Life cycle of *Calanus finmarchicus* in the lower St. Lawrence Estuary: the imprint of circulation and late timing of the spring phytoplankton bloom

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Abstract: The life cycle of *Calanus finmarchicus* in the lower St. Lawrence estuary is described based on observations of female egg production rate, population stage abundance, and chlorophyll *a* biomass collected over 7 years (1991–1997) at a centrally located monitoring station. The mean seasonal pattern shows maximum abundance of females in May, but peak population egg production rate and naupliar (N3–N6) abundance occur in early July just after onset of the late spring – early summer phytoplankton bloom. The population stage structure is characterized by low summer abundance of early copepodite stages C1–C3 and high stage C5 abundance in autumn. Between 1994 and 1997, there was important interannual variation in both timing (up to 1 month) and amplitude (five- to eight-fold) of population reproduction. Patterns of seasonal increase of C5 abundance in autumn suggest interannual variations of both timing and magnitude of deep upstream advection of this overwintering stage. Thus, the main features of *C. finmarchicus* population dynamics in the central lower St. Lawrence Estuary are (*i*) late reproduction resulting from food limitation prior to the onset of the summer phytoplankton bloom, (*ii*) probable export of early developmental stages during summer, and (*iii*) advection into the central lower St. Lawrence Estuary of overwintering stage C5 in autumn from downstream regions. These results support the hypothesis that circulation, mainly driven by discharge from the St. Lawrence River and its tributaries, is a key factor governing population dynamics of *C. finmarchicus* in this region.

Résumé : Le cycle de vie de *Calanus finmarchicus* dans l'estuaire maritime du Saint-Laurent est décrit en utilisant des mesures du taux de production d'oeufs des femelles, d'abondance des différents stades de développement et de la biomasse phytoplanctonique (chlorophylle *a*) effectuées durant une période de 7 ans (1991 à 1997) à une station de monitorage située dans la partie centrale de la région. Le patron saisonnier moyen est caractérisé par un maximum d'abondance des femelles en mai, mais un pic de reproduction de la population et de l'abondance de nauplii (N3–N6) au début juillet après l'amorce de la floraison du phytoplancton. La population montre une faible abondance des jeunes stades copépodites C1–C3 en été et une abondance élevée du stade C5 à l'automne. Nous observons d'importantes variations interannuelles du moment (jusqu'à 1 mois) et de l'amplitude (cinq à huit fois) de la reproduction de la population. Les patrons annuels d'abondance des C5 suggèrent des variations interannuelles du moment et de l'importance de l'advection en profondeur vers l'amont de ce stade d'hivernation à l'automne. Les caractéristiques principales de la dynamique de population de *C. finmarchicus* dans l'estuaire maritime du Saint-Laurent sont (*i*) une reproduction tardive induite par une limitation de la nourriture avant le début de la floraison estivale du phytoplancton, (*ii*) une exportation probable des jeunes stades de développement durant l'été et (*iii*) une advection en profondeur vers l'amont des C5 en hivernation à partir de régions en aval en automne. Ces résutltats supportent l'hypothèse que la circulation, principalement controlée par la décharge du fleuve Saint-Laurent et de ses tributaires, est un facteur clé du contrôle de la dynamique de population de *C. finmarchicus* dans la région.

Introduction

The marine calanoid copepod *Calanus finmarchicus* is an important component of the zooplankton community in the northwest Atlantic Ocean, including the regions located on the northeast America Continental shelf such as the Gulf of Maine – Georges Bank region, the Scotian Shelf, and the Gulf of St. Lawrence (GSL) (de Lafontaine et al. 1991; Sameoto and Herman 1992; Meise and O'Reilly 1996). *Calanus finmarchicus* has been hypothesized to be a critical

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link in some systems between lower (phytoplankton–microzooplankton) and higher levels (fish stocks) of the marine pelagic food web (Runge 1988; Cushing 1995). On Flemish Cap and in the GSL, the abundance of *C. finmarchicus* prey may control growth and survival rates of early life stages of redfish and mackerel (Anderson 1994; Runge and de Lafontaine 1996; Runge et al. 1999). The potential for a relationship between *C. finmarchicus* and fish recruitment is one reason why the Canadian Global Ocean Ecosystem Dynamics (GLOBEC) program has identified *C. finmarchicus* as a key species for study of how climate variability may affect recruitment of fish stocks in eastern Canadian waters.

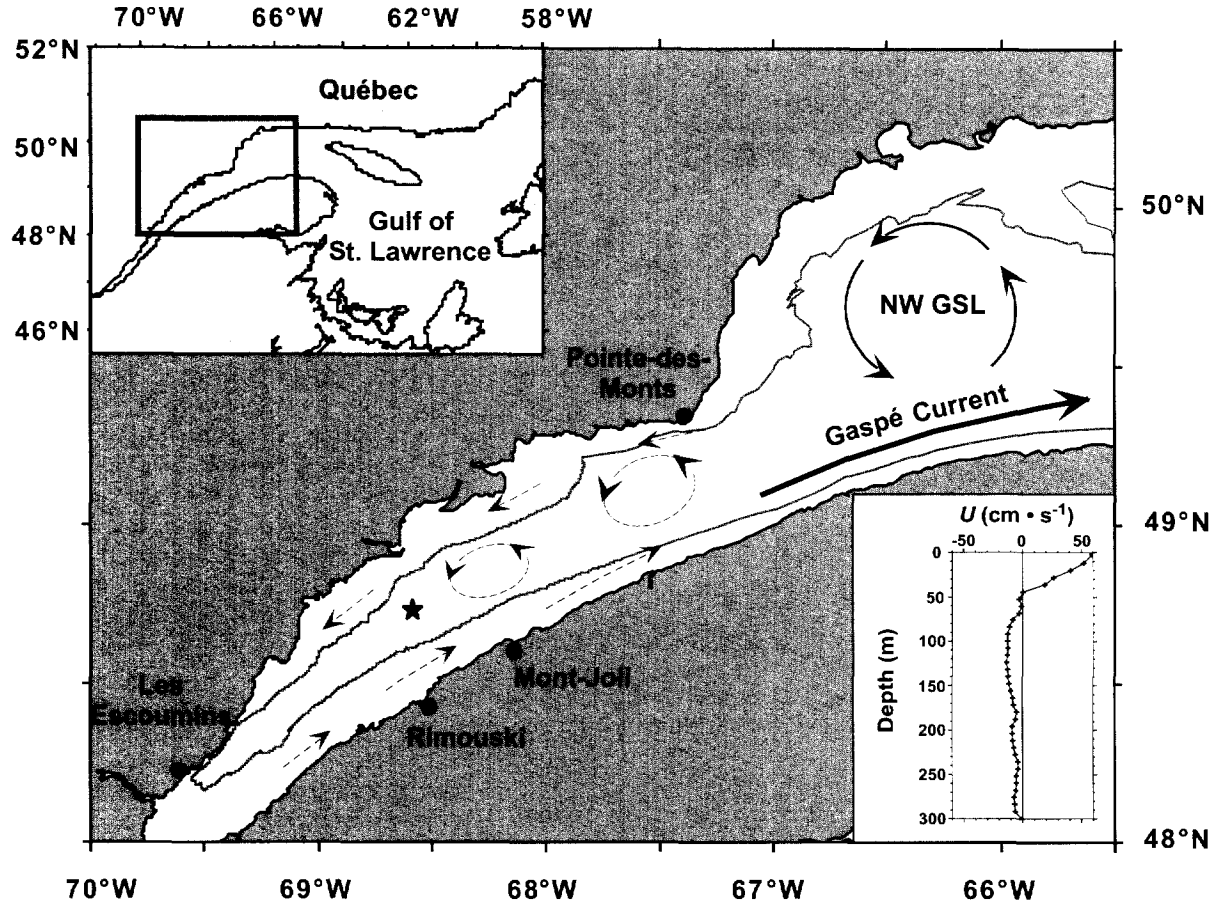
The life cycle strategy of *C. finmarchicus* is well adapted to the seasonal phytoplankton cycle occurring in higher latitudes. *Calanus finmarchicus* molt to adult stages and mate before the spring phytoplankton bloom in response to intrinsic or external environmental cues and reproduce as the spring bloom begins (Miller et al. 1991; Diel and Tande 1992; Plourde and Runge 1993). Cohort development takes place in food-rich surface waters, and overwintering from late summer to late winter in deep water occurs in a preadult stage (mainly copepodite C5) sustained by energy body reserves (Miller et al. 1991). The egg production rate (EPR) of *C. finmarchicus* adult females is a function of food and temperature, although such relationships have been difficult to establish in field conditions (Runge 1985; Hirche et al. 1997). *Calanus finmarchicus* body size varied both seasonally and spatially across its domain and is inversely related to temperature (Carlotti et al. 1993; Runge and Plourde 1996). In the natural environment, temperature has been considered as the main factor governing the development and growth rates of marine calanoid copepods, but recent studies based on field observations showed that food limitation may play an important role in some ecosystems (Richardson and Verheye 1999; Campbell et al. 2001).

In waters off eastern Canada, some important characteristics of the *C. finmarchicus* life history are known, but essential elements are still lacking for a complete understanding of its life cycle. *Calanus finmarchicus* starts to reproduce in early March on the Scotian Shelf, late April – early May in Baie-des-Chaleurs (southwest GSL), and late June in the lower St. Lawrence River estuary (LSLE) (Lacroix and Filteau 1970; Plourde and Runge 1993; McLaren et al. 2001). In the GSL, sparse information about the primary production cycle suggests that *C. finmarchicus* reproduction starts in April–May (de Lafontaine et al. 1991). Body size and stage composition data showed that *C. finmarchicus* produces two or three generations a year on the Scotian Shelf and in the southwest GSL (Lacroix and Filteau 1970; McLaren et al. 2001). It has been proposed that the *C. finmarchicus* population residing in deep basins over the Scotian Shelf may originate upstream from production in the GSL or from *Calanus*-rich slope waters to the east (Sameoto and Herman 1992; Head et al. 1999). However, little is known about other important aspects of *C. finmarchicus* population dynamics in the LSLE and GSL, such as timing of adult recruitment, variability in number of generations, and timing of entry into diapause at the end of the developmental season.

In the LSLE, physical and phytoplankton production cycle characteristics may greatly influence *C. finmarchicus* population dynamics. The LSLE is a large marine estuary (200 km long, 20–40 km wide, up to 330 m deep) with a two-layer circulation pattern in which the surface outflow (30–50 $cm \cdot s^{-1}$) driven by surface freshwater runoff from the St. Lawrence River is compensated by slow advection (5–10 $cm \cdot s^{-1}$) of deep water through the Laurentian Channel, a deep marine valley originating from the margin of the Continental Shelf and ending 2000 km upstream at the head of the LSLE (Fig. 1). The general summer surface circulation pattern is characterized by a seaward flow mainly located along the south shore in a jetlike structure that forms the Gaspé Current in the GSL and by the presence of several fronts and mesoscale features (Fig. 1) (Ingram and El-Sabh 1990). High freshwater discharge and light limitation are the likely factors determining delay of the onset of the spring diatom bloom until late June – early July, 1–2 months later than in the adjacent GSL (Therriault et al. 1990; Zakardjian et al. 2000). Upwelling of nutrient-rich deep cold water at the head and on the northern side of the Laurentian Channel in summer supports successive diatom blooms and maintains low surface temperatures (Ingram and EL-Sabh 1990; Therriault et al. 1990). In 1991, *C. finmarchicus* adult females initiated egg production 1 week after the onset of the phytoplankton bloom in June and sustained high specific EPR until late August (Plourde and Runge 1993). Based on the few studies conducted in the LSLE, there is evidence that *C. finmarchicus* stage structure is biased toward late copepodite stages C4 and C5 (Runge and Simard 1990). The authors proposed that the typical two-layer circulation pattern in LSLE favors the dominance of *C. finmarchicus* late copepodite stages by exporting surface-dwelling early developmental stages in the strong residual outward surface currents and transporting deep, overwintering late copepodite stages in the upstream deep circulation. Most water renewal in fjord systems isolated from adjacent water masses by a shallow sill occurs during sporadic seasonal events (Osgood and Frost 1996). Because of strong surface runoff and the Laurentian Channel, water exchange between the GSL and LSLE is continuous and the *C. finmarchicus* seasonal distribution patterns likely result from interaction between timing of population development, vertical distribution, and circulation. Clearly, a late start of the phytoplankton bloom and circulation pattern can have a great impact on the population dynamics of *C. finmarchicus* in the LSLE.

We present here a time series of chlorophyll *a* (Chl *a*) biomass, *C. finmarchicus* adult female EPR, population stage abundance, and body size of late copepodite stages collected over 7 years at a monitoring station in the central LSLE. We use both averaged and individual annual time series to answer the following questions about *C. finmarchicus* population dynamics in LSLE. (*i*) What is the long-term average of the timing, duration, and amplitude of the reproduction period in relation to the phytoplankton bloom? (*ii*) Is the stage structure dominated by late copepodite stages in summer, as hypothesized by Runge and Simard (1990)? (*iii*) What is the amplitude of interannual variations in *C. finmarchicus* life cycle parameters (abundance, reproduction, development)? Finally, we use all observations to evaluate the role of circulation as a control of population dynamics, propose mechanisms responsible for maintenance of the *C. finmarchicus* population in the LSLE, and estimate its contribution to the adjacent GSL.

Fig. 1. Map of the LSLE and the northwest GSL showing the sampling station (star) off Rimouski, the Laurentian Channel identified by the 200-m isobath (grey line), and the general surface circulation pattern in summer (adapted from Runge and Simard 1990). Lower right inset: representative depth profile of along-channel baroclinic velocities U showing the downstream (positive) and upstream (negative) residual currents in the central LSLE in summer (adapted from Zakardjian et al. 2000).



Materials and methods

Field sampling

Sampling was carried out from 1991 to 1997 at a station (330 m depth) located 16 km north of Rimouski in the central LSLE (Fig. 1). The basic protocol included an STD (Applied Microsystems STD-12) profile from the surface to 250 m, collection of water with 5-L Niskin bottles at eight depths (0, 5, 10, 15, 20, 25, 35, and 50 m), and collection of zooplankton with a 1-m-diameter, 333-μm-mesh ring net. The plankton net was fitted with a restricted-flow cod end and a TSK flowmeter. It was towed at <30 m·min^{-1} from 250 m to the surface and the catch was immediately diluted into 4-L jars filled with 0.2-μm-filtered seawater. Samples were consistently collected between 10:00 and 12:00; water samples (stored in dark bottles) and zooplankton were maintained at 5–6°C in coolers during transport to the laboratory at the Maurice Lamontagne Institute (Mont-Joli, Qué.). The laboratory analyses (filtration, copepod sorting) typically began between 14:00 and 15:00.

This basic protocol varied slightly among years. In 1991 and 1992, water was collected at three depths (0, 10, and 20 m) and five depths (between 0 and 25 m), respectively. As integrated Chl *a* biomass in the first 20 m of the water column represented >95% of the 0- to 50-m biomass measured in 1993–1997, we include data from 1991 and 1992 in our analysis. Additionally, we sampled zooplankton in 1992 with a bongo net equipped with 333-μm nets obliquely towed from a depth of 250 m to the surface. In 1994, 1996, and 1997, we added to the protocol a 1-m-diameter, 73-μm-mesh net towed from a depth of 50 m to the surface in order to collect early developmental stages (N1–C1).

Laboratory analyses

Chl a concentrations and adult females sorting

Duplicate 250- to 750-mL subsamples from each water bottle were filtered on GF/F filters and 5-μm Nuclepore screens. The screens and filters were placed in 95% acetone and Chl *a* was extracted at 5°C for 16–24 h; extracts were analyzed on a Turner Designs model 112 fluorometer and Chl *a* concentrations calculated according to Parsons et al. (1984) and integrated over depth sampled. Within 1–3 h of arrival, *C. finmarchicus* adult females used for measurement of the in situ EPR were sorted under a dissecting microscope at 6–12× magnification from the diluted zooplankton catch. Care was taken to maintain, with ice in the transport coolers, the zooplankton at 5–6°C during sorting. Only adult females smaller than 3.25 mm (see below) in prosome length were selected; larger copepods were assumed to be *Calanus glacialis*, which was also present although usually much less abundant. Most of these larger adult females had red-pigmented genital pores, which facilitated identification. The remainder of the zooplankton catch was preserved in 4% formaldehyde for analysis of composition and abundance.

EPR

We used two different incubation techniques to measure the

EPR of *C. finmarchicus* (Runge and Plourde 1996). In 1991 and 1992, we incubated five to10 *C. finmarchicus* adult females in each of four to six replicate 1.2-L egg separation containers closed off at the bottom end with 333-μm-mesh Nitex screen and immersed in 2-L glass beakers filled with 0.2-μm-filtered seawater. At the end of the incubation, egg separators and females were removed and the eggs counted. From 1993 to 1997, the EPR was measured by individually incubating 40 adult females in 50-mL petri dishes filled with filtered seawater. At the end of the incubation, the eggs were counted and spawning adult females removed for prosome length measurement. Both types of incubations (beaker and dishes) were run for 24 h at 5–6°C in the dark.

Calanus finmarchicus *enumeration and body size*

The formalin-preserved samples were rinsed in tap water and 10-mL aliquots were taken with a Stempel pipette. Species and stage composition were determined under a dissecting microscope at 6–50× magnification. Between 300 and 600 individuals were identified in each sample and no less that 1/100 of original sample was analyzed. Abundance of early developmental stages (nauplii and C1–C3) and older copepodite stages (C4 to adult C5) were determined from the 73- and 333-μm net samples, respectively. Naupliar stages N3–N6 were identified, whereas to save analysis time, N1 and N2 were grouped with nauplii of other calanoid copepod species such as *C. glacialis*, *Metridia longa*, and *Pseudocalanus* spp. Copepodite C1–C3 *C. finmarchicus* were distinguished from *C. glacialis* based on body size (Unstad and Tande 1991).

The 333-μm sample series collected from May to December 1996 was selected for analysis of the seasonal pattern of body size of the older copepodite stages. Because of the size overlap between *C. finmarchicus* and *C. glacialis*, a species that is present but not abundant in the lower estuary, distinction between these two species in the preadult stages is problematical. We first measured the bimodal size distribution of a natural *C. finmarchicus* – *C. glacialis* mixture in July and September in order to determine the stage-specific size distribution of both species. Based on this analysis, we used an upper cutoff limit for prosome length of 2.15 mm for C4, 2.85 mm for C5, and 3.25 mm for adult females to help distinguish *C. finmarchicus* C4, C5, adult males, and adult females. Usually, 50 individuals of each stage (all individuals of a given stage in samples if not sufficiently abundant) were sorted and measured at 25× magnification from a lateral view under a dissecting microscope coupled with BIO-QUANT, an image analysis system. The mean prosome length of each stage was calculated for each station.

Analysis of seasonal patterns

The LSLE is a highly dynamic environment characterized by several oceanographic features occurring at relatively short temporal scales (Ingram and El-Sabh 1990). These features may account for date-to-date high variation observed in annual time series. As one of our primary objectives is to identify general characteristics of *C. finmarchicus* population dynamics in the region, we combined data of different years for an averaged time series of Chl *a* biomass and *C. finmarchicus* life cycle. Data were grouped by 15-day periods. Calculated means for each 2-week period from May to September included at least six stations. Averaging for March, April, and October–December was more difficult because the station was infrequently visited. However, during this period, deep-living overwintering C5 dominate the population (Runge and Simard 1990) and are less affected by surface circulation than the summer population. Thus, we consider these points representative of the overwintering population (autumn to early spring). We used data collected from 1991 to 1997 to calculate Chl *a* and *C. finmarchicus* EPR averaged cycle and 1992–1997 data to represent adult female abundance and population EPR seasonal patterns. Finally, the averaged time series of stage structure was calculated from data collected in 1994, 1996, and 1997, years during which both 73- and 333-μm plankton nets were deployed.

Results

Mean seasonal patterns of phytoplankton biomass and *Calanus* reproduction

The seasonal cycle of Chl *a* standing stock in the LSLE is characterized by a late spring bloom starting in mid-June and persisting (Chl $a > 50$ mg·m^{-2}) throughout the summer months (Fig. 2A). The female-specific EPR (Fig. 2A) matches the timing and duration of the chlorophyll cycle. Prior to the bloom, from early May to mid-June, females produce eggs at low rates (mean of 10 eggs·female^{-1}·day^{-1}). Subsequently, up to 40–70 eggs·female^{-1} are laid daily once the bloom becomes well established (Fig. 2A). Females sustain this high EPR until late September, after which it drops to 20 eggs·female^{-1}·day^{-1} in October. The mean clutch size follows the pattern of specific EPR (Fig. 2A), with higher values observed during the bloom period (analysis of variance, $p < 0.0001$).

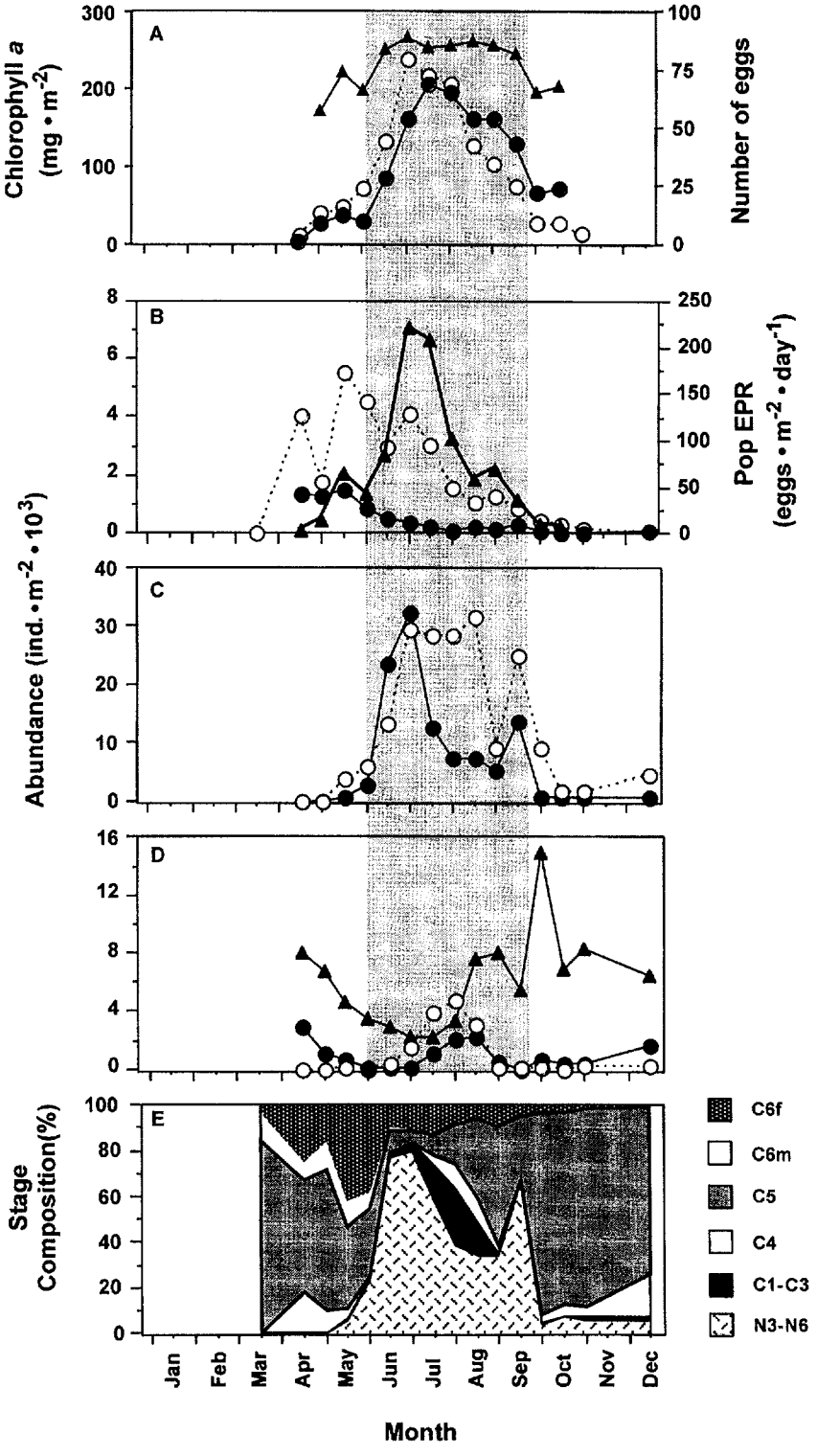
Calanus finmarchicus adult females are relatively abundant between late April and late July, with maximal abundance (5000 individuals·m^{-2}) observed in late spring (May–June) and a second smaller peak in July (Fig. 2B). The number of adult females steadily decreases from 1500 individuals·m^{-2} in August to near zero in autumn. Arousal from diapause probably begins earlier than mid-April in the LSLE, as suggested by maximal adult male abundance (1500 individuals·m^{-2}) at the start of the data series (Fig. 2B). The population EPR (eggs per square metre per day) is a function of patterns of specific EPR and adult female abundance. The *C. finmarchicus* population reproduces at high rates (>50 × 10^3 eggs·m^{-2}·day^{-1}) over the late spring and summer period, from early May to early September (Fig. 2B). The reproductive peak for the population (200 × 10^3 eggs·m^{-2}·day^{-1}) is centered in July.

Mean seasonal demographic pattern

Based on observations presented in Figs. 2C–2E, four main characteristics of *C. finmarchicus* population dynamics in the central LSLE are (*i*) domination of population number (40–80%) by naupliar stages (N3–N6) between late June and late September (Fig. 2E), (*ii*) a general pattern of cohort development between N3–N6 and C4, although abundance of naupliar (N3–N6) and early copepodite stages (C1–C4) is relatively low, (*iii*) year-round high numbers of stage C5, and (*iv*) drastic increases in stage C5 abundance in late summer – autumn.

The pattern of naupliar abundance (N3–N6) generally follows the population EPR (Figs. 2B and 2C) with a major (30 × 10^3 individuals·m^{-2}) and a minor (13 × 10^3 individuals·m^{-2}) peak occurring in early July and late September, respectively. The copepodite C1–C3 abundance maximum, occurring in late July – late August, is relatively low (3000–5000 individuals· m^{-2}), making up only 14–25% (18–40% considering only copepodite stages) of the population (Figs. 2D and 2E). The mean C4 abundance maximum occurs in August (2000 individuals·m^{-2}), but C4 abundance is also higher in late December and late April (Fig. 2D), at which times it constitutes 20% of the population (Fig. 2E). Despite the low abundance of stages C1–C3

Fig. 2. Mean (average in 15-day blocks over 3–6 years) seasonal pattern of *C. finmarchicus* reproduction dynamics, stage abundance, and structure in the central LSLE from late April to late December. (A) Estimated integrated total Chl *a* standing stock for the first 50 m of the water column (open circles), in situ specific EPR of adult females (solid circles), and clutch size (triangles); (B) abundance of adult females (open circles), males (solid circles), and population EPR (triangles); (C) abundance of calanoid naupliar stages N1–N2 (open circles) and naupliar stages N3–N6 (solid circles); (D) abundance of copepodite stages C1–C3 (open circles), C4 (solid circles), and C5 (triangles); (E) stage composition (C6f, adult females; C6m, adult males). Abundance and population EPR units are $\times 10^3$. The shaded area indicates the period of the phytoplankton bloom (Chl a > 50 mg·m^{-2}).



and C4, the development duration from the naupliar stages N3–N6 to the C4 stage is consistent with development time at ambient temperature measured in the laboratory (R.G. Campbell, University of Rhode Island, Kingston, R.I., unpublished data).

Stage C5 abundance does not follow the seasonal pattern of the previous life history stages (Figs. 2D and 2E). It decreases between late April and early July from 8000 to 2000 individuals·m^{-2} (80–10% of the population), probably reflecting molting to adult stages. During the main reproduction period in July – early August, C5 abundance never drops below 2000 individuals·m^{-2} and always outnumbers the adult stages (t test, $p < 0.05$). In mid-August, it rises to 8000 individuals·m^{-2}, at which level the mean C5 abundance in autumn, winter, and spring is maintained (Fig. 2D). During the overwintering period from October to April, stage C5 constitutes the bulk (80% or more) of the population (Figs 2D and 2E). The important C5 peak observed in early October (15 000 individuals·m^{-2}) reflects very high abundance of this stage observed in two of the four years studied (see Fig. 3).

Interannual variation in phytoplankton and *C. finmarchicus* reproductive cycles

There were year-to-year variations in the timing of reproduction in the LSLE (Figs. 3A–3D). The start of the phytoplankton bloom varied by 1 month, beginning in early June in 1997 and early July in 1994 and 1996 (Fig. 3A). In 1994, phytoplankton biomass remained high into September, and *C. finmarchicus* females responded by maintaining a high specific EPR (Figs. 3A and 3B). The period of maximum population EPR varied by 1 month among years but did not closely follow the seasonal pattern of phytoplankton biomass and specific EPR. For example, the latest date of peak population EPR (end of July) during the 4-year study occurred in the same year (1997) as the earliest onset of the spring bloom (Figs. 3A and 3D).

The annual time series observations (Figs. 3A–3D) are consistent with the hypothesis that adult female abundance determines population EPR after the onset of the spring phytoplankton bloom (Runge and de Lafontaine 1996). In all years, the late spring adult female abundance is decoupled from the phytoplankton bloom and the maximum female-specific EPR, resulting in moderate population EPR. In 1995, the year of lowest population EPR, adult female abundance in summer was correspondingly the lowest observed during the study period. In summer 1997, maximum female abundance occurred 3–4 weeks later (late July) than in 1996 and the peak naupliar abundance was also delayed. In general, then, the summer female abundance to a large extent controlled interannual variation in *C. finmarchicus* population EPR peak timing (up to 1 month) and magnitude (10-fold) over the 4-year study period.

Interannual variation in stage abundance and cohort development

Over the 4-year study, there is considerable interannual variation in stage abundance and in timing and coherence of cohort development (Figs. 3E–3I). There is a fivefold difference among years in maximal abundance of *C. finmarchicus* N3–N6 from 100×10^3 individuals·m^{-2} in 1996 to 20×10^3 individuals·m^{-2} in 1995. Peaks of *C. finmarchicus* nauplii (N3–N6) follow (1995) or slightly precede (1996) maxima in population EPR (Figs. 3D and 3F); missing data for 2 weeks in early July preclude interpretation of coherence in 1997. The 1-month difference in timing of the naupliar maximum (late June 1996 – late July 1997) reflects the different annual pattern of population EPR.

Stage C1–C3 maximal abundance varied by a factor of 3 among years (Fig. 3G). The highest C1–C3 abundance (22×10^3 individuals·m^{-2}) occurred in 1997 as compared with 1996 for naupliar abundance. The duration of maximal abundance varied between 2 weeks (1994 and 1995) and 6 weeks (1996 and 1997). Stage C4 abundance follows the C1–C3 peak in 1995 and is contemporaneous with the C1–C3 peak in 1996 and 1997 (Figs. 3G and 3H). In 1995 and 1997, high C4 abundances lasted 6 weeks, between early August and mid-September, despite the contrast in duration of C1–C3 abundance (Figs. 3G and 3H).

Stage C5 annual abundance cycles also exhibit important differences between years (Fig. 3I). The timing in the annual decline of C5 abundance in late spring varied by over a month, beginning in June in 1994, May in 1997, and possibly earlier in 1995 and 1996. Stage C5 abundance started to increase again in early August in 1995 and 1996, mid-August in 1997, and mid-September in 1994. There is a tremendous variability of peak abundance in autumn. In both 1995 and 1997, a maximum abundance $>20 \times 10^3$ individuals·m^{-2} was observed between September until (as least for 1997) mid-October. In 1996, the autumn C5 increase was distinguished by the lower maximum (12×10^3 individuals·m^{-2}) occurring in early November. Abundance were likely not directly dependent on local production in the central LSLE, as high C5 autumn numbers were observed in years of both low (1995) and high (1997) naupliar production and C1–C3 abundance (Figs. 3F, 3G, and 3I).

Seasonal pattern of body size

Mean prosome lengths of late copepodite stages in 1996 were measured in an attempt to identify successive generations and (or) different sources of life history stages. All stages followed a similar seasonal pattern, with mean prosome length generally increasing from late spring to late summer (Fig. 4). Stage C5 showed the largest variation, with a mean prosome length <2.6 mm in May–June, an increase to maximal values (2.75 mm) in late August – early September, and a decrease to 2.65 mm thereafter (Fig. 4C). The decrease in mean C5 prosome length corresponds to the autumn increase of abundance of this stage (see Fig. 3I, year 1996). We observe similar pattern for adult stages, with maximal mean prosome length attained somewhat later than for C5 in autumn (Figs. 4A and 4B). Nevertheless, no stepwise change in mean adult female prosome length was detectable, indicating no clear cohort succession in the LSLE.

Vertical distribution in summer

Calanus finmarchicus exhibits stage-specific vertical distribution in the central LSLE in July characterized by daily vertical migrations (Fig. 5). Copepodite stages C1–C3 stay in the upper 50 m of the water column with a shallower distribution (0–25 m) at night. Stages C4 and C5 show a bimodal distribution, especially at night. The shallower fraction of the population migrates from 25–50 m (C4) and

Fig. 3. Annual time series (1994 to 1997) of *C. finmarchicus* reproduction dynamics and stage abundance in the central LSLE from April to December. (A) Estimated integrated total Chl *a* standing stock for the first 50 m of the water column; (B) in situ specific EPR (eggs·female^{-1}·day^{-1}) of adult females; (C) abundance of adult females C6f); (D) population EPR (eggs·m^{-2}·day^{-1}); (E) abundance of large calanoid nauplii stages N1 and N2; (F–I) Abundance of nauplii N3–N6 and copepodite C1–C3, C4, and C5. Abundance and population EPR units are $\times 10^3$. The shaded area indicates the period of the phytoplankton bloom (Chl *a* > 50 mg·m^{-2}).

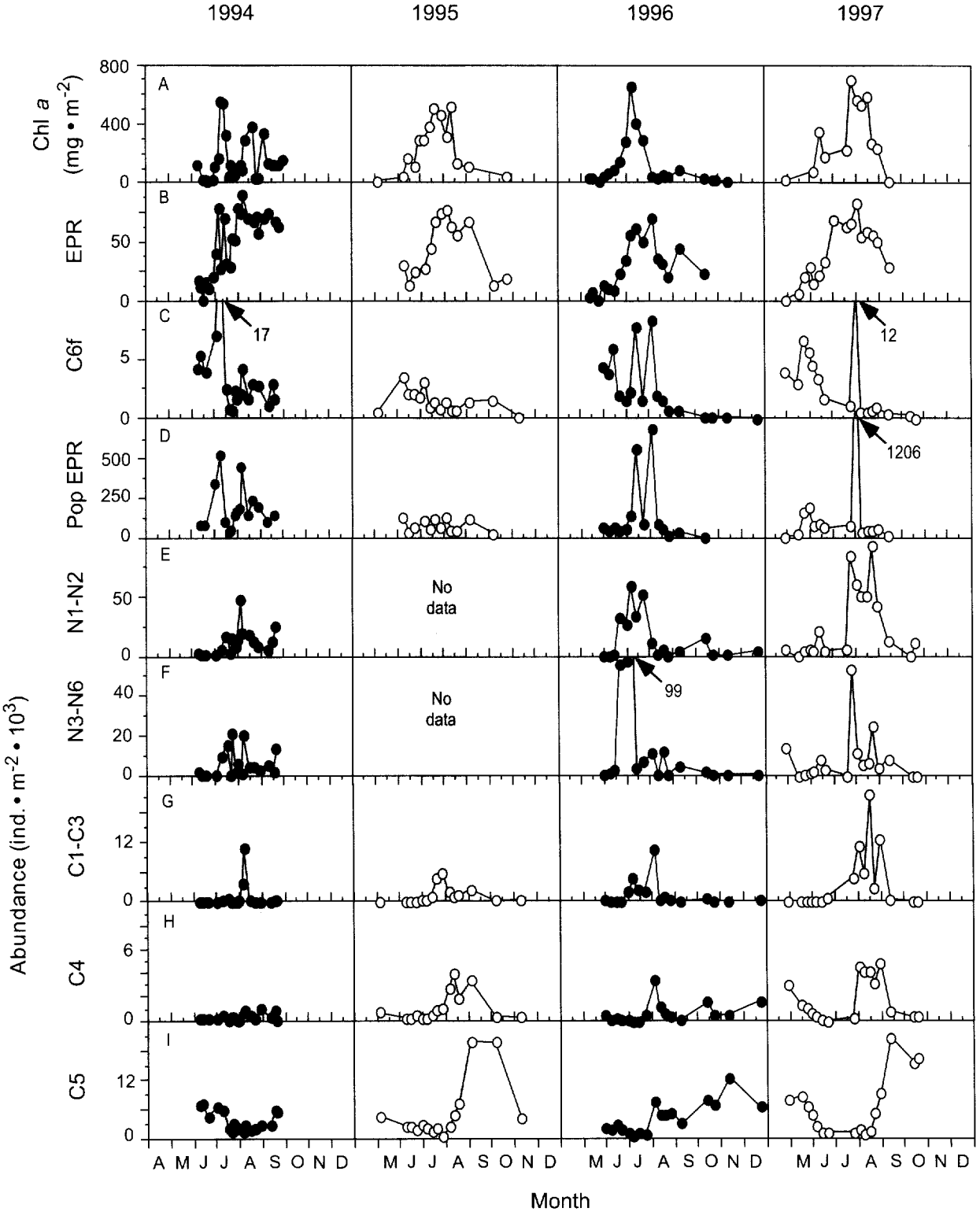
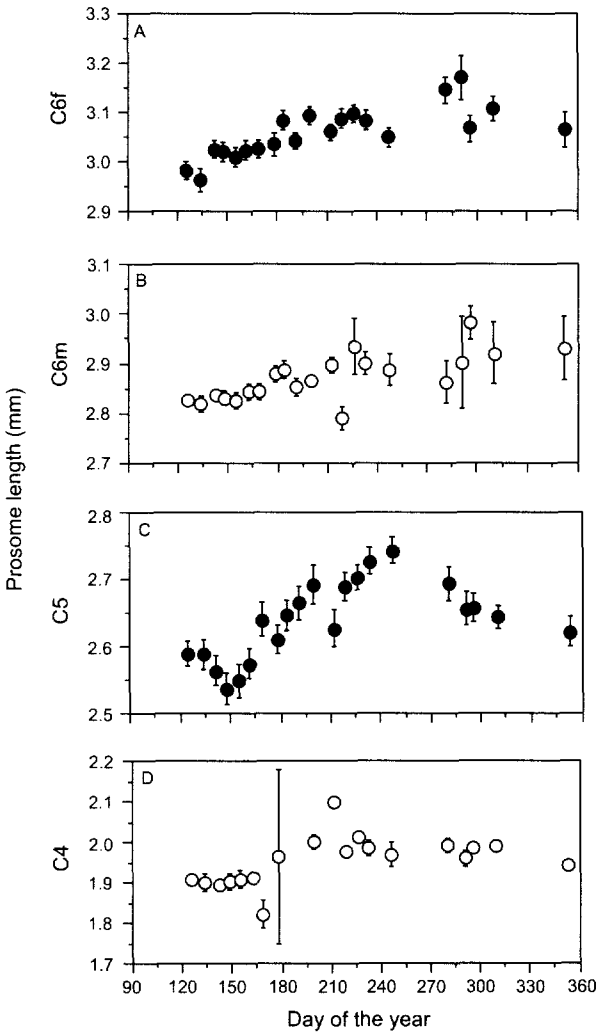


Fig. 4. Mean prosome length of *C. finmarchicus* late copepodite stages at each visit at the sampling station in the central LSLE in 1996. (A) Adult females (C6f); (B) adult males (C6m); (C) stage C5; (D) stage C4. Bars indicate standard error. Number of animals per sample was 7–50.



50–75 m (C5) depths during the day to the upper 25 m at night, whereas a large proportion (35–50%) remains below 100 m (and down to 250 m) both day and night. The adult females showed a marked daily vertical migration, with 100% of the population residing between 50 and 150 m during day and more than 75% in the upper 50 m of the water column at night.

Discussion

Timing, duration, and amplitude of the reproduction period in relation to the phytoplankton bloom

Reproduction of the *C. finmarchicus* population is strongly influenced by the phytoplankton bloom in the LSLE. The late start of the bloom delays the onset of the period of high specific EPR until July, but its long duration sustains these high rates until late summer. The main peak of population reproduction occurs in July, but despite low specific EPR before the bloom, significant population EPR is observed from late May to late September.

The late onset of the spring bloom is 2–3 months behind other that of regions of the northeast Atlantic Ocean such as the adjacent southwest GSL, the Scotian Shelf, and the Gulf of Maine – Georges Bank region (Lacroix and Filteau 1970; Durbin et al. 1997; McLaren et al. 2001). Despite this important delay, the mean population EPR during the bloom period (106×10^3 eggs·m^{-2}·day^{-1}) in the LSLE is threefold higher than in the Norwegian Sea (35×10^3 eggs·m^{-2}·day^{-1}), a region considered as a center of distribution of *C. finmarchicus* (Niehoff et al. 1999). This difference is likely due to larger female body size and consequently higher specific EPR (60–80 eggs·female^{-1}·day^{-1}) than in the Norwegian Sea (30–40 eggs·female^{-1}·day^{-1}), and females in the LSLE remain abundant after the start of the spring phytoplankton bloom, in contrast with the Norwegian Sea (Runge and Plourde 1996; Niehoff et al. 1999).

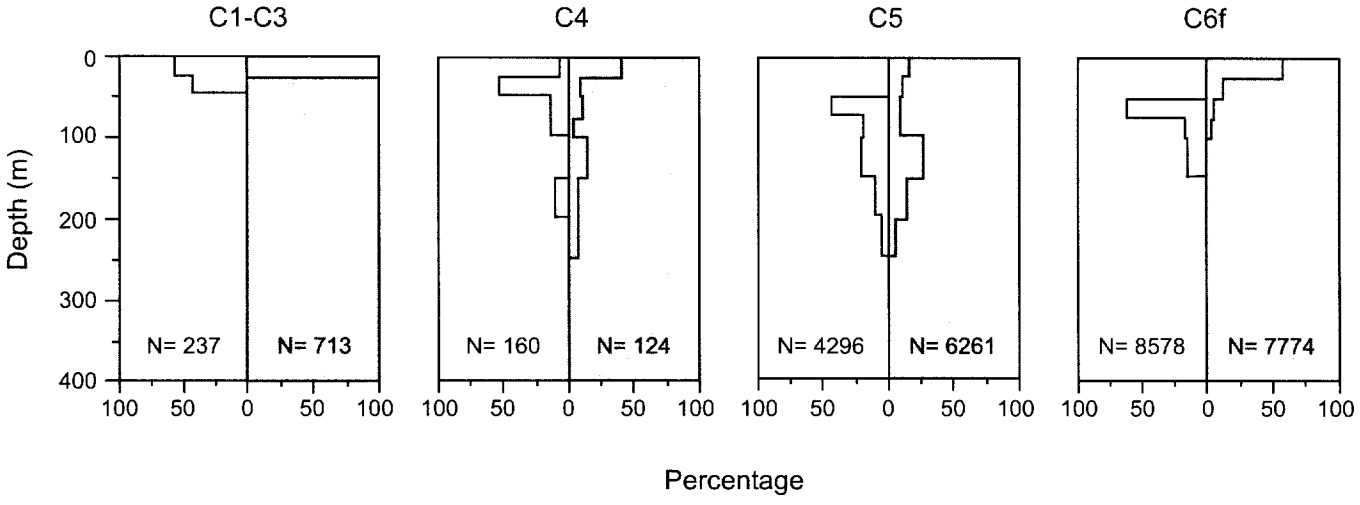
Because of the high abundance of adult females, the *C. finmarchicus* population reproduces in May and June prior to the bloom, despite a relatively low specific EPR. This is consistent with the pattern of reproduction described for the *C. finmarchicus* population in the Norwegian Sea (Niehoff et al. 1999). In our study, the mean Chl *a* biomass (20 mg·m^{-2}) and specific EPR (10 eggs·female^{-1}·day^{-1}) suggest that adult females are food limited during the prebloom period. Several lines of evidence support this statement. First, the mean Chl *a* biomass prior to the spring bloom is lower than the food concentration threshold at which *C. finmarchicus* adult females sustain maximum specific EPR (30–40 Chl *a* mg·m^{-2}) (Plourde and Runge 1993). Second, the large majority of the adult female population is in an immature state of gonad development prior to the bloom, which has been related to low food concentration (Plourde and Runge 1993; Niehoff et al. 1999). LSLE females brought into the laboratory in April and fed high food concentrations produced eggs at near-maximal rates well before the bloom in the estuary (Plourde and Runge 1993). Third, the lower clutch size observed during the prebloom period may be caused by food limitation, as has been proposed for the GSL, fjords of northern Norway, and the Norwegian Sea (Diel and Tande 1992; Runge and Plourde 1996; Niehoff et al. 1999).

The occurrence of a high specific EPR with significant abundance of females (>1000 individuals·m^{-2}) in late summer maintains a relatively high population EPR (50×10^3 eggs·m^{-2}·day^{-1}) into September. After the end of the phytoplankton bloom, population EPR falls off due to reduced specific EPR and the drop in adult female abundance (<500 individuals·m^{-2}).

Implications of copepodite stage structure in summer

Given the fivefold increase in population EPR in July, one would expect the development of an important cohort of early copepodite stages during summer in the central LSLE. However, the abundance of copepodite stages C1–C3 (4000–5000 individuals·m^{-2}) and C4 (2000 individuals·m^{-2}) is relatively low and the abundance of stage C5 (>2000 individuals·m^{-2}) relatively high. Excluding naupliar stages, copepodite stages C1–C4 and C5 represent 20–55 and 20–40%, respectively, of the population during summer. Both the abundance and the proportion of stages C1–C3 are lower than in other important

Fig. 5. Observed day (open) and night (shaded) vertical distributions of *C. finmarchicus* stage C1–C3, C4, C5, and adult females (C6f) in July 1997 in the central LSLE. Data represent means of oblique vertical tows taken with a BIONESS multinet sampler between 12:00 and 14:00 (day) and between 22:00 and 00:00 (night) at a single station off Les Escoumins at the head of the Laurentian Channel (Fig. 1). *N* is the integrated mean abundance (individuals·m^{-2}) of each developmental stage (J.A. Runge et al., unpublished data).



regions across the *C. finmarchicus* domain. In the southern GSL, on the Scotian Shelf, and in fjords of northern Norway, the abundance of stages C1–C3 during the main production period in spring is three- to 10-fold higher than in the LSLE and may represent 80–100% of the population (Lacroix and Filteau 1970; Sameoto and Herman 1992; Falkenhaug et al. 1997).

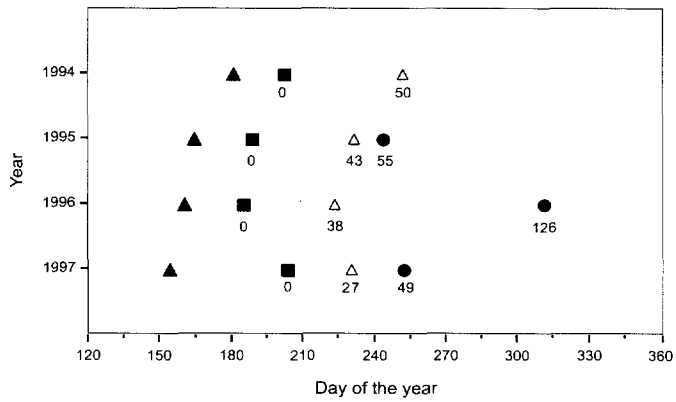
Stages C1–C3 of *C. finmarchicus* mostly occupy the top 50 m of the water column, the water layer strongly influenced by surface circulation in the LSLE. Our results are therefore consistent with the hypothesis that the population stage structure of the *C. finmarchicus* population in the central LSLE is biased toward the older copepodite stages due to the combined effect of the export of early developmental stages in the outward residual surface currents and the deep upward advection of older copepodite stages (Runge and Simard 1990). However, care must be taken when intepreting the observed abundances of the early copepodite stages. Two factors may determine the number of a given developmental stage: natural mortality and gain or loss by advection. The development from naupliar stages N3–N6 to copepodite stage C4 in the central LSLE roughly corresponds to development time measured in the laboratory at a similar temperature, suggesting that a consistent cohort development may occur in the central LSLE during summer. Assuming that there is no upstream gain of developmental stages and that the developing cohort originates from the summer peak of population EPR, we can estimate the stage-specific mortality rate using the abundance of each stage class (Ohman and Wood 1996). One would expect very high mortality rates in the case of strong loss due to advection. Using the maximal abundance of different developmental stages in the averaged time series, we calculated stage-specific mortality rates (0.25 and 0.12 individual·day^{-1} for naupliar and copepodite stages, respectively) falling in the range of natural mortality rates measured for *Pseudocalanus newmani* in Dabob Bay and for *C. finmarchicus* on Georges Bank (Ohman and Wood 1996). Although information on the abundance of potential invertebrate and vertebrate predators is lacking in the LSLE, high abundance of the suspension-feeding copepods *M. longa* and *Calanus hyperboreus*, various species of euphausiids and mysiids, the carnivorous copepod *Eucheata norvegica*, and the migratory fishes capelin and herring is observed in the region (de Lafontaine 1990; Runge and Simard 1990). Therefore, we cannot rule out natural mortality as an additional control on abundance of the *C. finmarchicus* early life stages in the central LSLE.

The relatively high mean abundance of stage C5 during summer in the LSLE may be the consequence of early timing of *C. finmarchicus* reproduction in the adjacent GSL and the upstream advection of its deep water. There is evidence that the phytoplankton spring bloom in the northwest GSL may start in April, more than 2 months earlier than in the LSLE (de Lafontaine et al. 1991; Fuentes-Yaco et al. 1997). Therefore, the *C. finmarchicus* spring cohort in the GSL likely develops to stage C5 by late May – early June at ambient temperatures (Campbell et al. 2000). A large proportion of this first generation would enter diapause and would be gradually advected upstream along the deepwater circulation. These animals would gradually replace the local C5 that molt to adults in late spring and early summer. This hypothesis is supported by the body size of C5 in LSLE, which shows a gradual increase from spring into summer. Generally, copepods attain a larger size in a colder environment, which would be the case in the GSL during spring compared with the central LSLE in summer (Carlotti et al. 1993). Consequently, the increase of C5 mean prosome length during summer may reflect an increasing proportion of C5 originating from the spring cohort in the GSL.

The composition of the overwintering C5 stock in the LSLE in winter might explain the seasonal pattern of adult female abundance. According to our observations, it is likely that the stage C5 overwintering stock in the LSLE originates from two distinct sources: the spring cohort in the GSL and local summer recruitment. We propose that the long period

of high adult female abundance in spring and early summer results from a difference in timing of arousal from diapause between the GSL and the LSLE component of the overwintering stock. The mechanisms proposed to control arousal from diapause are (*i*) the change in light intensity over the winter–spring period, (*ii*) temperature during overwintering, and (*iii*) an endogenous biological clock (Miller et al. 1991; Diel and Tande 1992; Hind et al. 2000). The light and temperature conditions during overwintering are likely similar in the GSL and LSLE (Gilbert and Pettigrew 1997). The biological clock implies a control of overwintering by physiological processes, with the consequence that timing of arousal is determined by the moment of entry into diapause during the previous year (Miller et al. 1991; Hind et al. 2000). Stage C5 that had begun to overwinter in late spring – early summer in GSL would arise from diapause in spring of the following year and constitute the bulk of the high abundance of adult females in late spring. Stage C5 issued from the summer production in LSLE that entered diapause in late summer would consequently come out of diapause 2 months later than the GSL component and represent the bulk of adult females in summer.

Fig. 6. Timing of key events of the *C. finmarchicus* life cycle in LSLE in 1994–1997. Events represented are the start of the phytoplankton bloom (Chl a > 50 mg·m^{-2}) (solid triangles), the maximum abundance of naupliar stages N3–N6 (squares), the laboratory estimate of development time at ambient temperature from the peak of N3–N6 peak to stage C5 (open triangles), and timing of the abundance maximum of stage C5 observed in each annual series (circles). Numbers indicate the development time in days from the abundance peak of N3–N6 (day 0) to the laboratory-predicted and observed stage C5 abundance peak.



Interannual variation in *C. finmarchicus* population dynamics

There is an important interannual variability in population dynamics of *C. finmarchicus* in the LSLE over the 4-year study period. The peak of the population EPR varied by a factor of 10 in magnitude and by 1 month in timing (although interestingly not in relation to the timing of the phytoplankton bloom). The impact of such variations on the population dynamics of *C. finmarchicus* in the LSLE is not understood.

Our results indicate that the timing and amplitude of the peak of females in summer control the timing and amplitude of the reproductive peak in the LSLE. The population EPR is lowest in the year of the lowest summer adult female abundance (1995). In 1997, the year of the highest and latest population EPR, timing and magnitude are correlated with the late peak in female abundance, not with the early onset of the phytoplankton bloom. These results agree with observations made along transects in the GSL and during a seasonal monitoring at a single station in the Norwegian Sea (Runge and de Lafontaine 1996; Niehoff et al. 1999). Therefore, the interaction between the timing of arousal from diapause of the overwintering C5 and the circulation pattern in early summer would likely govern the reproduction peak of the *C. finmarchicus* population in the central LSLE by determining the timing and abundance of adult females at our monitoring station.

Although the maximal abundance and timing of the naupliar N3–N6 peak are roughly correlated with the population EPR, there is little concordance between the abundance of the different copepodite stages and the reproductive output of the population. The abundance of stages C1–C3, C4, and C5 is similar during years of low and high population EPR and naupliar abundance. The highest abundance of C5 in late summer and autumn occurs during two years of very different population EPR. These results suggest that the seasonal pattern of abundance and distribution of development stages may be strongly influenced by natural mortality and advection.

The interannual variability in the population dynamics of *C. finmarchicus* in the central LSLE is within the range observed for the species in other regions. The timing of the spring bloom varied by more than 1 month in subarctic envrionments where significant interannual variation in cohort development has been related to food availability and temperature (Lacroix and Filteau 1970; Tande and Slagstad 1992; Hind et al. 2000). In our study, the mean temperature in the surface water layer (0–10 m) varied between 5.5 and 11°C among years, whereas onset and duration of the phytoplankton bloom varied by more than 1 month. Moreover, the temperature of the cold intermediate water layer and the amplitude and seasonal pattern of the freshwater runoff, one of the main factors controlling surface circulation and onset of the spring bloom in the LSLE, show significant interannual variations (Ingram and El-Sabh 1990; Gilbert and Pettigrew 1997). In addition to environmental conditions affecting the physiology of new recruits, interannual variation in circulation may determine *C. finmarchicus* abundance (Sameoto and Herman 1992; Tande and Slagstad 1992). Thus, several environmental factors may directly or indirectly affect the population dynamics of *C. finmarchicus* in the central LSLE. Coupled biological–physical modelling is needed for comprehensive investigation of the impacts of circulation and its interaction with the biology on *C. finmarchicus* population dynamics in the LSLE.

Mechanisms responsible for maintenance of the *C. finmarchicus* population in the LSLE

The seasonal pattern of stage C5 abundance in the central LSLE is characterized by a tremendous increase of abundance in late summer and early autumn. The abundance of C5 is three- to fivefold higher than the abundance of stage C1–C3 and C4, implying that factors other than those regu-

lating the development and survival rate of the cohort must explain this high C5 abundance. We propose that an increase of the residence time of surface water (retention) would allow the developing cohort to accumulate in high abundance. Additionally, the interaction between the development duration and the residence time of the surface water would determine the timing of abundance peak of stage C5 observed in late summer and early autumn in the central LSLE.

We illustrate our hypothesis using the annual time series of Chl *a* biomass and stage abundance, temperature-dependent predicted development times from naupliar stages N3–N6 to copepodite stage C5, and averaged surface and deep residual currents taken from the literature (Fig. 6). The mean temperature of the surface water (0–10 m) during July and August varied from 5.5°C in 1994 to 11°C in 1997, resulting in a twofold difference among years of the development time from N3–N6 to C5 (27–50 days). Based on these estimates, the abundance peak of C5 calculated from development time alone would follow the peak of N3–N6 by 27–50 days and roughly represent the timing of the expected peak of C5 in the absence of advection. Our observations show that the peak of C5 lags this estimate by 12, 88, and 22 days in 1995, 1996, and 1997, respectively. Assuming that (*i*) most of these C5 originate from the peak of abundance of naupliar N3–N6 in the LSLE, (*ii*) the early life stages mainly develop and grow in the surface water layer, and (*iii*) the inflowing current is 4–5 $cm \cdot s^{-1}$ at the overwintering depth of the C5, the *C. finmarchicus* stage C5 issued from the summer production peak in LSLE would have to enter diapause 50, 250, and 75 km (for the three study years, respectively) downstream of our monitoring station in the central LSLE before being advected back in order to be observed in our data series. The distance estimated in 1995 and 1997 implies that some retention process may occur in the lower portion of the LSLE. The occurrence and amplitude of this retention process would be a function of the interaction between the development time of the LSLE *C. finmarchicus* summer cohort and the surface circulation pattern in the region. Given this potential return of high abundance of stage C5, this hypothesis also explains the observed peak of adult females in summer (as discussed above) and provides a mechanism explaining the maintenance of the *C. finmarchicus* population in the region.

Contribution of the *C. finmarchicus* LSLE population to the adjacent GSL

The present study reinforces the idea that the LSLE may act as a *Calanus* pump by exporting a large proportion of its local population and production to the adjacent GSL (Plourde and Runge 1993). The high abundance of *C. finmarchicus* adult females yields a significant population EPR in the LSLE during the late spring – early summer period. This period corresponds to the peak of freshwater runoff in the LSLE, and according to our hypothesis, low abundance of naupliar (N1–N6) and early copepodite stages (C1–C3) is observed. We propose that most of the "early" production and adult female stock observed in the central LSLE before the onset of the spring bloom are exported to the adjacent GSL through the strong residual surface currents concentrated in the Gaspé Current (Fortier et al. 1992).

In early June, the Gaspé Current is the site of an intense copepod production compared with the adjacent northwest GSL, and it is an important site of growth for the abundant capelin and sand lance larvae spawned upstream in the LSLE (Fortier et al. 1992). Further dowstream, the Gaspé Current separates into a southern branch flowing into the southwest GSL, an important nursery site for several fish species, and a northern branch moving along the Laurentian Channel into the northern GSL (El-Sabh 1976; de Lafontaine et al. 1991). Recently, it has been shown that redfish larvae in the central GSL feed principally on *C. finmarchicus* early life history stages in early summer, and it has been hypothetized that the years of high mackerel recruitment in the southern GSL correspond to the years of high *C. finmarchicus* biomass and production (Runge and de Lafontaine 1996; Runge et al. 1999). Given the surface current velocities and the potential transport in the Gaspé Current during spring (40–95 $km \cdot day^{-1}$), it is possible that a large proportion of the adult females and the eggs produced in the central LSLE in late spring is advected into the GSL in May and June. This represents approximately half of the LSLE female stock and related potential production. Thus, the LSLE is located at the head of an extended estuary–shelf system and may play an important role in supplying key regions for the recruitment of fish stocks from spring to late summer.

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