (Fig. 3A). There was a minima between 80 and 100 m and the balance of the population was fairly evenly distributed below 100 m. Adult males were present at the base of the mixed layer between 40 and 80 m. During the day at the same location (Stn 9) a much greater proportion of the C4, C5 and C6F *C. finmarchicus* population resided be-

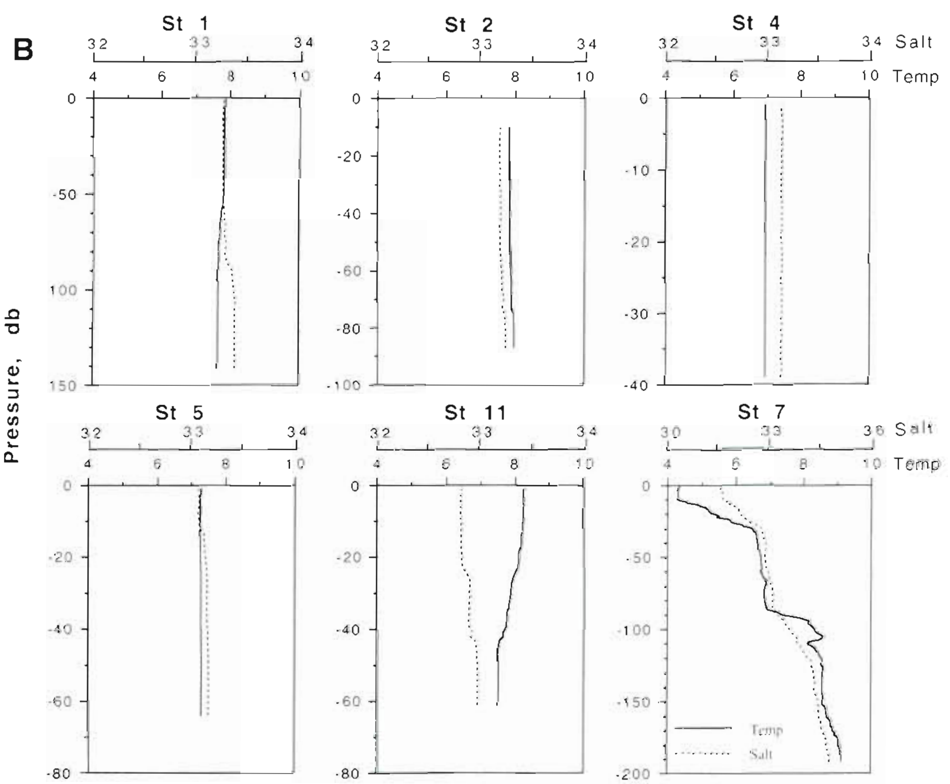



Fig. 2. CTD profiles (A) during RV 'Albatross' IV cruise 9410, 8 to 18 November 1994 in the southern Gulf of Maine (Stn 7), on the crest and southern flank of Georges Bank (Stns 6 and 19), and in slope waters (Stn 20) and (B) during RV 'Endeavor' cruise 259, 10 to 22 January 1995 in the Southern Gulf of Maine (Stns 1 and 2), on the crest (Stn 4), southern flank (Stn 11) and northeast peak (Stn 5) of Georges Bank, and in the Northeast Channel (Stn 7). Temperature is in °C, salinity in ‰ and fluorescence in arbitary units

Table 1. *Calanus finmarchicus*. Abundance and age structure of copepods at Stns 7 and 9 in the Southern Gulf of Maine, at Stns 6 and 19 on Georges Bank, and at Stn 20 in slope waters during November 1994. Abundance of nauplii are from pump samples collected in the upper 60 m while the 1 $m^2$ MOCNESS samples were taken over the entire water column (upper 400 m at Stn 20). Station depths are shown in parentheses. Data are presented as no. $m^{-2}$ over the depth range of the samples. nd: no data

| | Stn 7 (201 m) | Stn 9 (199 m) | Stn 6 (36 m) | Stn 19 (70 m) | Stn 20 (900 m) |
|---|---|---|---|---|---|
| N1 | 0 | nd | 0 | 0 | 0 |
| N2 | 0 | nd | 0 | 0 | 0 |
| N3 | 146 | nd | 0 | 0 | 118 |
| N4 | 27 | nd | 0 | 0 | 0 |
| N5 | 0 | nd | 0 | 0 | 118 |
| N6 | 0 | nd | 0 | 0 | 0 |
| C1 | 86 | 13 | 0 | 0 | 42 |
| C2 | 30 | 64 | 0 | 0 | 210 |
| C3 | 131 | 72 | 0 | 0 | 21 |
| C4 | 2849 | 5459 | 397 | 243 | 327 |
| C5 | 24050 | 30827 | 397 | 750 | 91 |
| C6F | 610 | 781 | 84 | 6 | 37 |
| C6M | 30 | 55 | 0 | 0 | 0 |

low 100 m (Fig. 3B). Weighted mean depths (WMD) for both stations were calculated from

$$WMD = \Sigma(n_i z_i)/\Sigma n_i$$

where $n_i$ is the number of copepods within each depth interval ($i$) (ind. $m^{-2}$) and $z_i$ the depth of the middle of the depth interval (Roe et al. 1984). During the night (Stn 7) values for the WMD were 72.8, 111.0 and 105.0 m for C4, C5 and C6F respectively, while during the day (Stn 9) they were 96.4, 131.9 and 124.3 m, about 20 m deeper. This suggests that a portion of the population was undergoing diel vertical migration.

By mid-January significant proportions of the *Calanus finmarchicus* population had molted to the adult stage and were reproducing. In the GSC region (Stn 1) about half the *C. finmarchicus* copepodite population was present as adult females (Table 2, Fig. 4). Most (73.9%) of these females were in the upper 40 m. Most (89.5%) of the C5 copepodites, however, were still below 40 m and presumably resting. Large numbers of young *C. finmarchicus* nauplii were present (Table 2, Fig. 5). In contrast, in Georges Basin (Stn 7), *C. finmarchicus* C5 copepodites were still dominant (73.4%

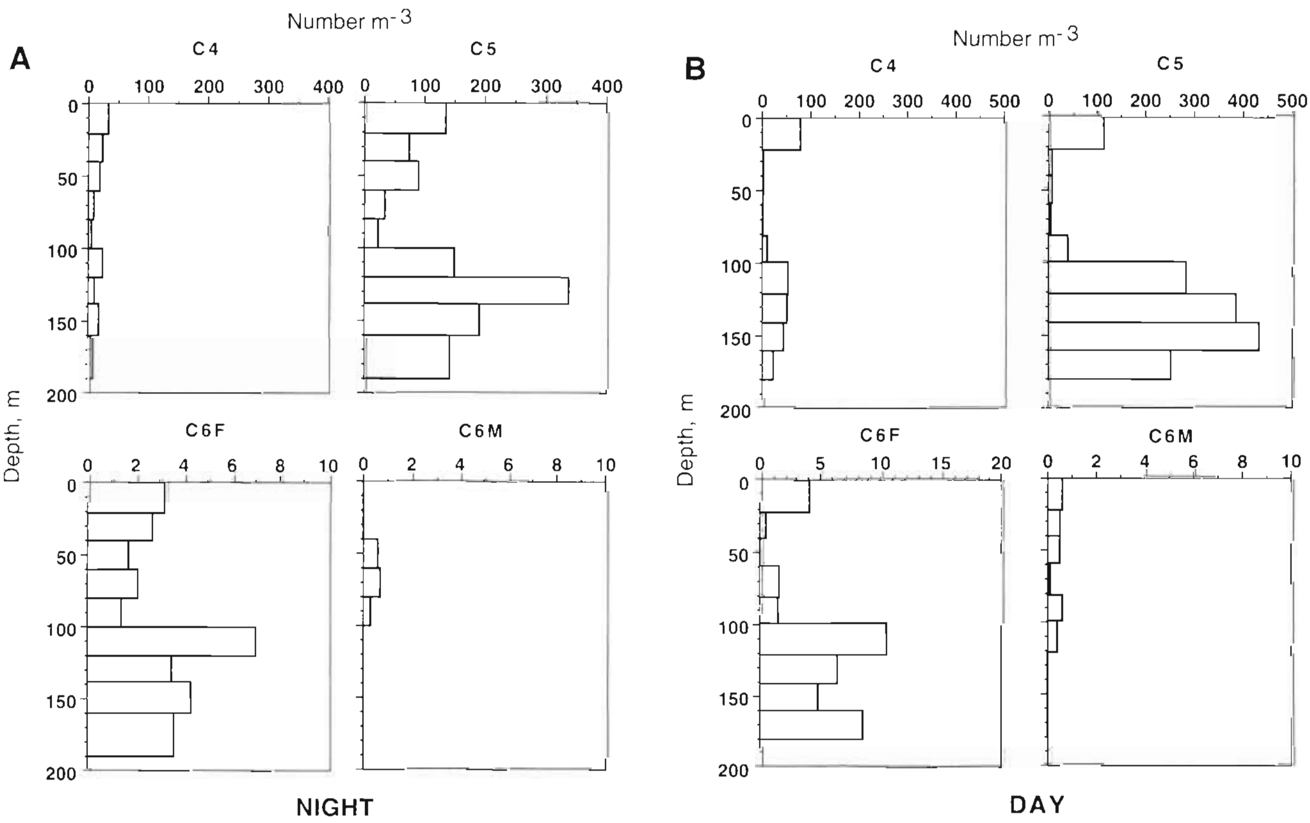



Fig. 3. *Calanus finmarchicus*. (A) Night-time (01:15 h) depth distribution at Stn 7 and (B) day-time (11:11 h) depth distribution at Stn 9 of older copepodites in the southern Gulf of Maine during RV 'Albatross IV' cruise 9410, 8–18 November 1994. Samples were collected with a 1 $m^2$ MOCNESS net with 0.15 mm mesh nets from the bottom to 100 m, and 0.33 mm mesh nets from 100 m to the surface. Water column abundances (no. $m^{-2}$) are given in Table 1

Table 2. *Calanus finmarchicus*. Abundance and age structure of copepods at Stns 1 and 7 in the Southern Gulf of Maine, at Stns 2, 4, 5, and 11 on Georges Bank and at Stn 16 in slope waters during January 1995. Abundance of nauplii are from pump samples collected in the upper 60 m while the 1 $m^2$ MOCNESS samples were taken over the entire water column (upper 400 m at Stn 16). Station depths are shown in parentheses. Data are presented as no. $m^{-2}$ over the depth range of the samples. nd: no data

| | Stn 1 (150 m) | Stn 7 (298 m) | Stn 2 (80 m) | Stn 4 (38 m) | Stn 5 (71 m) | Stn 11 (75 m) | Stn 16 (2500 m) |
|---|---|---|---|---|---|---|---|
| N1 | 1360 | 118 | 0 | 0 | 239 | 0 | nd |
| N2 | 7320 | 381 | 289 | 0 | 1710 | 0 | nd |
| N3 | 21050 | 1250 | 471 | 118 | 2940 | 352 | nd |
| N4 | 200 | 104 | 130 | 0 | 1010 | 0 | nd |
| N5 | 0 | 312 | 0 | 0 | 0 | 0 | nd |
| N6 | 0 | 312 | 0 | 0 | 0 | 0 | nd |
| C1 | 21 | 145 | 0 | 0 | 24 | 0 | 70 |
| C2 | 112 | 49 | 5 | 0 | 6 | 0 | 69 |
| C3 | 14 | 330 | 73 | 3 | 13 | 0 | 38 |
| C4 | 138 | 2390 | 36 | 7 | 0 | 0 | 85 |
| C5 | 2515 | 15900 | 175 | 36 | 308 | 0 | 1090 |
| C6F | 2420 | 1650 | 86 | 20 | 1500 | 0 | 405 |
| C6M | 747 | 1160 | 12 | 3 | 284 | 0 | 0 |

Table 3. *Calanus finmarchicus*. Length (L), carbon and nitrogen values and C:N ratio of copepods from surface and deep water on Georges Bank (GB), in the Gulf of Maine (GOM) and slope water during the fall and early winter of 1994-1995. Data were grouped by region and depth where the surface (S) samples were collected in the upper 40 m and the bottom (B) samples were from depths below 100 m. At each station, n groups of 5 animals each were measured

| Stage | Cruise | Region | Depth | L (mm) | SD | N (µg ind.$^{-1}$) | SD | C (µg ind.$^{-1}$) | SD | C:N | SD | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C5 | AL9410 | GOM | S | 2.09 | 0.08 | 15.1 | 3.3 | 132 | 37 | 8.65 | 1.16 | 24 |
| | | | B | 2.11 | 0.09 | 16.1 | 3.7 | 142 | 40 | 8.67 | 1.21 | 25 |
| | | GB | S | 2.03 | 0.10 | 15.0 | 2.9 | 127 | 33 | 8.37 | 0.77 | 20 |
| | | | B | 2.10 | 0.06 | 15.4 | 1.8 | 137 | 20 | 8.91 | 0.50 | 10 |
| | | Slope | S | 2.11 | 0.06 | 16.3 | 1.5 | 136 | 17 | 8.32 | 0.35 | 10 |
| | | | B | 2.02 | 0.08 | 14.9 | 2.9 | 134 | 28 | 8.97 | 0.35 | 10 |
| | EN259 | GOM | S | 2.04 | 0.08 | 12.2 | 1.7 | 91 | 18 | 7.37 | 0.62 | 37 |
| | | | B | 2.15 | 0.06 | 14.8 | 2.0 | 127 | 19 | 8.53 | 0.26 | 26 |
| | | GB | S | 2.09 | 0.07 | 15.7 | 2.2 | 121 | 28 | 7.66 | 0.89 | 31 |
| | | Slope | S | 2.13 | 0.07 | 13.1 | 1.6 | 105 | 19 | 7.99 | 0.67 | 8 |
| C6F | EN259 | GOM | S | 2.37 | 0.06 | 20.5 | 2.5 | 116 | 17 | 5.66 | 0.42 | 39 |
| | | | B | 2.46 | 0.07 | 16.3 | 2.4 | 127 | 23 | 7.79 | 0.89 | 26 |
| | | GB | S | 2.42 | 0.07 | 23.7 | 3.0 | 134 | 22 | 5.62 | 0.38 | 34 |

of total copepodites; Table 2, Fig. 5) and most of these were at depths >100 m (Fig. 6). About half (46%) of the adult females were found at depths <100 m, while most of the adult males (91%), which at this station were present in relatively high numbers (41% of the total adults in the water column), were found at depths >100 m (Fig. 6). At Stn 7 and at nearby Stn 5 on the NE peak, young *C. finmarchicus* nauplii were present (Table 2, Fig. 5), although in lower numbers than at Stn 1. On the shallow central region of the Bank (Stn 4) and on the southern flank (Stn 11), abundance of *C. finmarchicus* older stages (C5 and adults) was very low and there were few nauplii (Table 2), indicating that water from the GOM carrying the actively reproducing *C. finmarchicus* populations had not yet reached these regions.

### *Calanus finmarchicus* size

Data on body size were grouped according to region (GOM, GB and slope water) in order to examine differences between shallow and deep animals and between the GOM and GB. During November there were no significant differences ($p > 0.05$) in any measures of mass (carbon or nitrogen) of the C5 *C. finmarchicus* between depth layers within a region or between regions (Table 3).

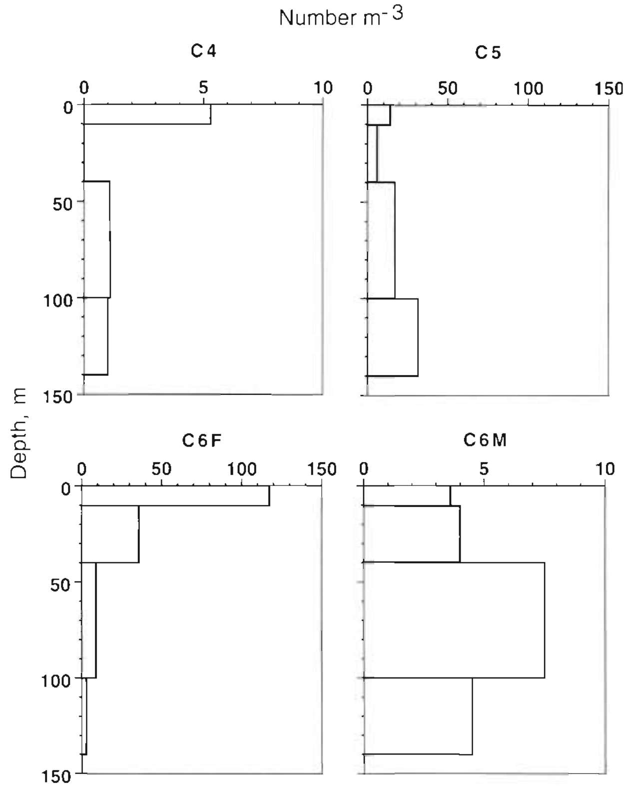



Fig. 4. *Calanus finmarchicus*. Night-time (03:15 h) depth distribution of older copepodites at Stn 1 in the southern Gulf of Maine during RV 'Endeavor' cruise 259, 10 to 22 January 1995. Samples were collected with a 1 $m^2$ MOCNESS net with 0.15 mm mesh nets. Water column abundances (no. $m^{-2}$) are given in Table 2

In January the carbon content of C5 *Calanus finmarchicus* in the bottom layer of the GOM and in the surface on GB was not different but was significantly ($p < 0.01$) greater than the carbon content of C5s at the surface in the GOM or in slope water (Table 3). Adult female *C. finmarchicus* collected from GB in January had significantly ($p < 0.01$) more carbon mass than females found at the surface in the GOM. The larger C5 and adult females were the same size as the C5s measured in November.

In contrast, in January nitrogen mass of adult females from the surface of the GOM and on GB was significantly ($p < 0.01$) higher than the nitrogen mass of adult females collected from the bottom layer in the GOM. These females also had significantly ($p < 0.01$) more nitrogen than the C5s collected both in November and January (Table 3). C:N ratios of the surface females were thus considerably lower than these other groups of *Calanus finmarchicus*. These results suggest that the females at the surface of the GOM and on GB in January have grown considerably in nitrogen but not carbon over the C5s collected in both January and in November.

## Gut pigments

Gut pigments of stage C5 *Calanus finmarchicus* in November were moderately high both on GB and in the GSC region of the southern GOM (Table 4) with values varying between 3.4 and 12.9 ng copepod$^{-1}$. While the mean gut pigment level of animals collected from GB was higher than in the GOM (7.28 and 4.77 ng copepod$^{-1}$, respectively), these differences were not significant. Gut pigments of copepods sampled at night on GB (Stns 18 and 22, Table 4) were significantly higher (p <

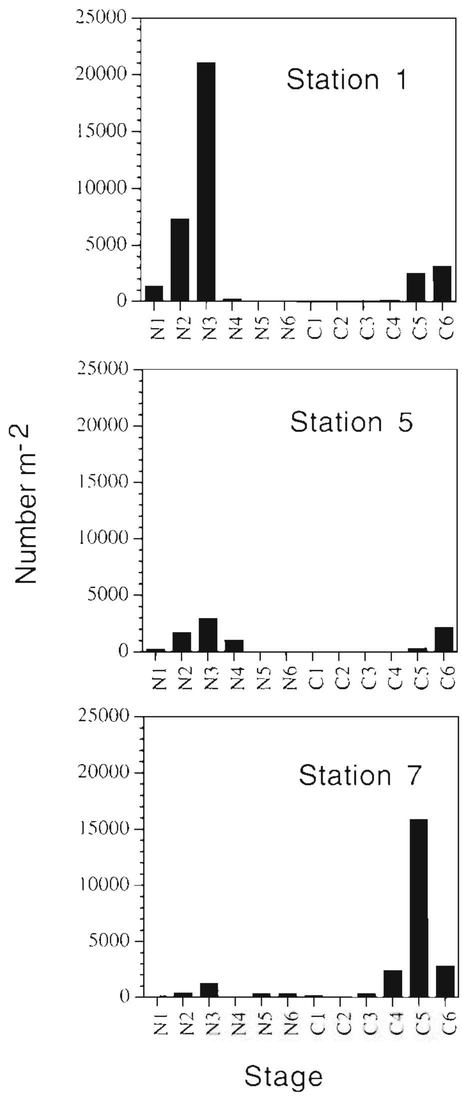



Fig. 5. *Calanus finmarchicus*. Abundance of nauplii and copepodites in the Southern Gulf of Maine (Stn 1), Georges Basin (Stn 7) and on the northeast Peak (Stn 5) during RV 'Endeavor' cruise 259, 10 to 22 January 1995. Copepodite numbers are from 1 $m^2$ MOCNESS net samples collected with 0.15 mm mesh nets between the bottom and the surface, while naupliar numbers are from vertically integrated pump samples collected between about 70 m and the surface

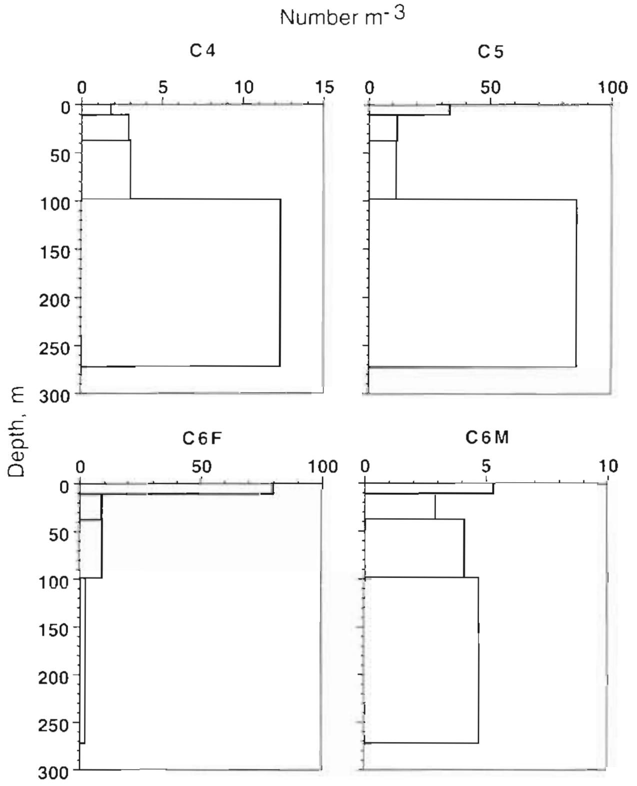



Fig. 6. Day-time (08:22 h) depth distribution of *Calanus finmarchicus* older copepodites at Stn 7 in Georges Basin during RV 'Endeavor' cruise 259, 10 to 22 January 1995. Samples were collected with a 1 $m^2$ MOCNESS net with 0.15 mm mesh nets. Water column abundances (no. $m^{-2}$) are given in Table 2

0.05) than those sampled during the day (Stns 19 and 24), suggesting diel changes in feeding rate. In the GOM there were no significant differences between night-time and day-time gut pigments. In January gut pigment levels of C5 and adult female *C. finmarchicus* collected from the GOM and GB ($\bar{x}$ = 2.96 ng copepod$^{-1}$) were significantly lower ($p < 0.01$) than values measured on C5 *C. finmarchicus* in November ($\bar{x}$ = 6.54 ng copepod$^{-1}$). There were no significant differences between the 2 regions. Gut pigment levels of the C6F collected in January ($\bar{x}$ = 3.75 ng copepod$^{-1}$) were significantly higher ($p < 0.01$) than levels in stage C5 ($\bar{x}$ = 1.90 ng copepod$^{-1}$).

## Egg laying and reproductive index (*RI*)

During November gonad maturation analysis indicated that there was little or no reproductive activity in the southern GOM (Stns 6 and 7, Table 5). In contrast on GB (Stns 16 and 19) 23 and 31% of the females were reproductively active (Table 5). From the relationship between *RI* and egg production rate developed for *C. finmarchicus* during EN259, the mean egg production rate at Stns 16 and 19 was between 5 and 10 eggs female$^{-1}$ d$^{-1}$. Egg production rates during January were between 14.2 and 33.6 eggs female$^{-1}$ d$^{-1}$ with highest rates on GB (Fig. 1B, Table 6). Daily population egg production rates were considerably higher than total naupliar abundance at Stns 5 and 7 (Table 6), suggesting that the development of the cohort was at the very earliest stages at these stations, or that the egg and naupliar mortality was high.

Table 4. *Calanus finmarchicus*. Mean gut pigment concentrations (GPC) of copepods in the southern Gulf of Maine (GOM) and on Georges Bank (GB) during November 1994 and January 1995. Groups of 5 were measured during AL9410 while individuals were measured during EN259

| Cruise | Region | Stn | Time (h) | Date | Stage | Mean GPC (ng ind.$^{-1}$) | SD | n |
|---|---|---|---|---|---|---|---|---|
| AL9410 | GOM | 7 | 1:15 | 12 Nov 1994 | C5 | 3.42 | 1.15 | 9 |
| | GOM | 8 | 13:16 | 12 Nov 1994 | C5 | 5.99 | 2.16 | 10 |
| | GB | 18 | 4:18 | 16 Nov 1994 | C5 | 8.39 | 3.73 | 11 |
| | GB | 19 | 13:35 | 16 Nov 1994 | C5 | 3.45 | 1.8 | 10 |
| | GB | 22 | 0:30 | 17 Nov 1994 | C5 | 12.95 | 7.23 | 10 |
| | GB | 24 | 11:53 | 17 Nov 1995 | C5 | 5.24 | 2.09 | 15 |
| EN259 | GOM | 1 | 3:15 | 11 Jan 1995 | C6F | 4.17 | 2.98 | 30 |
| | GOM | 7 | 11:30 | 15 Jan 1995 | C6F | 1.32 | 0.73 | 30 |
| | | | | | C5 | 1.12 | 1.07 | 30 |
| | GOM | 21 | 13:00 | 21 Jan 1995 | C6F | 3.27 | 3.38 | 30 |
| | | | | | C6M | 0.17 | 0.18 | 20 |
| | | | | | C5 | 1.76 | 1.78 | 30 |
| | GB | 4 | 16:30 | 12 Jan 1995 | C6F | 1.83 | 1.58 | 30 |
| | | | | | C5 | 1.33 | 2.53 | 30 |
| | GB | 5 | 10:30 | 14 Jan 1995 | C6F | 5.36 | 3.35 | 30 |
| | | | | | C5 | 2.67 | 2.57 | 30 |

Table 5. *Calanus finmarchicus*. Gonad maturation analysis for adult females collected during the AL9410 cruise, 17 to 18 November 1994, to the Gulf of Maine (GOM) and Georges Bank (GB). Reproductive states (RS) of 4 to 7 indicate reproductively active animals. *RI*: reproductive index

| Region | Stn | Sample depth (m) | Index | No. observed | Index frequency | *RI* |
|---|---|---|---|---|---|---|
| GOM | 7 | 0–40 | 1 | 23 | 0.45 | 0.00 |
| | | | 2 | 25 | 0.49 | |
| | | | 3 | 13 | 0.25 | |
| | | | 4 | 0 | 0.00 | |
| | | | 5 | 0 | 0.00 | |
| | | | 7 | 0 | 0.00 | |
| GB | 6 | 15–29 | 1 | 18 | 0.56 | 0.09 |
| | | | 2 | 10 | 0.31 | |
| | | | 3 | 1 | 0.03 | |
| | | | 4 | 0 | 0.00 | |
| | | | 5 | 2 | 0.06 | |
| | | | 7 | 1 | 0.03 | |
| GB | 16 | 15–37 | 1 | 13 | 0.43 | 0.23 |
| | | | 2 | 7 | 0.23 | |
| | | | 3 | 3 | 0.10 | |
| | | | 4 | 4 | 0.13 | |
| | | | 5 | 3 | 0.10 | |
| | | | 7 | 0 | 0.00 | |
| GB | 19 | 14–40 | 1 | 3 | 0.16 | 0.31 |
| | | | 2 | 3 | 0.16 | |
| | | | 3 | 7 | 0.37 | |
| | | | 4 | 4 | 0.21 | |
| | | | 5 | 1 | 0.05 | |
| | | | 7 | 1 | 0.05 | |

## DISCUSSION

In its typical life cycle in north Atlantic waters *Calanus finmarchicus* rests at depth during the fall in stage C5, with perhaps some in stage C4. Molting to the adult stage is observed to take place during winter and spawning by females is considered to commence when food reaches a sufficient level during or just prior to the spring bloom (Conover 1988). Resting copepods have low metabolic rates (Hirche 1983), empty guts and reduced epithelia (Hallberg & Hirche 1980), and low levels of digestive enzymes (Tande & Slagstad 1982, Hirche 1983). These observations indicate that little or no feeding occurs during the resting period. In the southern GOM, however, at least part of the *C. finmarchicus* population was physiologically active during November (Table 4) and began its reproductive cycle between mid-November and mid-January (Tables 5 & 6). Further, on GB *C. finmarchicus* was not only feeding at this time, but a fraction of the females were reproductively active, suggesting that the reproductive cycle is never broken. In the discussion below, we examine the implications of these results, both for the mechanisms controlling emergence from diapause or resting state and for the processes determining early spring abundance of *C. finmarchicus* on GB.

### Emergence from the resting phase in the southern GOM

Our observations suggest that there are 2 components to the fall-winter population of *Calanus finmarchicus* in the southern GOM. During November about one third of the population of *C. finmarchicus* resided in the upper 60 m. There was a minimum in abundance between 60 and 100 m and then a fairly even distribution of copepods between 100 m and the bottom (180 m). Stage C5 constituted most of both the surface and deep components. The surface component was actively feeding and appeared to be undergoing diel vertical migration, as fewer individuals were found within the surface layer during the daytime. The C5s at the surface were not significantly different in mass (C, N) from those at depth. Based on studies of stage in the molt cycle using the status of the hemocele and of tooth development in the mandibular gnathobase, the feeding C5s were not yet ready to molt to the adult stage and morphologically appeared to still be in the resting or diapause state (C. Miller pers. comm.). The deep component was not found in a discrete dense layer close to the bottom, as in the basins on the Scotian Shelf (Sameoto & Herman 1990, Herman et al. 1991), but rather was fairly evenly distributed in the lower 80 m. The deep copepodites were resting, showing the same quiescent behavior described for *C. finmarchicus* by Hirche (1983), i.e. floating motionless with their heads upwards. When brought back to the laboratory and provided with food, it took approxi-

Table 6. *Calanus finmarchicus*. Population egg production rates and total naupliar abundance in the Southern Gulf of Maine (GOM) and on Georges Bank (GB) during January 1995

| Region | Stn | C6F (no. $m^{-2}$) | Egg production rate (eggs $female^{-1}$ $d^{-1}$) | (eggs $m^{-2}$ $d^{-1}$) | Total nauplii (no. $m^{-2}$) |
|---|---|---|---|---|---|
| GOM | 1 | 2420 | 15.3 | 37000 | 29900 |
| GOM | 1 | 2420 | 23.5 | 56900 | 29900 |
| GOM | 7 | 1650 | 14.2 | 23500 | 2470 |
| GB | 2 | 175 | 20.3 | 3550 | 890 |
| GB | 4 | 20 | 33.6 | 672 | 118 |
| GB | 5 | 1500 | 30.7 | 46000 | 5900 |

mately 2 wk before they molted to the adult stage, a time similar to that described by Grigg & Bardwell (1982) for quiescent C5 *C. finmarchicus* collected during the fall.

In the GSC region of the southern GOM and Georges Basin the C5 *Calanus finmarchicus*, presumably the surface component, was molting to the adult stage and actively spawning by January. A cohort of young *C. finmarchicus* nauplii, predominantly stage N3, was present in January in the GSC, in Georges Basin and on the NE peak of GB. The highest abundance of nauplii was in the GSC. These observations indicate that *C. finmarchicus* is reproducing in the southern GOM at the very beginning of winter. The biomass peak of older copepodites observed on the Bank later in March and April (Davis 1987, Meise & O'Reilly 1996) does not provide a good indication of the timing of the onset of reproduction of this species.

There appears to be a difference between the GSC region of the southern GOM and Georges Basin in the timing of the arousal of the *Calanus finmarchicus* population. In January in the GSC region (Stn 1), 41% of the copepodite population was present as adult females and 42% as C5. In contrast, at about the same time in Georges Basin (Stn 7) most (73%) of the *C. finmarchicus* copepodites were still present as C5 and most of these were at depth. Adult females constituted only 8% of *C. finmarchicus* copepodites.

A more precise estimate of the timing of molting to the adult stage in the GSC region of the southern GOM and the start of reproduction can be obtained from the age structure of the young cohort observed in January and laboratory data on development rate. Surface temperature at Stn 1 in the GSC in January was 7.9°C. At 8°C, the development time in the laboratory of GB/GOM *Calanus finmarchicus* from egg laying to the midpoint of stage N3 is 9.1 d (Durbin unpubl.). We calculate that the young cohort would have hatched from eggs laid around the 1st of the year, implying that the molt from C5 to the adult stage took place some time prior to this. Plourde & Runge (1993) found a lag of 7 to 8 d between the rapid increase in phytoplankton abundance and the onset of egg laying by *C. finmarchicus* in the Gulf of St. Lawrence. If we assume a similar lag between molting to the adult stage and the onset of egg production, and a 2 wk period between arousal and molting, then emergence from the resting phase of *C. finmarchicus* in the GSC region of the southern GOM would have commenced in early December.

Miller et al. (1991) proposed that the arousal mechanism for *Calanus finmarchicus* depends on its winter habitat. In deep water, for example in the slope water off southern New England, *C. finmarchicus* overwinters at around 500 m, arousal and maturation appear to take place in February to March, and the stimulus for arousal is hypothesized to be the increasing photoperiod in late winter. However, if the resting C5 *C. finmarchicus* are transported to the surface by water circulation at a time other than the usual maturation time, then some cue, possibly involving a marked increase in intensity or duration of illumination, returns them to the active phase, in which case they mature and reproduce ahead of schedule. The survival value of this strategy is the reactivation of reproduction and predator avoidance behavior in the surface environment where mortality rates are undoubtedly higher.

Our results are consistent with this latter scenario. The surface component of C5s in the southern GOM in November could represent animals which have been advected into the surface layer, perhaps by deep convective mixing during the fall as the Maine Intermediate Water is beginning to form (Brown & Beardsley 1978, Hopkins & Garfield 1979). Once aroused, the copepodites resumed feeding. Phytoplankton concentrations on GB and in the southern GOM are relatively high during the fall where there is typically a diatom bloom (O'Reilly et al. 1987, see also Fig. 2A). During the winter the shallow water column depth enables phytoplankton production to continue (O'Reilly et al. 1987). Brief periods of reduced mixing also appear to allow diatoms to flourish in the absence of stratification during the winter in the southern GOM (Townsend et al. 1992). Thus food is probably normally sufficient in the southern GOM and on GB during late fall and early winter to enable *Calanus finmarchicus* to feed and grow after returning to the surface. Differences during January between the GSC and Georges Basin in the timing of emergence from resting may be related to depth: Georges Basin is about 270 m deep while the mean depth in the GSC is about 150 m.

Early maturation and onset of spawning of *Calanus finmarchicus* appears to occur in other areas, such as the Clyde Sea area (Nicholls 1933) and Loch Striven (Marshall et al. 1934), where the water column is relatively shallow and food is available. In these regions the bottom prevents *C. finmarchicus* from migrating to greater depths, and advection of animals into the surface mixed layer is more probable. The portion of the population at the surface would continue to develop and spawn, while those remaining at depth would wait until the proposed photoperiod cue. The interaction between food and illumination may be important in initiating emergence, as Pedersen et al. (1995) did not find any evidence of feeding or molting in surface-dwelling stage C5 in early winter in Grotsund north of Tromso, where the light level is very much lower than on GB at this time of year. Sufficient food is also necessary to initiate spawning. In the Lower St. Lawrence Estuary, *C. finmarchicus* females were clearly food-limited prior to the spring phytoplankton bloom, which

occurs quite late, typically in mid-June. Here, the final stages of oocyte development of *C. finmarchicus* females did not appear until the onset of the bloom with egg production beginning 1 wk later (Plourde & Runge 1993).

## Winter recruitment and the repopulation of Georges Bank

During November the abundance of *Calanus finmarchicus* on GB was very low. With the exception of the NE peak, a similar low abundance was observed in January. At the station on the southern flank, for example, no older stages of *C. finmarchicus* were found in the preserved samples (Table 2), and there were barely sufficient numbers of females in the live catch for egg laying measurements. It is unlikely that the density of *C. finmarchicus* copepodites on the Bank could serve as the parental stock for the winter-spring cohort which develops later. On the NE peak (Stn 5), abundance of older stage copepodites was relatively high and dominated by adult females (1500 $m^{-2}$). There was also a cohort of young *C. finmarchicus* nauplii present at this station. This suggests that recolonisation of the Bank initially occurs in this region. There are 3 potential sources for these animals: the adjacent Georges Basin water, the GSC region, or the Browns Bank region on the other side of the NE Channel. Extending along the northern flank of GB is a jet derived from rectification of the semidiurnal $M_2$ tidal current (Butman et al. 1987, Lynch & Naimee 1993, Chen et al. 1995), providing a mechanism by which animals from the GSC region could be transported along the northern flank and then deposited on the NE peak. Surface drifters deployed in the eastern part of the GSC region during late spring moved to the east and were entrained in this jet, moving onto the Bank in the region of the NE peak (Chen et al. 1995, Limeburner & Beardsley 1996). Alternatively, a winter-spring wind-driven surface layer in the GOM, which has a generally southward drift, may act as a conveyer belt for the transport of animals from adjacent waters to the north onto GB (C. Hannah, C. Namie, J. Loder & F. Werner unpubl.). This model, however, predicts that the shallow central region of the Bank will be recolonised as rapidly as the NE peak, something we did not see any evidence for based on the *C. finmarchicus* abundance at Stns 2 and 4 (Table 2). Filaments of Scotian Shelf surface water have been observed to jump across the NE Channel onto the NE peak (Flagg 1987, Bisagni et al. 1996). We saw evidence of cold, low salinity Scotian Shelf water at the surface in the GOM (Stn 7) during January but not on GB, suggesting that this was not an important source region. This suggests that either or both of the former 2 pathways could be operating.

The likelihood that the inputs of *Calanus finmarchicus* to the NE peak are controlled by these general circulation features (Butman & Beardsley 1987), and that reproduction is initiated in mid-winter as *C. finmarchicus* are carried onto the Bank, suggests that the NE peak has predictably high abundances of *C. finmarchicus* nauplii beginning in January. However, the mortality of egg and naupliar stages during this period may be high. For example, at Stns 5 and 7, naupliar abundance is much lower than might be expected from the daily input of eggs (Table 6). Potential winter sources of egg and naupliar mortality include low fertilization rate due to a paucity of males, food-quality or toxic effects of winter diatom blooms impairing embryogenesis (e.g. Poulet et al. 1995, Uye 1996) or the lack of suitable food to support naupliar growth. The rates and sources of mortality in *C. finmarchicus* populations have yet to be determined.

The NE peak is an important area for cod and haddock spawning (Smith 1983). Peak spawning for cod normally occurs between February and March, but it can vary from year to year (Smith 1983). Nauplii are major prey of the larvae of these species when feeding begins (Kane 1984, Buckley & Lough 1987). On an evolutionary time scale, fish may have adopted the NE peak as a focal point for recurrent spawning because of the predictable supply of prey for their larvae, starting in mid-winter.

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