ARTICLE

Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective

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Abstract: The timing of reproductive events of *Calanus glacialis* is closely coupled to the two major marine primary production events in the Arctic: the ice algal and phytoplankton blooms. Reproductive strategies vary between different physical and biological environments of the European and Canadian Arctic. In the Canadian Beaufort Sea and the high Arctic Rijpfjorden on Svalbard, *C. glacialis* utilized the ice algae bloom to fuel spawning in spring, while growth and development of the new generation was primarily supported by the phytoplankton bloom. In the predominantly ice-free Arctic Kongsfjorden (Svalbard), *C. glacialis* was mainly a capital breeder spawning early in the season in the absence of food. This enabled the offspring to synchronize their growth and development with the phytoplankton bloom and, thus, reproduce successfully despite the lack of an early ice algal bloom. The variability in life history traits observed in the Canadian and European Arctic is compared with data from other Arctic regions to present a pan-Arctic perspective on life cycle strategies of *C. glacialis*.

Résumé : La chronologie des évènements de reproduction de *Calanus glacialis* est étroitement liée à deux évènements majeurs touchant à la production primaire marine dans l'Arctique, soit les proliférations d'algues de glace et de phytoplancton. Les stratégies de reproduction varient selon les milieux physiques et biologiques dans l'Arctique européen et canadien. Dans la mer de Beaufort canadienne et dans la région de Rijpfjorden de Svalbard, dans l'Extrême Arctique européen, *C. glacialis* tire l'énergie nécessaire à son frai printanier de la prolifération d'algues de glace, alors que la croissance et le développement de la nouvelle génération s'appuient principalement sur la prolifération de phytoplancton. Dans la région arctique de Kongsfjorden (Svalbard), exempte de glace en bonne partie, *C. glacialis* est principalement un reproducteur sur capital qui fraye au début de la saison en l'absence de nourriture. Cela permet à sa progéniture de synchroniser sa croissance et son développement avec la prolifération de phytoplancton, ce qui en assure le succès de reproduction malgré l'absence d'une prolifération hâtive d'algues de glace. La variabilité des caractéristiques du cycle biologique observée dans l'Arctique canadien et européen est comparée à des données pour d'autres régions arctiques afin de brosser un portrait pan-arctique des stratégies associées au cycle de vie de *C. glacialis*. [Traduit par la Rédaction]

Introduction

Copepods of the genus *Calanus* are key species in the pelagic ecosystems of the Arctic seas (Jaschnov 1970; Conover 1988; Falk-Petersen et al. 2002). They convert low-energy carbohydrates and proteins from their algae diet into high-energy wax ester lipids (Lee et al. 2006; Falk-Petersen et al. 2009*a*), which makes them extremely lipid-rich (50%–70% lipids of dry mass) and thus important food items for higher trophic levels such as fish, birds, and mammals (Falk-Petersen et al. 1990). Their populations display various life history strategies that reflect adaptations to different environmental conditions (Conover 1988; Falk-Petersen et al. 2009*b*). These varying traits include life cycle length, size and age at maturation (Falk-Petersen et al. 2009*b*), and the degree of lipid-based gonad maturation and egg production (i.e., whether they primarily use stored energy (capital breeders) or are dependent on food (income breeders) for reproduction; Varpe et al. 2009). With a circumpolar distribution, *Calanus glacialis* populations experi-

ence a large range of environmental conditions, and high variability in life history traits are indeed observed along spatial and temporal gradients (Falk-Petersen et al. 2007; Pertsova and Kosobokova 2010; Leu et al. 2011). Much of the distribution area of *C. glacialis* is seasonally ice-covered and harbors two main algal production events: the ice algal bloom, when ice is present, and the later phytoplankton bloom, after the ice break-up (Horner et al. 1992; Legendre et al. 1992; Gosselin et al. 1997; Ji et al. 2013). The relative abundance and timing (including the time lag between the two blooms) of the two production regimes is subject to the prevailing sea conditions (Arrigo and van Dijken 2004; Ji et al. 2013).

Calanus glacialis is not strictly herbivorous (Ohman and Runge 1994; Levinsen et al. 2000*b*; Campbell et al. 2009), but it feeds mainly on microalgae during the spring bloom (Runge & Ingram 1988; Tourangeau and Runge 1991; Juul-Pedersen et al. 2006) and is also able to exploit ice algae at the ice–water interface (Runge &

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Ingram 1988; Tourangeau and Runge 1991; Plourde et al. 2005). *Calanus glacialis* fuels gonad maturation and egg production either solely with internal energy storage before the onset of the spring bloom or by utilizing the ice algal or pelagic blooms to fuel spawning (i.e., dependent on concurrent food intake; Smith 1990; Hirche and Kattner 1993; Kosobokova and Pertsova 2005; Plourde et al. 2005). The two strategies are referred to as capital and income breeding, respectively (Jönsson 1997; Varpe et al. 2009). The phytoplankton bloom is then utilized to fuel growth and development of nauplii and copepodites. This mixed reproductive strategy enables *C. glacialis* to extend the reproductive season beyond the brief periods of high primary production and optimize its growth and development. There are marked fitness consequences related to the ability to schedule annual events such as migrations, growth, and reproduction in relation to the seasonality in food availability and predation (Varpe et al. 2007; Varpe 2012). Specifically, the capacity to time reproduction in a way to match the peak of highest food quality and quantity with the occurrence of those stages that can utilize this food source may be a crucial adaptation that determines if growth and development are successful or not (cf. Cushing 1990).

Here we investigate how variability in the availability of the two prime food sources, the ice algae and the phytoplankton, influences the timing of reproductive events of *C. glacialis*. Because of logistical constraints in the high Arctic, data covering an entire year or even just the entire reproduction period of *C. glacialis* are scarce (Madsen et al. 2001; Søreide et al. 2010) as are data covering more than 1 year at the same location (Pertsova and Kosobokova 2010). We therefore chose to compare key life history traits of *C. glacialis* from Arctic regions displaying different environmental conditions to elucidate what drives the phenology of reproductive events in *C. glacialis* populations and how this species may be affected by environmental changes. The two main regions included in this study, the Canadian Arctic (Amundsen Gulf) and European Arctic (Svalbard) (Fig. 1), differ with regard to ice conditions, hydrography, light, and thus primary production regimes and the relative importance of ice algae versus phytoplankton. We assumed that the *C. glacialis* populations are mixed throughout the Arctic (e.g., Nelson et al. 2009) and that the responses of *C. glacialis* reflect primarily phenotypic plasticity, although we cannot exclude that evolution may have led to specialized local adaptations in resident populations. While we acknowledge that life history traits may also be top-down controlled (e.g., Kaartvedt 2008; Varpe and Fiksen 2010; Berge et al. 2012), we restrict our analysis to bottom-up processes mediated through variability in food availability and the particular role of the two blooms of ice algae and phytoplankton. We focus on plasticity shown in life history traits closely interrelated to food availability such as timing of reproduction (spawning, occurrence of young life stages), timing of seasonal vertical migration, and main overwintering developmental stage. Finally, we compared the variability in timing of reproductive events observed in our data with previously published data on population dynamics of *C. glacialis* from other Arctic regions to present a more extensive picture of the life history of *C. glacialis* in seasonal ice-covered waters. The environmental conditions encountered at one location in a given year may not be representative for that region, since interannual variability and local variation in ice formation and hydrography are large throughout the Arctic. The environmental conditions encountered in the different study areas will, however, illustrate the variety of conditions that *C. glacialis* may inhabit on a local as well as pan-Arctic scale.

Study area

Data on ice algal and phytoplankton production as well as on *C. glacialis* population dynamics were compiled for Rijpfjorden and Kongsfjorden in Svalbard (79°N–80°N) and the Amundsen Gulf and Franklin Bay (69°N–71°N) in the Canadian Arctic (Table 1).

These areas are located north of the Arctic Circle (Fig. 1) and experience pronounced seasonality in incident solar radiation (Table 1). The hydrographic conditions encountered in these areas during the study period are summarized in Table 1.

Svalbard

The archipelago of Svalbard is located in a border area between Atlantic and Arctic climatic (Stroemberg 1989) and biogeographic zones (Narayanaswamy et al. 2010). The main pathway of Atlantic water into the Arctic Ocean (the West Spitsbergen Current, WSC) runs along the western coast of Svalbard, and high interannual variability in the strength of the WSC and the inflow of Atlantic water to the Arctic (Saloranta and Haugan 2001; Walczowski and Piechura 2006) are observed in Svalbard waters, which are often modified by local oceanographic processes (e.g., freshwater run-off, wind-driven circulation, and cooling; Cottier et al. 2005).

Rijpfjorden is a north-facing fjord with a wide opening towards the broad shallow shelf (100–200 m deep), which extends to the shelf-break of the Polar Basin at ~81°N. Rijpfjorden is dominated by cold Arctic water masses, and the inflow of Atlantic water is much less pronounced compared with Kongsfjorden, which is a glacial fjord located on the west coast of Svalbard (79°N). The Kongsfjorden marine ecosystem functions under the balance of influx of Atlantic waters from the WSC and Arctic waters from the coastal current (Hop et al. 2002, 2006; Svendsen et al. 2002), and interannual variations in the inflow of Atlantic water are common (Svendsen et al. 2002; Cottier et al. 2005). In Rijpfjorden, ice formation usually starts in the inner part of the fjord in late autumn (November–December), the fjord is ice covered by January–February, and ice breakup starts in June (Søreide et al. 2010). Kongsfjorden used to be ice-covered in winter as recently as 2005. However, in the period 2006 to 2010 Kongsfjorden did not develop a fast ice cover during winter because of an extensive flooding of warm Atlantic water from the WSC during the winter 2005–2006 (Cottier et al. 2007).
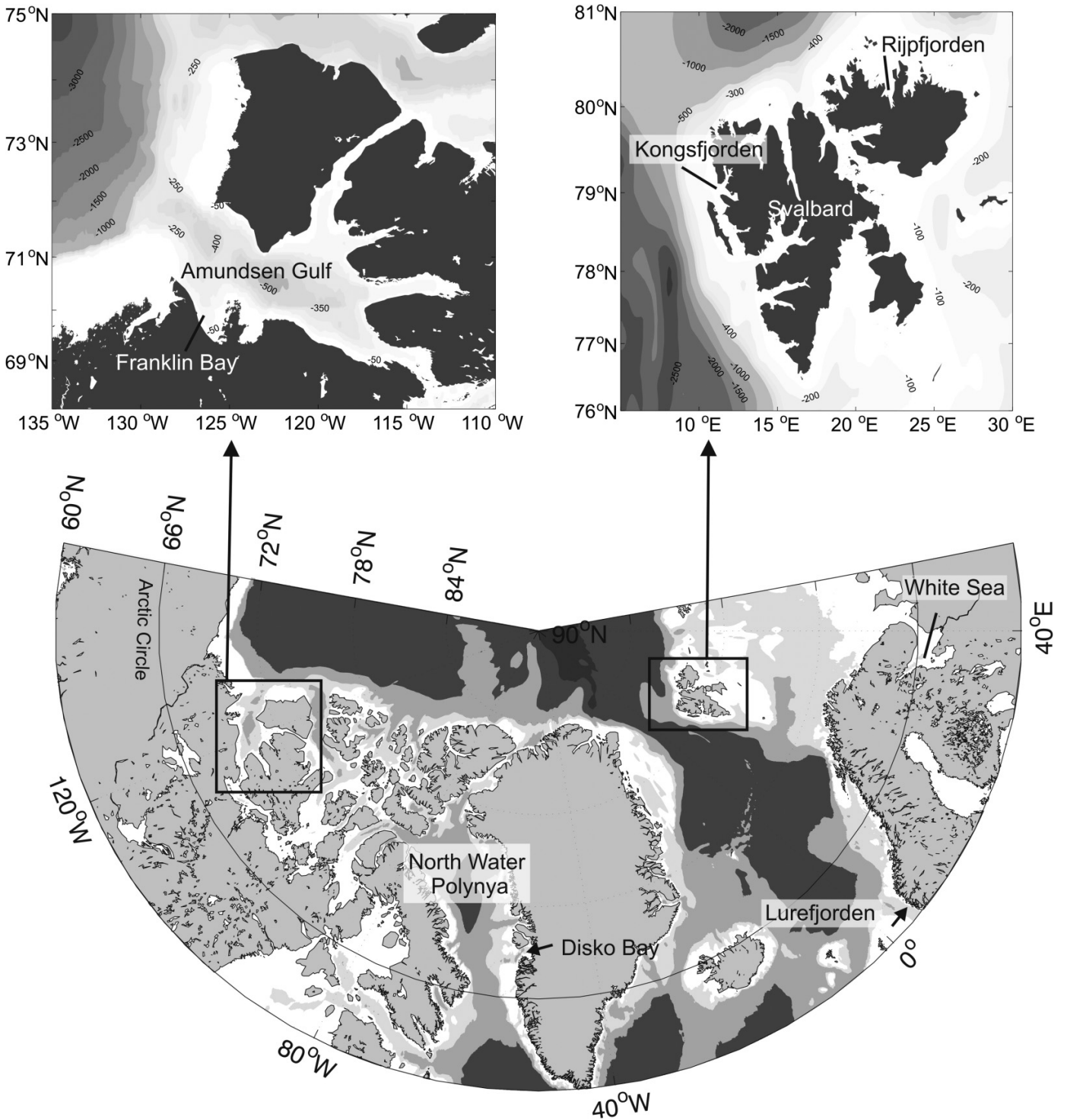
Amundsen Gulf and Franklin Bay

The Amundsen Gulf is located at 71°N, with Franklin Bay being a shallow bay south of the Amundsen Gulf. The Amundsen Gulf bridges the Beaufort Sea to the Canadian Arctic Archipelago. Offshore annual and multiyear sea ice is found beyond the Beaufort Sea shelf-break outside the Amundsen Gulf. The waters of the region typically comprise the Polar Mixed Layer (salinity < 31.6; 0–50 m), the Pacific Halocline (salinity of 32.4–33.1; 50–200 m), and the Atlantic water mass layer (salinity > 34; >200 m) (Carmack and MacDonald 2002). Along the inner shelf region, seasonal sea ice begins to form in October, and ice consolidates over the entire region in December (Galley et al. 2008). Ice breakup occurs between May and August. At the entrance of Amundsen Gulf the circum-arctic flaw lead polynya enlarges to form the Cape Bathurst polynya, which on average opens up in the second week of June (Darnis et al. 2008), but large interannual variability in the extent and persistence of open water regions are observed (Arrigo and van Dijken 2004). During the study period 2007–2008, land-fast ice did not consolidate in the Amundsen Gulf because of atmospheric forcing (ice formation starting 6 weeks later than usual), and the ice cover remained mobile throughout the winter, promoting a more rapid ice breakup in spring approximately 1 month earlier than normal (Barber et al. 2010; Forest et al. 2011b; Tremblay et al. 2011).

Materials and methods

Data from Rijpfjorden, Svalbard, were gathered during the Norwegian International Polar Year (IPY) projects "Climate effects on planktonic food quality and trophic transfer in Arctic Marginal Ice Zones" (CLEOPATRA) and Ice-edge. Field campaigns were carried out on a monthly basis in Rijpfjorden from February to October 2007. These data have been published previously, and zooplank-

Fig. 1. Study area: Amundsen Gulf, Franklin Bay, Kongsfjorden, and Rijpfjorden. Also marked are North Water Polynya, Disko Bay, Lurefjorden, and the White Sea (see Discussion).

ton sampling procedures, ice algal and phytoplankton sampling, and hydrographic conditions are described in detail in Søreide et al. (2010), Leu et al. (2010), and Leu et al. (2011) (see also Table 1).

In Kongsfjorden, zooplankton has been sampled regularly for the past 15 years along standard stations (Norwegian Polar Institute, unpublished data; Kwasniewski et al. 2003), but data on the entire annual cycle of *C. glacialis* are fragmented. Here, we compiled data from 2006 and 2007, when zooplankton were sampled several times over the season (April, May, July, August in 2006 and May, July,

August, October in 2007). *Calanus glacialis* abundance was compiled from three stations in the central part of Kongsfjorden (KB1, KB2, KB3, bottom depth ~300 m). Zooplankton samples were analyzed following procedures described by Kwasniewski et al. (2003) (Table 1). Chlorophyll *a* (Chl *a*) concentration measured in 2006 is based on fluorometrical analysis of filtered seawater samples and is published previously by Seuthe et al. (2011). In 2007, Chl *a* concentrations in the water column were based on weekly fluorescence measurements taken between May and

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Table 1. Overview of available data, sampling procedures, and main physical parameters in the study areas.

	Franklin Bay	Amundsen Gulf	Rijpfjorden	Kongsfjorden	
Program	CASES	CFL	CLEOPATRA	AEM–MOSJ	
Latitude (°N)	70	71	80	79	
Sampling period	Nov. 2003–Sept. 2004	Oct. 2007–July 2008	Mar.–Sept. 2007	Apr.–Sept. 2006	May–Oct. 2007
Max. sample depth (m)	220	600	140	300	
Sampling interval	~Weekly	~Weekly	~Monthly	4 times annually	
No. of stations	1	50	1	3	
Fluorescence from mooring	×	—	×	—	—
Fluorescence CTD casts	—	×	(*)	—	×
Chl *a* ice algae (ice core length)	× (4 cm)	× (3 cm)	× (5–8 cm)	—	—
Chl *a* phytoplankton	—	×	×	×	—
Zooplankton					
Net	MPS	MPS	WP2–MPS	MPS	
Mesh size (μm)	200	200	200	200	
Mouth opening (m²)	0.5	0.5	0.25	0.25	
Egg production rates	×	×	×	—	—
Nauplii abundance	—	×	×	×	×
Polar night	25 Nov.–17 Jan.	20 Nov.–22 Jan.	19 Oct.–23 Feb.	24 Oct.–19 Feb.	
Midnight sun	21 May–24 July	16 May–29 July	16 Apr.–28 Aug.	19 Apr.–25 Aug.	
Avg. winter water temperature (°C)	−1.8 to −1.2	−1.6	−1.8	−1 to +1	
Max. summer water temperature (°C)	0	7–8 (<0 under 50 m)	2–4	3–6	

Note: An asterisk (*) indicates data available but not presented in this study; an × symbol indicates a positive test; a long dash (—) indicates a negative test. Ice core length for ice algae chlorophyll *a* (Chl *a*) refers to the section of the ice core (measured from bottom of sea ice) that was analyzed for ice algae Chl *a* concentration. Abbreviations are as follows: CASES, Canadian Arctic Shelf Exchange Study; CFL, Circumpolar Flaw Lead Study; CLEOPATRA, Climate effects on planktonic food quality and trophic transfer in Arctic Marginal Ice Zones; AEM–MOSJ, Arctic Ecosystem monitoring–Miljøovervakning for Svalbard og Jan Mayen (Environmental monitoring for Svalbard and Jan Mayen); MPS, multiple plankton sampler (Hydrobios, Kiel).

September (Narcy et al. 2009; Table 1). Hydrographic conditions in 2006 and 2007 are described in Cottier et al. (2007) and Willis et al. (2008).

In Svalbard the morphologically similar Atlantic species *Calanus finmarchicus* co-occurs with *C. glacialis*. Most ecological investigations in this region adopt a morphological-based method for discriminating between the two species, and we used size classes derived from length–frequency analyses of prosome length by Kwasniewski et al. (2003) to distinguish between copepodite stages of *C. glacialis* and *C. finmarchicus*. Prosome length of *C. glacialis* may, however, vary interannually at the same location (Kwasniewski et al. 2003), and recently a molecular investigation has revealed a much higher overlap in terms of prosome length than previously assumed (Gabrielsen et al. 2012), documenting a high, but regionally variable, potential for misidentification when based on prosome length alone. However, these misidentifications seem for the most part to be unidirectional, in that errors occur as an underestimation of *C. glacialis* and a comparative overestimation of *C. finmarchicus*. Also, the importance of these misidentifications appears to vary both geographically and among developmental stages (Gabrielsen et al. 2012). For our data from Kongsfjorden and Rijpfjorden, this means that *C. glacialis* may have frequently been misidentified for *C. finmarchicus*, and we may therefore have underestimated the abundance of *C. glacialis* by ~20%. We cannot exclude that our dataset includes *C. finmarchicus*. However, since hardly any individuals of *C. finmarchicus* were found to be misidentified as *C. glacialis* based on prosome length (i.e., *C. finmarchicus* is not larger than suggested by previously established size classes; Gabrielsen et al. 2012), we believe that our dataset consist mainly of *C. glacialis*. Furthermore, since we are mainly interested in the abundance of different stages relative to each other and not the exact numbers, the underestimation of *C. glacialis* abundance by ~20% should not affect the overall interpretation of our data.

Data from the Canadian Arctic were collected within the framework of two large interdisciplinary research projects using the research icebreaker CCGS *Amundsen*: the Canadian Arctic Shelf Exchange Study (CASES) and the International Polar Year – Circumpolar Flaw Lead Study (IPY-CFL). As part of CASES, the ship overwintered in Franklin Bay in 2003–2004 to study the ecosystem throughout the winter. Hydrographic conditions during the study period are described in Forest et al. (2008). Zooplankton sampling was carried out on a weekly basis from November 2003 to June 2004, using vertically resolved net hauls from 220 m depth to the surface (Benoit et al. 2010). Sampling procedures are described in detail in Benoit et al. (2010). Chl *a* concentration of ice algae was measured from the bottom 4 cm of ice cores taken between 27 February and 20 June 2004 as described in Różańska et al. (2009) and Riedel et al. (2008). Chl *a* fluorescence at 30 m depth was recorded from October 2003 to mid-July 2004 by a fluorometer attached on a mooring nearby the overwintering station (Tremblay et al. 2008).

During CFL 2007–2008, the CCGS *Amundsen* was drifting in the Amundsen Gulf (70°N–71°N; Barber et al. 2010). Thus, sample location varied, and we restricted the data to the central Amundsen Gulf as defined as the area between 120°W and 127°W with a bottom depth >250 m (Forest et al. 2011*a*; Wold et al. 2011). Hydrographic conditions during the sampling period are described in detail by Barber et al. (2010). Zooplankton was sampled with vertical resolved net hauls on a weekly to monthly basis from October 2007 to July 2008 (Table 1). Zooplankton sampling procedures are described in detail in Wold et al. (2011), where these data have partly been published. Chl *a* concentration of ice algae was measured from ice cores taken between 16 March and 5 May 2008, as described by Wold et al. (2011). Only Chl *a* data retrieved from the bottom 3 cm of the ice core are presented here. In situ fluorescence was measured with a Rosette-mounted fluorometer from October to early August (Darnis and Fortier 2012). Water column Chl *a* concentration determined from regular water samples collected close to the mooring were used to calibrate the fluorescence signal (Forest et al. 2011*a*).

In Amundsen Gulf and Franklin Bay, the Pacific subarctic species *Calanus marshallae* may co-occur with *C. glacialis*, and because of uncertainties in distinguishing these two species, they are often pooled in a single taxon (Plourde et al. 2005; Hopcroft et al. 2010). We cannot exclude that our dataset from the Amundsen Gulf may include individuals of *C. marshallae*. However, while

C. marshallae prevails south of the Bering Strait, its abundances diminish towards the Chucki Sea and Amundsen Gulf (Frost 1974; Matsuno et al. 2011; Nelson et al. 2009), and the contribution of *C. marshallae* to the *Calanus glacialis–marshallae* population in the Amundsen Gulf region should not bias our interpretation (Nelson et al. 2009).

Calanus nauplii were not identified to species, and nauplii abundance was most likely underestimated at all locations since *Calanus* nauplii are not caught quantitatively with a mesh size of 200 μm. Nauplii abundance estimates should therefore be treated with caution, but the timing of nauplii occurrence is nevertheless shown as an additional indication of when reproduction may have started.

Calanus glacialis biomass was calculated from stage-specific dry masses as described in Daase et al. (2007). Nauplii were not included into biomass calculations.

Results

Rijpfjorden 2007

In 2007 a consolidated ice cover had formed in Rijpfjorden by the beginning of February and lasted until the end of June (Fig. 2*a*). The fjord was ice-free by 12 July. Water temperature remained close to –1.8 °C as long as the fjord was ice-covered. During summer, the surface water warmed up to 2–4 °C (Table 1). Highest ice algae Chl *a* concentrations were observed in late April 2007 (10–48 mg·m⁻²). By the beginning of June the ice algae Chl *a* concentration had decreased to 8–22 mg·m⁻² (Fig. 2*a*). The Chl *a* concentration below the sea ice began to increase in June (mainly washed off ice algae). During the period of ice breakup, a brief peak production period of phytoplankton had already occurred in the beginning of July. Thus there was a 1- to 2-month gap between peak ice algae and peak phytoplankton production in Rijpfjorden. Abundance of *C. glacialis* was low from March to June (~900–3800 individuals·m⁻²), and the population consisted mainly of the overwintering stages CIV and adults. Abundance increased sharply during summer and autumn (27 000–69 500 individuals·m⁻²; Fig. 2*a*). Spawning started at the end of April during the ice algae bloom, and maximum egg production rates were observed in early June (Table 2). Nauplii and young stages (CI and CII) appeared at high abundance first in July when the phytoplankton production peaked (Fig. 2*a*) and were present until September, at which time CIV and CV were the most common copepodite stages, forming the overwintering population (Fig. 2*a*). Most of the *C. glacialis* population was concentrated below 50 m in March (Fig. 3) and had surfaced to the upper 50 m by June. In July, the upper 20 m were avoided, and the population (now mainly young stages) was concentrated in the 20–50 m layer where maximum Chl *a* concentrations were recorded (Fig. 3). In August, part of the population had started to descend, and by September the population was concentrated below 100 m (Fig. 3). Biomass in Rijpfjorden increased from 500–2000 mg dry mass (DM)·m⁻² during spring and early summer to 5000–10 000 mg DM·m⁻² in summer and peaked in September, reaching 21 000 mg DM·m⁻² (Fig. 4).

Kongsfjorden 2006–2007

Sea ice did not form in Kongsfjorden in 2006 and 2007 (Fig. 2*b*). Water temperatures varied from 0–1 °C in winter to up to 3–6 °C in July to September (Table 1). Timing of onset and magnitude of the spring bloom varied between the 2 years in Kongsfjorden. In 2006, the bloom peaked as early as April (10 μg·L⁻¹; Fig. 2*b*), while Chl *a* concentrations were low in May (0.2 μg·L⁻¹), indicating a post-bloom situation. In 2007, a bloom was observed in the first half of May but Chl *a* concentrations were much lower than in 2006 (Fig. 2*b*).

In 2006, the total *C. glacialis* copepodite abundance peaked in late May (~233 100 individuals·m⁻², 31 May) but had decreased sharply by July and August (~18 000 individuals·m⁻²; Fig. 2*b*).

The population consisted mainly of females at the end of April 2006, and a peak of nauplii and CI occurred in May (Fig. 2*b*). In 2007, the total abundance varied little from May to October (20 000–30 000 individuals·m⁻²), and highest nauplii abundance was observed in May during the phytoplankton bloom (Fig. 2*b*). In both years, CI and CII dominated in middle to end of May (Fig. 2*b*). The overwintering population in 2006–2007 probably consisted mainly of CV, since it was the dominant stage in August 2006. There was still a high proportion of CIV in October 2007, and thus, the 2007–2008 overwintering population was most likely composed of CIV and CV (Fig. 2*b*). The *C. glacialis* population was concentrated in the upper 100 m in May (Fig. 3) and in a greater depth in August. In 2007 a deeper distribution signaled that the downward migration to overwintering depth had already started by July. High biomass was observed in Kongsfjorden in April 2006 (7000 mg DM·m⁻²), and it increased slightly over the summer to 11 000 mg DM·m⁻². In 2007, biomass was very low in May (700 mg DM·m⁻²), but a sharp increase was observed over the sample period, and by July and October biomass was as high as in summer 2006 (12 000 mg DM·m⁻²) (Fig. 4).

Franklin Bay 2003–2004

Franklin Bay was covered by first-year land-fast ice from December 2003 to June 2004 (Fig. 2*c*). Ice breakup started at the end of May (Fig. 2*c*). Water temperatures remained below 0 °C throughout the study period (Table 1). Ice algal Chl *a* concentration started to increase in April, forming an ice algal bloom in the third week of May (~30 mg Chl *a*·m⁻²), and biomass declined rapidly in June (0.72 mg Chl *a*·m⁻²). At the same time, water column Chl *a* concentrations (as estimated by fluorescence measurements), which had been low throughout spring, increased sharply as the ice broke up in June and remained relatively high until the beginning of July (Fig. 2*c*). Thus there was a 2- to 3-week time gap between peaks in the ice algal and phytoplankton blooms.
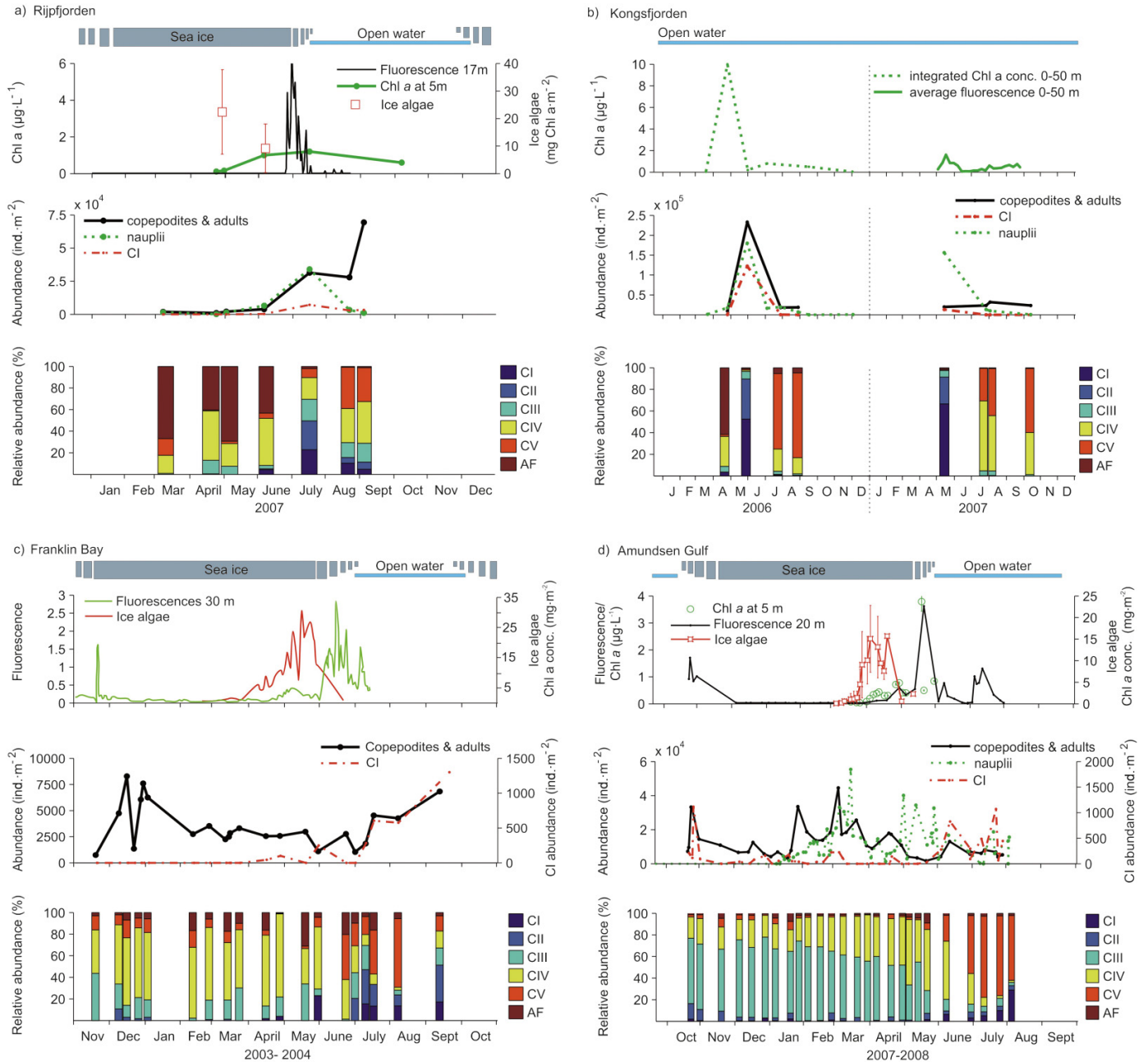
Calanus glacialis abundance in Franklin Bay was variable from November to January (700–8000 individuals·m⁻²). From January to June, a general decrease in *C. glacialis* abundance was observed (minimum 1000 individuals·m⁻² in June), followed by an increase during summer–autumn (6800 individuals·m⁻² in September; Fig. 2*c*). Copepodites CV increased in relative abundance in June. Spawning was first observed in May (Table 2), but a few young copepodites were already observed in April and May, indicating that some spawning occurred earlier in the season. However, high relative abundance of young copepodite stages occurred first in July in Franklin Bay (Fig. 2*c*), and a large part of the population was still composed of CI and CII in September (Fig. 2*c*).

The *C. glacialis* population was concentrated below 50 to 100 m from December to May, and CIV was the dominant overwintering stage (Fig. 3). Abundance in the upper 50 m increased in late May (Fig. 3). Nauplii abundance was not recorded in Franklin Bay in 2003–2004, and biomass of *C. glacialis* varied throughout the study period from 80 to 2000 mg DM·m⁻² (Fig. 4).

Amundsen Gulf 2007–2008

Ice started to form in Amundsen Gulf in October 2007, ice breakup started in the first week of May 2008, and ice concentration was <5% by mid June (Fig. 2*d*; see also Barber et al. 2010; Forest et al. 2011*b*; Tremblay et al. 2011). Water temperatures at the surface remained below 0 °C until early June and increased up to 7–8 °C during summer at the surface (Table 1). No visible ice algae were observed during the first 2 weeks of March in the Amundsen Gulf. Ice algal Chl *a* concentration increased from 0.2–3 mg·m⁻² in mid-March to 10–20 mg·m⁻² by the end of April (Fig. 2*d*) and had sharply declined by the beginning of May. Phytoplankton Chl *a* concentration peaked in mid-May (3.8 mg·m⁻³ at 5 m depth) about 2 weeks after the peak ice algae biomass. Chl *a* estimates derived from the fluorometer attached to the conductivity–temperature–depth rosette indicated a second peak in mid-July (Fig. 2*d*).

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Fig. 2. (*a*) Seasonal development of phytoplankton chlorophyll *a* (Chl *a*) concentration (based on Chl *a* measurements at 5 m and fluorescence measurements at 17 m) and ice algae Chl *a* concentration (mean values, error bars are standard deviations, SD) (upper panel), total abundance of *Calanus glacialis* (copepodites and adults), abundance of *C. glacialis* CI and *Calanus* nauplii (middle panel), and stage composition of *C. glacialis* (lower panel) in Rijpfjorden, Svalbard, in 2007; (*b*) Seasonal development of phytoplankton Chl *a* concentration (based on Chl *a* measurements averaged over upper 50 m in 2006 and average fluorescence in upper 50 m in 2007) (upper panel), total abundance of *C. glacialis* (copepodites and adults), abundance of *C. glacialis* CI and *Calanus* nauplii (middle panel), and stage composition of *C. glacialis* (lower panel) in Kongsfjorden, Svalbard, 2006 and 2007; (*c*) Seasonal development of phytoplankton Chl *a* concentration (estimated from mean fluorescence at 30 m at mooring site CA20, redrawn from Tremblay et al. (2008), arbitrary units) and ice algae Chl *a* concentration (redrawn after Różańska et al. (2009)) (upper panel), total abundance of *C. glacialis* (copepodites and adults) and abundance of *C. glacialis* CI (middle panel), and stage composition of *C. glacialis* in Franklin Bay, 2003–2004 (lower panel); (*d*) Seasonal development of phytoplankton Chl *a* concentration (based on Chl *a* concentration measured at 5 m and fluorescence measurements at 20 m) and ice algae Chl *a* concentration (mean values, error bars are SD) (upper panel), total abundance of *C. glacialis* (copepodites and adults), abundance of *C. glacialis* CI and *Calanus* nauplii (middle panel), and stage composition of *C. glacialis* in Amundsen Gulf, 2007–2008 (lower panel). Timing of ice formation and ice breakup is indicated on top of each subplot. AF, adult females.

Calanus glacialis abundance varied throughout autumn and winter (6000–43 000 individuals·m⁻²). Minimum abundance of *C. glacialis* (850 individuals·m⁻²) was observed in May (Fig. 2*d*). The population increased over the summer (maximum of 13 000

individuals·m⁻² in June; Fig. 2*d*). Until May, CIII and CIV were the dominant stages in all layers. During spring (March–May), the relative abundance of CIV increased, while CV made up a larger part of the population in June–August (Fig. 2*d*). Spawning started

Table 2. Timing of ice algae and phytoplankton blooms as well as life history events and population size and biomass of *C. glacialis* population from different areas across the Arctic.

	Unit	Rijpfjorden	Kongsfjorden	NOW polynya	Barrow Strait	Amundsen Gulf	Franklin Bay	Disko Bay	White Sea	Lurefjorden, Norway
Latitude	°N	81	79	76	76	71	71	69	66	60
Year		2007	2006, 2007	1998	1994–1995	2007–2008	2003–2004	1996–1997, 2005, 2008	1960–2003	1996
Ice melt	Week	26	no ice	20	27–31	19	22	16–17	18–22	No ice
Ice algae Start (week)		—	—	—	—	13	14	17	—	—
Ice algae Peak (week)		18	—	—	—	17	21	16–18	—	13
Phytoplankton bloom Start (week)		23	18	22	25	14	23	14–18	—	13
Phytoplankton bloom Peak (week)		28	17–20	25	27–28	21	24	17–22	19–21	15
Spawning Start (week)		18	—	—	—	15	20	10–15	18–22	10
Spawning Peak (week)		23	—	—	—	18	—	18–22	(18–25)	13
Nauplii Start (week)		22	15	—	—	5	—	13	—	11
Nauplii Peak (week)		28	19–22	—	—	11	—	22–23	—	16
CI Start (week)		24	15	19	27	16	16	20–21	20	—
CI Peak (week)		29	20–24	27	31	27	37	29	24	—
Max. egg production rates	Week	23	—	—	—	19	—	18–20	—	13
Descent	Month	Aug.	July–Aug.	—	—	Nov.–Dec.	Dec.	Aug.	July–Aug.	Feb.
Ascent	Month	Mar.	Mar. (?)	—	—	May	June	Mar.–Apr.	Apr.–May	ND†
Overwintering stage		CIV, CV	CIV, CV	CIV, CV, AF	CIII, CIV	CIII, CIV	CIII, CIV	CIV, CV, AF	CIV, CV, AF (CIII)	—
Population size	Individuals·m⁻²	970–70 000	13 000–270 000	2 000–11 000	500–4 500	850–44 500	740–8 300	3 500–23 000	—	10 000–200 000
Biomass	mg C·m⁻²	300–12 000	400–7 500	—	—	240–2 700	50–1 500	2 000–7 000	—	—
References*		1, 2, 3	1, 4, 5	6	6	1, 7, 8	1, 9, 10, 11	12, 13, 14, 15, 16	17, 18	19

*1, this study; 2, Søreide et al. 2010; 3, Leu et al. 2011; 4, Seuthe et al. 2011; 5, Narcy et al. 2009; 6, Ringuette et al. 2002; 7, Wold et al. 2011; 8, Forest et al. 2011a; 9, Tremblay et al. 2008; 10, Riedel et al. 2008; 11, Różańska et al. 2009; 12, Levinsen et al. 2000a; 13, Madsen et al. 2001; 14, Niehoff et al. 2002; 15, Madsen et al. 2008; 16, Swalethorp et al. 2011; 17, Kosobokova 1999; 18, Pertsova and Kosobokova 2010; 19, Niehoff and Hirche 2005.
†Not determined.

in the second week of April 2008, and maximum egg production rate was observed in early May (Table 2). Young copepodites (CI) appeared in mid-June (Fig. 2*d*), and their abundance peaked in late July shortly after the second peak in phytoplankton bloom. From November to April, the *C. glacialis* population was distributed mainly below 50 m, whereas abundance in the upper 50 m was high from April to May, indicating that the spring ascent took place in this period (Fig. 3). In mid-July, the upper 20 m were devoid of all stages, and young stages (CII–CIII) were abundant between 20 and 50 m depth (Fig. 3). *Calanus* nauplii appeared in January, and a first peak was observed in March. However, these were most likely nauplii of *Calanus hyperboreus*, whose reproductive period lasted until early April (Darnis et al. 2012). Nauplii remained abundant throughout the spring and summer, with peaks observed in May and at the end of June. These peaks in late spring and early summer were most likely nauplii of *C. glacialis*. Biomass of *C. glacialis* varied throughout the study period from 400 to 5000 mg DM·m⁻² (Fig. 4).

Discussion

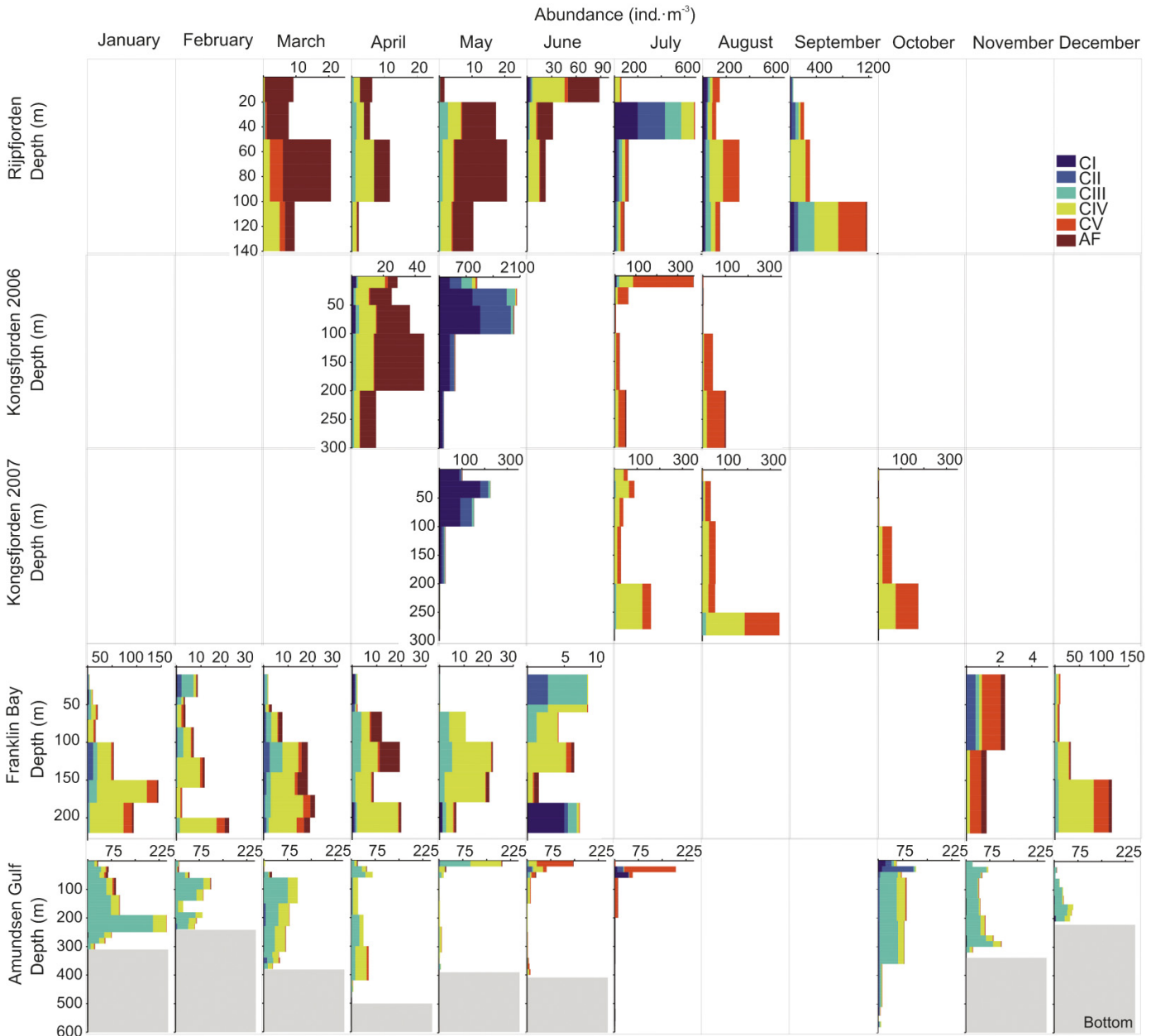### Timing of reproductive events in different environmental settings

Our findings suggest that ice conditions (and incident sunlight) determine the timing of ice algal and phytoplankton blooms and subsequently the timing of life history events of *C. glacialis* (such as egg production and recruitment to first copepodite stage) in different arctic regions (Fig. 5; Table 2). The environmental conditions that *C. glacialis* encounters on a pan-Arctic scale can be distinguished into three main categories: (I) regions with a long-lasting ice cover, primarily Arctic water and two major bloom events that occur with some time lag in between them; (II) open shelf systems with high variability in timing of ice formation and breakup, inflow of warmer water (Pacific or Atlantic), and two bloom events that may overlap; (III) regions with no or limited ice cover, inflow of warmer water (Pacific or Atlantic), and only one major pelagic spring bloom event.

Rijpfjorden is representative of the first type of environment (I, Fig. 5). There, *C. glacialis* adopted the strategy of income breeding by using ice algal bloom in April–May to fuel maturation, egg production, and spawning. The new generation (nauplii and CI) was prominent at the peak in the phytoplankton bloom, ensuring good conditions for growth and development of early stages. The advantage of this strategy in an environment with bimodal food supply is that food-independent developmental phases such as the development from egg to the first feeding nauplii stage III (NIII; Peterson 2001) can occur between the blooms. Thus, both food sources of the rather brief primary production season can be exploited if there is a match in timing between reproduction and ice algae bloom as well as between development to first feeding stage and phytoplankton bloom (Søreide et al. 2010; Varpe 2012).

Although at a lower latitude, Franklin Bay shares similarities with Rijpfjorden, such as a long-lasting ice cover and two major bloom events (Forest et al. 2008). Reproduction and occurrence of young stages of *C. glacialis* followed the same pattern as in Rijpfjorden, indicating that this species used the same strategy to exploit the sequence of bloom events in these two locations. However, the proportion of young stages (CI and CII) was highest later in the season (September) in Franklin Bay. Since development from egg to CI at water temperatures encountered during summer (<0 °C) takes ~46 days (Corkett et al. 1986), considerable reproduction must have taken place at the end of July.

A persistent ice cover and a tight coupling between ice algal bloom and timing of *C. glacialis* reproduction have also been observed in other locations, such as Barrow Strait, the Canadian Arctic archipelago, and subarctic Hudson Bay (Runge et al. 1991; Tourangeau and Runge 1991; Ringuette et al. 2002).
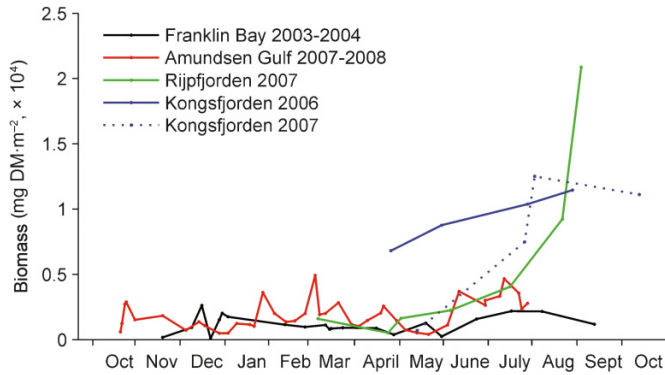
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Fig. 3. Vertical distribution and abundance (individuals·m⁻³) of copepodite stages of *C. glacialis* in Amundsen Gulf, Franklin Bay, Rijpfjorden, and Kongsfjorden from January to December. Note differences in scaling of *x* axis. AF, adult females.

Amundsen Gulf represents an open shelf system where the on-set, distribution, and duration of the seasonal ice cover may be highly variable (II, Fig. 5; Galley et al. 2008). Both an ice algal and a phytoplankton bloom occur, but their peaks may appear closer in time and be more variable in occurrence and distribution because of more dynamic ice conditions (Arrigo and van Dijken 2004). In 2008, spawning, growth, and development in Amundsen Gulf were also closely coupled with the two blooms. However, few *C. glacialis* females were present during the ice algal bloom in early April. At that time the population consisted mainly of CIII and CIV, indicating that the ice algae was more important for the development of CIII–CIV than for reproduction. Wold et al. (2011) and Tremblay et al. (2011) suggested that record low ice cover (NSIDC 2011) and favourable winds for nutrient replenishment provided favourable conditions for a second spawning event late in the productive season of 2007. These additional recruits would most likely not have had time to develop beyond CIII before the

onset of the overwintering period, explaining the high proportion of CIII in the 2007–2008 overwintering population and the surprisingly low numbers of CVs and females in spring 2008. A second reproduction event may also have occurred during summer 2008 in Amundsen Gulf, as the proportion of young stages (CI and CII) was highest relatively late in the season (end of July), suggesting that considerable reproduction must have taken place during the phytoplankton bloom in June. A similar scenario may explain the high numbers of CI and CII later in the season (August–September) as observed in 2004 in Franklin Bay. Wold et al. (2011) propose that *C. glacialis* is able to rapidly develop from CIII and CIV to females during spring and summer under favourable conditions. These females may then be able to spawn late in the season if food is available. Late spawning may be more successful in a system such as the Amundsen Gulf region than in Svalbard; a longer period of incoming solar radiation as well as wind-induced mixing and up-welling events can provide favourable conditions for growth and

Fig. 4. Seasonal variation in total *Calanus glacialis* biomass (mg DM·m⁻²) observed in all four study areas. *Calanus glacialis* biomass was calculated from stage-specific dry masses as described in Daase et al. (2007).
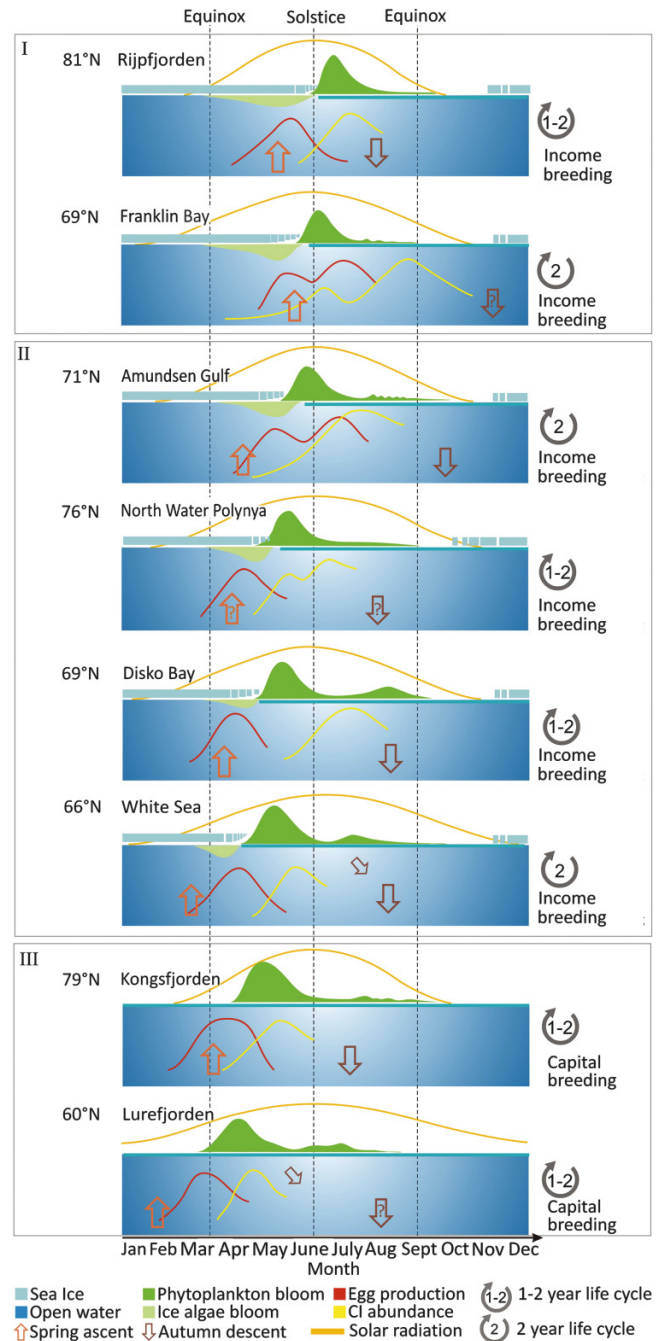

Fig. 5. Conceptual figure showing phenology of *Calanus glacialis* life history events at different locations and latitudes (based on data collected in Table 2). Roman numbers refer to three main types of environmental conditions (see Discussion).

development over a more extensive productive season (although nutrient replenishment of the surface layer is not systematic; Tremblay et al. 2008).

Calanus glacialis may encounter conditions similar to those in Amundsen Gulf in other polynyas, such as the North Water polynya (Ringuette et al. 2002) and the North East Water polynya (Hirche and Kwasniewski 1997), as well as on the European and Siberian shelves (Kosobokova and Hirche 2001) and in Disko Bay on the west coast of Greenland (Madsen et al. 2001) (II, Fig. 5). Differences in timing of recruitment across the North Water polynya could be related to lags in ice melt and onset of phytoplankton between the eastern and western sectors of the polynya (Ringuette et al. 2002). After experiencing early ice melt, the eastern polynya displayed an earlier phytoplankton bloom and recruitment of *C. glacialis*. Disko Bay can be ice-covered from January to April–May, with an ice algal bloom peaking just as the ice breaks up (Madsen et al. 2001), although a consolidated ice cover may also be absent in some years (Swalethorp et al. 2011). Ice algal and phytoplankton blooms occur closely in time (usually in April–May), functioning as one major bloom event. Thus, spawning is probably fueled more by the phytoplankton bloom (Swalethorp et al. 2011), and income breeding is the common strategy (Madsen et al. 2001). Also in Disko Bay, smaller blooms are observed throughout summer (Madsen et al. 2001), supporting growth and development until late in the season. Similar to the Amundsen Gulf in 2008, CIII and CIV can dominate the population prior to the bloom (Madsen et al. 2001; Swalethorp et al. 2011), indicating that part of the population overwinters as CIII and CIV and may develop to CIV and CV next spring.

Another combination of light regime, ice cover, and water temperature can be found in the White Sea, where an isolated relict population of *C. glacialis* exists (Kosobokova 1999). Similar to other Arctic regions, the White Sea is ice-covered during winter and spring. Water temperatures are below zero, and an ice algal bloom occurs here in addition to the phytoplankton bloom, which starts as soon as the ice breaks up. However, being on the Arctic Circle, the productive season starts much earlier here than further north. Kosobokova (1999) concluded that reproduction of *C. glacialis* was food-dependent in the White Sea, with eggs and nauplii peaking during the phytoplankton bloom. Growth and development of *C. glacialis* are also found to depend on water temperature during the growth season (Pertsova and Kosobokova 2010). Cold years defined by late ice breakup and low water temperatures can delay the appearance of the new generation by 3–4 weeks. Contrary to other Arctic regimes, water temperatures during summer often reach up to 15–25 °C in the White Sea, forcing *C. glacialis* to terminate reproduction and migrate to deeper waters

(Kosobokova 1999). In both cold and warm years, the growth season in the White Sea ended in July with the occurrence of CIV.

Despite being one of the northernmost locations included in this study, Kongsfjorden exhibits the least "Arctic-like" conditions. Sea ice does not consolidate every year or is completely lacking, relatively warm Atlantic water intrudes, and only one major bloom occurs in spring (III, Fig. 5). Our data show that a successful development and high recruitment of *C. glacialis* is possible in a high Arctic environment lacking an ice algal bloom. Unfortunately, no data on the onset of spawning and egg production rates are available for Kongsfjorden. However, young copepodites (CI) were present from late April to late May. Assuming

that development from egg to CI takes about 46 days at 0 °C (Corkett et al. 1986), spawning would have started in mid-March and peaked in April. Since the spring bloom in both years did not occur before mid-April, at least part of the *C. glacialis* population in Kongsfjorden had opted for reproduction without additional food supply (i.e., following the strategy of a capital breeder). This is in agreement with observations made in Kongsfjorden in spring 2003 and 2004 (Kwasniewski et al. 2013). Females were abundant in April 2006, while peak abundance of CI coincided with that of nauplii (Fig. 2b), indicating that the main reproductive period probably stretched over a time window of approximately 1 month, coinciding at least partly with the spring bloom.

Interestingly, this high number of recruits in spring 2006 could not be sustained until the end of summer, when abundance and biomass of *C. glacialis* in 2006 equaled those observed in 2007 (Fig. 4). Water mass exchange between Kongsfjorden and the shelf is common, however, during summer, and variability in *Calanus* abundance may be affected by advection (Cottier et al. 2005; Willis et al. 2006).

An ice-free regime such as Kongsfjorden seems to favour a capital breeding strategy. Similar observations have been made in Lurefjorden, an enclosed fjord on the west coast of Norway located at 60°N. Here a relict population of *C. glacialis* dominates the *Calanus* assemblage (Eiane et al. 1999; Niehoff and Hirche 2005). The fjord is not ice-covered during winter, and gonad maturation and egg production were found to be decoupled from the phytoplankton bloom (Niehoff and Hirche 2005). Conditions in Kongsfjorden and Lurefjorden may be indicative of the kind of environment *C. glacialis* could encounter in the future in areas where ice conditions will become severely reduced and water temperatures increase.

Since warmer water and lack of ice prolong the productive season in ice-free areas, a possible explanation for the capital breeding observed in Kongsfjorden and Lurefjorden is that *C. glacialis* takes advantage of long feeding seasons by storing resources that are used for breeding next spring. In such systems, one should expect interannual variability in the degree of capital breeding depending on the duration of the feeding season the year before. Feeding late in the season would be particularly advantageous if the predation risk is low at this time of the year (Varpe et al. 2009). However, capital breeding cannot be seen as an adaptation to a longer productive season. For one reason, this study showed that the population in Amundsen Gulf, where the productive season can last long into the autumn, uses an income breeder rather than capital breeder strategy. Furthermore, the arctic *C. hyperboreus*, which occurs in the central Arctic Ocean where primary production is low, is almost exclusively a capital breeder (Conover and Siferd 1993; Hirche and Niehoff 1996). However, the Atlantic *C. finmarchicus*, which occurs in area with a long primary productive season, is mainly an income breeder (Richardson et al. 1999).

For *C. glacialis*, the main difference between populations in ice-free and ice-covered areas is the lack of an ice algae bloom and thus the lack of a bimodal food distribution. Most likely, different annual routines may maximize fitness in these two cases (cf. Varpe 2012). The capital breeding strategy allows eggs to be produced independently of concurrent food intake and therefore potentially prior to the spring bloom. For situations with a pelagic bloom only, the offspring can develop through the food-independent development stages before the spring bloom starts and then utilize the bloom production. Model predictions suggest this to be the optimal strategy when the feeding season is early (Varpe et al. 2009). A head start on reproduction and development in spring also allows the overwintering stage to be reached early. Descent to diapause may therefore also take place early. In an area with ice algae blooms, the females may, through income breeding, produce offspring while feeding on ice algae, whereas the offspring utilize the pelagic bloom (Søreide et al. 2010). Indeed,

the pelagic bloom as well as the population development of *C. glacialis* in Kongsfjorden occurred 1–2 months ahead of that in Rijpfjorden. By the time young stages appeared in Rijpfjorden in July, the development in Kongsfjorden had already reached its final stage, and the descent to overwintering depths had started. In Rijpfjorden, the bulk of the population had descended to deeper layers first in September. Early descent to overwintering depths, prior to the end of the phytoplankton bloom, may increase fitness because it might reduce the predation risk (Kaartvedt 2000; Varpe et al. 2007) or exposure to unfavourable abiotic conditions (i.e., high temperature in Lurefjorden; Niehoff and Hirche 2005). Despite the differences in annual routines in Kongsfjorden and Rijpfjorden, both populations managed to build up a high amount of biomass by the end of the productive season (Fig. 4), indicating that the respective strategies are both successful.

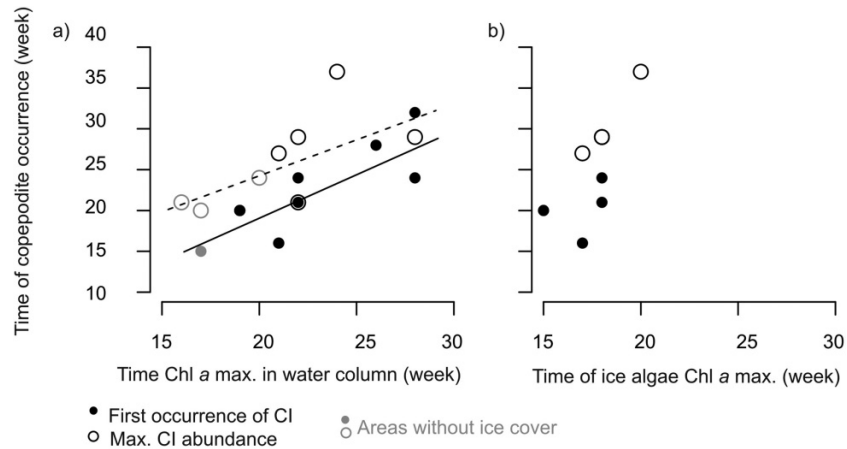### Life span and seasonal migration

While *C. glacialis* is capable of developing from eggs to wax ester-rich copepodite stages III and IV within a single year (Scott et al. 2000), the increase in body mass and lipid reserves during development from CIV to CV is only achieved in a single year under favourable conditions, and often a second year is necessary. Most studies therefore concluded that *C. glacialis* has a 1- to 2-year life cycle (Tande et al. 1985; Conover 1988; Kosobokova 1999; Fig. 5). Despite the differences in environmental settings and reproductive strategies in Rijpfjorden and Kongsfjorden, we did not find any evidence of differences in life span between these fjords. In both fjords, CIV and CV were found to be the main overwintering stages, supporting the assumption that *C. glacialis* is able to fulfil its life cycle in 1–2 years.

The high amount of CIII and CIV in the overwintering population of the Amundsen Gulf would indicate a 2-year life cycle. However, as discussed above, we suggest that overwintering CIII and CIV may develop into females during spring and summer under favourable conditions. By reproducing later in the season, these females would shorten the life cycle to 1 year. Nevertheless, late offspring bear the risk of running out of time to develop to a stage suitable for diapause (Varpe et al. 2007). In such cases, it may be beneficial for members of the parent generation to rather follow a 2-year life cycle, with the possibility of early and even capital breeding in their second year (Varpe et al. 2009).

Owing to lack of data from late summer and early autumn, it is difficult to estimate the time of descent in Amundsen Gulf and Franklin Bay. At both locations, young copepodites were abundant quite late in the summer. These copepodites would most likely need time to graze in surface waters to accumulate enough energy for overwintering. Data from October to December indicate that the bulk of the population reached greater depth as late as December (Fig. 3). Over the course of the production season, a variable vertical distribution of *C. glacialis* may be explained by the gradual deepening of the subsurface chlorophyll maximum in Amundsen Gulf (16 m in late April to 56 m in early August; Forest et al. 2011a) and Franklin Bay (Tremblay et al. 2008). This feature may have led to the deepening of the distribution of *C. glacialis* and not only the migration to depth of a fraction of the population ready to overwinter. Martin et al. (2010) found that diatoms contributed 10 times more in the subsurface chlorophyll maximum in the lower euphotic zone, and cells were larger (cells >20 μm) than in the upper mixed layer of Canadian Arctic waters in late summer. Thus, food seems to be still available to *C. glacialis* in late summer, but distributed deeper in the water column.

Favourable conditions early in the season do not guarantee a shorter life cycle if conditions become detrimental later in the season. In the White Sea, high water temperatures in the upper layers force *C. glacialis* to migrate to greater depth early in the summer (Kosobokova 1999; Pertsova and Kosobokova 2010), so despite favourable spring conditions such as an early onset of ice

Fig. 6. (*a*) Relationship between week of highest chlorophyll *a* (Chl *a*) concentration in the water column and week of first appearance of CI of *Calanus glacialis* and week of maximum CI abundance. Dotted line shows regression line of week of Chl *a* maximum versus week of maximum CI abundance ($R^2 = 0.36$, $p < 0.1$). Solid line shows regression line of week of Chl *a* versus week of first occurrence of CI ($R^2 = 0.6$, $p < 0.01$). Grey points depict data from areas without ice cover. Regression excluding these points: $R^2 = -0.19$, $p > 0.5$ (Chl *a* maximum versus maximum CI) and $R^2 = 0.56$, $p < 0.05$ (Chl *a* maximum versus first occurring CI). (*b*) Relationship between week of highest ice algae Chl *a* concentration and week of first appearance of CI of *C. glacialis* and week of maximum CI abundance (see Table 3 for details).

algal and spring bloom and a long productive season, *C. glacialis* has a 2-year life cycle in the White Sea.

Our data provided little insight into the interaction between life span and reproductive strategies. One unknown factor is the amount of energy actually needed for overwintering. How much lipids need to be stored before the descent, and how do energy reserves during diapause vary between populations and locations? If small lipid reserves are sufficient, and ice algae fuel reproduction, a late descent and thus a shorter life cycle may be beneficial. If large lipid reserves are needed, it may be worth postponing breeding to breed early in the second year, especially when capital breeding is beneficial (Varpe et al. 2009). These aspects of the life history may be state-dependent, with those individuals that have accumulated enough lipids benefitting from an early ascent, while those that still profit from continued feeding (late recruits) may remain in the surface layers until late in the season (Jónasdóttir 1999; Miller et al. 2000; Pond and Tarling 2011). This suggests that these strategies need to be investigated on an individual basis (i.e., Vogedes et al. 2010).

The phenology of *C. glacialis* in a changing Arctic

Søreide et al. (2010) suggested that variability in ice cover might lead to mismatch between the timing of ice algal and phytoplankton blooms and timing of reproduction and development, since the development from egg to the first feeding nauplius stage (NIII) of *C. glacialis* takes about 2 weeks (Daase et al. 2011). The offspring can therefore exploit the second bloom more efficiently if it does not follow the first one too closely. An early ice breakup may abbreviate the ice algal bloom period, and also the gap between ice algal and phytoplankton blooms, and hence lead to poorer growth condition for the *C. glacialis* population.

Ringuette et al. (2002) found a close relationship between the timing of the phytoplankton bloom and recruitment of *C. glacialis* CI. We expanded the dataset used by Ringuette et al. (2002) with data from the present study and from Disko Bay (Fig. 6; Table 3) and analyzed the relationship between the week of peak phytoplankton and ice algae bloom and week of first occurrence of CI and week of maximum CI abundance (Fig. 6). We used "time of first occurrence of CI" as a proxy for the start of reproduction. The variable "time of maximum CI abundance" provides an estimate for the time of peak reproduction activity. In both cases we assume mortality of young to be independent of time of the season. There was a positive relationship between the week of peak phy-

toplankton bloom and week of both first occurrence of CI and maximum CI abundance (linear regression $R^2 = 0.36$, $p < 0.1$ and $R^2 = 0.67$, $p < 0.01$, respectively; Fig. 6a). The relationship was also positive for week of first occurrence of CI after removing data points from locations without ice cover ($R^2 = 0.56$, $p < 0.05$). There was also a positive relationship between weeks of highest ice algal production and maximum CI abundance (Fig. 6b). These relationships imply that an earlier onset of the spring bloom (e.g., due to reduced ice cover) may lead to an earlier start of reproduction in *C. glacialis*, confirming the observations made by Ringuette et al. (2002). However, these results should be treated with caution as they are based on only a few data points, in particular the relationship with the timing of the ice algae bloom. The results illustrate the gap in data that needs to be addressed to make formal analyses of the relationships between timing of food availability and reproduction. Studies with high temporal resolution within seasons are needed to increase the precision of the estimates included in this kind of analyses.

Amundsen Gulf in 2008 represents a scenario where ice breakup and ice algal bloom occurred earlier than normal. Still, the tight coupling between the occurrence of eggs, nauplii, and early copepodite stages with ice algal and phytoplankton blooms indicates that reproduction did not fail for the population. However, the biomass in autumn was much lower in Amundsen Gulf than in Rijpfjorden (Fig. 4), where the estimated biomass is among the highest observed on a pan-Arctic scale (Table 2). Søreide et al. (2010) argue that in 2007 in Rijpfjorden the occurrences of ice algal and phytoplankton blooms and *C. glacialis* reproduction were perfectly timed. So one could argue that the recruitment in an "early-ice-break-up" scenario may not be as successful as in a "well-timed" scenario, which is in agreement with multiyear observations from Rijpfjorden (Leu et al. 2011). Kongsfjorden would be representative of an ice-free scenario, and as discussed above, *C. glacialis* can thrive under these conditions. The absence of an ice algal bloom seems to be compensated by applying a capital breeding strategy and thus timing the growth and development of recruits to the phytoplankton bloom.

In summary, *C. glacialis* populations subjected to various environmental conditions across the Arctic showed variability in the timing of reproductive events. Our study suggests that the seasonality of the environment and hence the timing of primary production are key drivers of this variability. The degree of capital versus

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Table 3. Overview of timing of ice algae and phytoplankton bloom and timing of CI recruitment in different Arctic regions.

Location	Year	Latitude (°N)	Ice-covered	Week of max. ice algae Chl *a* concentration	Week of max. Chl *a* concentration in water column	Week of first occurrence of CI	Week of peak CI abundance	Reference
Northern Iceland	1993	67	No		16		21	Gislason and Astthorsson 1998
Disko Bay	1996	69	Yes	18	22	21	29	Madsen et al. 2001
Disko Bay	1997	69	Yes	15	19	20		Madsen et al. 2001
Franklin Bay	2004	71	Yes	20	28	(*)	37	This study
Amundsen Gulf	2008	71	Yes	17	20	16	27	This study
Barrow Strait	1994	74	Yes		26	28		Ringuette et al. 2002
Barrow Strait	1995	74	Yes		28	>32		Ringuette et al. 2002
Barents Sea	1987	75	Yes		22		21	Melle and Skjodal 1998
Eastern North Water	1998	77	Yes (Polynya)		19	20		Ringuette et al. 2002
Western North Water	1998	77	Yes (Polynya)		22	24		Ringuette et al. 2002
Kongsfjorden	2006	79	No		17	15	20	This study
Kongsfjorden	2007	79	No		19		24	This study
Rijpfjorden	2007	81	Yes	18	28	24	29	This study

Note: Relationship between timing of bloom and CI recruitment is shown in Fig. 6. The asterisk (*) indicates that time of first occurrence of CI in Franklin Bay is not included because CI were present throughout the winter.

income breeding was found to vary with the feeding environment. Populations that have access to an ice algae bloom prior to the phytoplankton bloom seem to favour an income breeding strategy, perhaps with some capital breeding in parallel with the ice algae feeding, while those living in an open water system, with only one major bloom event, start reproduction prior to the onset of this bloom. The variability observed suggests that *C. glacialis* has a flexible reproductive strategy that may explain its wide distribution in Arctic continental shelf seas.

How much energy is actually needed for overwintering and reproduction, what triggers ascent and descent, and how does the male part of the population develop throughout the season are some of the questions that need to be addressed in future studies to better understand life history adaptations of *C. glacialis* to different environmental conditions and the eventual impact of climate change on this key species.

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