



# Sediment trap samples reveal regional differences in the population structure of *Calanus hyperboreus* from the Arctic Ocean

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## ABSTRACT

*Calanus hyperboreus* is one of the dominant copepod species in the Arctic zooplankton communities. The impact of climate change varies among regions within the Arctic, implying that *C. hyperboreus* populations may be differently affected at different locations, but knowledge on seasonal population dynamics in relation to biogeography is scarce. To fill this gap, we counted *C. hyperboreus* in samples from sediment traps that were moored from 2009 to 2014 in three regions of the Arctic Ocean (eastern Fram Strait, northern Chukchi Sea and MacKenzie Trough). The *C. hyperboreus* flux increased between April and May in all regions, likely associated with the ascent from overwintering depth to the surface. In the descent period, high fluxes were observed between July and September in the Fram Strait, between September and November in the northern Chukchi Sea, and between August and October in the MacKenzie Trough, suggesting that the timing of descent varied among the regions characterized by differences in light regime, phytoplankton development and water temperature. The copepodite stage composition in the eastern Fram Strait and the MacKenzie Trough varied with season, suggesting successful local reproduction while it was uniform in the northern Chukchi Sea, possibly because the population is fueled by advection.

**KEYWORDS:** sediment trap; *Calanus hyperboreus*; population structure; Arctic Ocean; regional differences

## INTRODUCTION

*Calanus hyperboreus* is distributed throughout the Arctic Ocean (Conover, 1988) and often dominates the biomass of Arctic zooplankton communities (Mumm *et al.*, 1998; Ashjian *et al.*, 2003; Kosobokova and Hirche, 2009). This copepod species feeds mainly on phytoplankton from spring to summer (Conover, 1988; Falk-Petersen *et al.*, 2009), and migrates to 500–2000 m in late summer and autumn where it overwinters in diapause (Conover, 1988; Falk-Petersen *et al.*, 2009; Kvile *et al.*, 2019). Overwintering stages are copepodite stage (C) 3, C4, C5 and females, and its life span has a wide range of 1–5 years (Falk-Petersen *et al.*, 2009), likely dependent on environmental conditions such as sea-ice coverage, water temperature, primary production and, thus, region (Conover, 1988; Madsen *et al.*, 2001; Falk-Petersen *et al.*, 2009). Overwintering in diapause at greater depth is common for the large, lipid-rich *Calanus* species in the Arctic Ocean, where light availability, water

temperature and food resources exhibit strong seasonality (Dahms, 1995), and has multiple evolutionary advantages such as reducing lipid consumption (Saumweber and Durbin, 2006), lowering the costs of swimming (Pond and Tarling, 2011) and avoiding surface-layer predation pressure (Kaartvedt, 1996). An increase in water temperature, predation pressure (Ji, 2011) and accumulation of a threshold amount of lipids (e.g. Häfker *et al.*, 2018; Schmid *et al.*, 2018) have been considered to induce diapause. A decrease in lipid content may trigger the end of diapause and migration to the surface layer during spring (Schmid *et al.*, 2018), and Häfker *et al.* (2018) suggest that an endogenous clock plays an important role in the termination of diapause in *Calanus finmarchicus*.

Global warming, i.e. increasing water and air temperatures, has already now severely reduced the sea-ice cover extent and duration of the Arctic Ocean (cf. Polyakov *et al.*, 2020), which in turn has consequences for algal growth (Arrigo and van Dijken, 2015;

Adyrna and Arrigo, 2020). Such changes are likely to affect the life cycle of key zooplankton species such as the herbivorous large copepod *C. hyperboreus*.

The impact of climate change varies, however, greatly among regions within the Arctic Ocean (e.g. Adyrna and Arrigo, 2020), which implies that also *C. hyperboreus* populations may be differently affected at different locations. In order to assess the response of this species to climate change scenarios, knowledge on seasonal changes in abundance and stage composition in several parts of the Arctic Ocean is required; however, harsh polar conditions make year-round ship observations difficult. This gap can potentially be filled by means of sediment trap sampling, which has been shown to be a semi-quantitative but viable method for evaluating seasonal dynamics in zooplankton communities (Ota *et al.*, 2008; Makabe *et al.*, 2010, 2016; Kraft *et al.*, 2012; Bauerfeind *et al.*, 2014; Matsuno *et al.*, 2014, 2015; Dezutter *et al.*, 2019; Tokuhiro *et al.*, 2019, 2020). Such traps were originally developed to collect passively sinking particles in the water column, but zooplankton that actively swim into the traps are also captured and preserved in the sampling bottles (Knauer *et al.*, 1979).

Only a few studies have used sediment trap samples to investigate seasonal variations in *C. hyperboreus* populations. Tokuhiro *et al.* (2019) studied the seasonal changes in developmental stages, lipid accumulation and gonad maturation stages in the northern Chukchi Sea. In sediment trap samples from the Amundsen Gulf, the succession of nauplii and copepodite stages has been followed over 1 year (Makabe *et al.*, 2010), while inter-annual differences in *C. hyperboreus* abundance and population structure were derived from sediment traps deployed in the MacKenzie Trough (Dezutter *et al.*, 2019). All three studies provide information on the population dynamics of *C. hyperboreus* in the Canadian Arctic, while no such information is yet available from the Eurasian Arctic. One objective of our study therefore was to study the population structure of *C. hyperboreus* in sediment trap samples deployed in the eastern Fram Strait, and compare these data to data from the northern Chukchi Sea and off the coast near the MacKenzie Trough. These three locations differ considerably with respect to environmental conditions (e.g. day length, water temperature, chlorophyll *a* and sea-ice concentration, SIC) and thus allow to improve our current understanding of how abiotic factors influence life history traits in a dominant Arctic copepod species.

## METHOD

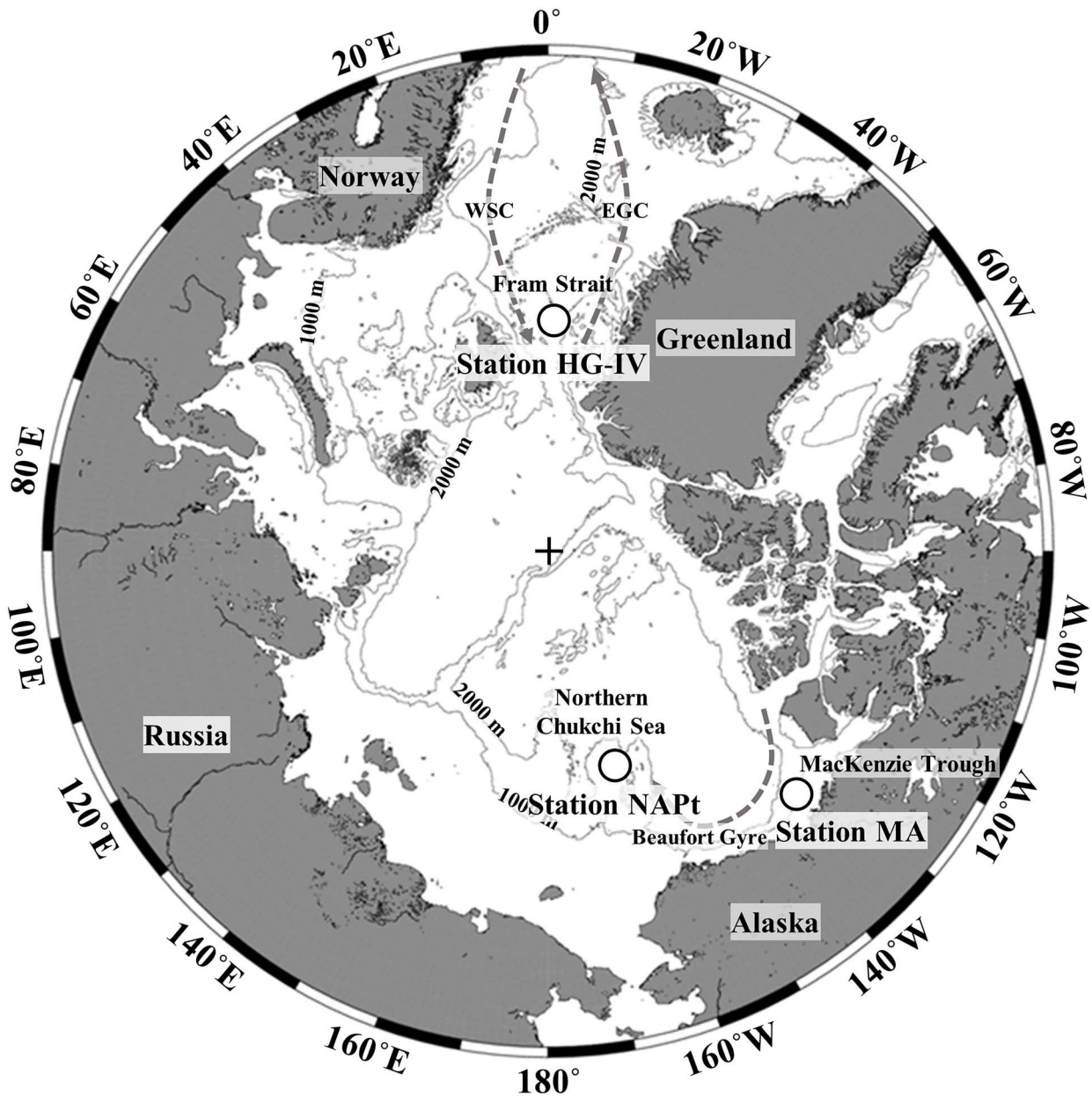
### Field sampling

The sediment traps were moored in the eastern Fram Strait, in the northern Chukchi Sea and in the MacKenzie Trough (Fig. 1). Sampling was conducted over several years, and the traps were recovered, and new ones redeployed at the same stations and depths once per year (Table 1).

The sediment traps (K/MT 234; K.U.M., Kiel, Germany; open-mouth area 0.5 m<sup>2</sup>) in the eastern Fram Strait were moored at a depth of ~200 m at the AWI LTER Observatory HAUSGARTEN Station (St.) HG-IV from summer 2010 to summer 2014 (Table 1). The collection intervals were short in summer (every 7 days) and long in winter (every 59 days). During each

Table 1: Time-series sediment trap deployments and collected samples at Stations HG-IV, NApT and MA

Mooring point (Station name)	Mooring period	Lat.	Long.	Bottom depth (m)	Trap depth (m)	Open area (m <sup>2</sup> )	Collection interval (days)	No. of samples
Eastern Fram Strait (Station HG-IV)	10.07.2010–30.06.2011	79.00 N	4.33E	2604	200	0.5	10–59	20
	01.08.2011–15.07.2012	79.01 N	4.33E	2605	200	0.5	10–32	20
	29.07.2012–30.06.2013	79.01 N	4.51E	2642	205	0.5	10–31	20
	10.07.2013–15.06.2014	79.06 N	4.03E	2577	205	0.5	7–31	20
Northern Chukchi Sea (Station NApT)	04.10.2010–28.09.2011	75.01 N	162.00 W	1973	186	0.5	13–15	26
	04.10.2011–18.09.2012	75.00 N	162.01 W	1975	260	0.5	10–15	26
	04.10.2012–18.09.2013	75.00 N	162.00 W	1975	222	0.5	10–15	26
	10.09.2013–10.09.2014	74.52 N	161.93 W	1681	189	0.5	14–15	26
MacKenzie Trough (Station MA)	21.07.2009–29.06.2010	70.45 N	136.00 W	688	198	0.125	3–31	25
	13.09.2010–31.08.2011	70.76 N	136.00 W	684	184	0.125	7–31	24
	14.09.2011–01.09.2012	70.45 N	136.00 W	659	172	0.125	8–17	24



**Fig. 1.** Location of the three sediment trap sites: the eastern Fram Strait, the northern Chukchi Sea and the MacKenzie Trough (off the coast). The eastern Fram Strait was sampled at Station HG-IV from 10 July 2010 to 15 June 2014. The northern Chukchi Sea was sampled at Station NAPt from 4 October 2010 to 10 September 2014. The MacKenzie Trough was sampled at Station MA from 21 July 2009 to 1 September 2012. WSC: West Spitzbergen Current, EGC: East Greenland Current.

deployment period, a total of 20 samples were collected. At least 17 of these were analyzed (Table I); the remaining were excluded because the sediment trap funnels were clogged.

In the northern Chukchi Sea, a time-series sediment trap (SMD26S-6000, Nichiyu Giken Kogyo, Co. Ltd; open-mouth area 0.5 m<sup>2</sup>) was moored from autumn 2010 to autumn 2014 at St. NAPt (Table I) located on the Northwind Abyssal Plain. Mooring depths were 186–260 m, and the collection interval varied between 10 and 15 days. Of all samples, 26 cups were analyzed per year.

Off the coast of the MacKenzie Trough, a time-series sediment trap (PPS 3/3, Technicap, open-mouth area 0.125 m<sup>2</sup>) was

moored at Station MA from summer 2009 to autumn 2012 at 172–198 m depth. The collection intervals were short during summer (every 3 days) and long during winter (every 31 days), and 24 or 25 samples were analyzed for each year (Table I).

To preserve particles and zooplankton, the sample cups at St. HG-IV were filled with mercuric chloride (0.14% final solution), while those at St. NAPt and St. MA were filled with sea water containing 5% neutralized formalin.

#### Environmental data

Daytime hours at each station were calculated following Brock (1981). The weekly average sea-ice coverage (%) near each



station during the mooring periods was calculated at a 25-km resolution from the SIC dataset (National Snow and Ice Data Centre). In this study, the Optimal Interpolation Sea Surface Temperature (OISST; °C) was used as sea surface water temperature (SST). OISST is a long-term climate data record that combines observations from multiple platforms (satellite, ship and mooring). Satellite data were obtained from the Advanced Very High Resolution Radiometer and the Advanced Microwave Scanning Radiometer. Ship and mooring data were extracted from the International Comprehensive Ocean–Atmosphere Datasets Release 2.4 (ICOADS R2.4) and the National Centers for Environmental Prediction Global Telecommunication System. OISST have a resolution of daily measurements of  $0.25^\circ \times 0.25^\circ$ . For chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ), MODIS/Aqua Level 3 binned chlorophyll *a* (Chl *a*) data were downloaded from the Distributed Active Archive Center of NASA's Goddard Space Flight Center, and a running mean of 9 days was calculated at 9-km resolution.

### Sample analysis

Sediment trap samples were gently filtered through a 0.5-mm-mesh net (St. HG-IV) and a 1-mm-mesh net (St. NAPt and St. MA), and the *C. hyperboreus* specimens retained on the net were determined to developmental stages. This study targeted copepodite stage of *C. hyperboreus*, which were identified following Brodsky (1967) and counted under a stereomicroscope (0–228 individuals per sample). Since the prosome width of C4 is on average 1.12 mm (Skjoldal, 2021), we likely underestimate the numbers of the younger developmental stages (C1–C3) in samples from the northern Chukchi Sea and the MacKenzie Trough. The prosome width of *C. hyperboreus* C2 is  $\sim 0.54$  mm (Skjoldal, 2021) and thus the numbers of C1 in samples from the Fram Strait are likely underestimated. Our study therefore is representative only for *C. hyperboreus* C4, C5 and adults, and all younger stages have been excluded.

The flux ( $F$ , individuals  $[\text{ind.}] \text{m}^{-2} \text{day}^{-1}$ ) of *C. hyperboreus* was calculated using the following equation:

$$F = N \times \frac{1}{O} \times \frac{1}{d}$$

where  $N$  is number of individuals,  $O$  is mouth area ( $\text{m}^2$ ) of the sediment trap and  $d$  is collection interval (days).

### Data analysis

Although the duration of the diapause varies in region and between years, the general timing of seasonal migrations seems to be relatively consistent. *Calanus hyperboreus* has been observed to diapause from September to April–May in the central Arctic Ocean (Dawson, 1978), from around mid-August to April in the Greenland Sea and the Resolute passage (Conover, 1988; Hirche, 1997), September to March–May in the Gulf of Saint Lawrence (Plourde *et al.*, 2003) and from September to March in the western Arctic Ocean (Ashjian *et al.*, 2003). Thus, the diapausing copepods migrate from the surface layer to the deep layer around August–September and vice versa around March–May. To compare among the stations, we defined the period from July to December as descent period and the period from

January to June as ascent period. Cumulative *C. hyperboreus* fluxes ( $\text{ind. m}^{-2}$ ) and copepodite stage compositions (%) during each period were then calculated per year.

## RESULTS

### Environmental conditions

In the eastern Fram Strait (St. HG-IV), the polar night lasts from mid-October to mid-February, and the midnight sun lasts from mid-April to mid-August (Fig. 2a). Around St. HG-IV, the sea surface temperature (SST) was low from winter to spring (minimum  $-1.8^\circ\text{C}$ ) and high from summer to autumn (maximum  $7.4^\circ\text{C}$ ). The SIC did not exhibit a clear seasonality. The surface Chl *a* concentration from April to September ranged between 0.020 and  $17 \text{ mg m}^{-3}$ .

In the northern Chukchi Sea (St. NAPt), the midnight sun lasts from late April to early August and the polar night from late October to early February (Fig. 2b). During open-water periods, the sea-surface water temperature was high (maximum  $2.3^\circ\text{C}$ ) and remained consistently low in ice-covered periods (minimum  $-1.8^\circ\text{C}$ ). The sea ice melted completely, and this station was always ice-free from August to October. New sea ice formed rapidly from October to November. Chl *a* was detected shortly after the sea ice melted in August, and the Chl *a* concentration increased until September but remained much lower than at the other two locations ( $0.019$ – $0.35 \text{ mg m}^{-3}$ ).

At the MacKenzie Trough station (St. MA), polar night and midnight sun occurred from mid-November to mid-January and early May to late July, respectively (Fig. 2c). As to be expected, the SST peaked during open-water periods and dropped during freezing periods when the SIC was above 80%. From late October to mid-November, the SIC increased rapidly and exceeded 90% from mid-September to mid-May. From mid-May to mid-June, the SIC decreased again. Chl *a* was detected at the surface after sea ice melted. The Chl *a* concentration then increased during open-water periods (from May to September) and was higher at the other two locations ( $0.03$ – $38.9 \text{ mg m}^{-3}$ ).

### *Calanus hyperboreus* population structure

The flux of *C. hyperboreus* showed seasonality at all stations. In the eastern Fram Strait, the *C. hyperboreus* flux ranged from 0 to  $46 \text{ ind. m}^{-2} \text{day}^{-1}$  (Fig. 3a), with high fluxes from April to May (ascent) and from July to September (descent) and no flux during winter. The cumulative flux during the descent period was lower than during the ascent period (Fig. 4). Copepodite stage VI females (C6F) were dominant throughout the year, while the copepodite stage 5 (C5) appeared mainly during high flux periods. C4 were observed only in the descent period 2011 and the ascent period 2012 (Fig. 4).

The *C. hyperboreus* flux in the northern Chukchi Sea varied between 0 and  $7.7 \text{ ind. m}^{-2} \text{day}^{-1}$ , with relatively high fluxes from April to May and September to October (Fig. 3b). The cumulative flux during the ascent period was slightly higher during the descent period (Fig. 4) and overall, fluxes were lower than at the other two stations (Fig. 3b). Other than in the Fram Strait, the flux decreased but did not cease completely in winter. Adult females (C6F) dominated throughout the year, and the number of C5 increased when the flux was high. Both the cumulative flux

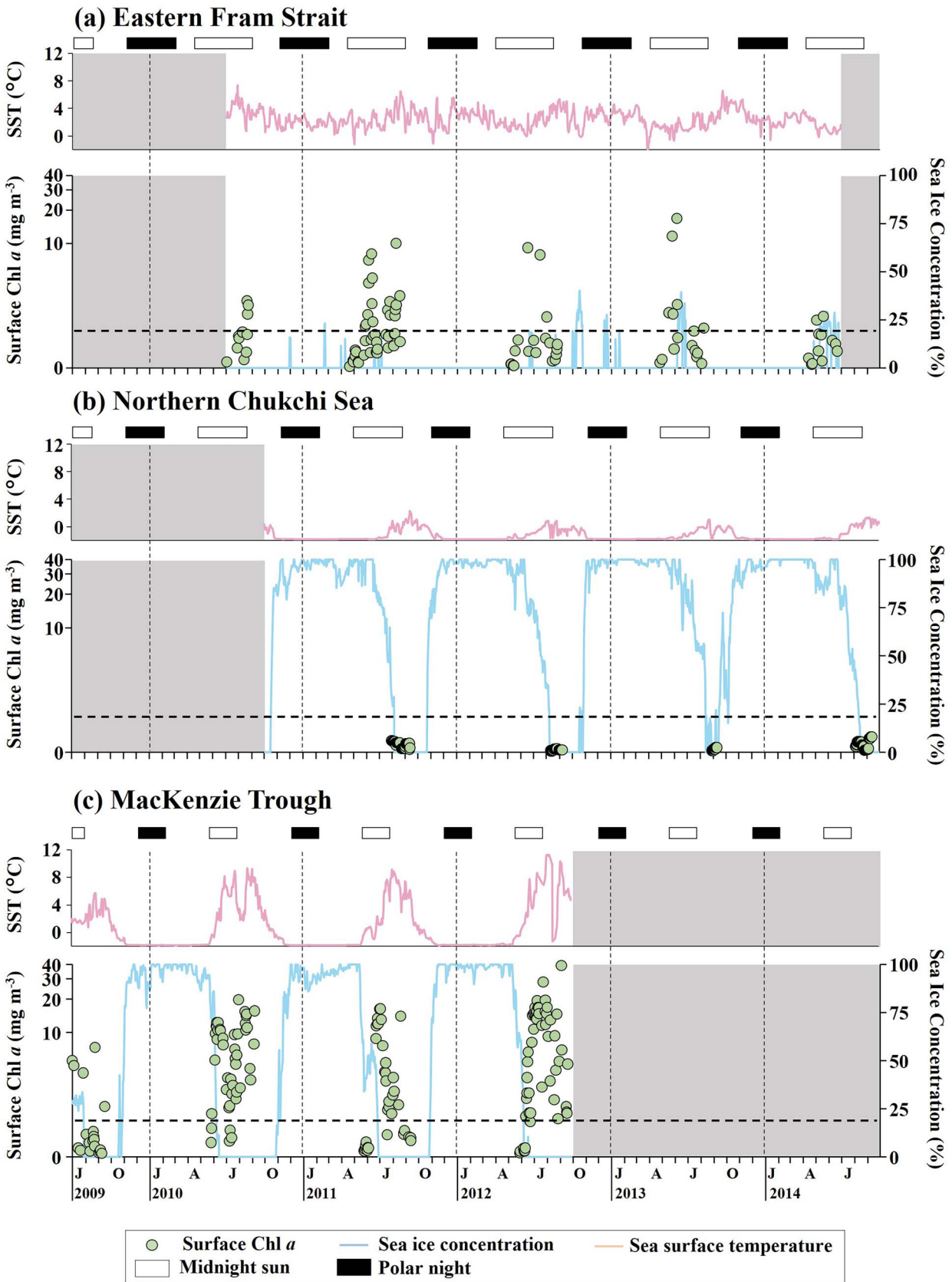
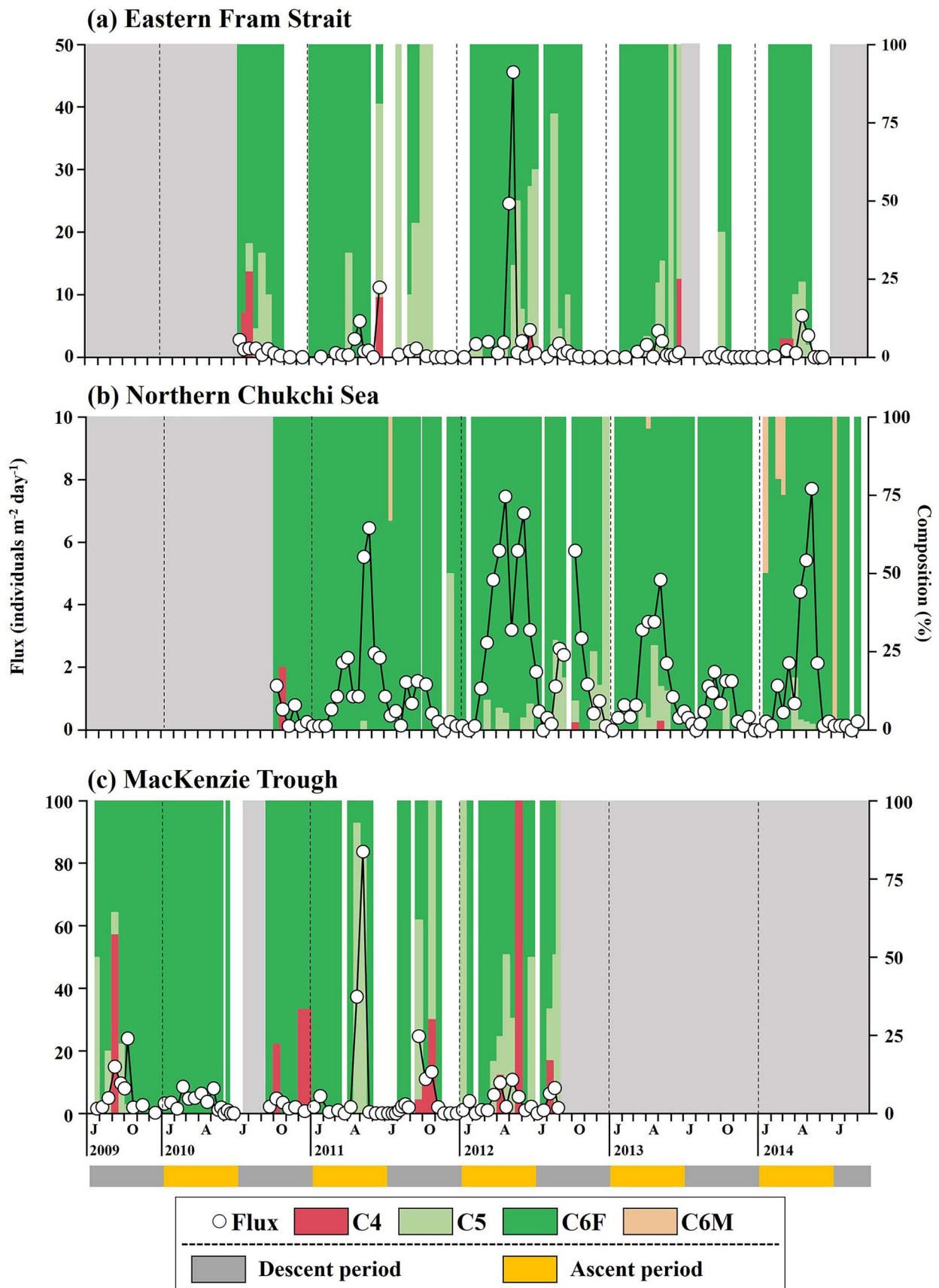
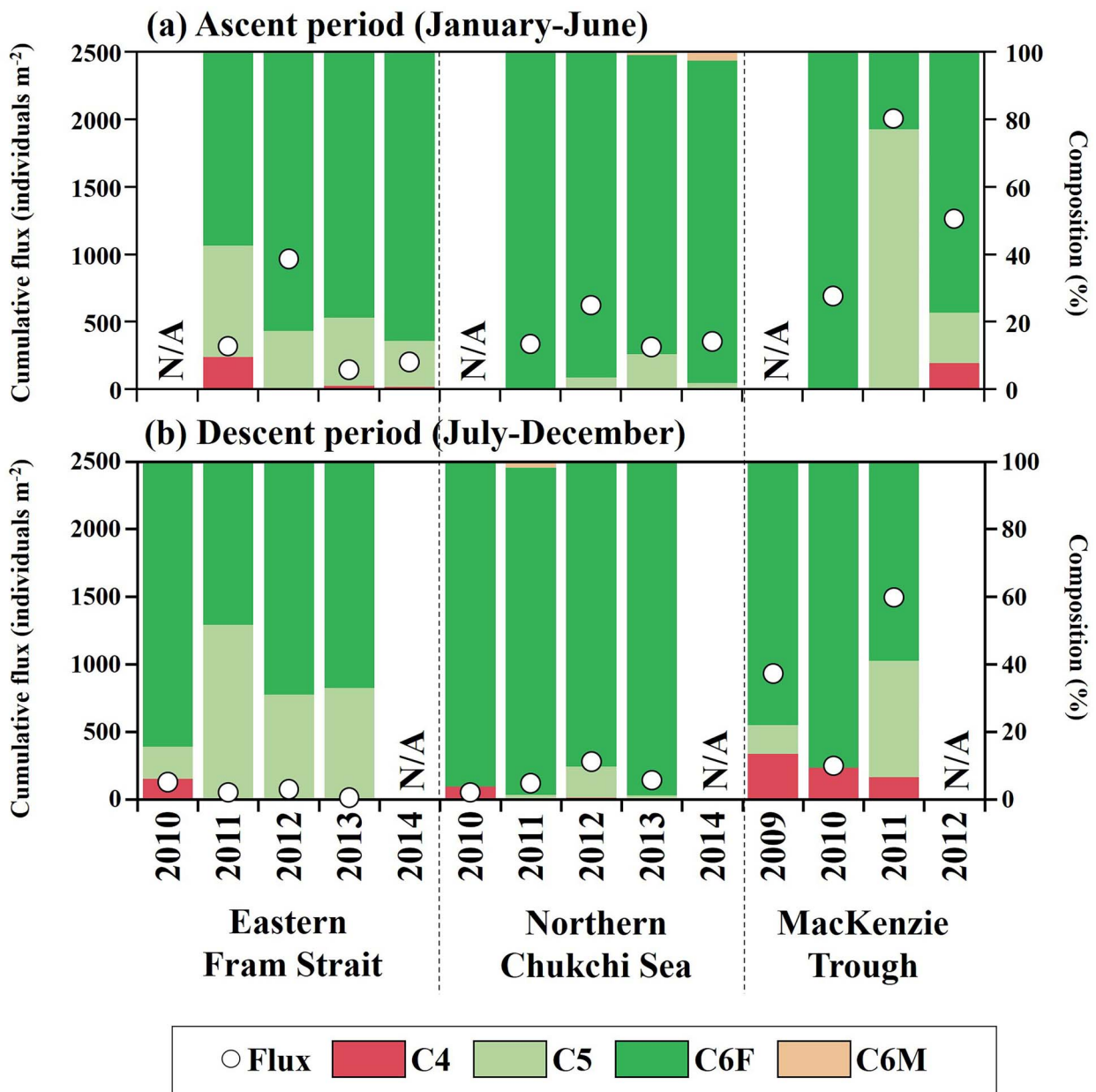


Fig. 2. Seasonal change in SST, SIC and surface chlorophyll *a* (Chl *a*) at each sediment trap station. Open and solid bars show midnight sun and polar night durations, respectively. Gray area shows no data.



**Fig. 3.** Seasonal change in flux and population structure of *Calanus hyperboreus* at each station. Black and yellow bars represent descent and ascent periods, respectively. Gray area shows no data and white area indicate 0 individuals  $\text{m}^{-2} \text{day}^{-1}$ . Please note that y-axis scales are different.



**Fig. 4.** Annual variation in *C. hyperboreus* cumulative flux and copepodite stage (C4–6, F: female, M: male) composition during the ascent (January to June) and descent (July to December) periods.

and population structure were comparably similar in the ascent and descent periods of the 4 years (Fig. 4).

The flux in the MacKenzie Trough ranged from 0 to 84 ind.  $m^{-2} day^{-1}$ , and was high from April to May and September to October (Fig. 3c) with similar levels of cumulative fluxes during ascent and descent periods (Fig. 4). As in the northern Chukchi Sea, low fluxes of *C. hyperboreus* sustained during winter. Adult females were dominant and the proportions of C5 increased during high flux period. The numbers of C4 increased in descent periods, but this developmental stage did not appear in ascent periods except in 2012. Comparing among years, cumulative fluxes were especially high in the ascent period 2011 and in the descent periods of 2009 and 2011 (Fig. 4).

## DISCUSSION

### Use of sediment traps to investigate *C. hyperboreus* population dynamics

There are several possible reasons why *C. hyperboreus* may appear in sediment trap samples. The first reason is that copepods, which die at depths shallower than the sediment trap mooring, sink into the traps (Sampei et al., 2009). The contribution of dead copepods is, however, usually small (Sampei et al., 2009), and in our analyses, we did not include carcasses. Thus, our data present the number of specimens that swam into the traps and were preserved. The second reason is that the copepods move vertically in the water column during diel vertical migration (DVM). However, *C. hyperboreus* in the Arctic Ocean does not



perform DVM during midnight sun (Hays, 2003; Blachowiak-Samolyk *et al.*, 2006). Even if there was DVM during diurnal light–darkness cycles in spring and autumn, the DVM amplitude in the Arctic is expected to be smaller than in low-latitude areas (Bandara *et al.*, 2018), and thus it is unlikely that *C. hyperboreus* would have reached the depth of the sediment trap due to DVM. The third reason is that *C. hyperboreus*, as the other two *Calanus* species *C. finmarchicus* and *C. glacialis*, performs seasonal vertical migration (SVM) (e.g. Conover, 1988). *Calanus hyperboreus* spends the productive spring/summer season in surface waters to feed on phytoplankton (Conover, 1988; Falk-Petersen *et al.*, 2009). In late summer/autumn, the copepods migrate to deeper water layers (>400 m) where it spends the winter in diapause, and in early spring *C. hyperboreus* returns to the surface (Conover, 1988; Niehoff *et al.*, 2002; Falk-Petersen *et al.*, 2009; Kvile *et al.*, 2019). During migration, individuals apparently indeed swim into sediment traps since the numbers of *C. hyperboreus* in the samples have previously been shown to change with season (Ota *et al.*, 2008; Matsuno *et al.*, 2015; Tokuhira *et al.*, 2019). We also observed clear seasonal patterns at all three stations in the *C. hyperboreus* flux, which are in agreement with the timing of SVM in this species. In conclusion, we believe that most of the individuals found in our samples swam into the traps during their vertical migration from overwintering depth to the surface and vice versa.

In the Arctic Ocean, it has been suggested that the timing of SVM varies among regions (Dawson, 1978; Conover, 1988; Hirche, 1997; Plourde *et al.*, 2003). In order to compare among regions, we included the months from January through June in our definition of the ascent period during within which the copepods migrate from deep waters (>200 m) to the surface (0–200 m). The period from July through December we defined as the descent period during which the copepods migrate from the surface to deep waters. As compared to the months the copepods stay in surface and in deep waters, respectively, the period of actual vertical migration is supposed to be short (Hirche, 1997; Ashjian *et al.*, 2003; Darnis and Fortier, 2014). Therefore, also the period during which *C. hyperboreus* passes the sediment traps is short, and we can assume that increases in flux reflect the SVM in *C. hyperboreus* and allow to determine the timing of ascent and descent.

#### Seasonal changes in fluxes of *C. hyperboreus*

The fluxes of *C. hyperboreus* increased in April/May just before the midnight sun, suggesting that the timing of the ascent did not differ much, neither among years nor among regions. The chlorophyll *a* concentration as derived from satellite data, which we use as an indicator of phytoplankton dynamics, however, did not increase at the same time, except for the Fram Strait. Satellite data, however, do not allow for the detection of chlorophyll *a* below the sea ice and of sub-surface maxima, and may thus not fully reflect algal development. Therefore, we also consider fluxes of phytoplankton and particulate organic carbon (POC) as determined from the sediment traps, and these did increase coincidentally with the ascent of *C. hyperboreus* in April/May. In the Fram Strait, fluxes of phytoplankton (mainly diatoms) and POC were usually high from April to July (Bauerfeind *et al.*, 2009; Lalande *et al.*, 2011, 2013). In the northern Chukchi Sea,

ice algae and diatoms appeared from April through September (Onodera *et al.*, 2015, 2016). In the MacKenzie Trough, the ice algae *Nitzschia frigida* were found in sediment trap samples in May and the total diatom flux lasted from May to August (Dezutter *et al.*, 2019). After ascending from the deep, *C. hyperboreus* thus immediately had access to food supply, allowing this species to feed during almost the entire productive season in the Arctic Ocean.

The timing of descent as reflected by increasing fluxes during the descent period was timed less closely. We observed increasing *C. hyperboreus* fluxes from July to September in the Fram Strait, in the northern Chukchi Sea from September to November and in the MacKenzie Trough from August to October. The descent coincided with a period of decreasing POC and phytoplankton flux in the Fram Strait and the MacKenzie Trough (Bauerfeind *et al.*, 2009; Lalande *et al.*, 2011, 2013; Dezutter *et al.*, 2019), but not in the northern Chukchi Sea (Onodera *et al.*, 2015, 2016). Decreasing food availability can therefore likely be excluded as a factor triggering the descent. Maximum sea-surface water temperatures were observed in July–August in the Fram Strait, in September in the northern Chukchi Sea and in August in the MacKenzie Trough, and the timing of rising temperature and increases in fluxes roughly coincided. Therefore, it is possible that changes in SST influenced the timing of the descent.

#### Seasonal changes on the population structure of *C. hyperboreus*

Studies based on net sampling have reported that adult females and C5 dominate during autumn and winter while young stages (C1–C4) are abundant during spring and summer in surface water layers (Hirche, 1997; Ashjian *et al.*, 2003). Our sediment trap sampling at ~200 m depth, however, does not reflect the total *C. hyperboreus* community but only the fraction of the population that seasonally migrates, i.e. potentially C3, C4, C5 and adults, which overwinter (Falk-Petersen *et al.*, 2009; Ji *et al.*, 2012). In agreement, we found only late developmental stages, mostly females and C5, and also C4 in low percentages (<10%) indicating that these were the overwintering stages at all three locations. Adult females were the most dominant stage in all regions during both the ascent and the descent periods, possibly because they reside at relatively shallow depths, also during winter, compared to other copepodite stages (C3 to C5; Ashjian *et al.*, 2003; Kvile *et al.*, 2019), and thus may swim more often into the traps except for ascent and descent phase. They were, however, found more frequently in spring and autumn, suggesting that they then migrated over more than 200 m depth. C4 and C5 were often absent in the sediment traps and frequently found in spring and autumn, contributing together with the females to an overall increase in total flux. The distribution patterns of these developmental stages thus seem to differ from that of the females, confirming previous studies (e.g. Ashjian *et al.*, 2003).

The population structure is expected to reflect the duration of the life cycle, i.e. if we find overwintering copepods as young as C3, the life cycle should be 4 years while a population consisting of C5 and females suggests a 2-year life cycle. In our data, we found the lowest percentage of C4, which would be indicative of life cycle of more than 3 years, in the northern Chukchi Sea. In the Fram Strait, C4 were found in each year,



but their percentage did not exceed 20% while they—at times of seasonal migration—reached >25% in the MacKenzie Trough. This could suggest that the copepods in the latter area have the longest life cycle while copepods in the Chukchi Sea had the shortest.

It is generally assumed that the life cycle is shorter in low-latitude and coastal areas than at high latitudes (Falk-Petersen *et al.*, 2009), mainly because growth rates increase with high water temperature and food availability (Ji *et al.*, 2012). In the Fram Strait, despite being located at the highest latitude of all three locations, our data suggest that a large part of the population quickly develops to the subadult stage C5. It is possible that here the relatively warm Atlantic Water allows for the rapid growth, and thus, for life cycles of 1–2 years, similar to the Greenland Sea and the Norwegian Sea (Falk-Petersen *et al.*, 2009). Usually, the percentage of the C5 was higher during descent periods than during ascent periods, which suggests that the overwintering C5 molted at depth into C6F and migrated to the surface (<200 m) in the following year as shown previously (e.g. Conover, 1988).

In the northern Chukchi Sea, the open-water period was shorter and the SST was much lower than in the two other areas. Under these harsh conditions, it is possible that the population consisted mostly of surviving adult females and only few C5, and that recruitment was limited. This is also in agreement with the overall lowest fluxes, which may mirror the small size of the *C. hyperboreus* population in this area. It is possible that some younger stages (C1–C5) might have been advected from the continental slopes where they are more abundant than in the basins (Hirche, 1991; Hirche and Mumm, 1992; Kosobokova and Hirche, 2009; Kvile *et al.*, 2018; Ershova *et al.*, 2021). However, current direction and velocity near the sediment trap were almost constant and slow throughout the year (Matsuno *et al.*, 2014; Onodera *et al.*, 2016) and, therefore, we believe that the contribution of copepods being transported into the region was minimal.

In the MacKenzie Trough, the copepodite stage composition differed between the ascent and descent periods; specifically, the proportion of C4 during the descent was higher during the ascent. This suggests that overwintering C4 molted at depth into C5 and migrated to the surface (<200 m) in the following year (e.g. Conover, 1988). In this area, the highest numbers of *C. hyperboreus* were found in the sediment traps, suggesting that in this a large population exists. The MacKenzie Trough might thus be a suitable habitat for *C. hyperboreus* as has been shown for other locations close to the coast (Kvile *et al.*, 2018; Ershova *et al.*, 2021).

## CONCLUSIONS

In this study, time-series sediment trap samples were used to investigate regional differences in *C. hyperboreus* population dynamics in the Arctic Ocean. The flux of *C. hyperboreus* varied with season, which likely reflected the SVM. While the timing of the ascent was similar in all three regions, the descent was more variable in time, with the population in the Fram Strait being the earliest migrating downwards. Also, the total flux was different among regions. If we assume that the flux reflects the size of the

population inhabiting the water column in the respective areas, the population at the MacKenzie Trough is the largest, followed by the populations in the eastern Fram Strait and the northern Chukchi Sea.

In the future, changes in hydrography (e.g. reduction in sea-ice coverage, increasing water temperatures) and in primary production (e.g. timing of phytoplankton blooms, composition of phytoplankton communities) will likely affect the life cycle and distribution of the herbivorous *C. hyperboreus*. With increasing water temperature, the duration of their diapause decreases (Ji *et al.*, 2012), and gonad maturation proceeds faster, which may lead to earlier spawning (Hildebrandt *et al.*, 2014). *Calanus hyperboreus* might also become more frequent at higher latitude in the Central Arctic Ocean (Carstensen *et al.*, 2012; Ji *et al.*, 2012; Chust *et al.*, 2014) where its contribution to the biological pump could increase due to their overwintering at great depths where they respire carbon that had been stored during feeding at the surface (Jónasdóttir *et al.*, 2015). It is thus important to fully understand the relation of environmental conditions and life cycle events in *C. hyperboreus*, and our data suggest that time-series data from sediment traps deployed in various areas of the Arctic Ocean could in the future help to assess the impact of climate change on this Arctic key species.

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## DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author, K.T., upon reasonable request.

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