

Accelerated recruitment of copepod *Calanus hyperboreus* in pelagic slope waters of the western Arctic Ocean

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Abstract

Shelf-basin advection is essential to subsistence of the Arctic copepod *Calanus hyperboreus* population in high basin area. Its abundance, population structure and body size in pelagic layer were investigated with samples collected over a large range in the western Arctic Ocean during summer 2003, to evaluate the geographical variation in recruitment pattern. *Calanus hyperboreus* was absent from the shallow areas of the Chukchi Sea and most abundant in the slope area between the Chukchi Sea and Chukchi Abyssal Plain (CS-slope). Total abundance varied between 1110.0 and 5815.0 ind./m² in the CS-slope area and ranged from 40.0 to 950.0 ind./m² in the other areas. Early stages (CI–IV) dominated in the CS-slope area, whereas CV and adult females were frequently recorded only in deep basin areas. Geographical difference of prosome length was most evident in CIII, with average ranging from 2.48 to 2.61 mm at the CS-slope stations and 2.16–2.37 mm at the others. Abundance of early developmental stages (CI–CIV) correlated positively with Chl *a* concentration, but negative correlation was observed in late stages (CV–adult). Our results indicated that *C. hyperboreus* can benefit from primary production increase through accelerated development in the first growth season and the productive CS-slope area is a potential source for slope-basin replenishment.

Key words: continental slope, prosome length, population structure, food availability, life cycle

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1 Introduction

Calanus hyperboreus is a large calanoid copepod widely distributed in the Arctic Ocean, accounting for a large proportion of the zooplankton biomass. In adaptation to the extreme polar environment, it has evolved capability of pre-bloom spawning fueled by lipid accumulation, diapausing at earlier copepodite stages and utilizing ice-algae as a food source (Smith and Schnack-Schiel, 1990; Hirche, 1997; Ji et al., 2012). However, based on evidences from population structure, grazing capacity and simulated development duration, populations of *C. hyperboreus* may still be not self-sustaining in the central Arctic Basin, but must be replenished by advection of individuals produced in the shallow and coastal regions (Rudiyakov, 1983; Olli et al., 2007; Ji et al., 2012). High abundance of early copepodites (CI–CIV) had been frequently reported in shelf regions in the Atlantic sector, but it is uncertain whether shallow areas of the western Arctic Ocean can serve as possible origins, as *C. hyperboreus* was absent from some shelf waters such as the Chukchi Sea (Hopcroft et al., 2010).

Comparing to the central Arctic Basin, higher water temperature and longer growth season in shallow shelf regions lead to shorter life cycle and thus higher recruitment rate. Over its geographical distribution, *C. hyperboreus* developed flexible life history durations ranging from 1 to >4 years. In the first year, the

new cohorts develop to copepodite Stage III (CIII) and accumulate energy for overwintering in deep layers (Conover, 1988). For the following years, they can overwinter further in Stages CIV, CV or CVI, depending on various development rates (Hirche, 1997). Annual life cycle was proposed only in warmer regions of the North Atlantic, such as the Gulf of Maine and Norwegian Sea (Conover, 1988). An at least 4-year life cycle was observed in the central Arctic Basin and other high latitude areas. Meanwhile, in the Greenland Sea shorter life cycle was observed in warm West-spitsbergen Current waters comparing to cold Greenland Sea Gyre waters (Hirche, 1997). Until now, there is no report on shortened life cycle duration of *C. hyperboreus* in the western part of the Arctic Ocean, as southern distribution into subarctic or shelf waters is not observed in this sector.

Furthermore, distribution and recruitment rates of *C. hyperboreus* can be influenced by food supply. Longer lifespan and higher egg production were observed in fed females than those starved in both laboratory incubations and natural environments (Conover, 1967; Hirche, 2013). In the North Water polynya and Barrow Strait area, recruitment success of early copepodites (CI–CIV) increased primarily with Chl *a* concentration for *C. hyperboreus*, and the availability of Chl *a* rather than temperature was suggested the factor triggering *Calanus* recruitment

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(Ringuette et al., 2002). On shelf-basin transects, elevated biomass of *C. hyperboreus* was observed in margin parts off the Laptev Sea with the recurrent polynya as a feeding hot spot for filter feeders (Kosobokova and Hirche, 2009).

In the western Arctic Ocean with significant geographical variation in primary production rate, elevated standing stocks of zooplankton had been recorded in the Chukchi Shelf areas receiving more nutrient-rich Pacific and fluvial waters (Grebmeier et al., 1995). Although the perennial northward current and shallow water depth prevent the arrival of *C. hyperboreus* into the Chukchi Sea, it can still reach the slope areas with high primary production. Thereafter, accelerated development elevated recruitment is expected. Moreover, this area has shown the largest changes in sea-ice coverage (Parkinson and Cavalieri, 2008) and massive under-ice phytoplankton bloom (Arrigo et al., 2012). Studies on the response of the predominant large calanoid copepods can favor the prediction of climate-induced effects on secondary production.

The objectives of our study include: (1) if the productive shelf region in the western Arctic Ocean can serve as a resource for advection to central basin; (2) how development of *C. hyperboreus* benefits from slope environments. Based on 43 zooplankton samples collected in pelagic layers from 37 stations in the Canada Basin, Chukchi Plateau, Chukchi Abyssal Plain and Chukchi Sea, distribution pattern of *C. hyperboreus* was defined. Its development regime was investigated with population structure and size frequency distribution of prosome length of CIII-adult. Their correlation with environment condition was statistically analyzed. Potential impact of global warming is also discussed, based on environmental preferences of this species.

2 Materials and methods

2.1 Field observations

The 2nd Chinese Arctic Research Expedition was carried out

from 29 July to 7 September 2003 over a large area including the Chukchi Sea, Chukchi Abyssal Plain, Chukchi Plateau and Canada Basin (Fig. 1). Multi-disciplinary observation was carried out at 37 stations, with six of them (R06–14, P11) investigated twice (Table 1).

At each station, ice coverage was estimated by direct visual observation. Temperature and salinity were measured with a Mark III CTD. Water samples for Chl *a* concentration were collected with Niskin bottles at depths of 1, 10, 20, 30, 50, 75, 100, 150 and 200 m. A total of 250 mL of natural seawater was taken from each sample and filtered through Whatman GF/F filter. Each filter was extracted with 90% acetone for 24 h at 0°C and fluorescence was measured with a Model 10 Turner Designs fluorometer.

Quantitative zooplankton sampling was conducted at all stations with a conical net (mouth area 0.5 m²; mesh size 330 μm). The net was hauled vertically from within 3 m of the bottom to the surface at 0.5 m/s at stations shallower than 200 m and from 200 m to surface at deep stations. Samples were preserved in buffered 5% formalin seawater.

2.2 Sample counting and prosome length measurement

In the laboratory, copepodite stage compositions were determined with the aid of a dissecting microscope according to morphological characters for *Calanus* species (Marshall and Orr, 1955; Li and Fang, 1990) and body size for *C. hyperboreus* (Hirche, 1997; Melle and Skjoldal, 1998). Integrate abundance of *C. hyperboreus* in the uppermost 200 m were here presented as individuals per m² (ind./m²) taking into account the different sampling depth (Plourde et al., 2003; Ota et al., 2008; Thor et al., 2008; Broms et al., 2009). Prosome length, from the anterior end of the cephalosome to the posterior lateral edge of fifth metasome segments, was measured using a graticule in the microscope eyepiece. Prosome lengths measurement was carried out only for later stages with fully developed prosome somites and making up the vast majority of overwintering population. The

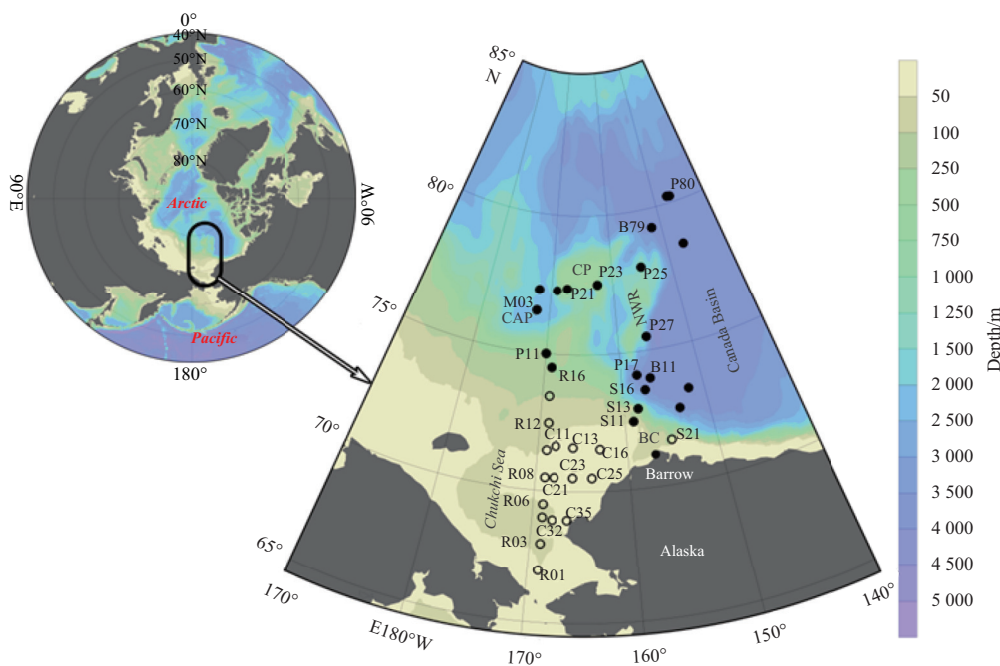


Fig. 1. Location of the study area and zooplankton sampling stations in the 2nd Chinese Arctic Research Expedition during 29 July to 7 September 2003 in the western Arctic Ocean. Black dots represent stations where *Calanus hyperboreus* was observed. Geographical locations are abbreviated as follows: BC, Barrow Canyon; CAP, Chukchi Abyssal Plain; CP, Chukchi Plateau; NWR, Northwind Ridge.

Table 1. Water depth (m), date and ice coverage (%) of all zooplankton stations in the 2nd Chinese Arctic Research Expedition during 29 July to 7 September 2003 in the western Arctic Ocean

Station	Depth/m	Date	Ice/%	Station	Depth/m	Date	Ice/%
R01	49	29 Jul.	0	R16	180	9 Aug.	50
R03	57	29 Jul.	0	P11	260	9 Aug.	60
R06	51	30 Jul.	0	P17	2 500	11 Aug.	20
R08	35	30 Jul.	0	B11	3 000	11 Aug.	20
R10	48	30 Jul.	0	B13	3 000	14 Aug.	50
R12	76	31 Jul.	5	S25	3 000	14 Aug.	20
R14	115	1 Aug.	80	S11	52	17 Aug.	20
C11	48	3 Aug.	50	S13	1 330	17 Aug.	10
C13	43	3 Aug.	10	S16	3 000	17 Aug.	5
C16	42	3 Aug.	80	P27	3 050	18 Aug.	50
S21	70	5 Aug.	20	B80	3 800	24 Aug.	95
C25	41	6 Aug.	0	P80	3 800	25 Aug.	95
C23	44	6 Aug.	0	B79	3 800	26 Aug.	20
C21	46	6 Aug.	0	B78	3 800	29 Aug.	95
C35	32	7 Aug.	0	P25	1 805	4 Sep.	80
C32	50	7 Aug.	0	P23	2 200	5 Sep.	70
R05	51	7 Aug.	0	P21	530	6 Sep.	70
R06-2	51	8 Aug.	0	M01	1 546	6 Sep.	50
R08-2	37	8 Aug.	0	M02	2 400	6 Sep.	60
R10-2	51	8 Aug.	0	M03	2 400	7 Sep.	80
R12-2	75	8 Aug.	0	P11-2	250	7 Sep.	20
R14-2	118	9 Aug.	50				

Note: Repeat samplings at same stations was marked by the suffix “-2”.

original sample was divided with plankton sample splitter, and at least 10% of that was counted for population structure and abundance. For prosome length measurements, no more than 150 individuals from each stage were measured at each station.

2.3 Data analysis

In the present study, hydrological conditions and Chl *a* concentrations were shown in detail only at those stations with *C. hyperboreus* present. In order to check the possible overlap of cohorts with different geographical and temporal origins, normality of size frequency distribution was checked with one-sample Kolmogorov-Smirnov Test on all measured stages from each station and the entire investigation, respectively. Significance of influence from food availability and temperature was analyzed with Spearman rank correlation on abundance and proportion of each stage, as well as average prosome length of CIII-adult. As diel vertical migration was unknown, food availability was analyzed in terms of column averaged and maximum Chl *a* concentration, respectively. Their correlation with temperature was tested as both column average and surface value. All the statistics were run with software SPSS 16.0.

The relationships between abundances of each development stage and environmental variables were examined with Canonical Correspondence Analysis (CCA) on software CANOCO 4.5. After test of the length of gradients with Detrended Correspondence Analysis, CCA was performed on log transformed data. The significance of environmental variables to explain the variance of abundances in CCA was tested using forward selection of Monte Carlo simulations.

3 Results

3.1 Environmental conditions

This investigation covered a large area varying from ice-free

shallow neritic to fast ice-cover deep basin areas. *Calanus hyperboreus* was presented at all stations deeper than 200 m, but was absent from all shallow stations except Stas R16 and S11 close to the basin (Fig. 1). Ice coverage at stations with *C. hyperboreus* occurrence varied from 10% to 95%. The highest ice coverage was observed at 80°N stations, where sampling was conducted in narrow polynias surrounded by thick sea ice. Ice coverage was lowest in the slope area near Barrow, Alaska. Sea ice retreat was observed at duplicated stations. At Sta. P11, ice coverage decreased from 65% on 9 August to 20% on 7 September (Table 1).

Temperature-salinity characteristics identified various hydrographic regimes among stations where *C. hyperboreus* was observed. Warm high-salinity water ($S > 34$, $T > -1.0^{\circ}\text{C}$) was observed in 150–200 m layer at stations in the north Canada Basin and Chukchi Plateau, as well as Stas P11 and R16 in the slope area between the Chukchi Sea and Chukchi Abyssal Plain (CS-slope), but absent at stations in the south Canada Basin and slope areas (Fig. 2). Salinity higher than 34.5 was observed only at 200 m depth at Sta. P11, where temperature was also as high as 0.25°C . At the adjacent Sta. R16, temperature and salinity were -0.53°C and 34.3 respectively. At all stations, surface temperature varied between -1.56 (M03) and -0.56°C (S16), and surface salinity varied between 27.56 (B13) and 29.86 (B80 and P80). High sub-surface temperature ($>0^{\circ}\text{C}$) was detected only at Stas S25 and P27 in the south Canada Basin. Halocline was commonly observed at all stations in 30–60 m layers.

Chl *a* concentration was high and more variable above 100 m depth, and lower than $0.10\ \mu\text{g/L}$ at all stations under 100 m depth (Fig. 2). At the northernmost Stas P80 and B80 with highest ice coverage, Chl *a* concentration was highest (0.21 and $0.23\ \mu\text{g/L}$) in surface layer, whereas sub-surface maximum was observed at the other stations. Extremely high concentrations of 8.60 and $39.10\ \mu\text{g/L}$ were observed at 20 m and 30 m depth at Stas R16 and S11, respectively. Except these two stations, the maximum Chl *a* con-

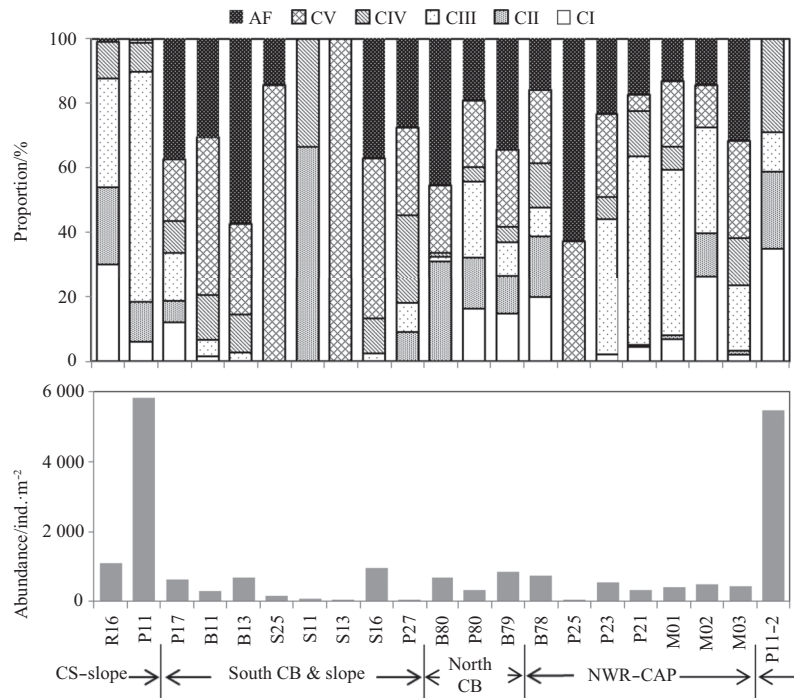


Fig. 3. Total abundance and proportion of each development stages of *Calanus hyperboreus* (AF, adult female) in the western Arctic Ocean, with geographical regions shown in same abbreviations with Fig. 2.

Table 2. Spearman’s rank correlation coefficient (r_s) between column average (Ave.) and maximum (Max.) Chl *a* concentrations and abundance, proportion, and average prosome length of each development stage of *Calanus hyperboreus* from various samples (*N*) in the western Arctic Ocean during 29 July to 7 September

Stage	Abundance				Proportion				Prosome length			
	Ave.		Max.		Ave.		Max.		Ave.		Max.	
	r_s	<i>N</i>	r_s	<i>N</i>	r_s	<i>N</i>	r_s	<i>N</i>	r_s	<i>N</i>	r_s	<i>N</i>
CI	0.220	21	0.306	21	0.157	21	0.211	21	-	-	-	-
CII	0.171	21	0.179	21	0.193	21	0.155	21	-	-	-	-
CIII	0.463*	21	0.497*	21	0.384	21	0.390	21	0.441	18	0.534*	18
CIV	0.391	21	0.485*	21	0.414	21	0.519*	21	0.067	18	0.260	18
CV	-0.532*	21	-0.557**	21	-0.522*	21	-0.546*	21	0.414	19	0.520*	19
AF	-0.427	21	-0.441*	21	-0.537*	21	-0.442*	21	-0.051	19	-0.121	19

Note: ** Significant at the 0.01 level (2-tailed); * significant at the 0.05 level (2-tailed).

ant correlation between average prosome length at each station and Chl *a* concentration was detected only in CIII and CV (Table 2), in which average prosome length increased with maximum Chl *a* concentration.

According to one-sample Kolmogorov-Smirnov Test, normality was accepted for each developmental stage from all stations ($P > 0.05$; Table 3), except CIV at Sta. P11-2 ($P < 0.05$). However, normality was rejected for all the measured developmental stages as a whole, and asynchronous recruitment in various regions was accepted. The frequency distribution was positively skewed for CIII and negatively skewed for the other stages, indicating that asynchrony in newborns may be resulted from accelerated growth in some individuals and that in overwintered stages was induced by retarded development. The absolute values of skewness increased from CIV to AF, showing that individuals shorter than mode size increased in number with age.

3.4 Canonical correspondence analysis

The two first axes in CCA, with eigenvalues of 0.085 and 0.018, explained a total of 20.1% of cumulative variance in abundance

data, and 98.2% of the correlations between environmental variables and abundance. After forward selection, four variables (in descending order, average Chl *a* concentration, surface temperature, ice coverage and surface salinity) played significant role ($P < 0.05$) on the geographical distribution of each development stage. Based on the intersect correlations, Chl *a* and salinity were largely related to the first axis, while temperature and ice coverage were respectively positively and negatively related to the second axis.

With regard to the ordination (Fig. 5), environmental conditions were less variable at deep basal stations comparing to shelf stations. Most of the basal stations located near the ice coverage arrow, whereas scattered distribution was observed on the CS-slope stations. Abundance of each development stage was associated mainly with Chl *a* concentration, with CI and CII at higher but CV and female at lower value.

4 Discussion

Although *C. hyperboreus* is absent from shelf waters of the

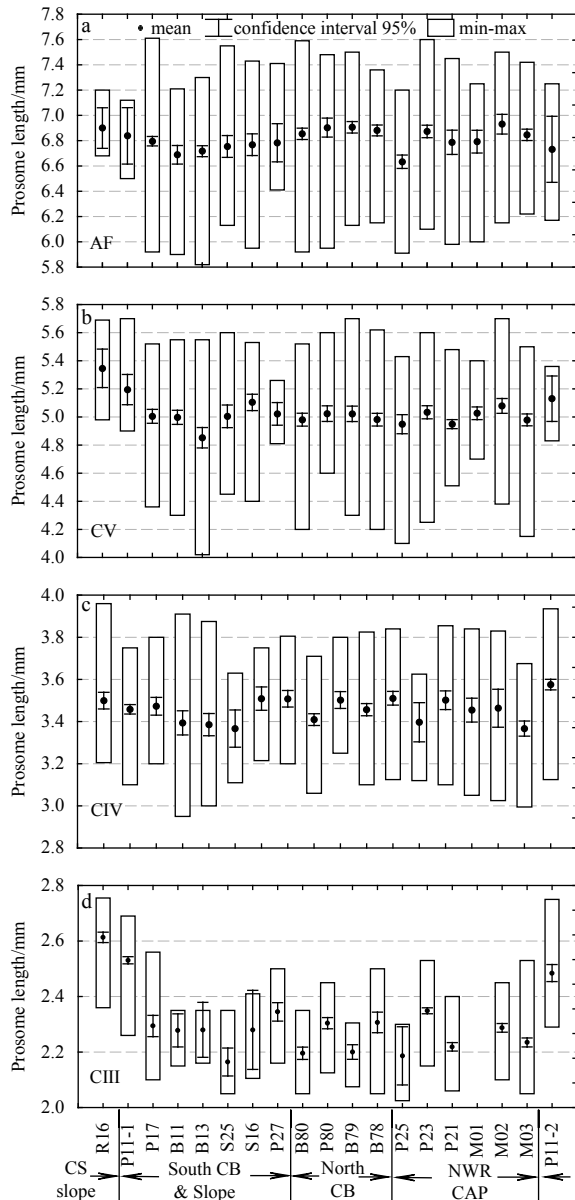


Fig. 4. Geographical variation in prosome length of *C. hyperboreus* in late Stages CIII, CIV, CV and adult female (AF), shown by average, range and 95% confidential intervals at each station. Geographical regions were shown in same abbreviations with Fig. 2.

Chukchi Sea, we find that the slope area between the Chukchi Sea and Chukchi Abyssal Plain (CS-slope) was a hotspot for population development. As outlined in the introduction, shorter life cycle and high recruitment rate were expected in shelf waters with high food availability. Here we first assess variation in life cycle through geographical distribution, population structure and body size, and subsequently consider the possibility of slope-basin advection.

4.1 Accelerated development in slope area

The most important finding in our study is that CIV can be achieved in one growing season in the productive CS-slope area. In the multi-year life cycle of *C. hyperboreus*, it was commonly accepted that CIII is attained in the first year and descended to

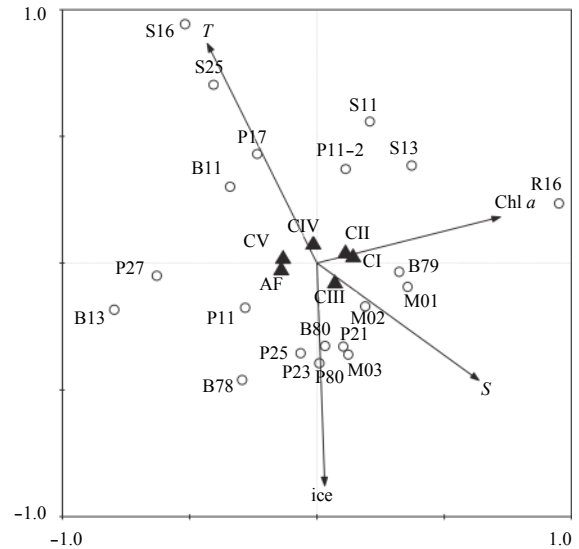


Fig. 5. Ordination diagram of canonical correspondence analysis showing abundance of each development stage (triangle) and selected environmental variables (arrows) at sampling stations (circle). Chl *a* represents average Chl *a* concentration, *S* surface salinity, *T* surface water temperature, and *Ice* ice coverage.

the deep layer as the main overwintering stage (Hirche, 1997). Most of the overwintered CIIIs molted to CIV from May to July in the next year (Dawson, 1978; Hirche, 1997). At the SHEBA station, which drifted from the Canada Basin over the Northwind Ridge and Chukchi Plateau and back over the basin, average prosome length of CIII was highest in May, the claimed molting season for overwintered individuals (Ashjian et al., 2003), but it was still lower than that in CS-slope area in our study. In our study, an overwhelming majority of CIIIs in CS-slope area were larger than the median of its size range in previous reports (Table 4). Meanwhile, at the other stations, prosome length of most CIIIs were shorter than the median of reported size range, and on average shorter than the station specific minimum at SHEBA station. We suggest that, only in CS-slope area, CIII can reach molting size in August of the first growing season.

According to temporal variation at the same sampling site from August (Sta. P11) to September (P11-2), molting from CIII to CIV was suggested during this period, as both abundance and proportion decreased in CIII but increased in CIV. Simultaneously, prosome length of CIII decreased on average, the same as the SHEBA station results. Normality was not significant for size frequency distribution of CIV at Sta. P11-2, indicating overlap of different cohorts. In the Resolute Passage (Conover, 1988) and Barrow Strait (Conover and Siferd, 1993), CIV had been recorded as the dominant overwintering stage, although its achievement in one growing season was still doubted. However, its further development to CV was suggested occurring separately in early spring and summer (Conover and Siferd, 1993), showing that the overwintered CIVs contained cohorts with different temporal origin. Thus, at least a part of the newborns of *C. hyperboreus* can develop to CIV before winter in the shelf waters of the western Arctic Ocean.

In previous studies carried out in semi-closed coastal regions, no marked temporal pattern was observed in prosome length of *C. hyperboreus* in Stages CIII–CV during the bloom period, and its somatic growth was detected mainly as an increase in dry weight or carbon content (Plourde et al., 2003; Swalethorp et al., 2011).

Table 3. Normality test on frequency distribution of *Calanus hyperboreus* prosome length, calculated with one-sample Kolmogorov-Smirnov Test

Station	CIII		CIV		CV		AF	
	N	A.S.	N	A.S.	N	A.S.	N	A.S.
R16	92	0.11	60	0.73	11	0.97	9	0.89
P11	129	0.17	124	0.42	20	0.36	6	1
P17	36	0.43	50	0.92	122	0.73	219	0.09
B11	8	0.72	42	0.64	106	0.56	80	0.32
B13	5	0.92	45	0.61	77	0.85	180	0.23
S25	13	0.84	15	0.98	51	0.96	41	0.79
S13	12	0.95	6	0.99	11	1	10	0.67
S16	6	0.83	26	0.89	77	0.49	66	0.7
P27	28	0.93	44	0.35	13	0.92	14	0.45
B80	40	0.56	122	0.44	92	0.69	164	0.08
P80	55	0.82	53	0.59	61	0.77	68	0.96
P79	26	0.89	124	0.35	82	0.76	149	0.13
P78	33	0.77	87	0.12	102	0.57	126	0.14
P25	7	0.91	14	1	58	0.64	102	0.96
P23	140	0.09	43	0.82	89	0.57	109	0.23
P21	106	0.31	33	0.62	119	0.59	50	0.59
M01	–	–	–	–	53	0.79	45	0.35
M02	106	0.10	21	0.89	73	0.94	56	0.81
M03	129	0.06	74	0.93	140	0.07	113	0.43
P11-2	59	0.23	149	0.04	7	1	10	0.99
Total	1 018	0	1 126	0.01	1 126	0	1 607	0

Note: N represents number of measured individuals from each developmental stages, and normal distribution was identified by A.S. (asymptotic significance) greater than 0.05 (boldface).

Table 4. Comparison of individual and station average prosome length (PL) of *Calanus hyperboreus* from previous reports and our study in the western Arctic Ocean during 29 July to 7 September 2003

Location	Data type	Time	Range of PL/mm			
			CIII	CIV	CV	AF
LSLE	individual	main and post bloom period	no data	3.0–3.8	4.0–5.2	5.0–6.5
GSG & WSC	individual	Feb.–Dec.	2.0–3.0	2.9–4.1	4.2–5.8	5.9–7.4
WAO	average	Feb.–Oct.	2.42–2.60	3.49–3.71	5.02–5.09	6.62–6.90
Our study	individual	Jul.–Sep.	2.00–2.75	2.80–3.95	4.00–5.60	5.90–7.50
	average		2.16–2.61	3.37–3.58	4.85–5.35	6.63–6.93

Note: LSLE represents the lower St. Lawrence Estuary (Plourde et al., 2003), GSG & WSC the central Greenland Sea Gyre and the West Spitsbergen Current (Hirche, 1997), and WAO the western Arctic Ocean (Ashjian et al., 2003).

However, according to our results, the prosome length achieved in various regions might increase with local food availability. Significant correlation between prosome length and Chl *a* concentration was observed in both CIII (the new-born generation) and CV (the overwintered population). Additionally, prosome length of CIV increased significantly from August to September at the same Sta. P11. Thus, its somatic growth pattern may change with various environmental conditions. In the Barrow Strait, less lipid storage was recorded in CIII and CIV, but they can still successfully overwinter along with the lipid-rich CV stages (Conover and Siferd, 1993).

The recorded abundance of early stages (CI–CIV) in CS-slope area was as high as that observed in other shallow Arctic areas (Hirche et al., 1994; Hirche, 1997; Swalethorp et al., 2011). Cross shelf abundance gradients of *C. hyperboreus* have been observed along the margins of the deep Nansen, Amundsen and Makarov Basins, and an elevated biomass was observed in the margin off the Laptev Sea (Kosobokova and Hirche, 2009). It was indicated that, though *C. hyperboreus* is absent from shallow shelf areas of the western Arctic Ocean, the CS-slope area can serve as a hot-

spot of population recruitment, through acceleration in both development and recruitment rates.

4.2 Food-dependent development

Food limitation to *C. hyperboreus* was commonly observed in natural environments. Estimated *in situ* grazing rates for the large copepod species were less than 10% of their maximum rates in a melt water influenced Greenlandic fjord (Tang et al., 2011) and *in situ* rates for *C. hyperboreus* and *C. glacialis* in the central Arctic Ocean were only about 3% and 20% of the expected food-saturated ingestion rates (Olli et al., 2007). However, *C. hyperboreus* has great potentiality to take advantage of the elevated food supply, as non-selective and non-saturated feeding was observed. It removed all types of phytoplankton in direct proportion to their abundance at Chl *a* concentrations ranging from 0.53 to 12.1 mg/m³ (Huntley, 1981). Thus, recruitment success in early copepodites (CI–CIV) of *C. hyperboreus* increased primarily with food availability once the recruitment had started (Ringuelette et al., 2002).

In the western Arctic Ocean, alleviated primary production

was induced mainly by intrusion of nutrient-rich Pacific water (Nishino et al., 2008). However, in agreement with previous report (Hopcroft et al., 2010), *C. hyperboreus* cannot arrive the productive shelf waters of the Chukchi Sea. High food availability is also expected in the CS-slope area, as mesoscale eddies can bring episodic pulses of nutrients into the euphotic zone. During an investigation on a warm-core eddy in the southwestern Canada Basin, 30% higher biomass of pico-phytoplankton was sustained than in the surrounding water (Nishino et al., 2011). In another study, elevated concentrations of most zooplankton taxa were observed in eddies (Llinás et al., 2009). Though Chl *a* concentration at Sta. P11 was low on average, subsurface maximum was observed in both August and September, indicating high food availability.

Besides higher Chl *a* concentration in the CS-slope area, earlier onset of spring bloom may also contribute to the flexible life cycle. Under-ice phytoplankton blooms were observed widely in polar regions, including the Canadian Beaufort Sea and north part of Chukchi Sea (Mundy et al., 2009; Arrigo et al., 2012). Spawning of *C. hyperboreus* is fueled by lipid storage; the spring ascent was prior to or in association with the break-up of sea ice and the development of the spring phytoplankton bloom (Madsen et al., 2001). In the eastern sector of the North Water, the recruitment of the first cohort of copepodites of *C. hyperboreus* coincided with the onset of the bloom and occurred before any significant increase in temperature (Ringuette et al., 2002).

As our investigation was carried out in summer, positive correlation between abundance and Chl *a* concentration and accelerated development were observed mainly in CIII. Reproduction of *C. hyperboreus* starts before May, and most of the new generation has developed to CIII in August, so that correlation between abundance and Chl *a* concentration was not significant in CI and CII. Besides simultaneous food availability, body size and abundance of late stages (CIV–adult) can be influenced by conditions in the past growing seasons and physical advection. Well-developed individuals can be transported from productive shelf waters to barren basin areas, but we still cannot explain the significant negative correlation in CV.

4.3 Possibility of slope-basin advection

The mismatch between distribution centers of early (CI–IV) and late (CV–adult) stages demonstrates the importance of advection processes to population recruitment of *C. hyperboreus*. Prevalence of late stages (CV–adult) had been observed in the central Arctic Basin, the Norwegian Sea and the Chukchi Plateau (Rudiyakov, 1983; Ashjian et al., 2003; Broms et al., 2009). Accordingly, different hypotheses of cross shelf-basin replenishment and insufficient sampling of individuals beneath the ice were put forward as explanations. As our investigation was carried out in August and September and significant ice melting was observed at most stations, underestimation of nauplii and early copepodites was unlikely. According to the reported reproduction season, *C. hyperboreus* spawns from January to May in the central Arctic Ocean (Brodskiĭ and Nikitin, 1955; Johnson, 1963), and CII was commonly observed in the basin area after July (Ashjian et al., 2003). It was also suggested by numerical simulation that some of the new cohort cannot develop to CIII in one growing season (Ji et al., 2012). Considering the shorter prosome length, the early stages observed in the high latitude area in our study might be recruited locally, but the abundance of CIII was much lower than that of CIV–AF. On the other hand, net emigration was indicated by high abundance of early stages and scarcity of late ones in the CS-slope area. Thereafter, it is more likely that the *C. hyper-*

boreus population in the high latitude area is at least partially replenished by advection, and the CS-slope area may be an important potential source.

As early generations can be advected into deep water by the offshore current, backward supplement may also play an important role in the slope-basin interaction, as the CS-slope area tends to be an unfavorable overwintering site for *C. hyperboreus*. In previous reports, copepodite stages later than CIII were observed only at deeper than 300 m in winter, whereas both early and late stages entered upper layers in summer (Hirche, 1997; Ashjian et al., 2003). The two CS-slope stations with high early stage abundance observed in our study are shallower than 300 m. In our results, adult female were extremely scarce at Stas R16 and P11, and their prosome length showed no significant difference with basin stations.

According to previous reports on current regimes, advection between the central Arctic basin and CS-slope area is possible on both back and forth directions. Currents in deep areas in the western Arctic Ocean, such as the Barents Sea Branches of the Arctic Circumpolar Boundary Current flowing continuously along the Siberian Shelf, can reach as far as the Chukchi Plateau (Aksenov et al., 2011). Meanwhile, *C. hyperboreus* can be transported from overwintering depths in the deep basin to the Chukchi Shelf by upwelling (Lane et al., 2008; Llinás et al., 2009). Elevated abundances of Arctic-origin copepods, including *C. hyperboreus*, were recorded in a cold-core eddy in slope area between the Beaufort Sea and Chukchi Sea in summer (Llinás et al., 2009), even though most such eddies probably originated from the edges of the Chukchi and Beaufort shelves and contained water of Pacific origin (Muench et al., 2000). In our study, deep water with higher temperature and salinity reached shallower depth in the northern Chukchi Sea, indicating upwelling of deep waters. On the other hand, its absence in slope area between the Beaufort Sea and Chukchi Sea may be a reason for scarcity of *C. hyperboreus*. Shelfbreak eddies in the western Arctic Ocean last from weeks to more than a year before moving from the Chukchi Shelf into the interior Canada Basin (Manley and Hunkins, 1985), which can act as a possible pathway carrying *C. hyperboreus* from CS-slope into central basin.

Although this is the first time that early stages (CI–CIV) of *C. hyperboreus* was recorded in high abundance in the CS-slope area, its prosperity is always expected whenever overwintered cohort was transported into productive regions influenced by the Pacific waters. In previous studies, both intrusion of *C. hyperboreus* and elevated primary production had been recorded separately in slope regions in the western Arctic Ocean (Llinás et al., 2009; Nishino et al., 2011). Along the margins of the deep Nansen, Amundsen and Makarov Basins, the Arctic Ocean Boundary Current can transport the Atlantic pelagic copepod population into the Siberian shelf waters, where its abundance was further elevated by higher food availability (Kosobokova and Hirche, 2009). Furthermore, based on food-dependent development, accelerated population recruitment was expected in any other regions with elevated primary production or reduced ice coverage, supporting an increase in biomass of *C. hyperboreus* even in the Canada Basin with low phytoplankton biomass through advection (Hunt et al., 2014).

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