

Reproduction of the planktonic copepod *Calanus finmarchicus* in the Lower St. Lawrence Estuary: relation to the cycle of phytoplankton production and evidence for a *Calanus* pump

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ABSTRACT: Due to the dynamic physical environment of the Lower St. Lawrence Estuary, the spring phytoplankton bloom in the Laurentian Channel occurs late in the season, typically in mid-June, but the high phytoplankton biomass is sustained throughout the summer months. In this study, relationships between the phytoplankton production cycle, water temperature, and the reproductive cycle of *Calanus finmarchicus* Gunnerus, a predominant planktonic copepod in the Lower Estuary, were investigated during spring–summer 1991. Field observations showed that the final stages of oocyte maturation in *C. finmarchicus* females did not begin until the onset of the spring phytoplankton bloom in mid-June. High egg production rates, as estimated by the number of eggs released by females incubated immediately after capture, commenced 1 wk later and persisted until late August. Egg production rates were significantly correlated with an index of gonadal maturity in females and were consistent with a rectilinear or curvilinear relationship with chlorophyll *a* standing stock. Laboratory experiments showed that: (1) in presence of food (the diatom *Thalassiosira weissfloggii*), maturation of oocytes would proceed and females could spawn eggs at least 2 mo before the spring bloom; (2) without food, the oocytes did not develop past immature stages, except in a small minority of the population; and (3) colder temperatures in early spring would prolong the lag between the onset of the spring bloom and the start of egg production by less than 4 d. Combined with concurrent microscopic measurements of oil sac volume, the results do not rule out the possibility that lipid reserves were used to support the early stages of oogenesis, but do show that the majority of females did not use lipid reserves for vitellogenesis prior to the spring phytoplankton bloom. It is suggested that the Lower St. Lawrence Estuary is an important region of *C. finmarchicus* production in summer which, because of the residual surface circulation, may act as a *Calanus* 'pump' to influence levels of zooplankton biomass in the Gulf of St. Lawrence and on the shelf off Nova Scotia.

KEY WORDS: *Calanus* · Egg production · Primary production cycle · Zooplankton

INTRODUCTION

The Lower St. Lawrence Estuary is a long (200 km), narrow (50 km) and deep (350 m) body of water connecting the Upper Estuary, into which the St. Lawrence River flows, with the Gulf of St. Lawrence. The dynamic physical environment of the Lower Estuary has a large influence on the pattern and processes of its marine planktonic inhabitants. Due to the large runoff from the St. Lawrence River, residence times in the surface layer in spring are short (Sinclair et al.

1981) and seeding of diatoms into the surface layer may be restricted during the runoff period (Levasseur et al. 1984). As a consequence, the spring phytoplankton bloom in the Lower Estuary typically does not start until mid-June. However, tidal mixing at the head of the Laurentian Channel supplies nutrients to the surface waters of the Lower Estuary periodically throughout the summer, and the phytoplankton bloom, in which diatoms and dinoflagellates predominate, usually persists into September (Levasseur et al. 1984, Theriault & Levasseur 1985).

Calanus finmarchicus is a predominant member of the planktonic copepod community of the Lower St. Lawrence Estuary. Its prominence in this region is even greater than in the coastal northwest Atlantic. This amplified dominance is thought to result principally from the residual circulation, which rapidly exports surface water containing smaller copepods and imports *Calanus*-rich deep water (Runge & Simard 1990). How the *Calanus* that are present in the Lower Estuary in spring respond to the timing of the phytoplankton production cycle is not known with certainty.

Heinrich (1962) classified the life history of *Calanus finmarchicus* as one in which propagation in spring cannot begin earlier than the vernal development of phytoplankton. His analysis was based primarily on studies conducted in the northeast Atlantic and adjacent seas, in which the spring bloom typically commences sometime between February and early May. In general, subsequent field observations of *C. finmarchicus* and related species in the genus continue to support this conclusion (e.g. Frasz 1975, Runge 1985a, Skjoldal et al. 1987, Diel & Tande 1992), although there are reports of spawning before the onset of the spring bloom (Marshall & Orr 1955, Skjoldal et al. 1987, Melle & Skjoldal 1989, Diel & Tande 1992). Experimental studies indicate that there is a curvilinear or rectilinear relationship between *Calanus* egg production rate and external food supply and that females stop producing eggs in the complete absence of food (Marshall & Orr 1955, Runge 1984, Peterson 1988).

Understanding the response of *Calanus finmarchicus* to the timing of the spring bloom also requires consideration of its reproductive cycle and of the role of its stored lipids in the production of eggs. Overwintering C5 copepodites typically molt into adults and mate in winter, 1 to 3 mo after solstice (Miller et al. 1991). In the female, the oocyte maturation can begin in stage C5 and continue until a certain point prior to the spring bloom. The role of stored lipids during oogenesis is still in need of clarification. Tande (1982) concluded that the source of materials and energy for sexual differentiation, molting and the first stages of gonad maturation is the female's lipid reserves, but that the final stages of oogenesis, in which large quantities of yolk are accreted, require materials derived from feeding on sufficiently high phytoplankton concentrations. However, it has also been proposed that lipid reserves are sufficient to sustain considerable egg production without an external food supply (Gatten et al. 1979, 1980), which may account for observations of spawning in *C. finmarchicus* before the spring bloom. Diel & Tande (1992) suggested that there is a direct relationship between the level of lipid reserves at the initiation of gonadal development and the stage of oocyte maturation achieved at the time of the spring bloom.

We present here a study of the reproductive response of *Calanus finmarchicus* to the unusual primary production cycle in the Lower St. Lawrence Estuary. Laboratory experiments and field observations were employed to address the following 5 questions: (1) What is the relationship between oocyte development and the timing of the spring phytoplankton bloom? (2) Does the start of spawning correspond with the onset of the spring bloom? (3) Does the high phytoplankton biomass in the Lower Estuary sustain egg production by *C. finmarchicus* throughout the summer months? (4) What is the relationship between lipid reserves and oocyte development? (5) How might temperature variation in spring influence oocyte development and consequently the response of *C. finmarchicus* to the spring bloom? Our results lead to the conclusion that the Lower Estuary functions as a *Calanus* 'pump', which may have important implications for understanding zooplankton population dynamics in the Gulf of St. Lawrence and perhaps on the coastal shelf of Nova Scotia.

METHODS

Observations in the Lower Estuary. The field work was conducted at a single station (330 m depth) located in the Laurentian Channel approximately 16 km N of Rimouski (48° 40' N, 68° 35' W; Fig. 1). The protocol for each of 28 visits to the station between 18 April and 26 August 1991 included a CTD profile (Applied Microsystems STD-12) from 0 to 250 m, collection of water samples with a Niskin bottle at 0, 10 and 20 m, and collection of zooplankton with a 1 m diameter, 333 μ m mesh plankton net towed at $<30 \text{ m min}^{-1}$ from 250 m to the surface. The water samples were transferred to dark bottles and the zooplankton, which were captured in a large (8 l), restricted-flow cod end, were immediately diluted into 4 l jars filled with filtered seawater. The bottles and jars of zooplankton were kept at 5 to 6°C in coolers during transport to the laboratory at the Maurice-Lamontagne Institute, Mont-Joli. Sampling was consistently done between 10:00 and 12:00 h and laboratory analyses (filtrations, sorting for experiments) typically began between 14:00 and 14:30 h. On 2 final sampling visits to the station (2 and 9 September), only a net tow was taken, and the zooplankton catch was preserved in 4 % formaldehyde.

In the laboratory, 250 to 750 ml subsamples from each water bottle were filtered in duplicate on GF/F filters and 5 μ m Nuclepore screens. The screens and filters were extracted in acetone at 5°C for 16 to 24 h, the extract analysed on a Turner Designs model 112 fluorometer, and chlorophyll *a* concentrations calculated according to Parsons et al. (1984). Within 1 to 3 h

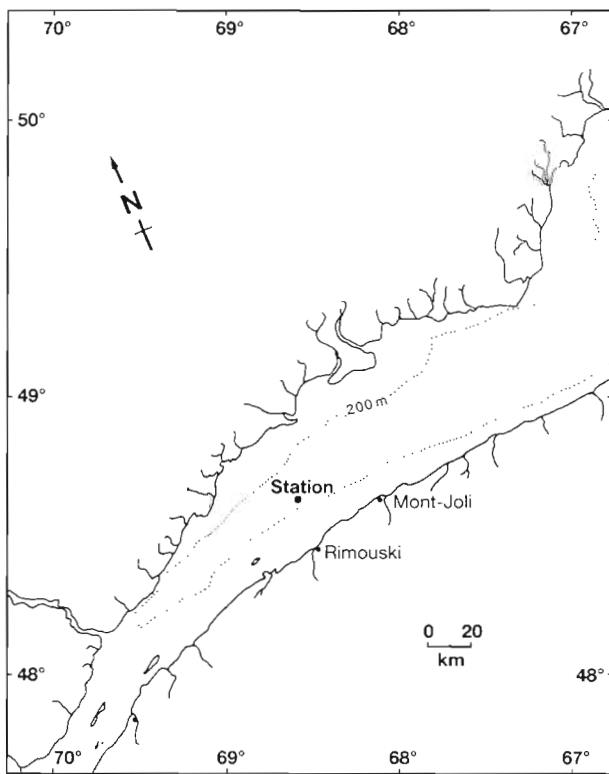


Fig. 1. Sampling station location off Rimouski in the Lower St. Lawrence Estuary

of arrival, approximately 200 *Calanus finmarchicus* females were sorted from the live zooplankton using a dissecting microscope. Only females smaller than 3.32 mm in prosome length were selected; larger copepods were assumed to be *C. glacialis*, which were also present although usually much less abundant. Most of these larger females had red-pigmented genital pores, which facilitated identification. *C. glacialis* eggs, which are distinctly different from those of *C. finmarchicus* (McLaren et al. 1988), were extremely rare in our incubation experiments, confirming the accuracy of our selection technique. Immediately after sorting, 30 females were preserved in 4% formaldehyde with BHT added, for later measurement of stages of oocyte development and oil sac volume. The remaining females were used for the measurement of egg production rate.

Egg production rates of *Calanus finmarchicus* were determined by incubating females over a 24 h period in 1 l egg separation containers, as described in Runge (1985b). The containers consisted of plexiglass cylinders closed off on the bottom end with a 571 μ m mesh nitex screen and immersed in 2 l glass beakers containing 0.2 μ m filtered seawater. Four different incubation conditions, involving 2 food treatments (enriched and filtered seawater) and 2 temperature regimes

(1 and 5.5°C) were employed. Once a day, the enriched treatments received approximately 8000 cells ml^{-1} of the diatom *Thalassiosira weissflogii* (in exponential growth), which was cultured at 15°C in 40 l plastic bags using natural seawater (filtered at 0.2 μ m) enriched with f/2 medium (Stein 1973). Salinity of the seawater used in laboratory experiments and cultures ranged between 25 and 30 PSU (Practical Salinity Units). Ten female *C. finmarchicus* were placed into each container and there were 4 replicate containers per treatment. The incubations typically started between 15:00 and 17:00 h. After 24 h, the females were removed and the eggs, which were left behind in the beakers, were counted.

Laboratory experiments. Females for laboratory experiments were collected at the station from 8 to 12 April 1991. To study the effect of temperature and food regime on gonad maturation and lipid utilization rates, 2400 females were distributed among twenty-four 4 l containers (100 females container^{-1}), which were then randomly allocated to 1 of the 4 treatments described above. Every 2 d the medium in each container was renewed. On the alternate days, the algal concentration in the enriched containers was assessed with a Coulter Counter TAIL and *Thalassiosira weissflogii* culture was added to obtain 8000 cells ml^{-1} . For the first 14 d of the experiment, 30 females treatment^{-1} (6 females container^{-1}) were removed during medium changes. For the remainder of the experiment, females were removed every 3 to 4 d. The females were preserved in 4% formaldehyde with BHT added.

Egg production rates were measured during the same period, using the basic methodology described above (10 females container^{-1}). Each day, the females in their egg separator were placed in a new beaker filled with fresh medium and the number of released eggs was recorded. Both sets of experiments commenced on 14 April. The containers were kept in controlled temperature rooms in the dark for the duration of the experiment.

Stages of oocyte maturity. The classification of stages of oocyte maturity in female *Calanus finmarchicus* followed descriptions provided by Runge (1987) and Tourangeau & Runge (1991). Females were classified according to the most advanced stage of oocyte maturity observed in the reproductive tract. Evaluations were made under a Wild M-8 binocular microscope at 25 \times . Copepods carrying only pre-vitellogenic and early vitellogenic oocytes (stages 1 to 3) were considered to be in a non-spawning or pre-spawning state. Females in stages 4 to 7 were classified as actively spawning because of the presence of oocytes undergoing secondary vitellogenesis.

Lipid reserves. Following Arts & Evans (1991), female lipid reserves were estimated from oil sac

volume. A BIOQUANT image analysis system coupled to a binocular microscope and video monitor was used to measure body and oil sac dimensions, in lateral view, of the same females preserved for assessment of oocyte development. Volumes were calculated assuming that both oil sac and prosome were ellipses, according to the formula:

$$V = (4/3)\pi (A/2) (B/2) (C/2)$$

where A = maximum length; B = height; and C = width. Based on observations that the transversal shape of both objects is nearly circular, C was assumed to be equal to B . Oil sac volume was divided by prosome volume in order to normalize the effect of body size. The data are presented as the mean of individual relative oil sac volume in each sample.

RESULTS

Reproduction of *Calanus finmarchicus* in the laboratory

Food and temperature strongly influenced long-term egg production of *Calanus finmarchicus* in the laboratory incubations (Fig. 2A, B). Daily egg production rates in filtered seawater were typically zero and never exceeded 5 eggs female⁻¹ d⁻¹. Egg production rates in food-enriched seawater were consistently higher at 5.5°C than at 1°C (ANOVA, $p < 0.025$) except for the last 17 d, when they were approximately equal (ANOVA, $p > 0.3$). Rates were highest in the first 3 wk of the experiments; maximum daily egg production (43 eggs female⁻¹ d⁻¹ at 5.5°C and 30 eggs female⁻¹ d⁻¹ at 1°C) occurred on Day 9 and 13, respectively, of the experiment. Mean total egg production in enriched seawater over the 2 mo period was 913 eggs female⁻¹ at 5.5°C and

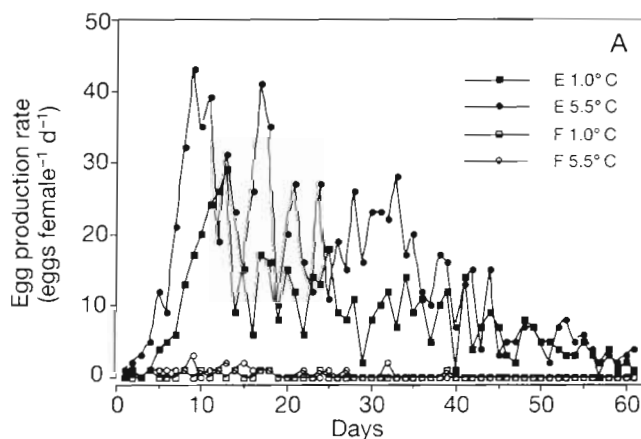


Fig. 2. *Calanus finmarchicus*. Egg production of females during the laboratory experiment between 14 April and 13 June 1991. (A) Egg production rate in food-enriched (E) and filtered (F) seawater at 1 and 5.5°C. Points represent mean of 31 to 40 females. (B) Total egg production per female for the 61 d of experiment in the 4 treatments

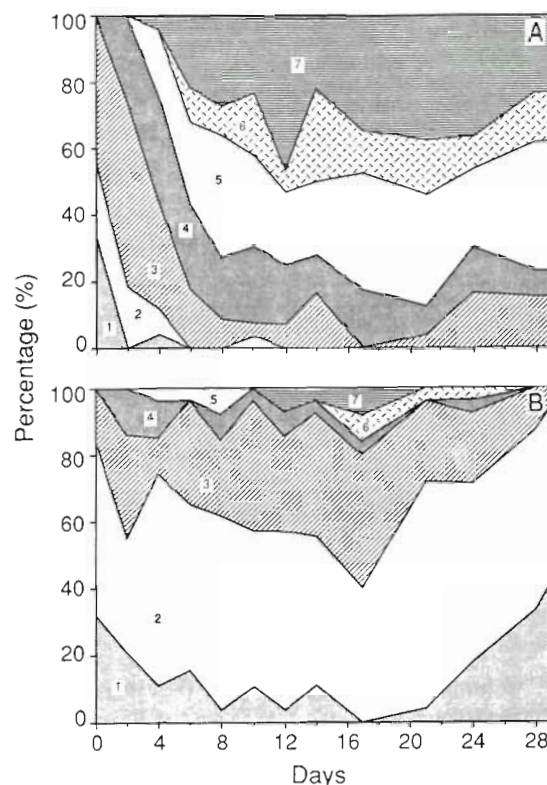
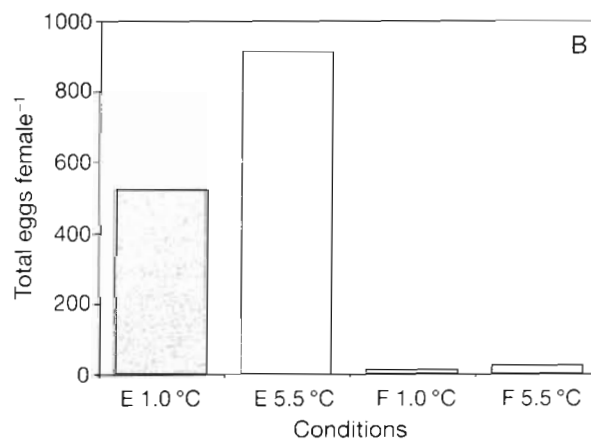


Fig. 3. *Calanus finmarchicus*. Gonad maturation (proportion of total population in each stage) of females in laboratory experiment (14 April and 13 May 1991) at 5.5°C in (A) enriched and (B) filtered seawater. No. of females per sampling date = 23 to 33

523 at 1°C. Total egg production in filtered seawater was negligible in both temperature regimes.

These results are consistent with our observations of gonad maturation in the laboratory population. At the start of the experiment, oocytes of all females were immature (stages 1 to 3; Fig. 3). After 6 to 7 d, >80%



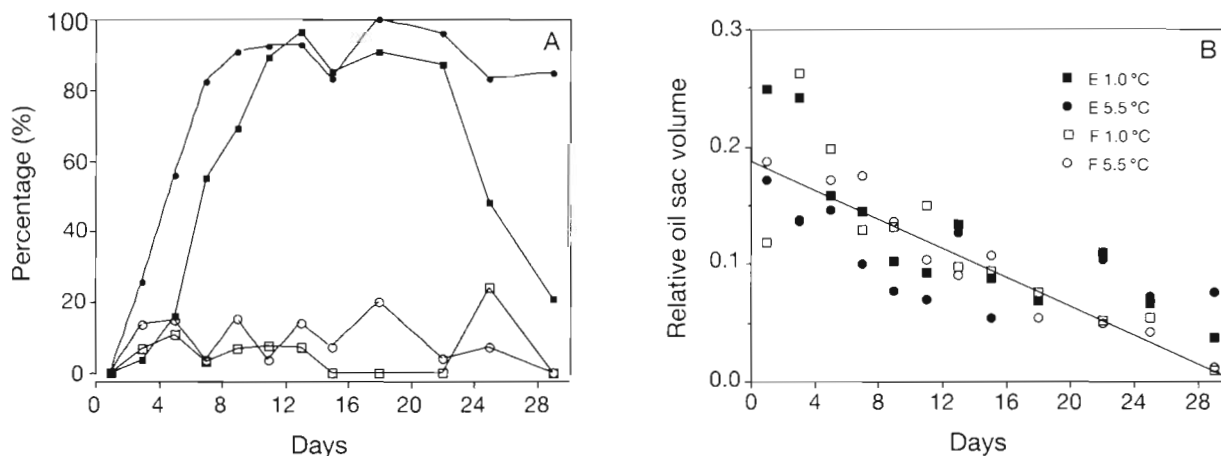


Fig. 4. *Calanus finmarchicus*. Laboratory experiment with females (14 April to 13 June 1991). (A) Percentage reproductive (stages 4 to 7) females in the 4 experimental conditions. For each point, $n = 23$ to 33. (B) Relative oil sac volume [oil sac volume (prosoma volume) $^{-1}$] for the same individuals in food-enriched (E) and filtered (F) seawater. Equation of the regression line: $y = 0.187 - 0.006x$, $r^2 = 0.90$

of females in food-enriched seawater at 5.5°C carried oocytes that were in the process of or had completed vitellogenesis (stages 4 to 7; Fig. 3A). A similar oocyte development was observed at 1°C, but with a delay of 5 d (Fig. 4A). The start of maximum egg production in the laboratory population coincided with the timing of gonad development (cf. Figs. 2A & 4A). In the filtered seawater treatments, oogenesis did not progress and the majority (>80%) of the females remained immature at both temperatures (Figs. 3B & 4A). However, in a small proportion of the population (ca 15%), oocytes proceeded to maturity despite the absence of food.

The relative oil sac volume decreased steadily, from approximately 20% at capture to <5% after 2 mo in all treatments (Fig. 4B). There was no detectable effect of food or temperature on the rate of decline (ANCOVA, $p > 0.3$).

Reproduction of *Calanus finmarchicus* in the Lower St. Lawrence Estuary

Representative temperature and salinity profiles during the study period are shown in Fig. 5. Surface temperature rose from 4°C in mid-May to between 8 and 9°C in August. The upper depth of the intermediate water, a layer of cold (−0.5 to 1°C) water which is characteristic of the Lower Estuary in summer (Koutitonsky & Budgen 1991), varied between 30 and 75 m. Salinities at the surface were as low as 24 PSU, reflecting discharge of spring runoff from the St. Lawrence River in early summer, but were consistently 32 to 33 PSU deeper in the water column.

In 1991, the transition from low to high phytoplankton biomass took place within a 10 d interval in mid-June, marking a distinct beginning to the spring phytoplankton bloom. A prolonged, summertime period of high phytoplankton biomass ensued (Fig. 6A). Between June 13 and August 15, integrated chlorophyll *a* concentrations over the first 20 m of the water column were typically between 75 and 125 mg m $^{-2}$.

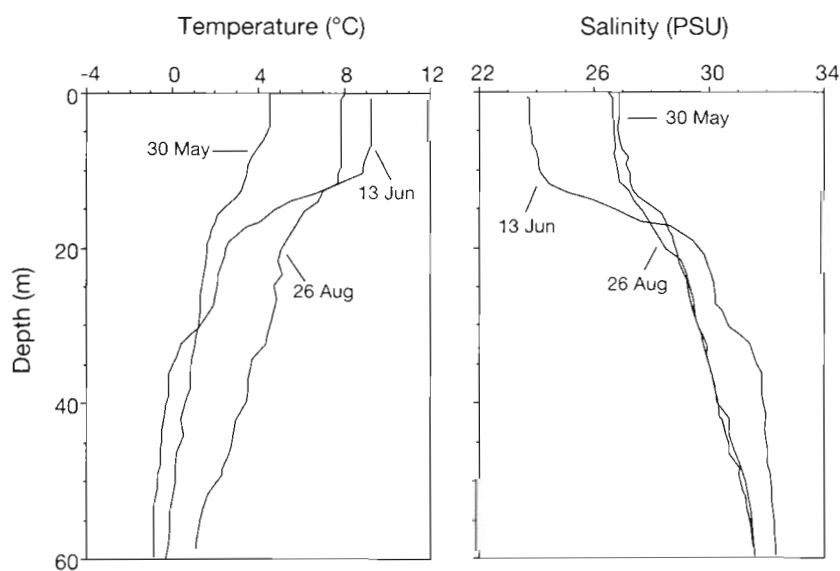


Fig. 5. Temperature and salinity profiles (0 to 60 m only; station depth 330 m) on 30 May, 13 June and 26 August 1991 at the sampling station

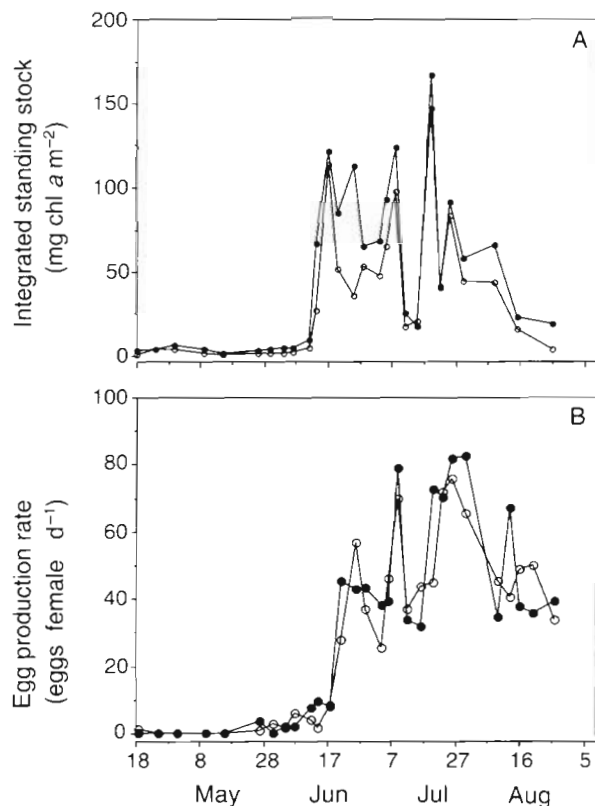


Fig. 6. *Calanus finmarchicus*. Time series from the Lower St. Lawrence Estuary station between 18 April and 26 August 1991. (A) Estimated integrated total (●) and > 5 µm (○) chl *a* (mg m⁻²) standing stock for the first 20 m of the water column. (B) Estimated *in situ* egg production rate of females at 5.5°C in enriched (●) and filtered (○) seawater. Points represent mean of 4 replicates

Maximum values (up to 166 mg chl *a* m⁻²) were observed in July. During this period, algae > 5 µm constituted more than 50% of the phytoplankton biomass. By late August, values were smaller than 25 mg m⁻², indicating that chlorophyll concentrations had started to decline.

The spawning of *Calanus finmarchicus* was synchronised with the timing of the phytoplankton bloom (Fig. 6). Observations showed zero or near-zero egg laying in the Lower Estuary between mid-April (the start of the study) and the end of May. Some egg production occurred at the beginning of June, but rates for the population remained low (< 10 eggs female⁻¹ d⁻¹). Egg production rates increased dramatically in the third week in June, 7 to 8 d after the distinct rise in phytoplankton biomass. *C. finmarchicus* continued to produce eggs at high rates (between 22 and 82 eggs female⁻¹ d⁻¹) until the end of August. Highest rates were observed in July (Fig. 6B).

The short-term (24 h) incubations employed to estimate egg production were conducted at 2 different temperatures and food treatments. Females held at

1°C released 24% fewer eggs (ANOVA, $p < 0.025$), on average, as compared to those maintained at 5.5°C. However, the general seasonal pattern of egg production did not vary significantly between temperatures (Fig. 6B). Except for the period of rapid increase in phytoplankton biomass in mid-June, females incubated in food-enriched or filtered seawater released the same number of eggs (ANOVA, $p > 0.3$).

The fluctuations in egg production rate in summer, after the onset of the bloom, were not well correlated with variations in phytoplankton biomass (Fig. 6). When the 2 data points taken between 13 and 17 June (when egg production rates had not yet equilibrated with the rapid increase in food concentration) are removed, the relationship between egg production and chlorophyll biomass is consistent with a curvilinear or rectilinear response to food concentration (Fig. 7).

Changes in gonadal maturity in the population (Fig. 8A) match the observations of egg production rates. There were 4 distinct phases in the seasonal cycle of gonad maturation. An increase, from 10 to 35%, in the proportion of stage 3 females and a corresponding decrease in the proportion of stage 1 females occurred during the period prior to the spring bloom. Females carrying oocytes in advanced stages of vitellogenesis (stages 4 to 7) made up less than 20% of the population. The second phase started with the spring bloom on 12 June and lasted for 1 wk, during which more than 80% of the female population attained reproductive maturity. This period corresponds to the

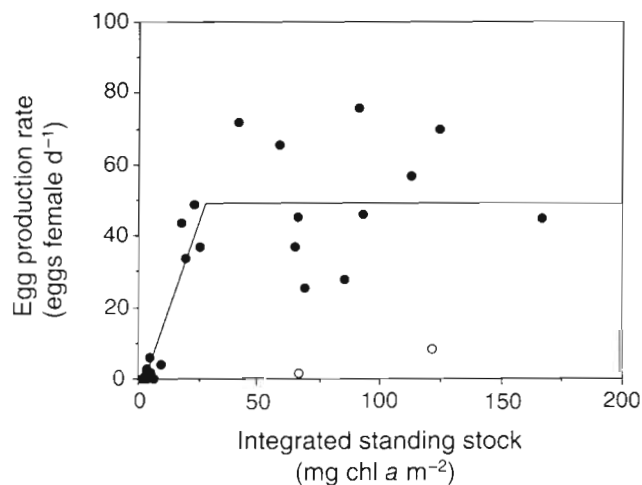


Fig. 7. *Calanus finmarchicus*. Estimated *in situ* egg production rate of females in the Lower St. Lawrence Estuary in 1991 as a function of the total chl *a* concentration (mg m⁻²) integrated over the first 20 m of the water column. Data are fit to a rectilinear model: $y = 2.00x - 6.00$ (for $x < 50$ mg chl *a* m⁻²), $r^2 = 0.93$; $y = 49.4$ (for $x \geq 50$ mg chl *a* m⁻²). The 2 measurements (○) taken during the lag between the rapid increase in food concentration and the increase in egg production (13 to 19 June) are not included in the fit

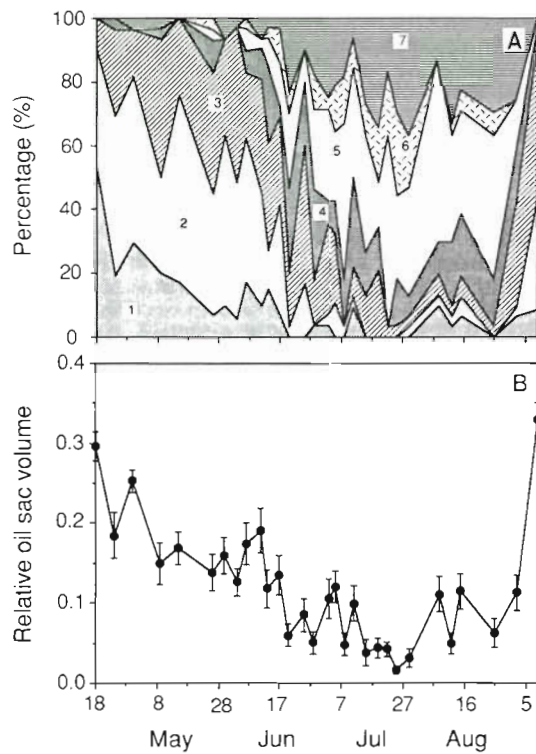


Fig. 8. *Calanus finmarchicus*. Time series from the Lower St. Lawrence Estuary station between 18 April and 9 September 1991 of (A) gonad maturation stages of females and (B) relative oil sac volume for the same individuals. No. of females per sample = 22 to 42

lag time between the onset of high phytoplankton biomass and the start of high egg production rates. The third phase, during which most of the females were reproductively mature, corresponds to the period of high summer egg production (21 June to 31 August). The final phase shows a marked decline in the proportion of reproductively active females between 31 August and 9 September, signaling the end of the reproductive season.

The empirical relationship between egg production rates and the state of reproductive maturity of the population is shown in Fig. 9. Following Runge (1987), estimates of *in situ* egg production rate in filtered seawater at 5.5°C were regressed on an index of reproductive maturity (the cumulative proportion of the female population in stages 4 to 7). A simple linear regression showed a strong correlation between the 2 variables ($r^2 = 0.79$).

The relative oil sac volume followed a similar 4-phase pattern over the sampling period (Fig. 8B). During the interval prior to the spring phytoplankton bloom, the oil sac/body volume ratio decreased from an initial value of 0.3 to about 0.17 to 0.20, a reduction of 30 to 40%. The decrease was most noticeable in late April–early May, when there was also a marked

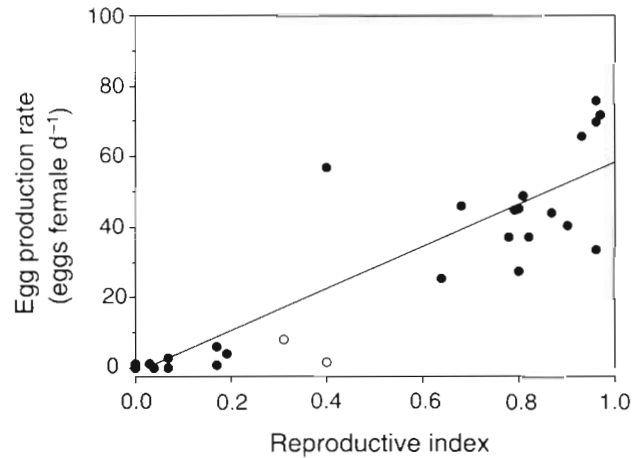


Fig. 9. *Calanus finmarchicus*. Relationship between *in situ* egg production rate at 5.5°C in filtered seawater and reproductive index (proportion of females, stages 4 to 7 inclusive) for females in the Lower St. Lawrence Estuary, 1991. The equation is a simple linear regression: $y = 59.8x - 1.6$ ($r^2 = 0.79$). The 2 measurements (○) taken during the lag between the rapid increase in food concentration and the increase in egg production (13 to 19 June) are not included in the fit. The regression of egg production rate on reproductive index, using enriched seawater at 5.5°C (data not shown) is: $y = 68.0x - 3.4$ ($r^2 = 0.80$)

decrease in the proportion of gonadal stage 1 females. A pronounced decline in oil sac volume occurred during the phase of rapid gonad maturation corresponding to the onset of the spring bloom. By 3 July, the oil sac was about 25% of the volume it had 3 wk earlier. Its longitudinal axis no longer extended the length of the cephalothorax, but rather was reduced to the posterior end. During the phase of high summer egg production, the oil sac was thin, making up only 5 to 10% of the prosome volume, and confined to the posterior end of the cephalothorax. In September, after mature stages disappeared from the population, oil sac volume increased to high pre-reproductive values.

DISCUSSION

Oocyte development, egg production, and the cycle of phytoplankton production in the Lower Estuary

The results are consistent with the prevailing understanding of the relationship between egg production and external food supply for *Calanus finmarchicus* and related species of the genus. Based on the correspondence of egg production with the spring bloom and confirmed by feeding experiments reported elsewhere (Ohman & Runge in press), females in the Lower Estuary relied on ingested phytoplankton as the source of materials for the final stages of oocyte maturation. Egg

production commenced with the late spring bloom, after a 1 wk lag corresponding to the time required for the oocytes to complete vitellogenesis. High phytoplankton concentrations apparently supported egg production throughout the summer.

There is a clear relationship between oocyte maturation and egg production (e.g. Fig 9), supporting the proposal that egg production rates of *Calanus finmarchicus* can be predicted from preserved samples of females staged for reproductive maturity (Runge 1987). The slope of the linear regression (59.8) is about 50% greater than the value obtained by Runge (1987) for *C. finmarchicus* on the Scotian shelf. However, the females from the Lower Estuary were considerably larger (2.9 to 3.1 mm mean prosome length; unpubl. data) than their counterparts in waters off Nova Scotia (2.7 to 2.8 mm). This difference in body size is sufficient to account for the high rates (60 to 80 eggs female⁻¹ d⁻¹) observed in July in the Lower Estuary, compared to measurements of egg production (using a similar method) in the southwest Nova Scotia population (20 to 40 eggs female⁻¹ d⁻¹; Runge 1985b), or in populations in fjords of Northern Norway (20 to 35 eggs female⁻¹ d⁻¹), where female body size was smaller (2.5 mm prosome length; Diel & Tande 1992). Given an egg carbon weight of 0.23 µg and a female carbon weight ranging between 160 and 220 µg (pers. obs., Ohman & Runge in press), maximum egg production rates in the Lower Estuary in July and August, when surface temperature were 7 to 9°C, were on the order of 0.08 to 0.11 µg C egg µg C⁻¹ d⁻¹. This is a reasonable *P/B* range for these temperatures based on previous experiments (Runge 1984, 1985a). It is therefore not clear that a general relationship can be found that is applicable to all *Calanus* populations; our results nevertheless advance the possibility of developing a specific relationship for a given region.

The relationship between egg production rate and integrated standing stock indicates that the critical density for maximum rates occurred at about 25 mg chl *a* m⁻² (Fig. 7). Even taking into account that the Lower Estuary value represents just the upper 20 m of the water column, this is considerably lower than what Runge (1985a) found for *Calanus pacificus* in Puget Sound and is consistent with the suggestion, based on few data, that the empirical response of the 2 species to chlorophyll standing stock is different (Runge 1985b). In addition to possible species-specific differences in the functional response to 'optimal' food, any number of factors could contribute to differences in the chlorophyll-egg production relationship, including the variable relationship between chlorophyll and what the females are actually eating (including microzooplankton; Ohman & Runge in press), the vertical distribution of prey, and the proportion of females in a pre-

reproductive state. Nevertheless, the results shown in Fig. 7 support the idea that region-specific (in this case the Lower St. Lawrence Estuary), empirical relationships between chlorophyll standing stock and *C. finmarchicus* egg production rates have predictive value in studies of the *Calanus*-prey interactions.

Comparison of egg production rates in the Lower Estuary with the laboratory observations must take into account possible temperature differences between laboratory incubations (5.5°C) and the ambient environment. The mean equilibrium rate in the first 3 wk of the laboratory experiment was 31 eggs female⁻¹ d⁻¹. Assuming that surface water temperatures (7 to 9°C) have a predominant influence on *Calanus* egg production and using the relationship between egg production and temperature developed by Runge (1985b), a mean rate of 40 to 50 eggs female⁻¹ d⁻¹ for well-fed females in summer would be predicted based on our laboratory results. This rate is equalled or surpassed by the Lower Estuary population, in contrast to the situation in Puget Sound, where egg production rates of *C. pacificus* were always less than the temperature-corrected from laboratory experiments in which *Thalassiosira weissflogii* was also the sole source of food (Runge 1985a). A reduction in egg production rate after 3 wk is similar to laboratory observations of *C. pacificus* (Runge 1984) and indicates either onset of senescence (Diel & Tande 1992) or that *T. weissflogii* does not contain all the essential dietary elements necessary to sustain long-term egg production. It is possible as well that senescence (with respect to egg production) was brought on prematurely in the laboratory by the rapid decline in lipid reserves, if depot lipids are required for the early, generative phase of oögonial production, as discussed below. That a similar reduction in egg production was not also observed in the ambient environment suggests some combination of the following factors: (1) new females were being input into the Lower Estuary population; (2) wild females were ageing more slowly; or (3) the food composition in the Lower Estuary was more nutritious for *C. finmarchicus* than the laboratory food.

Role of depot lipids in oocyte development

The presence of a high proportion of females in stages 2 and 3 at the start of the study confirms that females realize the first steps of oögenesis well before the start of the spring bloom. While we cannot rule out the possibility that female *Calanus finmarchicus* also sustain oocyte proliferation in early spring by ingesting suspended particulate material, including microzooplankton (e.g. Butler et al. 1970, Corner et al. 1974, 1976, Stoecker & McDowell Capuzzo 1990), lipid

reserves are a likely source of materials and energy during the early stages of development (Tande & Hopkins 1981, Tande 1982). Moreover, the result that a small proportion of females develop oocytes to maturity in the absence of food (Fig. 3B) indicates that the capability of relying solely on internal reserves exists in the species. This could explain the presence of a small proportion of reproductively mature females in the Lower Estuary in April and May.

Results of our laboratory and field observations of oil sac depletion do not, however, provide unequivocal evidence for a relationship between lipid stores and oocyte development. The corresponding decline in both the depot lipid index and the proportion of stage 1 females before the spring bloom in the Lower Estuary population is consistent with the idea that lipid reserves support early stages of oogenesis. The rapid decline in lipid stores at the start of the phytoplankton bloom could represent either rapid development of stage 1 oocytes in remaining immature females or increased metabolic costs associated with feeding and other behaviour changes in response to the spring bloom. Laboratory experiments, however, show no difference between fed and unfed treatments in depletion of depot lipids. As previously mentioned, the rate of decline of lipid volume in the laboratory was much higher than in the natural environment; it is possible that the conditions of the experiments exacted an increased metabolic cost that masked the contribution of lipids to the early stages of oocyte development.

Our results therefore only allow several general conclusions with regard to the role of lipids in oogenesis: (1) the data do not rule out the possibility that lipid reserves were used to support the generative phase (i.e. proliferation of oogonia in the ovary) and early pre-vitellogenic growth of primary oocytes; and (2) prior to the spring bloom, the majority (but not necessarily all) of females did not use lipid reserves for secondary vitellogenesis (stages 4 to 7).

Effects of temperature on the timing of egg production

The purpose of the low temperature experiment was to understand the extent to which temperature variation in early spring may influence reproductive processes in the Lower Estuary. Interannual differences of several degrees centigrade have been observed in April–May in surface (e.g. Lacroix & Filteau 1970) and deep (Budgen 1991) waters of the region; our choice of 1 °C represents an extreme minimum that female *Calanus finmarchicus* would experience if they resided in the cold intermediate layer. The results show that, while the lower temperature reduces daily egg production rate, the start of egg production

relative to the spring bloom was only 4 d later than the response of females incubated at 5.5 °C, a relatively short delay compared to the length of the spawning season. Therefore we conclude that interannual temperature variation in the Lower Estuary would have a minor influence on the timing of the copepod's reproductive cycle.

The Lower St. Lawrence Estuary: a *Calanus* pump?

Our results lead to the conclusion that the Lower St. Lawrence Estuary is a regionally important zone of *Calanus finmarchicus* reproduction. Although it commenced late, the spawning period of *C. finmarchicus* lasted over 12 wk, during which egg production reached the highest rates ever recorded for the species. The cycle of egg production is typically shorter and frequently episodic in other regions where *C. finmarchicus* predominates (e.g. Wiborg 1954, Marshall & Orr 1955, Davis 1976, Williams & Lindley 1980a, b, Tande et al. 1985, Skjoldal et al. 1987, Diel & Tande 1992); maximum egg production rates are also substantially lower, due to the smaller body size of the resident females. Although we do not yet have extensive measurements of the concentration of *C. finmarchicus* females in the Lower Estuary, this species is predominant in the region's zooplankton community and there is no indication that *C. finmarchicus* is any less abundant there than elsewhere (Runge & Simard 1990).

A dominant feature of the surface circulation in the region is the Gaspé Current, a rapidly moving coastal jet moving the mass of the discharge from the St. Lawrence River out along the Estuary's southern side. Net transport in the surface layer (0 to 30 m) of the Lower Estuary is therefore outward to the Gulf of St. Lawrence (El-Sabh 1988). Fortier et al. (1992) observed high concentrations of copepod eggs (most of which would be *Calanus* spp.) and *Calanus* spp. copepodites in summer in the Gaspé Current as it leaves the Lower Estuary proper and rounds the Gaspé Peninsula into the Gulf of St. Lawrence. These concentrations are 1 to 2 orders of magnitude higher than in the adjacent Anticosti Gyre, reflecting differences in *Calanus* spp. production cycles between the Lower Estuary and Gaspé Current and waters of the Northern Gulf of St. Lawrence. Although there is not yet complete seasonal coverage of the phytoplankton production cycle in the Northern Gulf, there is every indication that the spring phytoplankton bloom typically ends by mid-June (de Lafontaine et al. 1991) and a stratified condition dominated by the microbial loop sets in for the summer months (Levasseur et al. 1992, Ohman & Runge in press). While *C. finmarchicus* females continue to produce eggs in the Northern Gulf in early summer

(June–July), egg concentrations in the water column are ca 5 times lower than in the Lower Estuary/Gaspé Current.

Hence, the evidence indicates that the Lower Estuary/Gaspé Current system acts as a *Calanus* 'pump', supplying fish larvae with abundant food (Fortier et al. 1992) and exporting zooplankton to the Gulf of St. Lawrence during the summer months. Examination of the residual surface circulation patterns in the Gulf (e.g. Koutitonsky & Budgen 1991) suggests that some of the developing copepodites will drift with a branch of the Gaspé Current into the Southern Gulf of St. Lawrence; others will disperse into the northern gyres on the western and eastern sides of Anticosti Island. A portion of the current moves out through Cabot Strait along the southern side of the Laurentian Channel, where it becomes the Nova Scotia Current. Recent studies indicate that the Gulf of St. Lawrence is a major supplier of species of *Calanus* to populations on the Scotian Shelf (Herman et al. 1991, Sameoto & Herman 1992). The Lower St. Lawrence Estuary may be the heart of a complex system that influences cycles of marine production over a wide region of eastern Canada.

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