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Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic

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Abstract

The Arctic bloom consists of two distinct categories of primary producers, ice algae growing within and on the underside of the sea ice, and phytoplankton growing in open waters. Long chain omega-3 fatty acids, a subgroup of polyunsaturated fatty acids (PUFAs) produced exclusively by these algae, are essential to all marine organisms for successful reproduction, growth, and development. During an extensive field study in the Arctic shelf seas, we followed the seasonal biomass development of ice algae and phytoplankton and their food quality in terms of their relative PUFA content. The first PUFA-peak occurred in late April during solid ice cover at the onset of the ice algal bloom, and the second PUFA-peak occurred in early July just after the ice break-up at the onset of the phytoplankton bloom. The reproduction and growth of the key Arctic grazer *Calanus glacialis* perfectly coincided with these two bloom events. Females of *C. glacialis* utilized the high-quality ice algal bloom to fuel early maturation and reproduction, whereas the resulting offspring had access to ample high-quality food during the phytoplankton bloom 2 months later. Reduction in sea ice thickness and coverage area will alter the current primary production regime due to earlier ice break-up and onset of the phytoplankton bloom. A potential mismatch between the two primary production peaks of high-quality food and the reproductive cycle of key Arctic grazers may have negative consequences for the entire lipid-driven Arctic marine ecosystem.

Keywords: *Calanus glacialis*, climate change, food quality, ice algae, lipids, mismatch-hypothesis, phytoplankton, PUFAs

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Introduction

Although the dramatic loss of Arctic sea ice during the last decade is indisputable (Smetacek & Nicol, 2005; Stroeve *et al*., 2007; Comiso *et al*., 2008), the consequences of this loss on key biological processes remain largely unknown. Of the studies addressing potential impacts of climate change on polar marine ecosystems, few have focused on the biochemical aspects of trophic interactions (e.g., food quality and transfer) (but see (Falk-Petersen *et al*., 2007; Kaartvedt, 2008).

Sea ice plays a dual role for primary production in polar seas (Smetacek & Nicol, 2005), both providing a habitat for ice algae and regulating the available light for primary production. Ice algae begin growing in low light levels in March and continue growing until their sea ice substratum melts (Hegseth, 1998). In contrast, phytoplankton production starts after the ice break-up, giving a temporal discontinuity between sea ice and open-water production. As the window of opportunity for primary production becomes narrower at higher latitudes, the timing and availability of essential omega-3 fatty acids become increasingly crucial for all marine organisms. The long-chain eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are omega-3 fatty acids produced exclusively by marine algae. These polyunsaturated fatty acids (PUFAs) play a key role in reproduction, growth, and physiology for all organisms in marine ecosystems (Ackman, 1989), as well as for human health (Riediger *et al*., 2009). The importance of omega-3 fatty acids for copepod egg production, egg hatching, and zooplankton growth has been well documented in field (Pond *et al*., 1996; Swadling *et al*., 2000; Jonasdottir *et al*., 2005) and experimental studies (Breteler *et al*., 2005; Jonasdottir *et al*., 2009), and has furthermore been proven to be essential for proper fish development (Watanabe *et al*., 1983).

Among the zooplankton in the arctic shelf seas, the arctic grazer *Calanus glacialis* accounts for up to 80% of the biomass (Tremblay *et al*., 2006; Blachowiak-Samolyk *et al*., 2008; Søreide *et al*., 2008) and plays a key role in the pelagic lipid-based arctic food web (Falk-Petersen *et al*., 1990). *C. glacialis* accumulates essential PUFAs from its algal diet, and converts the low-energy carbohydrates and proteins in algae into high-energy wax ester lipids (Lee *et al*., 2006; Falk-Petersen *et al*., 2009). These lipids make it an extremely energy-rich food

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(>70% lipids of dry weight) for higher trophic levels (Falk-Petersen *et al*., 1990).

C. glacialis has a 1–3 year life cycle, depending on the temperature and food regime. The life-cycle includes six nauplii and six copepodite stages that follow a pronounced seasonal migration pattern. *C. glacialis* develops through the various stages mainly during summer. In autumn, it accumulates lipids before it descends towards the deep and enters a diapause to survive the long and dark food-poor winter. The main overwintering stages are copepodite stage IV (CIV) and V (CV) (Falk-Petersen *et al*., 2009). Overwintering CV individuals develop into females in mid-winter and ascend to surface waters in spring to feed and reproduce (Kosobokova, 1999). The evolutionary success of *C. glacialis* depends on its ability to synchronize its seasonal migration, reproduction, and growth to the primary production regime in Arctic shelf seas (Falk-Petersen *et al*., 2009). As sea ice becomes thinner and has less coverage, the underwater light climate will change significantly (Tremblay *et al*., 2006; Pabi *et al*., 2008). This change will alter the onset, duration, and magnitude of the sea ice algal and phytoplankton blooms. Because the peak growing season for ice algae is confined to consolidated ice, the qualitative and quantitative importance of sea ice algae for the development of key Arctic grazers remain poorly studied.

To predict ecological consequences of climate change on the algal blooms and PUFA production, we carried out an extensive field study during the International Polar Year (IPY, 2007) in the seasonally ice-covered Rijpfjord in northern (>80°N) Svalbard. We followed the seasonal development of ice algae and phytoplankton, including biomass variation and food quality (i.e., the proportion of PUFAs) simultaneously with population development of the key grazer *C. glacialis*. This study aimed at unravelling the intimate coupling between the solar cycle, food quality peaks, and the onset and duration of primary and secondary production.

Materials and methods

Study area

The study was performed in 2007 in Rijpfjorden, Svalbard (Appendix S1) as part of the Norwegian IPY-project CLEOPATRA (Climate effects on planktonic food quality and trophic transfer in Arctic marginal ice zone). Rijpfjorden is a north-facing, relatively shallow fjord (max. 240 m deep) that opens towards the Arctic Ocean. It has a wide opening that is in direct contact with a broad shallow shelf (100–200 m deep), which extends to the shelf-break of the Polar Basin at ~81° N (Appendix S1). Rijpfjorden is dominated by cold Arctic water masses and is covered by sea ice up to 9 months a year (Ambrose *et al*., 2006; Wallace *et al*., 2010). The zooplankton community in Rijpfjorden is dominated by Arctic species, with *C. glacialis* representing up to 90% of the zooplankton biomass (Daase & Eiane, 2007; Blachowiak-Samolyk *et al*., 2008).

Physical data

Temperature, salinity, and *in situ* fluorescence were measured at hourly intervals by a mooring placed in close vicinity of our main sampling station (Stn. SH; Appendix S2). The mooring was equipped with SBE microcats (model: 37-SM MicroCAT; Sea-Bird Electronics, Bellevue, WA, USA) at 27 and 205 m that recorded temperature, conductivity, and pressure. In addition, Vemco temperature mini loggers (Minilog12; accuracy ± 0.1 °C) were located at 3–30 m intervals between 20 and 200 m. At 17 m deep, a Seapoint Chlorophyll Fluorometer (Seapoint Sensors Inc., Exeter, NH, USA) was attached to the mooring. Only approximate chlorophyll *a* data were available from this fluorometer due to absence of suitable water samples for exact calibration, but for identifying the approximate timing of the phytoplankton bloom is was useful. Samples for exact chlorophyll *a* concentrations were collected at lower resolution, monthly from April to August, and in October. The mooring was deployed in September 2006 and recovered in August 2007. For more detailed information about the mooring, see Berge *et al.* (2009) and Wallace *et al.* (2010).

We measured the photosynthetically active radiation (PAR; 400–700 nm) hourly with a PAR LITE Kipp & Zonen Quantum Sensor (Campell Scientific, Edmonton, AB, Canada), mounted 4 m above sea level at the Rijpfjorden field station. Sea ice thickness and snow depth were determined for all sites from which ice cores for ice algae analyses were taken.

Primary producers

Samples of primary producers were collected monthly from March to August and in October (Appendix S2). We took core samples of ice algae using a SIPRE type corer (12.5 cm diameter). For each sampling spot, we took three core replicates (50–100 cm apart). We sawed off the lowest part (5–8 cm) of the core that contained visible amounts of ice algae. This core section was protected against light exposure and immediately transported to the field station. In the field laboratory, we slowly (24–36 h) thawed the cores in the dark in 500 mL of GF/F filtered seawater. After the samples were completely thawed, subsamples were filtered through precombusted GF/F-filters (1 h at 450 °C) to estimate the concentration of chlorophyll *a*, the total particulate carbon (C), and the fatty acid composition of the total lipids. Pelagic algae (phytoplankton) were sampled with a 10 L Niskin-bottle (Ocean Test Equipment Inc., Fort Lauderdale, FL, USA) at six depths between 0 and 50 (80) m (Appendix S2). At each depth, samples were measured in triplicate (0.5–3 L depending on the algae concentrations) and filtered on precombusted GF/F-filters (1 h at 450 °C) to estimate the concentration of chlorophyll *a*, the total particulate C, and the fatty acid composition of the total lipids.

Chlorophyll *a* concentration was determined by high-performance liquid chromatography (HPLC). The pigments were

extracted from the filters with 1.6 mL methanol. The extract was sonicated for 30 s using a Vibra-cell sonicator (Sonics and Materials Inc., Danbury, CT, USA) equipped with a 3 mm diameter probe. The extraction and HPLC analysis continued according to Wright & Jeffrey (1997), using an absorbance diode-array detector (Spectraphysics UV600LP, Newport Corp., Thermo Fisher Scientific, Waltham, MA, USA). The column was a C18 Phenomenex Ultracarb (Torrance, CA, USA) 3 μm ODS (20) (150 × 3.20 mm). The HPLC system was calibrated with pigment standards from DHI, Water and Environment, Denmark.

For particulate C analyses, samples of 20–100 mL for ice algae, and 250–2000 mL for phytoplankton, depending on biomass density, were filtered. All filter samples were frozen (−20 °C) until analysis. Particulate C was analyzed on a Thermo Finnigan FlashEA 1112 elemental analyser (Waltham, MA, USA).

Secondary producers

Zooplankton was sampled monthly by WP2 closing nets with a $0.225\,m^2$ opening, vertically at four standard depths: 0–20, 20–50, 50–100, and 100 m bottom (Appendix S2). To gather data on *Calanus* copepodites and nauplii, we used WP2 nets with mesh size 200 μm. To estimate *Calanus* egg abundance, we used modified WP2 nets with mesh size 63 μm. In August and October, *Calanus* copepodites and nauplii were sampled with a multiple plankton sampler (MPS; Hydro-Bios, Kiel, Germany) consisting of five closing nets with the same opening diameter and mesh size (200 μm) as the WP2 closing net. *Calanus* specimens were identified to the species level based on morphology and prosome lengths of individual copepodite stages (Kwasniewski *et al.*, 2003). Eggs and nauplii were identified to *Calanus* genus level. Although sampling depth ranged from 130 m in July and October to 186 m in September, *Calanus* density (ind. m^{-2}) was calculated for 0–140 m in all months (Appendix S2).

To estimate egg production rates, we incubated females for 24 h at near to *in situ* temperatures, obtained by placing the incubator chambers in a large cooling box filled with sea water and sea ice. Each female was placed alone in a 200 mL chamber with a false bottom of 500 μm mesh. Incubations started within 2–3 h of sampling in prescreened (60 μm mesh size) surface sea water collected from the same site as the females.

Fatty acid analysis

Fatty acids of particulate organic matter (POM) were analyzed at Unilab (Tromsø, Norway), whereas fatty acid and fatty alcohol of *C. glacialis* were analyzed at Alfred-Wegner-Institute (Bremerhaven, Germany).

For POM, triplicate samples of 100–200 mL from each ice core and 0.5 to 3 L from each water depth (Niskin samples) were filtered onto precombusted glass fibre filters (GF/F). The filters were transferred to glass vials with Teflon-lined caps and 8 mL dichloromethane–methanol (2 : 1, v/v) was added. The vials were stored at −80 °C until analyzed. Total lipid was extracted according to the procedure described in Folch *et al.* (1957). A known amount of heneicosanoic acid (21 : 0) was added as internal standard, and an acid-catalysed transesterification was carried out with 1% sulfuric acid in methanol (Christie, 1982). The extract was then cleaned using a silica column (Christie, 1982). The relative composition of the fatty acid methyl esters (FAME) was determined in an Agilent 6890 N (Agilent Technologies Deutschland GmbH & Co. KG, Waldbronn, Germany) gas chromatograph, equipped with a fused silica, wall-coated capillary column (50 m × 0.25 mm i.d., Varian Select FAME, Agilent Technologies Deutschland GmbH & Co. KG) with an oven thermal gradient from an initial 60 to 150 °C at 30 °C min^{-1}, and then to a final temperature of 230 °C at 1.5 °C min^{-1}. Individual components were identified by comparison with two known standards and were quantified using HPChemStation software (Hewlett-Packard, Agilent Technologies Deutschland GmbH & Co. KG).

For *Calanus*, 10–30 individuals were pooled and transferred to glass vials with Teflon-lined caps and 8 mL dichloromethane–methanol (2 : 1, v/v) was added. These vials were stored at −80 °C until analyzed. Specimens from two discrete layers, the surface (0–50 m) and bottom layer (>100 m), were analyzed separately. *Calanus* specimens were homogenized and lipids were extracted according to Folch *et al.* (1957). Methyl esters of fatty acids and free fatty alcohols were prepared by transesterification of the lipid extract with 3% concentrated sulfuric acid in methanol for 4 h at 80 °C under nitrogen atmosphere. FAME and free alcohols were then simultaneously analyzed with a gas liquid chromatograph (HP 6890N, Agilent Technologies Deutschland GmbH & Co. KG) on a 30 m × 0.25 mm i.d. wall-coated open tubular column (film thickness: 0.25 μm; liquid phase: DB-FFAP), equipped with split/splitless injector (250 °C) and flame ionization detector (280 °C) using temperature programming as described above. Fatty acids and fatty alcohols were quantified with an internal 19 : 0 fatty acid standard added to the sample before the extraction. Individual components were identified by comparisons to standards or, if necessary, by additional GC-mass spectrometry runs. The samples were quantified using ChemStation software (Agilent, Agilent Technologies Deutschland GmbH & Co. KG). Total lipid composition was calculated as sum of total fatty acids and fatty alcohols.

All identified PUFAs and omega-3 fatty acids (Appendix S4) were included when calculating the proportions of PUFAs and omega-3 fatty acids in algae and *C. glacialis*.

Statistical analyses

Statistical tests were performed using STATISTICA 7.0 (StatSoft Inc., Tulsa, OK, USA): *t*-tests were used when comparing two independent groups, and one-way ANOVA followed by the *post hoc* tests Tukey's honestly significantly different (HSD) and unequal Tukey's HSD were used when comparing multiple groups with similar or unequal number of replicates per group, respectively (Winer *et al.*, 1991). If the variance between independent groups was unequal (i.e., Levene's *T*-test $P \leq 0.05$), we used the Mann–Whitney *U*-test (MWU-test) and Kruskal–Wallis multiple comparisons of mean ranks for all groups (Siegel & Castellan, 1988). The significance level was set to $P \leq 0.05$ in all tests.

Results

Physical properties: hydrography, sea ice, and light

Rijpfjorden froze solid February 2, 2007 (J. Berge, personal observations). During the ice covered period from

February to end of June there was a cold (−1.8 °C) homogenous water mass from surface to bottom (Fig. 1). The sea ice thickness was on average 0.5 m in March, and around 1 m thick from April to June (mean 0.9 ± 0.1 m). By the end of June, the sea ice started to break up, and on 12 July, the fjord was ice free (J. E. Søreide, personal observations). In Rijpfjorden (80.27°N and 22.29°E), the sun appeared for the first time in late February (22 February) (http://www.esrl.noaa.gov/gmd/grad/solcalc/). The mean daily light intensities increased rapidly the following months (Appendix S3), and the midnight sun appeared from 11 April to 31 August. The 4 months of the long polar night period began when the sun disappeared on 21 October.

Primary producers: ice algae and phytoplankton

Between March and October there were two distinct algal blooms, corresponding to the two peaks in PUFA-production. The earlier PUFA-peak was associated with the ice algal bloom in late April, and the later PUFA-peak corresponded to the phytoplankton bloom just after ice break-up in early July (Figs 1 and 2). Omega-3 fatty acids accounted for most of the PUFAs in both ice algae (65%–74%) and phytoplankton (57%–83%) (Table 1, Appendix S4). Ice algae were present as early as March, but biomass began to build up in April and lasted until June. Similarly high biomass in terms of particulate carbon was found in April and June, but the

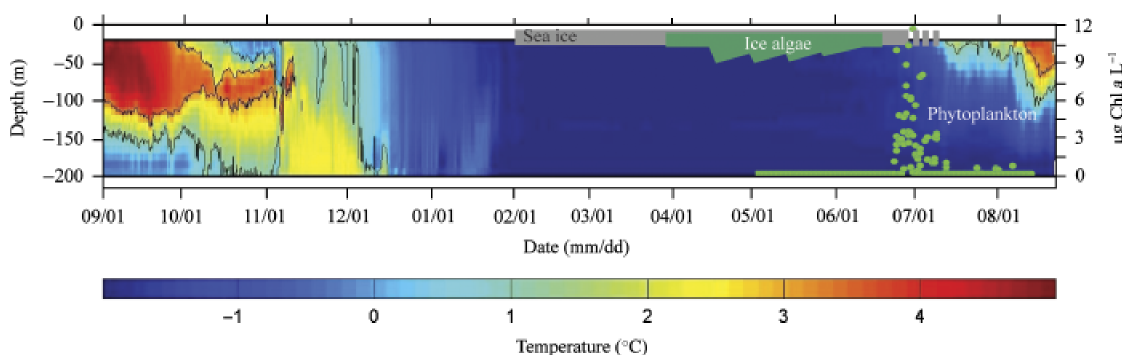

Fig. 1 The temperature profile measured from September 2006 to September 2007 in Rijpfjorden by a mooring equipped with temperature loggers spaced through the water column. Timing of sea ice and ice algae are indicated by drawings at the plot, whereas phytoplankton are chlorophyll *a* (Chl *a*) measurements from a fluorometer placed at the mooring at 17 m depth. Peak biomass of ice algae occurred from mid-April to approx. mid-June. The phytoplankton chlorophyll *a* values are only approximate values due to lack of suitable water samples for proper calibration.

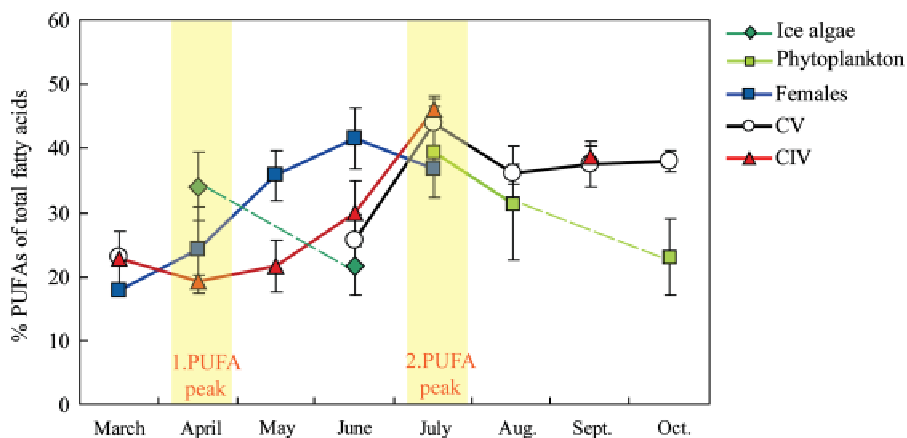

Fig. 2 The relative polyunsaturated fatty acids (PUFA) content (as percentage of total fatty acids; mean ± SD) in algae and females, copepodite stage V (CV) and stage IV (CIV) of *Calanus glacialis* from March to October 2007 in Rijpfjorden. Only ice algae were present from April to June, whereas from July to October only phytoplankton was available for grazers. Hatched lines were drawn when data between monthly points were missing. For algae average values per month are shown, based upon three to five independent station measurements for ice algae (with three replicate ice cores each), and two to four stations with six sampling depths for phytoplankton. For *C. glacialis* average values based upon three to nine samples of 10–30 individuals per sample are shown per month.

Table 1 Integrated (0–50 m) total carbon (C) and chlorophyll *a* (Chl *a*) biomass, and relative amount of polyunsaturated fatty acids (PUFAs) of total lipids and the relative amount of omega-3 fatty acids of total PUFAs (mean ± SD; nd, not determined) in ice- and pelagic-particulate organic matter (POM) in Rijpfjorden 2007

	Total C ($g\,m^{-2}$)	Chl *a* ($mg\,m^{-2}$)	PUFAs/total lipids (%)	Omega-3/PUFAs (%)
Ice-POM				
April	0.2 ± 0.1	22.4 ± 15.3	36.7 ± 1.4	65.0 ± 1.5
June	0.2 ± 0.1	9.2 ± 8.8	22.3 ± 2.8	73.7 ± 2.6
Pelagic-POM				
April	nd	3.5 ± 0.6	14.3	56.5
June	4.4 ± 0.2*	15.9 ± 2.2*	20.2 ± 2.8*	75.9 ± 1.1*
July	21.6 ± 4.8	77.5 ± 30.5	40.3 ± 3.1	83.4 ± 4.1
August	12.7 ± 3.2	12.7 ± 3.2†	32.5 ± 4.5	82.4 ± 2.6
October	9.7 ± 3.1	23.1 ± 9.1	23.9 ± 5.4	80.4 ± 3.1

*Mainly ice algae sloughed off from the bottom ice.
†Approximate values estimated from fluorometer readings.

Table 2 *Calanus glacialis* egg production measurements from Rijpfjorden in 2007

	3–4 March	25–26 April	1–2 May	5–6 June	7–8 June
Number of females incubated	30	29	29	33	30
Incubation temperature (°C)	−1.7	−1.6	−1.5	0	0.5
Prosme length in mm (mean ± SD)	3.3 ± 0.3	3.4 ± 0.3	3.5 ± 0.3	3.5 ± 0.2	3.7 ± 0.4
% Egg laying females	0	27.6	13.8	27.3	63.3
Egg production day^{-1} (mean ± SE)*	0	7.4 ± 2.8	5.7 ± 4.7	14.8 ± 5.2	17.4 ± 3.6
Max egg clutch size day^{-1}	0	16	15	46	59

*Per egg laying female.

ice algal PUFA content decreased from 37% in April to 22% in June (*t*-test, $P = 0.001$) (Table 1, Fig. 2). The phytoplankton biomass was negligible during the ice-covered period from February to June (Fig. 1). The ice break up in June/July was followed by a phytoplankton bloom in early July (Table 1, Fig. 1). The quality of the phytoplankton as food also peaked during this bloom when the phytoplankton contained up to 40% PUFAs (Table 1, Fig. 2). The pelagic POM (P-POM) had a low PUFA content in April (<15%). In June, P-POM consisted primarily of ice algae sloughed off the bottom of the sea ice, so in June, ice algae and P-POM had a similar PUFA content (*t*-test, $P = 0.667$).

Secondary producers: C. glacialis

During April and May, females of *C. glacialis* had a pronounced increase in their relative PUFA content (Fig. 2; Appendix S5a). In contrast, CIV and CV individuals in these months had no significant increases in relative PUFA content (Fig. 2, Appendix S5b and c). *C. glacialis* females produced eggs during the ice algal bloom (Table 2), which mirrored an increase in egg abundance in the net samples from April to June (Fig. 3). We could not estimate egg production after June due to very low female abundance in this period (<1 ind. m^{-3} in the upper 50 m). Similarly, we found very low egg abundance from July to October (Fig. 3). The total lipid content in surface dwelling females dropped in April at the onset of spawning, but remained stable during the spawning period from April to June (Kruskal–Wallis median test, $P = 0.0563$) (Fig. 5). In contrast, the total PUFA content in females slightly increased from March to June (Fig. 5).

The peak abundance of *C. glacialis* nauplii and young copepodites coincided with the pelagic bloom in July, which provided the offspring with excellent food (Figs 3 and 4). Young nauplii stages dominated during the ice-covered period, whereas older feeding nauplii stages (≥ NIII) dominated at the onset of the phytoplankton bloom (Fig. 4b). In July, the youngest copepodite stages (CI–CIII) accounted for most of the population (70%), whereas the overwintering stages CIV and CV dominated from August (Fig. 4a). Females (40%–69%) and CIV individuals (17%–46%) were the most common *C. glacialis* stages from March to June, followed by CIV (17%–46%) (Fig. 4a). *C. glacialis* males were absent from March to September, but started to appear below 100 m depth (0.5 ind. m^{-3}) in October.

By early March, 23% of the female population had already migrated to the upper 50 m (Fig. 5). In contrast, during the same time, only 1% of *C. glacialis* CIV

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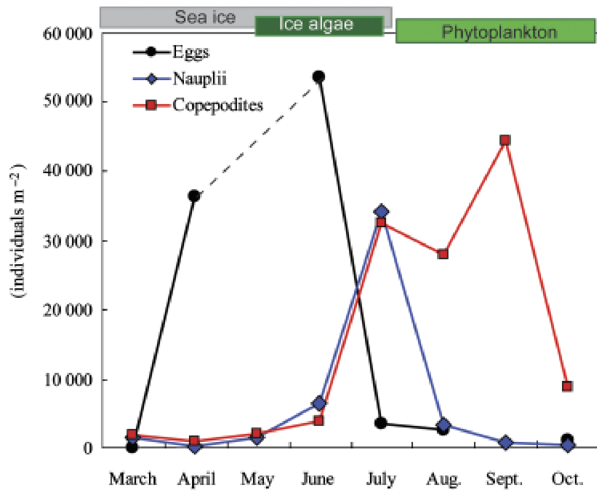

Fig. 3 Seasonal abundances of eggs, nauplii and copepodites of *Calanus glacialis* in Rijpfjorden 2007. Eggs collected with mesh size 63 μm (hatched line from April to June since data from May is missing), whereas nauplii and copepodites were collected with mesh size 200 μm.

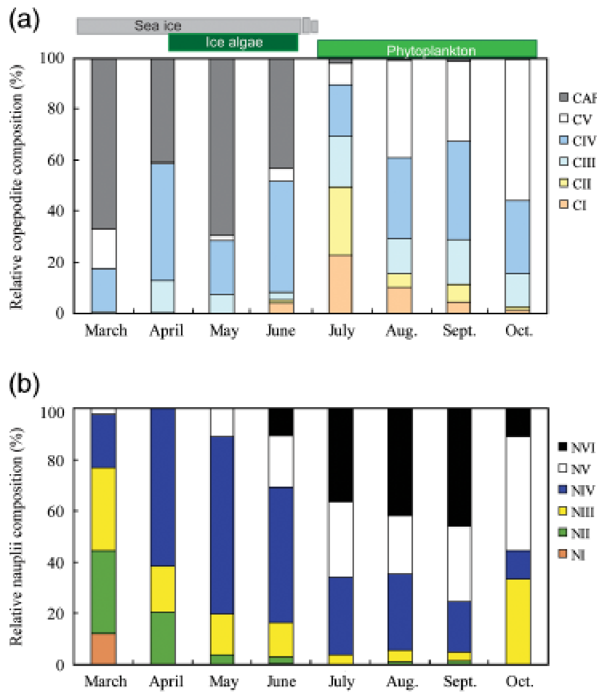

Fig. 4 Relative copepodite (a) and nauplii (b) composition of *Calanus glacialis* from March to October 2007 in Rijpfjorden (CAF; adult females).

individuals were present in surface waters. The seasonal descent started in August (data not shown), and by October, <1.5% of the population remained in the upper 50 m. The copepods that did remain at the

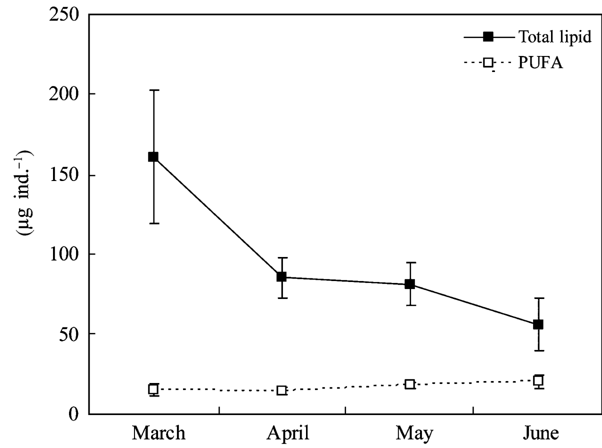

Fig. 5 Total lipids and polyunsaturated fatty acids (PUFAs) in surface dwelling (0–50 m) *Calanus glacialis* females (mean ± SD) from March to June 2007 in Rijpfjorden.

surface in October were almost entirely of young copepodites (CI–CIII). From August to October, CIV and CV specimens in the bottom layer were more lipid-rich than their counterparts in the surface (Fig. 6).

Discussion

Our findings show a close coupling between the solar cycle, onset of ice algae and phytoplankton blooms, and the reproductive success and growth of *C. glacialis* in a high Arctic ecosystem. More specifically, both the timing of the reproduction and the ontogenetic developmental time for *C. glacialis* are synchronized with the two distinct blooms of available high-quality algal food. *C. glacialis* females efficiently use the ice algae bloom as food for maturing and fueling early egg production. The progress of *C. glacialis* development then allows the offspring to take advantage of the second bloom of high-quality food produced by phytoplankton (Fig. 7a). As the Arctic ice cap shrinks and sea ice thins, the ice will break-up earlier in the season, resulting in an earlier onset of the pelagic bloom (Arrigo *et al.*, 2008). However, the overall ice algal growth season will shorten as its onset is limited by light availability, which again is restricted by the low solar angle at high latitudes. Hence the onset of ice algal growth season will not be influenced by a thinner Arctic ice cap, but the end will be shifted forward following the earlier ice break-up. The time lag between the ice-associated and pelagic blooms will therefore shorten, resulting in a potential mismatch between the phytoplankton bloom and the temperature-controlled ontogenetic development of *C. glacialis* (Fig. 7b) (McLaren *et al.*, 1988).

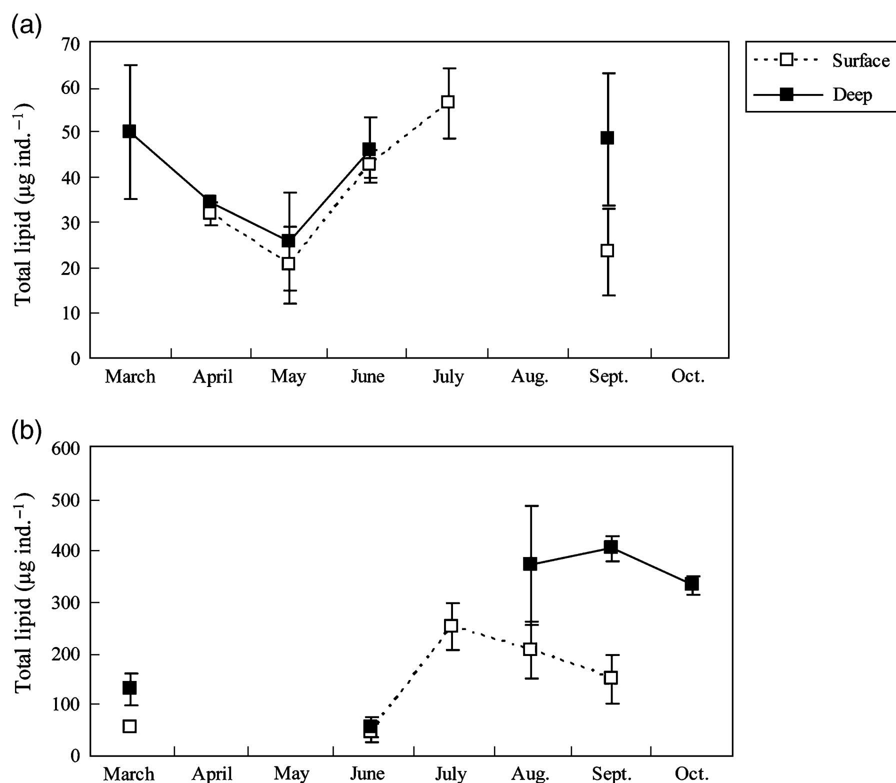

Fig. 6 Total lipid content (mean ± SD) in *Calanus glacialis* copepodite stage IV (CIV, a) and stage V (CV, b) in the upper 50 m (surface) and in the deep (100–140 m) from March to October 2007 in Rijpfjorden.

Female reproduction

The exact effect of food in *C. glacialis* maturation and reproduction remains unclear (Hirche & Bohrer, 1987; Hirche, 1989; Hirche & Kattner, 1993). It has been suggested that early reproduction in *C. glacialis* can be fueled by internal lipid reserves (Hirche & Kattner, 1993), but there is no doubt that food speed up maturation (Tourangeau & Runge, 1991) and increases egg production (Hirche, 1989; Hirche & Kattner, 1993). Females of *C. glacialis* may need up to 4 weeks to mature, dependent on the food accessibility (Tourangeau & Runge, 1991). *C. glacialis* can produce up to 90 eggs per day during bloom conditions (Melle & Skjoldal, 1998), suggesting that we missed the peak egg production period when measuring the egg production rates in late April and June. During prebloom and late bloom conditions, the egg production rates of *C. glacialis* are highly variable (Melle & Skjoldal, 1998) and comparable to the egg production rates we measured in April/May and June, respectively. Based on the prevailing sea water temperatures and the peak nauplii abundance, the peak egg production most likely occurred in late-May in Rijpfjorden 2007. *C. glacialis* needs about 3 weeks to develop to the first nauplii feeding stage (NIII) at temperatures below −1 °C (M. Daase & J. E. Søreide, unpublished results), suggesting that the total time from female maturation and spawning to when the new generation is ready to feed takes about 2 months. This timeline fits our monthly population data from Rijpfjorden and appears optimized for successful *C. glacialis* recruitment and growth, which is reflected in the high population biomass of *C. glacialis* in this fjord (Daase & Eiane, 2007; Blachowiak-Samolyk *et al.*, 2008; Søreide *et al.*, 2008).

Particularly females took advantage of the ice algae bloom of high food quality. During the ice cover from February to June, both the fluorescence measurements and high nutrient levels (E. Leu , J. Wiktor, J.E. Søreide, J. Berge & S. Falk-Petersen, unpublished results) indicated very low phytoplankton biomass and production. Active ice algae grazing in females were supported by a pronounced increase in PUFA content during the ice algal growth season and green guts already in April (field observations, not shown). The difference in female abundance – high during the ice algal bloom and few at the onset of the phytoplankton bloom – further supports the importance of the ice algae bloom for *C. glacialis* reproduction. Gonad maturation is energetically costly (Jonasdottir, 1999; Rey-Rassat *et al.*, 2002;

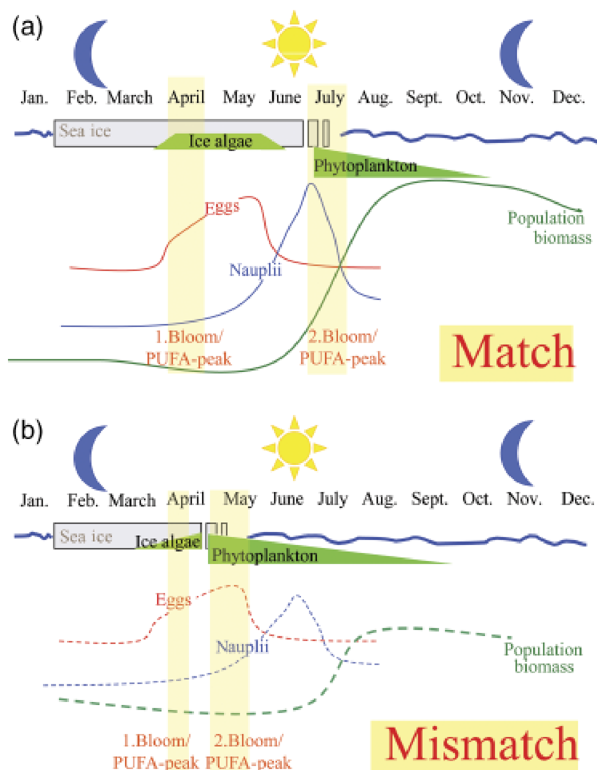

Fig. 7 Current primary production regime in Arctic shelf seas (a) with highest food quality [highest poly unsaturated fatty acid (PUFA) content] during the ice algal and phytoplankton blooms. *Calanus glacialis* efficiently uses the high-quality ice algal food in early spring to fuel reproduction, which allows the offspring (nauplii and copepodites) to fully exploit the high food quality in the later occurring phytoplankton bloom. This perfect primary producer–grazer match ensures high population biomass of *C. glacialis*. Future primary production regime (b) with shorter growth season for ice algae due to earlier ice break up, will lead to shorter time between the two PUFA-peaks associated with the ice algal and phytoplankton blooms. This decrease may lead to a mismatch between primary producers and the ontogenetic development of the offspring. Because *C. glacialis* requires roughly 3 weeks to develop to first feeding nauplii stage (NIII) after spawning, it may partially or totally miss the high-quality phytoplankton bloom during its most critical growth phase.

Lee *et al.*, 2006). *C. glacialis* females can loose up to half of their lipid content during gonad maturation despite access to food (Hirche & Kattner, 1993). After maturation is completed, however, the lipid content stabilizes since egg production is being driven by ingested food (Hirche & Kattner, 1993). Although the lipid content in females from Rijpfjorden decreased and stabilized as descried above, the PUFA content remained constant or slightly increased during gonad development and egg formation (Fig. 5). This maintenance of PUFAs might reflect their role as essential structural units in membranes (Ackman, 1989). *C. glacialis* eggs have high proportions of both EPA (>17%) and DHA (>13%) (Hirche & Kattner, 1993). As such, senescent diatoms with low PUFA content are poor food for copepods, resulting in lower egg production (Mayzaud *et al.*, 1989; Jonasdottir, 1994; Breteler *et al.*, 2005) and lower hatching success (Jonasdottir *et al.*, 2005).

Ontogenetic development

Ice algae provided females high-quality food for early and successful reproduction. In turn, there was also high-quality food during nauplii and early copepodite development. Later in the season, the PUFA content of food may be less important because the overwintering stages CIV and CV that dominated at this time (Fig. 4a) mainly invested food into storage lipids (monounsaturated fatty acids and alcohols) for overwintering (Lee *et al.*, 2006).

C. glacialis needs approximately 2 months to develop from CI to their overwintering stages CIV and CV at temperatures around 3 °C (Corkett *et al.*, 1986). CI individuals started to appear in Rijfjorden in June and July, which corresponded to the dominance of CIV and CV in late August (Fig. 4a) and known sea water temperatures in the upper 50 m from July to August (Fig. 1). The earlier *C. glacialis* reaches its overwintering stage, the earlier it can accumulate lipids and descend to its overwintering depth, reducing the predation risk (Dale *et al.*, 1999; Varpe *et al.*, 2007). In October, CV dominated (55%), followed by CIV (29%), suggesting that *C. glacialis* completes its life cycle in 1–2 years despite the relative extreme environment in Rijpfjorden. In general, the *C. glacialis* life cycle is biennial north of the polar front and annual over the rest of its range (Conover, 1988). However, in Rijpfjorden, *C. glacialis* can take advantage of both ice algae and phytoplankton production and have optimized timing of reproduction and growth in accordance with the two bloom- and PUFA-peaks. This schedule ensured early reproduction and a long growth season for *C. glacialis*, allowing this Arctic population to complete its life cycle within 1 year.

Concluding remarks

C. glacialis elongated its grazing and growth season by efficient use of both the early ice algae and the late phytoplankton as food resources. The effects of a shorter ice algal growth season and a corresponding earlier onset of the phytoplankton bloom on the *C. glacialis* population remains unknown, and further research is required to examine the adaptability of *C. glacialis* under these future scenarios. However, based on this study and an earlier study (Tourangeau & Runge, 1991), we propose that an earlier onset of the pelagic spring

bloom will decrease the time between the two bloom- and PUFA-peaks, since the onset of the ice algal bloom is mainly determined by the solar angle. This decrease may not only have a direct and negative influence on the reproduction, growth, and abundance of *C. glacialis*, but may also potentially affect the entire lipid-driven Arctic marine ecosystem. Many important predators in the Arctic ecosystem such as the little auk (Karnovsky *et al*., 2003; Steen *et al*., 2007) and the bowhead whale (Rogachev *et al*., 2008) depend on the small but very energy rich *C. glacialis* as their main prey.

The current dramatic reduction is sea ice thickness and coverage area may therefore have direct negative impacts on higher trophic levels, such as sea birds and large predators, since lipid-rich key Arctic grazers are likely to be replaced by temperate and less lipid-rich organisms (Falk-Petersen *et al*., 2007; Steen *et al*., 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Rijpfjorden, the study area in north-eastern Svalbard with bathymetry indicated by different colour shadings.
Appendix S2. Samples collected during 2007 in Rijpfjorden. Additional zooplankton samples were collected for lipid, dry weight and egg production measurements of *C. glacialis*.
Appendix S3. Photosynthetically active radiation (400–700 nm) in air measured in Rijpfjorden from February to October 2007. Monthly average values based on hourly measurements.
Appendix S4. The relative polyunsaturated fatty acid (PUFA) composition (mean ± SD) in ice algae and phytoplankton, i.e. Ice- and Pelagic (P)- particulate organic matter (POM), in Rijpfjorden in 2007 (number of stations in brackets). All identified PUFAs are shown. The proportions of PUFA, monounsaturated fatty acids (MUFA) and saturated fatty acids (SAFA) of total lipids are also given.
Appendix S5. The relative polyunsaturated fatty acid (PUFA) composition (means ± SD) in *Calanus glacialis* females (a), *C. glacialis* CV (b) and *C. glacialis* CIV (c) in Rijpfjorden in 2007 (number of samples in brackets). All identified PUFAs are shown. The proportions of PUFA, monounsaturated fatty acids (MUFA) and saturated fatty acids (SAFA) of total fatty acids (FA), and the absolute amounts of FA, fatty alcohols (Falc) and total lipids (TL) are also given. Samples collected in surface (0–50 m) and deep water (>100 m) are pooled which resulted in high variability in absolute values.

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