

# Seasonal changes in nauplii and adults of *Calanus hyperboreus* (Copepoda) captured in sediment traps, Amundsen Gulf, Canadian Arctic

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## Abstract

Arctic copepods were collected using time-series sediment traps in the Amundsen Gulf, Canadian Arctic, as part of the CASES (Canadian Arctic Shelf Exchange Study) program. Four sediment traps were deployed at three stations (200 m depth for CA15, 200 and 400 m depths for CA18, and 200 m depth for CA20) from October 2003 to July 2004. We collected many copepod nauplii ranging in body length from 155 to 811  $\mu\text{m}$ , among which nauplii (mostly N1–2) of *Calanus* with a size of  $\sim 190 \mu\text{m}$  apparently increased in abundance from February to mid-March. Mature-stage adult females (AF) of *Calanus hyperboreus* were collected in the traps from February to March, and adult males of *C. hyperboreus* appeared from November to December at all stations. The likely spawning period of these AF coincided with the occurrence period of  $\sim 190 \mu\text{m}$ -sized nauplii. This finding suggests that these nauplii were derived from *C. hyperboreus* and that their breeding began at the beginning of November or December at the latest, continuing through April in the Amundsen Gulf.

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## 1. Introduction

The planktonic copepod *Calanus hyperboreus* is a key species in the Arctic pelagic ecosystem because of its large abundance and body size (e.g., Grice, 1962). Its main distribution area is the subarctic–Arctic seas, from where it spreads south into the

Norwegian Sea and Gulf of Maine (Conover, 1962, 1988) and north into the Arctic Ocean (Hirche, 1991; Hirche and Mumm, 1992). Due to its remote and often inaccessible habitat, little year-round information on its life and reproductive cycles has been obtained in the open ocean, except for several studies of drifting ice islands in the Arctic Ocean (Dawson, 1978; Lee, 1974; Rudyakov, 1983). Annual observations in the Norwegian Sea were made by Sømme (1934) and Østvedt (1955). The life cycle and metabolism of *C. hyperboreus* have been studied in coastal waters, such as the

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eastern Greenland fjords by Ussing (1938) and Digby (1954), the Norwegian fjords by Wiborg (1954) and Matthews et al. (1978), the Gulf of Maine by Conover (1962, 1965), the Northwest Passage by Conover and Siferd (1993), and the Greenland Sea by Hirche and Niehoff (1996). The results of these studies demonstrate that the generation time of *C. hyperboreus* ranges from 1 to 4 years. The egg production of adult female (AF) of *C. hyperboreus* takes place from November to May, when no food is available. They are fuelled only by stored lipids, mainly of wax esters (e.g., Lee, 1974); however, the generation time and reproduction periods stated above vary with location.

Due to the difficulty of zooplankton sampling in ice-covered pelagic waters, it is difficult to perform time-series observations of reproductive biology at multiple locations in winter. Since the AF and adult male (AM) of *C. hyperboreus* are known to reside within a certain depth layer (>100 m) during the ice-covered period, they cannot be effectively caught using plankton nets towed vertically from a single hole in the sea ice. To understand the spawning periods of *C. hyperboreus*, the occurrence of early developmental stages, including nauplii, must be ascertained in the natural environment; however, such individuals are not easily caught using plankton nets because of their small body length (approx. <200 µm) (Gallienne and Robins, 2001). Zooplankton collected using sediment traps, known as “swimmers”, are usually removed from collected samples because they are not regarded as passively sinking particles (PSPs). In high-latitude waters, however, swimmers commonly represent a significant component of PSPs (in mass weight) recovered in trap samples. Although the collection efficiency of swimmers in sediment traps has yet to be determined, time-integrated trap sampling can provide valuable information on seasonal variations in swimmers in areas where only limited zooplankton sampling has been performed in ice-covered polar waters (Forbes et al., 1992). Provided that small-sized copepods, including nauplii stages, are not active swimmers, they can be quantitatively collected in sediment traps as PSPs. In this study, we present data on the occurrence of nauplii and adults of *C. hyperboreus* in winter, based on sequential 9-month collections of zooplankton using sediment traps in the Amundsen Gulf, Canadian Arctic, during 2003–2004.

## 2. Materials and methods

We used Nichiyu SMD 26S, Nichiyu SMD-12S, and TECHNICUP PPS5/5 time-series sediment traps, which

have collection areas at the mouth of 0.502, 0.018, and 1.000 m<sup>2</sup>, respectively. At the bottom of each trap, a platform contained 13–26 sampling bottles filled with buffered formalin in filtered seawater (final conc. 5% v/v). A stepping motor brought one sampling bottle at a time to the opening of the trap and closed the previous one such that each sampling bottle was open for programmed periods of 2–60 days.

The sediment traps were deployed at three stations (CA15, CA18, and CA20) in the Amundsen Gulf as part of the CASES (Canadian Arctic Shelf Exchange Study) program from October 2003 to July 2004 during the cruise of the Canadian research ice-breaker, the CCGS *Amundsen* (Fig. 1). The traps were deployed at depths of 200 m (CA15, sample number CA15<sub>200</sub>), 200 m (CA18, CA18<sub>200</sub>), 400 m (CA18, CA18<sub>400</sub>), and 200 m (CA20, CA20<sub>200</sub>). A recording current meter and acoustic Doppler current profiler were attached to the mooring line just below the sediment traps, except for CA20<sub>200</sub>. After recovery, samples were divided into aliquots on board the ship for later microscopic observations of zooplankton and chemical analysis (Particulate Organic Carbon (POC) and stable isotopes), the latter of which will be published elsewhere.

In the laboratory, trap-collected zooplankton were separated into two fractions by sieving through a 1 mm mesh net: large-sized (>1 mm) zooplankton and small-sized zooplankton (<1 mm), along with non-living particle samples. Large-sized zooplankton samples were used for the identification of AF and AM of *C. hyperboreus* under a dissecting microscope. Small-sized zooplankton with non-living particles were divided into 8, 16, or 32 fractions using a Motoda splitter (Motoda, 1959). Copepod nauplii were picked out under a dissecting microscope and identified, counted, and their body lengths measured. *Calanus* nauplii were identified according to Sømme (1934) and

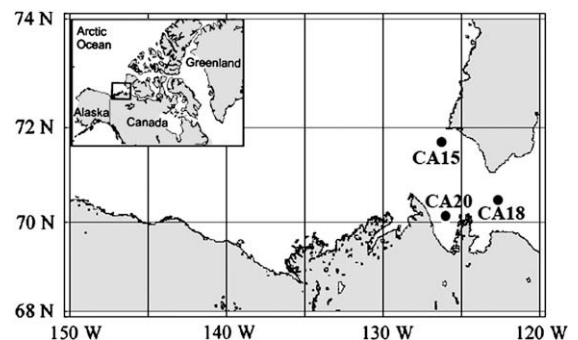


Fig. 1. Location of sampling stations in the Amundsen Gulf. Closed circles indicate stations at which sediment traps were deployed.

Koga (1984). In this study, the abundances of AF and AM of *C. hyperboreus* and nauplii of *Calanus* were standardized as the flux (individuals  $m^{-2} d^{-1}$ ).

A gonad maturity stage in AF *C. hyperboreus* was determined according to the method of Hirche and Niehoff (1996). The first gonad maturity stage is the immature stage of AF, which has diverticula and empty oviducts (Fig. 2a). The second and third stages are the semi-mature stage of AF, which has diverticula with small oocytes (Fig. 2b and c). The fourth stage is the mature stage of AF, which has diverticula filled with large oocytes (Fig. 2d); the pouches for large oocytes are visible inside the oviducts. The fifth stage is the spent stage of AF, which has completed egg spawning. The spent stage of AF has diverticula and thin band-like oviducts that commonly include several eggs. It was commonly impossible to distinguish the immature stage and the two semi-mature stages in this study, because of their similar appearances. Therefore, these three stages are treated as a single immature stage on the result for the seasonal development of adults.

### 3. Results

#### 3.1. Hydrography

Relatively subtle seasonal variations in water temperature were found at the trap deployment depths

at all three stations (Table 1). Water temperature varied from  $-1.5$  to  $-0.5$  °C at 200 m at CA15 over the period November–February. Relatively warm water ( $0.3$  °C) was found at CA18 from April to July. During the period February–April, the water temperature increased to  $>0$  °C at  $<200$  m water depth at two stations (CA15 and CA18). The obtained seasonal variations in salinity largely correspond to those for water temperature. Salinity at 200 m at CA15 from November to February varied from 33.0 to 34.2 psu, and was largely stable from March to July ( $\sim 34.0$  psu). Near-constant salinity was observed at 400 m at CA18 (34.7–34.8 psu).

#### 3.2. *Calanus nauplii*

In the small-sized zooplankton fractions, we counted many copepod nauplii at the three stations, among which early developmental stages of *Calanus* nauplii (N1 and N2) dominated from January to July 2004 (Fig. 3). *Calanus* nauplii collected in the traps were identified based on morphological features and a body length of about 190  $\mu m$ , as suggested by Sømme (1934) and Koga (1984). Other nauplii (i.e., excluding the 190  $\mu m$  size group) were identified as Oithonidae ( $<190$   $\mu m$ ), *Paraeuchaeta* sp. ( $>190$   $\mu m$ ), or unidentified in the case of those with a body length of 155–700  $\mu m$ .

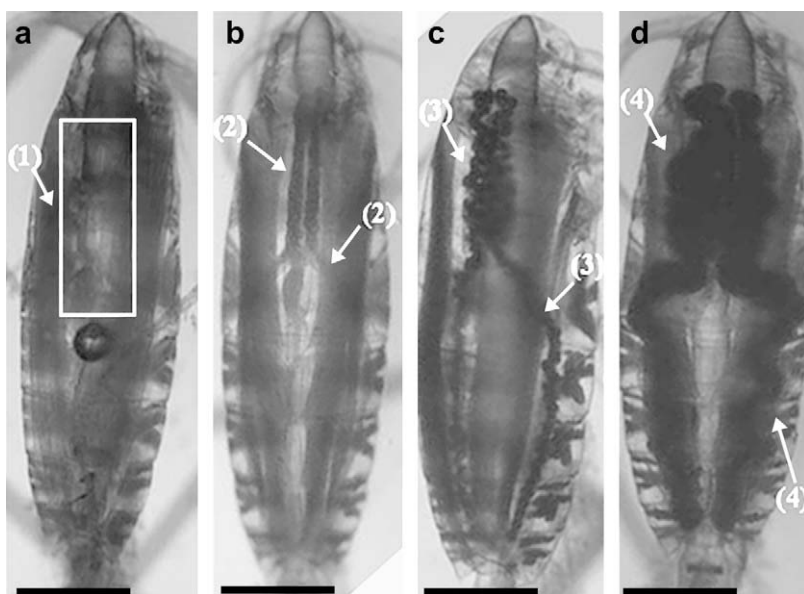


Fig. 2. Gonads of AF *C. hyperboreus*, a: diverticula and empty oviducts, b: diverticula with a single row of small oocytes, c: diverticula with several rows of small oocytes visible in oviducts, and d: diverticula filled with several rows of large oocytes and pouches of large oocytes visible in oviducts. Scale bar is 1 mm.

Table 1

Location of trap deployment and bottom depth, deployment period and depth of each sediment trap type, and ranges of water temperature and salinity during the study period (October 2003–August 2004)

	Station			Deployment			Hydrography		
	Latitude (N)	Longitude (W)	Bottom depth (m)	Period	Depth (m)	Sediment trap type	Sample no.	Temperature (°C)	Salinity (psu)
CA15	71°32.232'	127°1.434'	400	11/10/03–22/7/04	200	Nichiyu26s	CA15 <sub>200</sub>	–1.5 to 0.5	33.0–34.2
CA18	70°38.557'	123°6.042'	500	14/10/03–29/7/04	200	Nichiyu12s	CA18 <sub>200</sub>	–1.1 to 0.0	No data
–	–	–	–	–	400	TECHNICUP PPS5	CA18 <sub>400</sub>	0.2–0.3	34.7–34.8
CA20	71°09.745'	133°52.630'	250	12/10/03–16/7/04	200	Nichiyu26s	CA20 <sub>200</sub>	>0.0–1.2*	>34.0*

Temperature and salinity at CA20<sub>200</sub> (\*) are from CTD (Sea-Bird Electronics Inc., Model SBE-911plus) data (Makabe, unpublished).

*Calanus* nauplii first occurred in CA15<sub>200</sub> during November 2003 (Fig. 4a). They were found in CA18<sub>200</sub> from January to June (Fig. 4b), and in CA18<sub>400</sub> from January to July (Fig. 4c). *Calanus* nauplii were abundant in CA18<sub>400</sub> during March and June. In CA20<sub>200</sub>, a marked increase in abundance was recorded in February (Fig. 4d). A lower abundance was recorded from April to July than that during winter. At all stations, the abundance of *Calanus* nauplii increased from February to March. The maximum abundances in CA15<sub>200</sub>, CA18<sub>200</sub>, CA18<sub>400</sub>, and CA20<sub>200</sub> were 24 individuals (ind.) m<sup>-2</sup> d<sup>-1</sup> in February, 277 ind. m<sup>-2</sup> d<sup>-1</sup> in March, 10 ind. m<sup>-2</sup> d<sup>-1</sup> in March, and 83 ind. m<sup>-2</sup> d<sup>-1</sup> in February, respectively.

### 3.3. Adult female and adult male of *C. hyperboreus*

In CA15<sub>200</sub>, most gonads of AF *C. hyperboreus* were of the immature stage from October to November

2003 (Fig. 5a). In December, some semi-mature AF in the gonad developmental stage appeared, and increased numbers of 2nd- and 3rd-stage semi-mature AF were observed in January. Most of the AF with an abundance of 2–3 ind. m<sup>-2</sup> d<sup>-1</sup> were in the mature stage from February to March, although a few AF gonads were still in the immature stage or the spent stage.

In CA18<sub>200</sub>, immature AF were found in November (Fig. 5b). The mature AF appeared in December, with a maximum abundance in March (32 ind. m<sup>-2</sup> d<sup>-1</sup>). The AF *C. hyperboreus* were in the immature stage in November in CA18<sub>400</sub> (Fig. 5c). The mature AF first appeared in January; the maximum abundance in March (<1 ind. m<sup>-2</sup> d<sup>-1</sup>) was lower than that at 200 m (CA18<sub>200</sub>).

In CA20<sub>200</sub>, AF gonads were in the immature stage in October (Fig. 5d). Mature AF first occurred in late February, increasing to a maximum abundance of

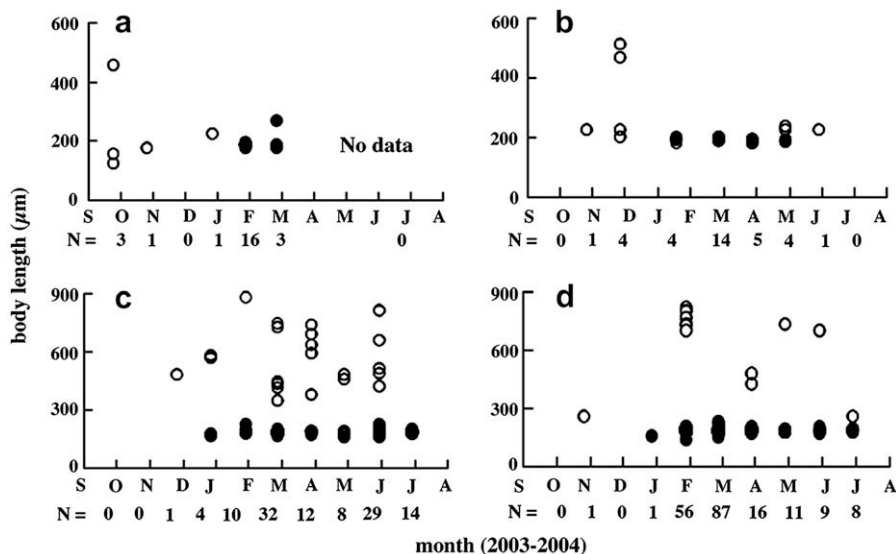


Fig. 3. Seasonal variability in body length of copepod nauplii collected in samples CA15<sub>200</sub> (a), CA18<sub>200</sub> (b), CA18<sub>400</sub> (c), and CA20<sub>200</sub> (d). Copepod nauplii with sizes of 160–260 µm (closed circles) were identified as those of *Calanus* based on morphological features. There were some unidentified nauplii with sizes of 155–811 µm (open circles). *N* = number of individual nauplii.

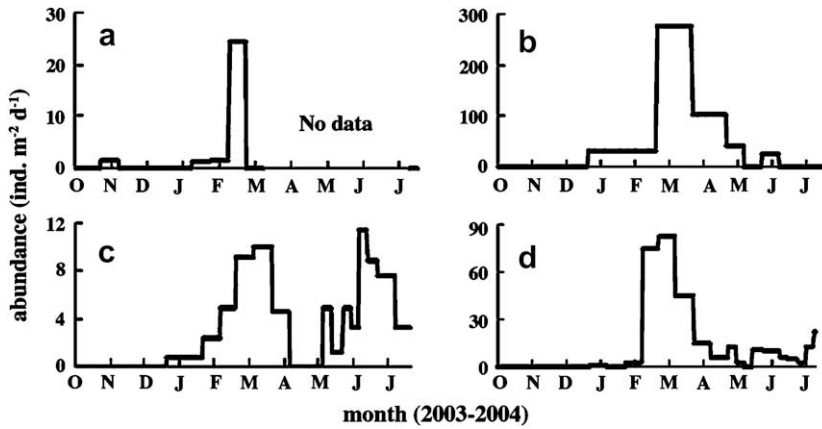


Fig. 4. Seasonal variability in the abundances of *Calanus* nauplii collected in samples CA15<sub>200</sub> (a), CA18<sub>200</sub> (b), CA18<sub>400</sub> (c), and CA20<sub>200</sub> (d). Abundances of nauplii are indicated as the flux (ind. m<sup>-2</sup> d<sup>-1</sup>); ind. = individuals.

4 ind. m<sup>-2</sup> d<sup>-1</sup> in early March. Most of the mature AF disappeared in May. The AM of *C. hyperboreus* appeared at 200 m at all three stations from November to July, although with abundances far less than those for AF. The maximum abundances were <1 ind. m<sup>-2</sup> d<sup>-1</sup> in CA15<sub>200</sub>, 12 ind. m<sup>-2</sup> d<sup>-1</sup> in CA18<sub>200</sub>, and 2 ind. m<sup>-2</sup> d<sup>-1</sup> in CA20<sub>200</sub>. The AM found in CA18<sub>400</sub> occurred at much higher abundances than that of AF (maximum abundance of 2 ind. m<sup>-2</sup> d<sup>-1</sup>).

**4. Discussion**

In many previous studies (e.g., Angel, 1984), minute trap-collected organisms such as phytoplankton

and protozooplankton with little or no swimming activity have been used for quantitative flux estimates, primarily because they are regarded as non-swimmers. This raises the questions of whether copepod nauplii collected in sediment traps are swimmers or non-swimmers. The early stages of nauplii (N1–2) of *Calanus finmarchicus*, subarctic copepods, do not swim actively before they start to feed (see Titleman and Kjørboe, 2003). These nauplii should be considered as “non-swimmers”, primarily because they are eventually captured in traps, even though some of them make slight jump–sink movements (Titleman and Kjørboe, 2003). The nauplii N1–4 of *C. hyperboreus* can also be regarded as “non-swimmers” because they do not feed (Conover, 1962). Therefore, copepod

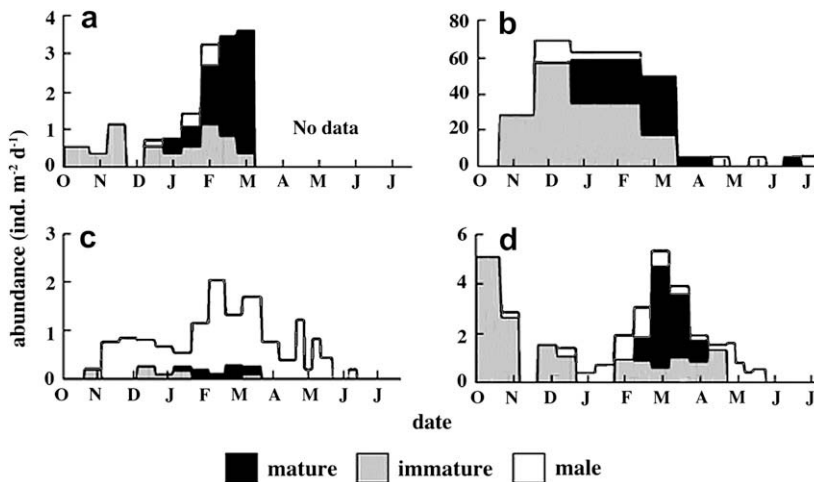


Fig. 5. Seasonal variability in the abundances of the immature stage of AF, mature stage of AF, and AM of *C. hyperboreus* caught in samples CA15<sub>200</sub> (a), CA18<sub>200</sub> (b), CA18<sub>400</sub> (c), and CA20<sub>200</sub> (d).

nauplii (N1–2) collected in the present study can be considered non-swimmers, and the abundances in terms of flux recorded in different periods can be quantitatively compared with each other. We were unable to make a quantitative comparison between the trap-collected nauplii and plankton-net-collected nauplii, the latter of which demonstrate the true abundance in a unit water volume; however, small-sized nauplii (mostly <200  $\mu\text{m}$ ) were not effectively caught using conventional plankton nets with a mesh size of 200–300  $\mu\text{m}$ . On the other hand, active swimmers represented by later stages of nauplii, copepodites, and adults have their own specific downward or upward movements. Consequently, these vertical migrants might be collected periodically using sediment traps (R. Makabe, unpublished). Although the abundances of AF and AM in the present study may not represent real movements in the water column, their occurrence periods in the trap provide a reliable indication of the period of migration. *C. hyperboreus* is a well-known species, as they undertake a seasonal ontogenetic migration in the northern North Atlantic (Hirche, 1997), spending the winter period below 500 m depth, ascending in April to the surface, and spawning their eggs before their spring ascent from the overwintering depths (Hirche and Niehoff, 1996). In the Arctic Ocean, Dawson (1978) found abundant copepodites (C2) of *C. hyperboreus* at 200–300 m in March–April. Based on the coincidence of the occurrence periods (January–March) of mature AF of *C. hyperboreus* and their nauplii in the present study, these nauplii were most likely derived from *C. hyperboreus* (Figs. 4a–d and 5a–d). This finding also suggests that the spawning of *C. hyperboreus* started during February–March in the Amundsen Gulf. Furthermore, the occurrence of AM, which indicates the breeding season (Conover, 1965; Sømme, 1934), was confirmed in CA15<sub>200</sub> and CA18<sub>200</sub> during December, and in CA18<sub>400</sub> and CA20<sub>200</sub> during November (Fig. 5a–d). This finding is supported by Hirche (1997), who demonstrated that the AM develop their spermatophores and fertilize AF as soon as they meet. Thus, their breeding should start in November/December at the latest, and is probably largely completed by April.

*Calanus glacialis*, another dominant *Calanus* in the Amundsen Gulf, were not the major producers of the 190  $\mu\text{m}$ -sized nauplii in mid-winter, as their reproduction is known to occur within a certain period between April and August (Asjian et al., 1995, 1997; Hirche and Bohrer, 1987; Hirche et al., 1994; Smith, 1990). In fact, we found abundant *Calanus* nauplii with

a size of  $\sim 190 \mu\text{m}$  during summer (Fig. 3c); these were derived from *C. glacialis*, but probably not from *C. hyperboreus*.

Previous studies reported that the reproduction periods of *C. hyperboreus* are from November to late March in the ice-free Greenland Sea (Hirche and Niehoff, 1996), February to March in the Norwegian Sea (Østvedt, 1955; Wiborg, 1954), January to May in the central Arctic Ocean (Brodskii and Nikitin, 1955; Johnson, 1963), mid-March to May in the Northwest Passage (Conover and Siferd, 1993), and February to mid-April in Disko Bay, West Greenland (Niehoff et al., 2002). Relatively short reproduction periods were also reported in the Foxe Basin (May–June; Grainger, 1965) and in the Billefjorden, Svalbard (January–February; Arnkværn et al., 2005). These regional and temporal differences in production period are thought to reflect the local timing of the phytoplankton bloom (Conover and Siferd, 1993; Hirche and Niehoff, 1996). Eggs and nauplii of *C. hyperboreus* contain substantial lipid reserves used to support development until the first feeding starts when they migrate upward to the surface. Feeding probably starts at nauplius stage N5 in *C. hyperboreus* (Conover, 1962), which were rarely collected in the present traps. The lag time between spawning and the onset of the phytoplankton bloom is regarded as the “buffer” time (Conover, 1988).

Based on the data obtained from laboratory experiments at temperatures of 4–6 °C (Conover, 1967), it takes 18 days from hatching to N5. As the temperature in the present study area was lower than that of this previous laboratory experiment, the development of nauplii probably takes longer than 18 days in the natural environment. If we assume  $Q_{10}$  (metabolic increase due to 10 °C temperature increase) = 2–3, nauplii of *C. hyperboreus* take 36 days to develop to N5 during March–April. According to Mauchline (1998), the development time to C1 can be greater than 40 days; thus, they must survive for several weeks or even months before food becomes available (Conover, 1965; Hirche and Niehoff, 1996). Food for nauplius stage N5 could be scarce from March to April, as chlorophyll *a* concentrations at CA20 were less than 1  $\mu\text{g Chl. } a \text{ l}^{-1}$  in surface layers in April, and an ice algal bloom was observed in mid-May (Renaud et al., 2007). Although we obtained no information on the main food items for the nauplii N5 and further developmental stages prior to the phytoplankton bloom, they possibly feed on microheterotrophs and/or non-living detrital particles.

The largest number of nauplii of *C. hyperboreus* occurred at 200 m within the eastern Amundsen Gulf

(CA18<sub>400</sub>). The abundance at this site (277 ind. m<sup>-2</sup> d<sup>-1</sup>) was approximately 10 times greater than that at other sites. It is unclear why these nauplii accumulate at this location. According to A. Forest (unpublished), who measured regional and temporal changes in POC flux in the Amundsen Gulf during 2004–2006, the annual POC fluxes at eastern sites were 20–85% greater at 200 m than that at 100 m depth, even during the wintertime. This finding suggests that lateral POC transport from the west (close to the Cape Bathurst polynya) to the east may occur within the eastward current that flows in the intermediate layer. The horizontal advection of particles possibly forms a food-particle-rich environment for later stages of these nauplii in the eastern Amundsen Gulf. If the mid-water lateral current is sufficiently strong to transport copepod zooplankton including nauplii and AF in the area west of CA18, it is possible that both copepods and non-living sinking particles would accumulate in this area.

Nauplii N3–6 of *C. hyperboreus* were not effectively caught using sediment traps at any station or any time of the year. It is possible that they start to migrate upward to surface layers, but we obtained no information on whether they remained within specific depth layers. We identified the breeding and spawning periods of *C. hyperboreus* based on the occurrence data of early nauplii in the Amundsen Gulf in winter. To fully understand the life cycle of *C. hyperboreus*, further investigations are needed to cover the developmental stages of later nauplii and early copepodites of *C. hyperboreus* in ice-covered Arctic waters.

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