



Importance of feeding for egg production in *Calanus finmarchicus* and *C. glacialis* during the Arctic spring

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ABSTRACT: The vertical distribution and *in situ* egg production of *Calanus finmarchicus* and *C. glacialis* were studied in Disko Bay, western Greenland, from winter throughout the spring bloom. The 2 species entered the surface water simultaneously, but their spawning patterns differed significantly. Maximum egg production for *C. glacialis* of 48 ± 8 eggs female⁻¹ d⁻¹ was measured on May 1, 2005 in association with the culmination of the bloom, while the highest egg production rate of *C. finmarchicus* of 44 ± 7 eggs female⁻¹ d⁻¹ was measured on May 25 after termination of the bloom. During 3 phases of the spring bloom, the impact of starvation and saturating food conditions on the egg production rates of the 2 *Calanus* species was investigated in the laboratory. Experiments with starved and ad libitum fed females showed a significant difference in the egg production rate between the 2 species, depending on sampling time, i.e. gonad maturity and feeding history. The results showed varying use of saturating food during the 3 phases of the bloom. For *C. finmarchicus*, no effect of food was observed during the first experiment in late April, whereas females collected in early May, during the peak of the spring bloom, responded strongly to changes in food concentration, with egg production which was 3 times higher than that of the starved controls. In contrast, *C. glacialis* responded strongly to food concentration in both late April and early May. The present investigations illustrate that *Calanus* females from the Disko Bay area continue to produce eggs without food more than twice as long as those reported from other northern populations. This observation could indicate an adaptation to the Disko Bay environment, which has unpredictable ice conditions and consequently large variations in the initiation of the spring bloom.

KEY WORDS: *Calanus glacialis* · *C. finmarchicus* · Egg production · Starvation · Spring bloom

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INTRODUCTION

Copepods of the genus *Calanus* are key players in high latitude marine ecosystems. They dominate the mesozooplankton communities, are significant grazers on the primary production (Nielsen & Hansen 1995, Levinsen & Nielsen 2002), and constitute an important prey item for numerous fish, bird, and whale populations (Heide-Jørgensen & Acquarone 2002, Karnovsky et al. 2003). At the same time, *Calanus* have a role in the supply of high quality food to the benthic communities by acceleration of the vertical flux through production of large fast-sinking fecal pellets (Pedersen et

al. 2006). In Greenlandic waters, 3 species of *Calanus* dominate the mesozooplankton community during spring and early summer (Madsen et al. 2001, Møller et al. 2005, Nielsen et al. 2007). *C. hyperboreus* and *C. glacialis* are true arctic species inhabiting polar waters, while *C. finmarchicus* is a temperate species associated with Atlantic waters (Conover 1988, Hirche et al. 1991). In Disko Bay, western Greenland, the northern border for *C. finmarchicus* and the southern for *C. glacialis*, the 2 species meet and co-exist (Madsen et al. 2001). The life-history strategies of *Calanus* are adapted to the arctic, involving hibernation in deep waters during winter followed by an ascent to

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the productive layers in early spring, where spawning, feeding, and refueling of lipid stores take place (Lee et al. 2006). In late summer, first *C. hyperboreus*, then *C. glacialis* and later *C. finmarchicus* descend to deep waters. *C. glacialis* initiates spawning prior to the spring bloom, with gonad maturation and egg production (EP) fueled by internal lipid reserves (Smith 1990). EP reaches a maximum during the spring bloom, when a correlation between EP and chlorophyll *a* (chl *a*) concentration can be found (Nielsen & Hansen 1995, Hirche & Kosobokova 2003). Being a temperate species, *C. finmarchicus* has smaller lipid reserves and depends on food in order to finish gonad maturation and initiate spawning. EP is therefore highly dependent on the phytoplankton concentration, and spawning is initiated after feeding on the phytoplankton spring bloom has begun (Madsen et al. 2001, Niehoff et al. 2002). As *C. hyperboreus* spawns during winter (Hirche & Niehoff 1996, Madsen et al. 2001), it was not considered in the present study.

Disko Bay is located at the southern border of the arctic sea ice and is therefore likely to be affected by climatic changes. The break-up of sea ice in Disko Bay normally takes place between April and May, but oscillates considerably from year to year (Heide-Jørgensen et al. 2007), thereby influencing the timing of the phytoplankton spring bloom (Nielsen & Hansen 1995, Madsen et al. 2001, Hansen et al. 2003, Thor et al. 2005). As the mechanisms triggering the termination of *Calanus* winter hibernation are not fully understood (Fiksen 2000, Hansen et al. 2003, Thorisson 2006), it is not yet known to what degree copepods are capable of timing their ascent from deep waters with the occurrence of the spring bloom. Modeling scenarios suggest that a possible mismatch between ascent and ice break-up could result in copepods experiencing periods of starvation or bad food quality. If the ice remains longer than normal, copepods may ascend at a time when no food is available, and if the ice breaks up early, then the phytoplankton bloom has already sedimented, making protozooplankton and ciliates the main food items (Hansen et al. 2003). Starvation experiments with *C. finmarchicus* (Hirche 1990, Hirche et al. 1997, Niehoff 2000, 2004) and with *C. glacialis* (Hirche & Bohrer 1987, Hirche 1989, Hirche & Kwasniewski 1997, Kosobokova & Hirche 2001, Hirche & Kosobokova 2003) have shown a pronounced decrease in reproductive activity following even short periods of starvation. Knowledge about the sensitivity of reproduction in relation to starvation is therefore crucial for understanding future dynamics of the copepod community in order to quantify their role in the marine food web in a changing environment.

The aim of the present study was to describe the spring migration of the *Calanus* populations to the surface layer in relation to spring bloom formation in Disko Bay, western Greenland, and to investigate how the surface food conditions on arrival influence EP rate of the 2 co-occurring copepod species *C. finmarchicus* and *C. glacialis* during 3 phases of the spring bloom development.

MATERIALS AND METHODS

Study site. Sampling was conducted from RV 'Porsild' (Arctic Station, University of Copenhagen) in the Disko Bay area close to Qeqertarsuaq in western Greenland from February 22 to May 30, 2005. The sampling was carried out at the permanent station located 1 nautical mile off Qeqertarsuaq (69° 15' N, 53° 33' W) (Fig. 1), previously used for studying the pelagic community (Nielsen & Hansen 1995, Hansen et al. 1999, Madsen et al. 2001, Levinsen & Nielsen 2002, Thor et al. 2005, Pedersen et al. 2006). From February 22 to May 30, weekly cruises were made to the permanent station, where CTD profiles, chl *a*, nutrient, and stratified copepod samples were taken. From late April to the end of May, additional measurements of *Calanus finmarchicus* and *C. glacialis* EP were included in the program.

Hydrography and nutrients. The vertical distribution of salinity and temperature was measured down to 80 m using a Seabird SBE25-01 CTD. Water samples from 1, 15, 30, 50, and 100 m were taken using a Niskin 10 l water bottle, and stored in dark 10 l plastic containers. Subsamples of 10 ml for determination of nutrient concentration were frozen immediately after sampling. The nutrient concentrations were later analyzed at the National Environmental Research Institute (NERI) on an automatic nutrient analyzer (Dansk Havteknik) following Grasshoff (1976). All nutrient samples were analyzed in duplicate with a precision of 0.06, 0.1, 0.3, and 0.2 μM for phosphorus, nitrate, ammonia, and silicate, respectively.

Phytoplankton. Three samples of 500 ml were filtered onto GF/F filters. Chl *a* was extracted overnight in 5 ml 96% ethanol (Jespersen & Christoffersen 1987) and measured before and after acid addition on a Turner Designs Model 700 Fluorometer calibrated against a pure chl *a* standard. Phytoplankton biomass was calculated from chl *a*, applying a C/chl *a* conversion factor of 42.8 (Pedersen et al. 2006).

Ciliates and heterotrophic dinoflagellates. The abundance and species composition of ciliates and heterotrophic dinoflagellates were quantified in 100 ml seawater from 1 and 15 m depth, preserved in Lugol's solution (2% final concentration). The samples were allowed to settle for 24 h in 50 ml chambers, prior to quantification under an inverted microscope at 200 \times

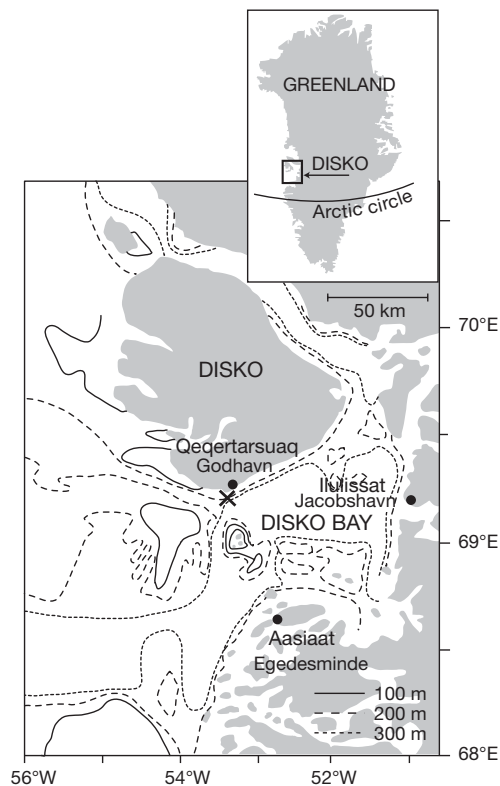


Fig. 1. Location of study site

magnification. The identification of species or morphologic types was based on Nielsen & Hansen (1999). Cell volume was calculated from measurements of linear dimensions and simple geometric shapes, and the biomass estimated from volume according to equations in Menden-Deuer & Lessard (2000).

Mesozooplankton. Zooplankton distribution was sampled using a submersible pump (900 l min⁻¹, HOMA-H500, DIFRES design) equipped with a flowmeter (Hydrobios), conical net (50 µm mesh size), and a nonfiltering cod end. Samples were collected in 4 depth strata (0–50, 50–100, 100–150, and 150–200 m). The pump was lowered to deepest part of the strata, switched on, and retrieved to the upper layer at speed 10 m s⁻¹ and turned off. From 0 to 50 m, strata triplicate samples were taken on each sampling occasion. The samples were immediately preserved in buffered formalin (2% final concentration) for later analyses. In the laboratory, the samples were split by a plankton splitter to obtain sample sizes of approximately 500 individuals, and all identifiable zooplankters were identified to either species or genus and developmental stage. Prosome lengths were measured on 10 individuals from each copepodite or adult stage of

each species. The biomass values of the different copepods were calculated based on measurements of their length in the different depth strata and length–weight regressions from the literature (Thor et al. 2005).

In situ EP. Approximately once a week, live copepods were sampled in the upper 100 m using a WP-2 net (mesh size 200 µm) and transferred to a 25 l plastic jar and stored under dark and cold conditions. Within 3 h, 10 fertilized females of *Calanus glacialis* and *C. finmarchicus* were carefully sorted out and individually incubated in 600 ml polycarbonate bottles filled with surface water at *in situ* temperature. During sorting, the copepod-containing beakers and Petri dishes were kept in trays with ice-cold seawater. The incubation bottles were placed in the cold room in 100 l buckets with snow and seawater to keep the temperature at 0°C. After 24 to 36 h incubation, the content of the bottles were concentrated on a 45 µm sieve and the female and the eggs rinsed to a counting chamber, where the eggs were counted and length of the females measured. Carbon content in females was estimated from length, using conversion factors found by Nielsen & Hansen (1995) (Table 1).

Laboratory experiments. On 3 occasions (April 26, May 10, and May 30) representing different phases of the spring bloom (Table 2), additional EP experiments were initiated. Live females were collected as described above, and 2 levels of food concentration were set up for each of the experiments (Expts 1 to 3).

EP during starvation: Ten fertilized females of *Calanus finmarchicus* and *C. glacialis* were incubated individually in 600 ml polycarbonate bottles with GF/F filtered surface water ($0.15 \pm 0.02 \mu\text{g chl } a \text{ l}^{-1}$).

Table 1. *Calanus finmarchicus* and *C. glacialis*. Prosome length and carbon content (mean \pm SE) in females collected for *in situ* measurement of egg production

Species	Length (µm)	Weight (mg C)	n
<i>C. finmarchicus</i>	2600 \pm 13.2	0.15 \pm 0.00	150
<i>C. glacialis</i>	3416 \pm 25.8	0.40 \pm 0.01	120

Table 2. *Calanus finmarchicus* and *C. glacialis*. *In situ* nutrient conditions and pelagic carbon in plankton on the day females were collected for experiments, i.e. prior to addition of *Rhodomonas salina*, and carbon content (mean \pm SE) of the incubated females. BD: below detection limit

Biomass	Expt 1	Expt 2	Expt 3
Nitrate (µM)	6.9 \pm 0.5	BD	BD
Phytoplankton (µg C l ⁻¹)	298.9	532.7	176.04
Protozoa (µg C l ⁻¹)	14.7	5.1	6.6
<i>C. finmarchicus</i> (mg C female ⁻¹)	0.16 \pm 0.01	0.17 \pm 0.01	0.14 \pm 0.01
<i>C. glacialis</i> (mg C female ⁻¹)	0.46 \pm 0.03	0.45 \pm 0.03	0.45 \pm 0.03

EP at saturated food concentration: Ten females of each species were incubated individually in 600 ml polycarbonate bottles with 45 μm screened surface water (9, 12, and 4 $\mu\text{g chl } a \text{ l}^{-1}$ for the 3 experiments, respectively) spiked with a phytoplankton culture (*Rhodomonas salina*) until an average chl *a* concentration of $56.2 \pm 6.6 \mu\text{g chl } a \text{ l}^{-1}$ was achieved.

On a daily basis, the contents of the bottles were gently concentrated on a 45 μm submerged sieve and rinsed to a counting chamber. The females were immediately transferred using a large mouth pipette to new bottles with either fresh GF/F filtered water or diluted *Rhodomonas salina* culture and brought back to the cold room. The spawned eggs were then counted. In order to keep the temperature subzero, all handling of the copepods was done in containers submerged in ice-cold seawater. After 10 to 13 d, the experiments were terminated and the length of the females measured. Results of all experiments are presented as average values \pm SE, unless otherwise stated.

RESULTS

Hydrography and phytoplankton

In winter 2005, no permanent ice cover of Disko Bay was formed; hence, when the present investigation was initiated in February, only drift ice was present. Until early April, the temperature in the upper 50 m was rather homogeneous and $< -1.5^\circ\text{C}$ (Fig. 2A). There was a weak salinity difference of about 0.1 from the surface to 100 m (Fig. 2B) and the chl *a* concentration was $< 0.1 \mu\text{g l}^{-1}$ (Fig. 2C). In mid-April, an upwelling or inflow of water with higher salinity stratified the surface layer (Fig. 2B), and the shallower mixed layer triggered the plankton bloom (Fig. 2C). From April 8 to May 2, the chl *a* concentration increased from 1 to $17 \mu\text{g l}^{-1}$ (Fig. 2C). The nutrients were rapidly consumed by the bloom, after which the bloom gradually settled. In the middle of May, meltwater reduced the mixed-layer salinity and mixed-layer depth down to 33.1 and 5 m, respectively (Fig. 2B). Throughout the winter, the surface chl *a* concentration was low ($0.06 \pm 0.01 \mu\text{g l}^{-1}$), which lasted until April, when it exceeded $1 \mu\text{g l}^{-1}$ (Figs. 2C & 3A). The spring bloom started in mid-April and peaked May 2 at $16.4 \pm 0.4 \mu\text{g chl } a \text{ l}^{-1}$, after which chl *a* concentration rapidly declined, reaching $4.1 \pm 0.9 \mu\text{g l}^{-1}$ on May 30, as a result of a nitrate depletion in the photic zone. Small phytoplankton ($< 45 \mu\text{m}$) dominated the surface waters from February 25 to April 27, when they contributed on average $81 \pm 6\%$ to the total phytoplankton biomass. As the bloom developed, a shift in size composition was observed. The proportion of small phytoplankton decreased to an average of $23 \pm 2\%$, and during the rest

of the investigative period, the phytoplankton community was dominated by phytoplankton $> 45 \mu\text{m}$ (Fig. 3A). This observation was corroborated by microscopic examination of the plankton, which showed that large diatoms (*Thalassiosira* spp., *Chaetoceros* spp., and *Detonula* spp.) dominated the phytoplankton community during the bloom.

Protozooplankton (ciliates and heterotrophic dinoflagellates)

The succession of microprotozooplankton followed the development of the phytoplankton community. Heterotrophic dinoflagellates dominated the protozooplankton community, and were responsible for $69 \pm 4\%$ of the protozooplankton biomass (Fig. 3B,C). Until late April, the protozooplankton biomass was low, and thereafter it followed the developing phyto-

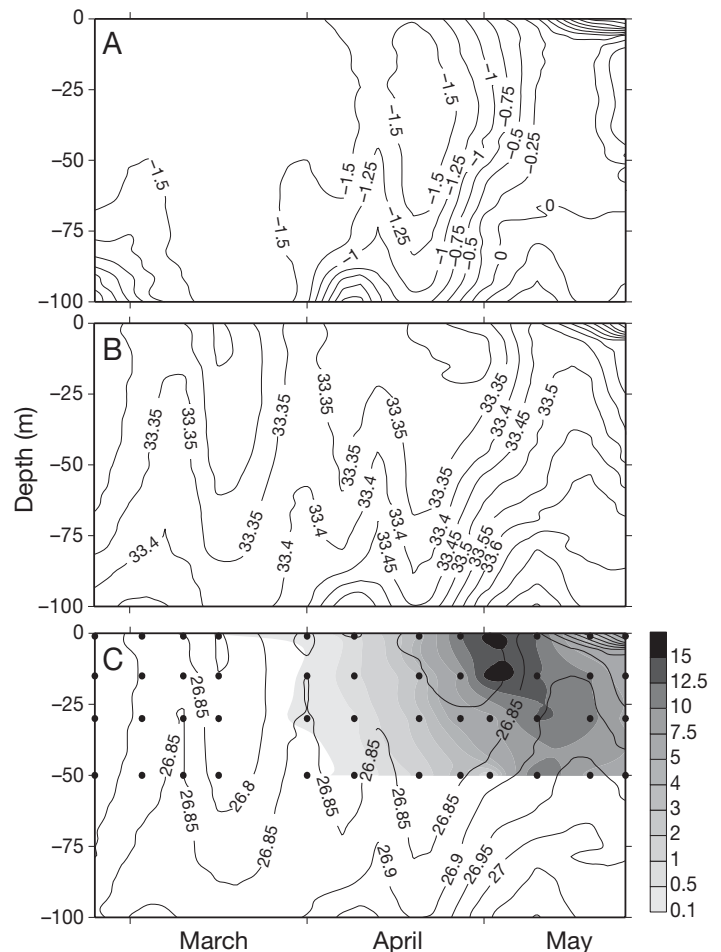


Fig. 2. Depth distribution of (A) temperature ($^\circ\text{C}$), (B) salinity, and (C) density (1000 kg m^{-3} , lines) and chlorophyll *a* concentration ($\mu\text{g l}^{-1}$, shading) in Disko Bay February 25 to May 30, 2005

plankton spring bloom (Fig. 3B,C). Dinoflagellates were found to correlate strongly with phytoplankton <45 μm ($r^2 = 0.70$, $n = 25$, $p < 0.01$), whereas ciliates correlated weakly with total phytoplankton biomass ($r^2 = 0.34$, $n = 74$, $p < 0.05$). Total protozooplankton biomass correlated with phytoplankton <45 μm ($r^2 = 0.72$, $n = 25$, $p < 0.01$). Biomass decreased after a peak of 23 $\mu\text{g C l}^{-1}$ on April 24, and from May 10, the biomass stabilized at $5 \pm 0.5 \mu\text{g C l}^{-1}$. The contribution of dinoflagellates and ciliates to total protist carbon dropped from 12% in late February to 2% in late May. From April 24 to May 30, the average protozoan biomass was $12 \pm 2 \mu\text{g C l}^{-1}$, which corresponded to approximately $3.6 \pm 0.7\%$ of the total protist biomass.

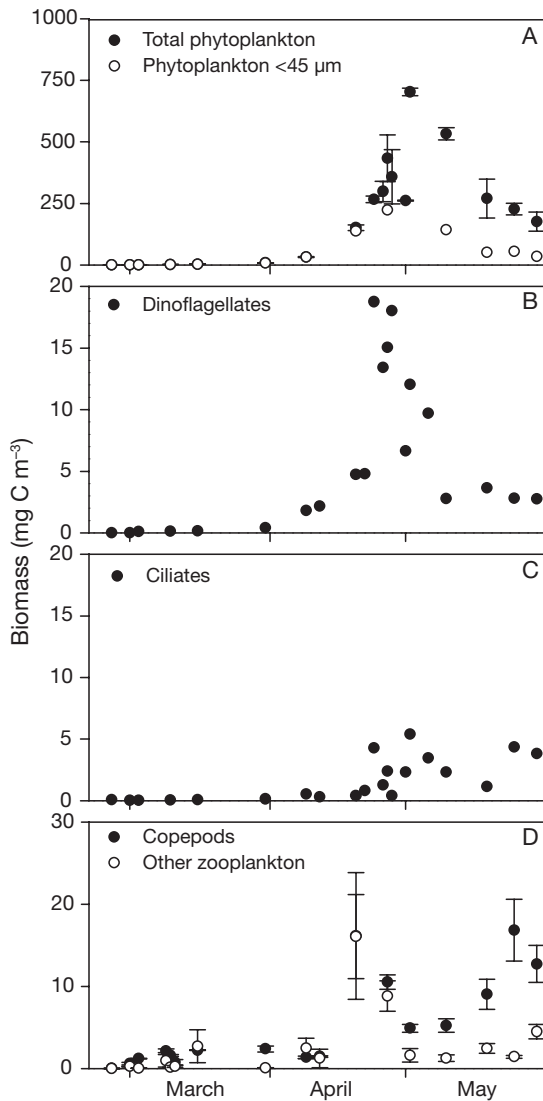


Fig. 3. Biomass of (A) total phytoplankton and phytoplankton <45 μm , (B) dinoflagellates, (C) ciliates, and (D) copepods and other zooplankton. Values are means of measurements (A–C) at 1 and 15 m or (D) in the upper 50 m. Error bars indicate \pm SE

Biomass and depth distribution of the copepod community

Copepods dominated the mesozooplankton and contributed on average $79 \pm 3\%$ to total integrated biomass (0 to 200 m). The biomass included in the group 'other zooplankton' mainly consisted of *Clione limacina* and *Balanus* spp. In the upper 50 m, the proportion of copepods in the zooplankton samples was 36 to 97%, and on average $73 \pm 6\%$ during the investigation (Fig. 3D). The total biomass of copepods and 'other zooplankton' increased gradually from February 25 to April 20 with a maximum biomass of 16 mg C m^{-3} .

Calanus spp. dominated the copepod biomass at all depth strata (Fig. 4), contributing on average $69 \pm 4\%$

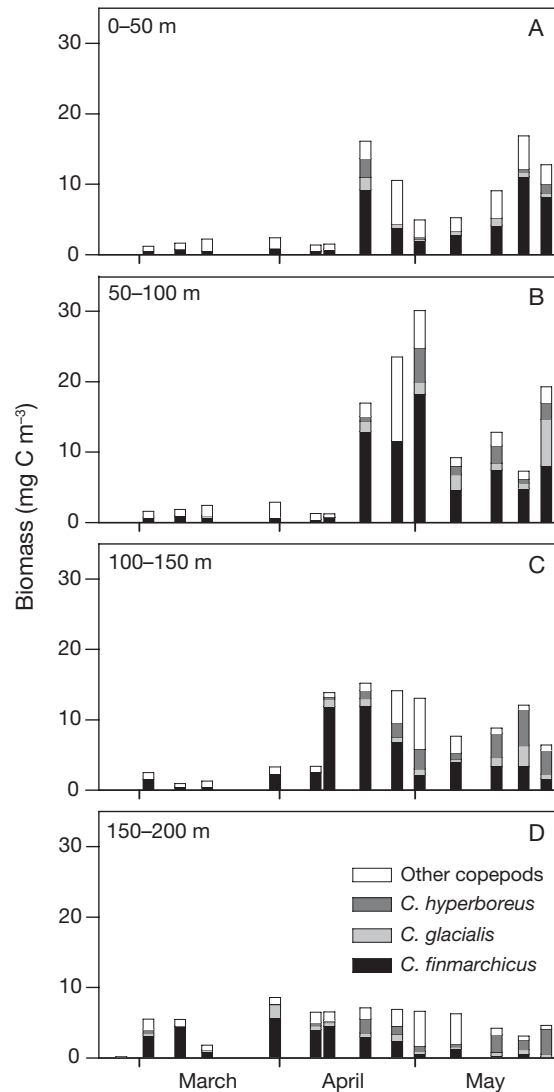


Fig. 4. *Calanus* spp. and other copepods. Vertical distribution and composition of the copepod biomass in 4 depth strata: (A) 0–50 m, (B) 50–100 m, (C) 100–150 m, and (D) 150–200 m

to the integrated copepod biomass (0 to 200 m). *C. finmarchicus* was by far the most abundant species, responsible for on average $75 \pm 4\%$ of the integrated *Calanus* biomass, with the other 25% equally divided between *C. glacialis* and *C. hyperboreus*. The group of 'other copepods' primarily consisted of *Pseudocalanus* sp., *Metridia longa*, and *Oithona similis*. Until mid-April, the biomass of copepods was low and relatively constant at all depths. During April, the copepods gradually migrated towards the surface, and from April 20, the majority of the biomass was located above 100 m, with a maximum biomass of 30 mg C m^{-3} measured at 50 to 100 m depth on May 2.

Calanus finmarchicus and *C. glacialis* arrived simultaneously to the surface layer, where they could be

found in low proportions from the end of February (Fig. 5A,E). Both species exhibited a clear seasonal migration pattern, where a decline in the proportion of copepods in the deeper depth strata was followed by a rise in the proportion of copepods in the overlaying strata. The overall migration patterns for *C. finmarchicus* (Fig. 5A–D) and *C. glacialis* (Fig. 5E–H) were very similar, but with a tendency for *C. glacialis* to be located in deeper strata.

In situ EP rate

Despite simultaneous arrival to the surface layers, the spawning pattern differed significantly between

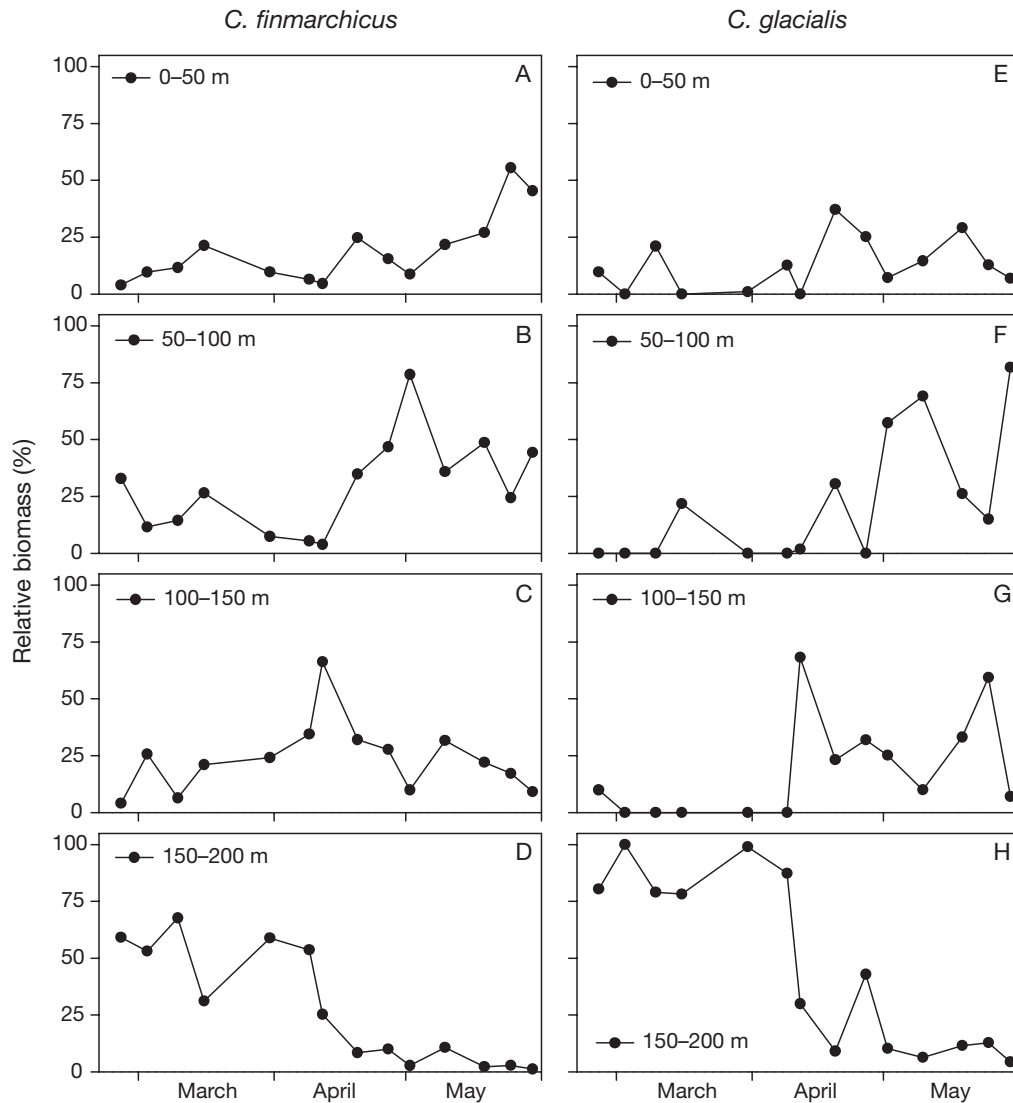


Fig. 5. *Calanus finmarchicus* and *C. glacialis*. Vertical distribution of the relative biomass (% of total biomass) of (A–D) *C. finmarchicus* and (E–H) *C. glacialis* at 4 depth strata

the 2 *Calanus* species. In late April, when EP experiments were initiated, <25% ($20 \pm 4\%$) of *C. finmarchicus* were spawning, and the EP rate was correspondingly low (2.8 ± 0.9 eggs female⁻¹ d⁻¹, Fig. 6B,D). Thereafter the spawning percentage increased and >90% of females were spawning at the beginning of May. However, EP did not peak before May 25 (43.5 ± 6.9 eggs female⁻¹ d⁻¹), when the spring

bloom was decreasing (Fig. 6A,F). Specific EP (SEP) varied between 0.16 ± 0.12 and 8.5 ± 1.5 $\mu\text{g C } \mu\text{g C}^{-1}$ d⁻¹ (Fig. 6E) and clutch size was on average 23.8 ± 2.1 eggs, with the largest clutches found at the end of May (Fig. 6C). In contrast to *C. finmarchicus*, >75% ($80 \pm 10\%$) of *C. glacialis* females were spawning by late April and EP reached a maximum of 48.3 ± 8.3 eggs female⁻¹ d⁻¹ on May 1, simultaneously with the

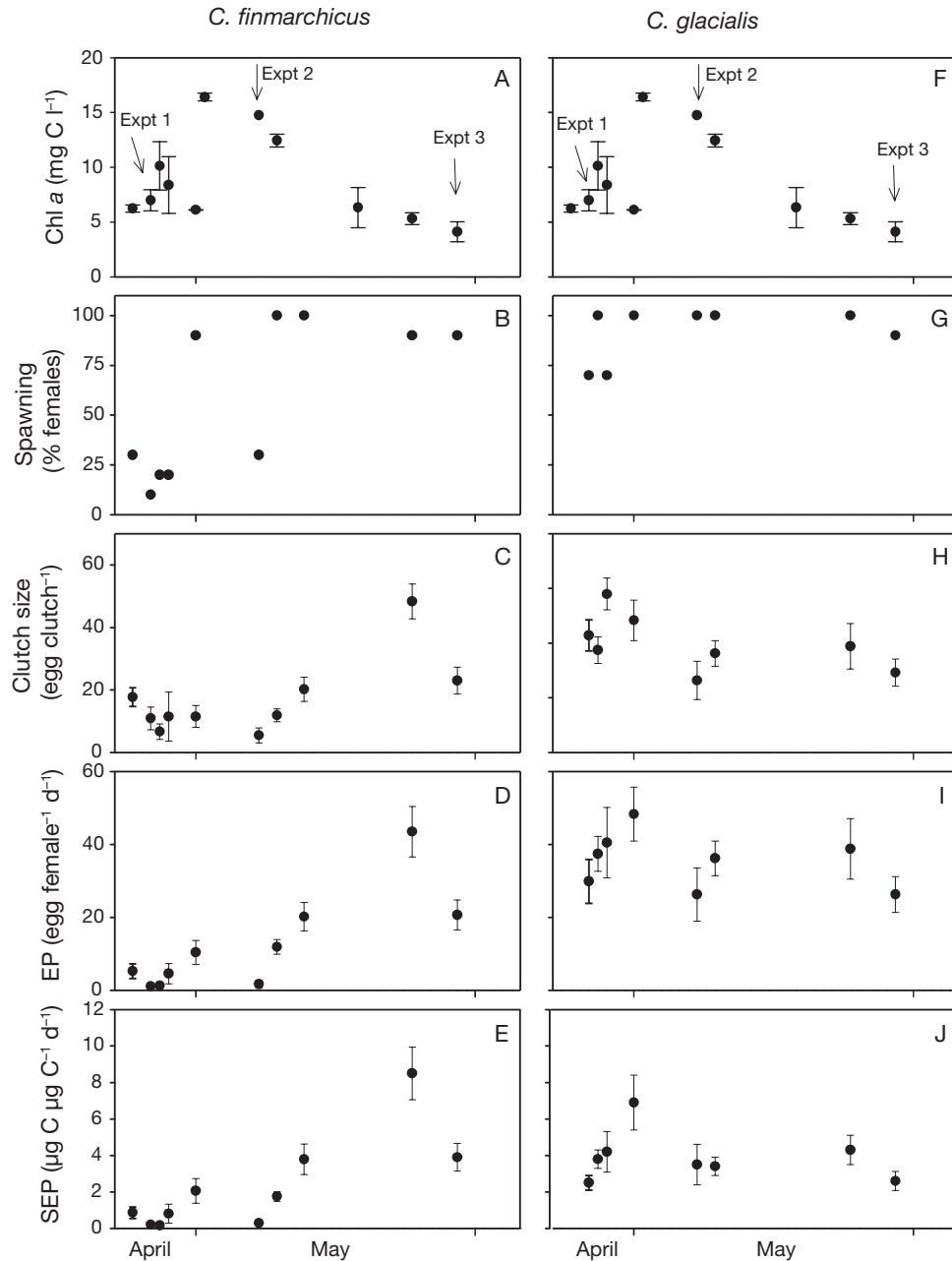


Fig. 6. *Calanus finmarchicus* and *C. glacialis*. Reproduction of (A–D) *C. finmarchicus* and (F–J) *C. glacialis* from April 24 to May 30, 2005 in Disko Bay. (A,F) Mean chlorophyll *a* concentrations at 1 and 15 m; arrows indicate when females were collected for starvation experiments. (B,G) Percentage of actively spawning females; (C,H) clutch size; (D,I) *in situ* egg production (EP); and (E,J) specific egg production (SEP). Values are the means of 10 to 20 females. Error bars indicate \pm SE

peak of the spring bloom (Fig. 6G,I). During May, average EP remained high (31.7 ± 2.9 eggs female⁻¹ d⁻¹) and spawning percentage never dropped below 90% ($98 \pm 2\%$). SEP for *C. glacialis* varied between 2.5 ± 0.5 and 7.0 ± 1.5 $\mu\text{g C } \mu\text{g C}^{-1} \text{d}^{-1}$ (Fig. 6J) and the average clutch size was 38 ± 2 eggs, with the largest clutches recorded from the end of April to the beginning of May (Fig. 6H).

There was no significant correlation between the EP of *Calanus finmarchicus* and *C. glacialis* and the biomass of any of the potential prey organisms, i.e. phytoplankton, protozooplankton, or total protist biomass. A day-by-day comparison of SEP rates between *C. finmarchicus* and *C. glacialis* revealed a significant

difference in the reproductive activity over the season (Mann-Whitney *U*-test $p < 0.05$). *C. glacialis* was found to spawn earlier, with an EP peaking almost a month before that of *C. finmarchicus*.

Laboratory experiments

Expt 1 was initiated April 24 during the early phase of the spring bloom (Fig. 7). During the 10 d incubation, no differences in reproductive activity of *Calanus finmarchicus* females were detectable between the 2 food concentrations (Mann-Whitney *U*-test $p > 0.05$). The spawning percentage for the entire period aver-

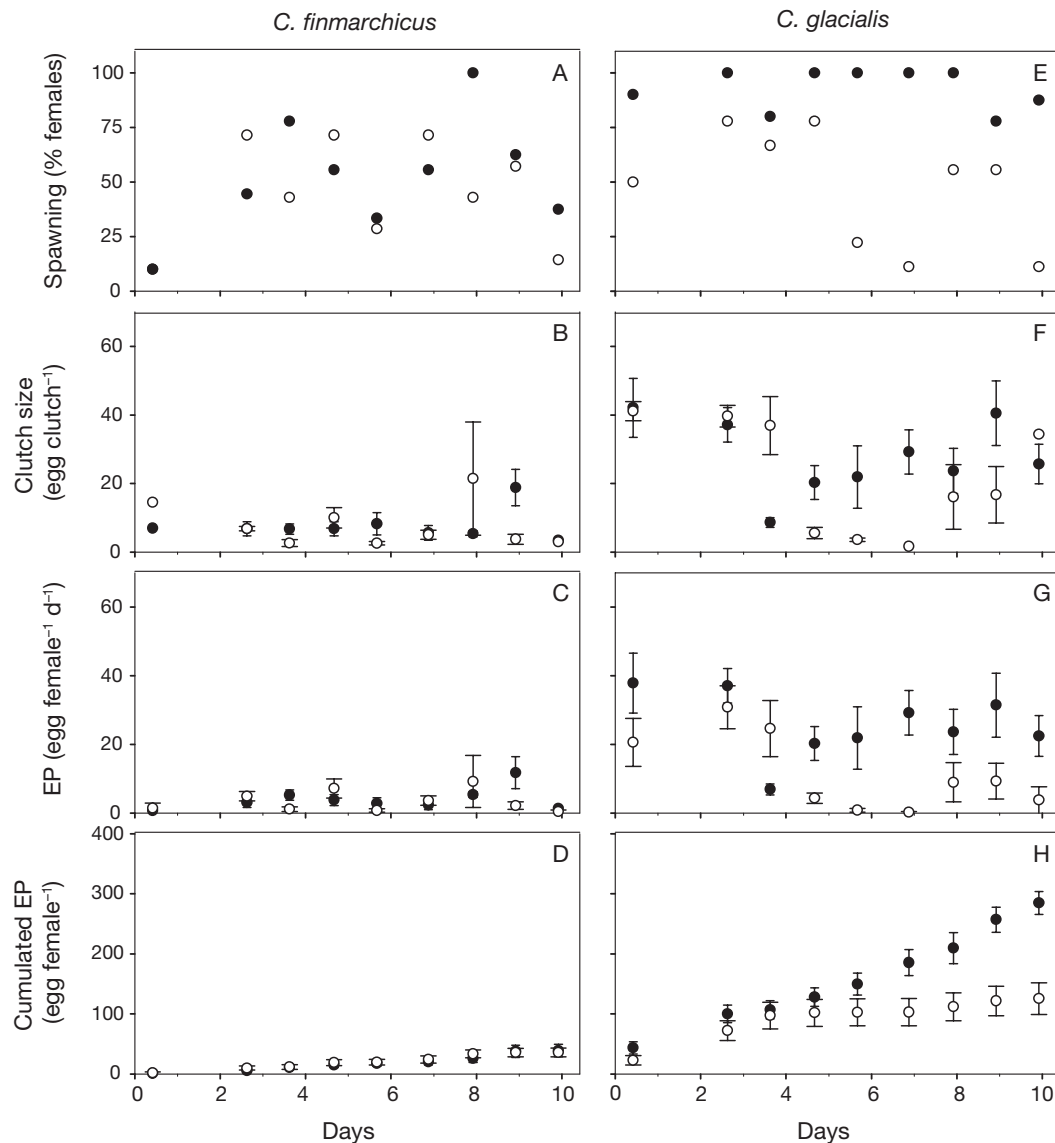


Fig. 7. *Calanus finmarchicus*, and *C. glacialis*. Expt 1. (A,E) Spawning %; (B,F) clutch size; (C,G) egg production (EP); and (D,H) cumulative EP for fed (●) and starved (○) females during 238 h incubation. Values are mean of 10 females. Error bars indicate \pm SE

aged 50% for both fed and starved females (54 ± 9 and $46 \pm 8\%$, respectively, Fig. 7A) and clutch size averaged 7.5 ± 1 and 7.7 ± 1.8 eggs, respectively (Fig. 7B). Rates of EP were 4.0 ± 0.7 for fed females and 3.4 ± 0.9 eggs female⁻¹ d⁻¹ for starved females (Fig. 7C), and cumulative EP after 10 d were 38.9 ± 9.2 and 35.9 ± 6.3 eggs female⁻¹ for fed and starved females, respectively (Fig. 7D).

In contrast to *Calanus finmarchicus*, *C. glacialis* showed a clear decrease in reproduction due to starvation, with a significant difference in EP between fed and starved females after 5 d (Mann-Whitney *U*-test $p < 0.05$). While the spawning percentage of fed females remained constant at $92.3 \pm 3.1\%$ during the entire period, the spawning percentage for starved females averaged $68.1 \pm 6.6\%$ the first 5 d and fell to $31.1 \pm 10.2\%$ thereafter (Fig. 7E). Clutch sizes for fed and starved females were high the first 3 d, averaging 39.5 ± 3.2 and 39.1 ± 3 eggs, respectively (Fig. 7F). Thereafter the clutch size for starved females fell to an average of 17.6 ± 3.6 eggs, whereas for fed females it was averaging 23.9 ± 2.7 eggs. As a consequence of the drastic decrease in the amount of females spawning and clutch size, EP for starved females dropped rapidly from averaging 20.1 ± 3.4 eggs female⁻¹ d⁻¹ after 5 d, to an average of 4.6 ± 1.8 eggs female⁻¹ d⁻¹ (Fig. 7G). In contrast, EP for fed females remained at 25.1 ± 3.3 eggs female⁻¹ d⁻¹. Furthermore, starved females had a cumulative EP after 10 d which was half the size of the fed ones (125 ± 24 and 285 ± 17 eggs, respectively), with differences between fed and starved females becoming significant after 6 d (Mann-Whitney *U*-test $p < 0.05$) (Fig. 7H).

Expt 2 was initiated May 10 during the peak of the spring bloom, when both females of *Calanus finmarchicus* and *C. glacialis* had high EP rates (Fig. 8). Comparison of EP between fed and starved females revealed a significant effect of food concentration after 4 and 5 d for *C. finmarchicus* and *C. glacialis*, respectively (Mann-Whitney *U*-test $p < 0.05$). The proportion of *C. finmarchicus* females spawning was high from the beginning of the experiment, averaging $90 \pm 4.1\%$ for fed females (Fig. 8A). For starved females, spawning percentage declined from 100% after 2 d to 50% after 11 d, averaging $66.3 \pm 6.7\%$. Clutch size averaged 33.5 ± 2.7 for fed and 15.3 ± 1.9 eggs for starved females (Fig. 8B). During the first 4 d, no difference in EP between fed and starved females was observed (Mann-Whitney *U*-test $p > 0.05$). Thereafter the difference became significant as EP for fed females increased to average 33.3 ± 3.3 eggs female⁻¹ d⁻¹ for the remainder of the experiment, while for starved females it averaged 9.3 ± 1.8 eggs female⁻¹ d⁻¹ (Fig. 8C). This resulted in a 3-fold higher cumulative EP after 11 d for fed females (342 ± 26 eggs) than for starved females

(118 ± 40 eggs), with differences becoming significant after 4 d (Mann-Whitney *U*-test $p < 0.05$) (Fig. 8D).

The proportion of fed *Calanus glacialis* females spawning remained approximately constant during the experiment, averaging $94.3 \pm 1.7\%$ (Fig. 8E). Spawning percentage for starved females was high the first 5 d, averaging $92.5 \pm 4.8\%$, after which it dropped to average $44.3 \pm 2.8\%$. Clutch size of fed females was on average 30.4 ± 2.8 eggs, while clutch size for starved females averaged 22.4 ± 3.5 eggs (Fig. 8F). Consequently the rate of EP for fed and starved females was similar the first 5 d, after which it became significantly different (Mann-Whitney *U*-test $p < 0.05$) (Fig. 8G). EP for starved females dropped from an average of 27.0 ± 5.0 to an average of 5.3 ± 1.5 eggs female⁻¹ d⁻¹, while for fed females it remained high, averaging 29.2 ± 2.7 eggs female⁻¹ d⁻¹. Cumulative EP after 11 d was 324.3 ± 40.6 and 154.7 ± 40.3 eggs female⁻¹ for fed and starved females, respectively, with a difference observable after 7 d (Mann-Whitney *U*-test $p < 0.05$) (Fig. 8H).

Expt 3 was initiated on May 30 after the spring bloom (Fig. 9). The data for both *Calanus finmarchicus* and *C. glacialis* showed a decrease in reproduction, with only minor differences between fed and starved females recorded. The proportion of *C. finmarchicus* females spawning varied considerably during the experiment, averaging 87.1 ± 3.4 and $74.3 \pm 5.3\%$ for fed and starved females, respectively (Fig. 9A). Differences in clutch size and EP were small, with a tendency for values for starved females to be lower than for fed females (Fig. 9B,C). Mean clutch size and EP rate for starved females were 14 ± 1.7 eggs and 10.4 ± 1.4 eggs female⁻¹ d⁻¹, respectively, and for fed females were 18 ± 1.3 eggs and 15.7 ± 1.3 eggs female⁻¹ d⁻¹, respectively. That added up to a cumulative EP after 13 d of 210.6 ± 21.8 eggs for fed females and 116.7 ± 13.7 eggs for starved females (Fig. 9D). EP rate between fed and starved females did not differ significantly in this experiment, but by comparing the cumulated EP curves, differences were observed after 8 d (Mann-Whitney *U*-test $p < 0.05$).

The proportion of *Calanus glacialis* females spawning averaged 92.5 ± 3.9 for fed females and $69.3 \pm 6.7\%$ for starved females (Fig. 9E). Also here, differences in clutch size and EP between fed and starved females were found to be small (Fig. 9F,G). Mean clutch size and EP rate for starved females were 14.3 ± 1.8 eggs and 9.8 ± 1.4 eggs female⁻¹ d⁻¹, respectively, and for fed females were 16.6 ± 1.4 egg and 15.3 ± 1.4 eggs female⁻¹ d⁻¹, respectively. That added up to a cumulative EP after 13 d of 194.4 ± 18.5 eggs for fed females and 119.4 ± 14.9 eggs for starved females, with differences between fed and starved females noted only in the cumulative EP curves after 7 d (Mann-Whitney *U*-test $p < 0.05$) (Fig. 9H).

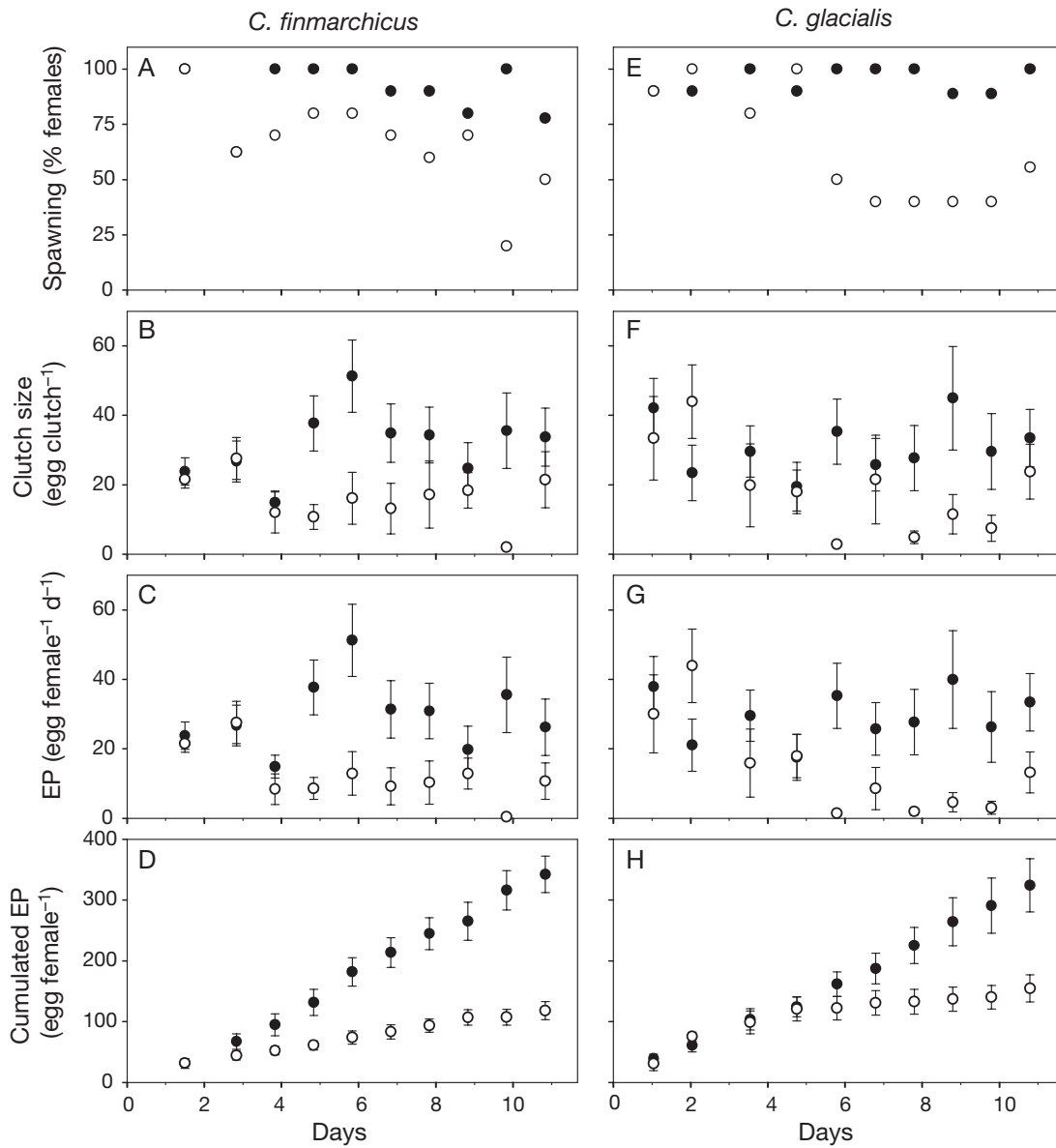


Fig. 8. *Calanus finmarchicus* and *C. glacialis*. Expt 2. (A,E) Spawning %; (B,F), clutch size; (C,G), egg production (EP); and (D,H) cumulative EP for fed (●) and starved (○) females during 260 h incubation. Values are mean of 10 females. Error bars indicate ±SE

Effect of season

The effects of food concentration on EP rate were different between the 3 experiments. The slopes of the cumulative EP curves of copepods of the same species held under the same experimental conditions were compared using a *t*-test. Significant differences ($p < 0.01$ or 0.02) were detected between all curves except between fed *Calanus glacialis* females in Expts 1 and 2, starved *C. glacialis* females in Expts 1 and 2, and starved *C. finmarchicus* females in Expts 2 and 3 (Table 3).

Table 3. *Calanus finmarchicus* and *C. glacialis*. Significance levels for *t*-test comparisons of the slopes of the cumulative egg production (EP) curves. ns: not significant

Cumulative EP	<i>C. finmarchicus</i>		<i>C. glacialis</i>	
	Fed	Starved	Fed	Starved
Expt 1><Expt 2	0.01	0.01	ns	ns
Expt 1><Expt 3	0.01	0.01	0.01	0.02
Expt 2><Expt 3	0.01	ns	0.01	0.01

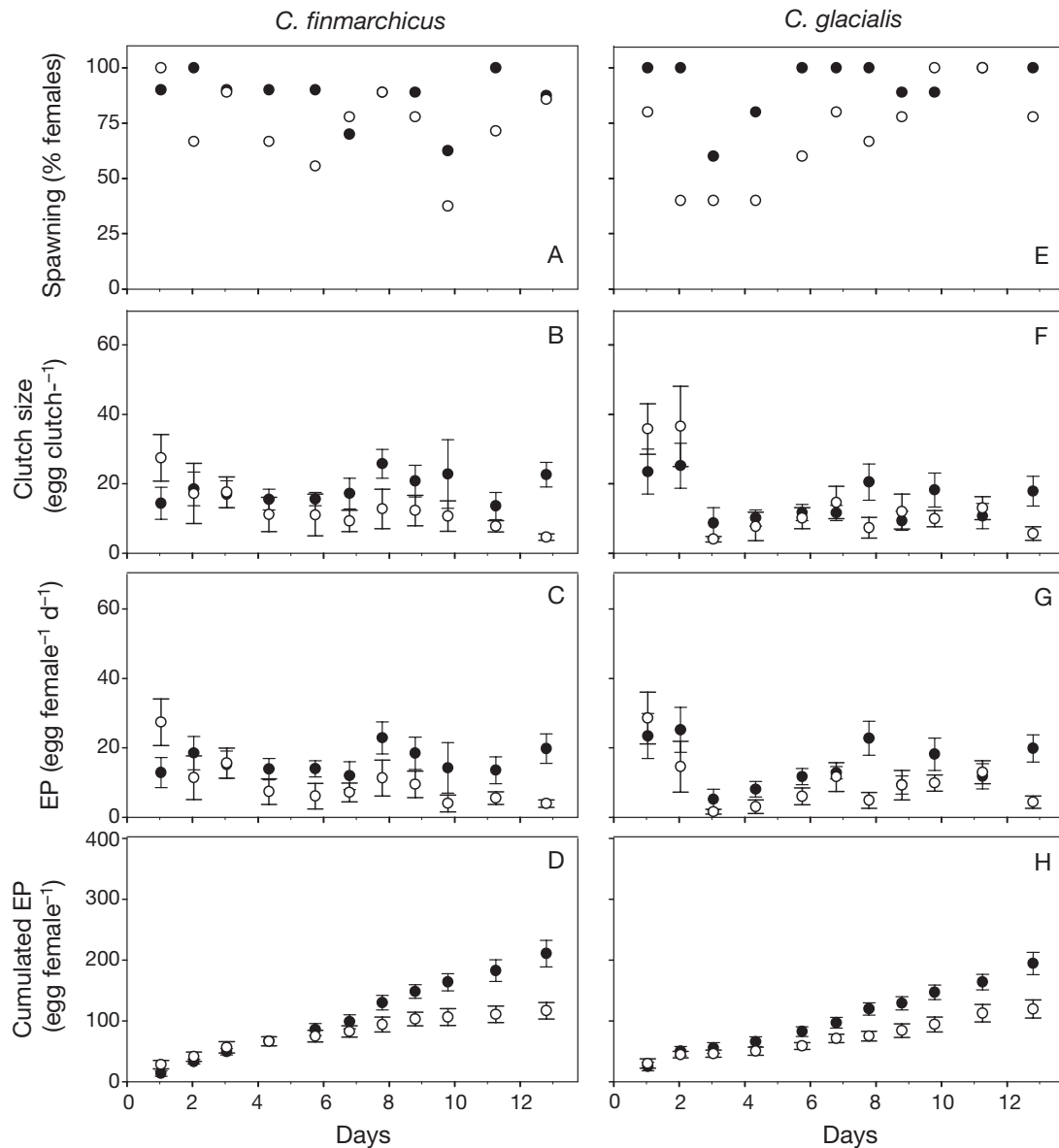


Fig. 9. *Calanus finmarchicus* and *C. glacialis*. Expt 3. (A,E) Spawning %; (B,F), clutch size; (C,G), egg production (EP); and (D,H), cumulative EP for fed (●) and starved (○) females during 307 h incubation. Values are mean of 10 females. Error bars indicate \pm SE

DISCUSSION

The plankton community

The spring bloom is the trigger for the pelagic production cycle and is the single most important event determining the production capacity of arctic marine food webs. The onset of the bloom varies between years depending on the duration of ice cover and the meteorologic conditions. In Disko Bay, the duration of ice cover is highly variable from year to year (Heide-Jørgensen et al. 2007). In 1992, the break-up of sea ice

occurred in mid-May, with the subsequent bloom peaking in late June (Nielsen & Hansen 1995), whereas in 2005 during our study, no stable sea ice was formed and the bloom developed early. During the present investigation, the spring bloom was triggered by a salinity-based stratification in late April, and peaked in early May. Duration of the bloom was around 2 wk, after which nitrate was depleted from the photic zone.

The estimated protozoan biomass was within the range of estimations from earlier years, and maximum biomass was found during the spring bloom (Levinsen

et al. 2000). Top-down control by omnivorous copepods often regulates the protozooplankton community after the spring bloom when phytoplankton biomass is low (Levinsen & Nielsen 2002). During the spring bloom, the copepods are primarily herbivores, as phytoplankton is by far the most abundant food resource (Levinsen et al. 2000).

As previously documented (Nielsen & Hansen 1995, Madsen et al. 2001, Thor et al. 2005), we found that copepods dominated the mesozooplankton, and the copepod community was dominated by *Calanus* spp. In the upper 50 m, the highest biomasses were found during the spring bloom, and were comparable to previous values measured in the area (Madsen et al. 2001). *C. finmarchicus* was by far the most abundant species of *Calanus*, responsible for 75% of the *Calanus* biomass, which differs from previous observations in which the 3 *Calanus* species were found in equal biomasses (Madsen et al. 2001). *C. finmarchicus* and *C. glacialis* exhibited a clear migration pattern and entered the surface layers simultaneously at the end of February, 2 mo before the development of the spring bloom.

The timing of the reproductive cycle in relation to the spring bloom confirmed results of previous investigations of life cycles and reproductive strategies of *Calanus finmarchicus* and *C. glacialis*. (Nielsen & Hansen 1995, Madsen et al. 2001, Niehoff et al. 2002), i.e. *C. glacialis* was observed spawning prior to the spring bloom, with highest EP coinciding with the phytoplankton spring bloom, whereas the EP of *C. finmarchicus* was low prior to the bloom and peaked after termination of the bloom. The highest EP rates were similar or higher than previously measured rates from Disko Bay (Nielsen & Hansen 1995, Madsen et al. 2001, Thor et al. 2005), but still within range of EP rates recorded from other arctic areas (Hirche 1990, Hirche & Kwasniewski 1997, Kosobokova & Hirche 2001).

Effect of food

The 2 *Calanus* species responded differently to the manipulated food concentrations and a clear effect of season on the female's ability to exploit the elevated food concentrations and endure starvation was observed. The copepods from Disko Bay were able to withstand starvation considerably longer than previously reported. Starved *C. finmarchicus* reproduced unaffected for 4 d, twice as long as that found in starvation studies by Hirche (1990) and Hirche et al. (1997) at similar temperatures. *C. glacialis* females were found to withstand starvation for 5 to 6 d before EP was reduced, which was 2 to 3 times longer than previously observed. Other studies conducted at 0°C have re-

corded response times at 2 d (Hirche 1989, Hirche & Kwasniewski 1997, Kosobokova & Hirche 2001, 2003), and experiments with females from Fram Strait have showed a decrease in EP rate after only 24 h of starvation (Hirche & Bohrer 1987). The observed decrease in EP following starvation could mainly be explained by the decrease in clutch size and percentage of females spawning, reported by Niehoff (2000, 2004). Spawning intervals were not measured in the present study, but have previously been shown to be affected negatively by starvation (Hirche et al. 1997). The responses to the manipulated food concentration varied between the 3 experiments according to the *in situ* conditions of the collected females in terms of maturity and feeding history. *C. finmarchicus* collected in the early phase of the spring bloom (Expt 1, Fig. 7) had a very low EP, as was expected from the *in situ* measurements (Fig. 6) and previous studies (Nielsen & Hansen 1995, Madsen et al. 2001), and no effect of food concentration on EP was observed. The lack of response in Expt 1 was probably due to the short feeding history of the females, as the initial gonad maturation seems to be dependent on freshly ingested food and the females consequently were not ripe (Niehoff 2004). Females collected during the peak of the spring bloom (Expt 2, Fig. 8) maintained high EP in the bottles with saturated food concentrations, whereas EP of the females incubated without food decreased to a minimum after 4 d. *C. glacialis* females were reproducing at rates close to maximum, both in the early phase and during spring bloom (Expts 1 and 2), with EP of the starving females decreasing after 5 d. In late May when the last experiment was initiated (Expt 3, Fig. 9), the *in situ* EP rate of both species had dropped to a lower level (Fig. 6). Compared to Expt 2 (Fig. 8), fed females were producing around 40% fewer eggs during the incubation period, whereas the decrease seen in the cumulative EP of the starved females was less obvious. Females of both *C. finmarchicus* and *C. glacialis* maintained unaffected EP for 6 to 8 d during starvation. Comparison of the slopes between the cumulative EP curves revealed that this was not the response to starvation that had changed between the 2 experiments, but rather the precondition of the females to exploit the food. It can be hypothesized that the females had become less sensitive to changes in food conditions because of an ability to recycle part of the established lipid, or that a part of the ingested food was being used to refuel lipid stores in preparation for the coming hibernation period instead of being allocated to EP. Even though the EP rate for fed females during Expt 3 had decreased profoundly, it was still in the range of *in situ* rates obtained by Madsen et al. (2001) in the post-bloom situation.

In conclusion, both species investigated entered the surface layer prior to the development of the spring

bloom and depended on food to maintain maximal EP. Before the spring bloom, *Calanus finmarchicus* was less able to handle an extended period of starvation than was *C. glacialis*, but once the bloom was underway, both species had a similar response to starvation. Females of *C. glacialis* and *C. finmarchicus* from Disko Bay seemed to be capable of enduring considerably longer starvation periods than females collected from other areas before lipid stores were exhausted and an effect on reproductive output was observed. This could be an adaptive response to the highly unpredictable environment of Disko Bay, and a possible explanation of the reproductive success of the Atlantic copepod *C. finmarchicus* in this Arctic area.

The strategy of *Calanus glacialis* to spawn prior to the spring bloom could be an adaptation to the unpredictable food conditions in the arctic environment with oscillating ice cover. In a future warmer climate, the initiation of the spring bloom will be more predictable, as the bloom will develop according to the light cycle rather than the ice break-up. In such a scenario, the advantages of early spawning could change to a burden in the competition with the co-occurring *C. finmarchicus*. Consequently, in a warmer future, the smaller, faster-growing *C. finmarchicus* with a shorter life cycle could have an advantage and take over as the dominating copepod in this Arctic ecosystem.

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