



Regional patterns and controlling factors on summer population structure of *Calanus glacialis* in the western Arctic Ocean



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ABSTRACT

In the Arctic Ocean, *Calanus glacialis* is the most dominant species in zooplankton biomass. While important, little information is available concerning the factors controlling their population. In this study, we evaluated regional patterns and environmental factors controlling the population structure of *C. glacialis* in the western Arctic Ocean in summer months (July–October) in 1991, 1992, 2007, 2008, 2010, 2012, 2013 and 2014. To evaluate regional patterns, environmental parameters (temperature, salinity and chlorophyll *a*) and *C. glacialis* population parameters (abundance, biomass, mean copepodid stage and lipid accumulation) were divided into three latitudinal regions. In all three regions from July to October, chlorophyll *a* decreased, while the mean copepodid stage increased. These results suggest phytoplankton blooms occurred early in the sampling period, and *C. glacialis* grew during the period. From Structural Equation Model (SEM) analysis, the controlling factors on the *C. glacialis* population were evaluated. The results of the SEM analysis indicated positive correlations between abundance and biomass; Julian day and mean copepodid stage; and temperature and mean copepodid stage. Additionally, a negative correlation between abundance and mean copepodid stage was observed.

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1. Introduction

Over recent years, drastic sea ice reduction has been observed in the western Arctic Ocean (Markus et al., 2009). As a result of the decreases in sea ice, sea surface water is heated by solar radiation and has warmed over the recent summers in the Arctic Ocean (Steele et al., 2008). As the effect of temperature increases, lower trophic levels of the marine ecosystem structure are reported to be changing in the western Arctic Ocean (Grebmeier, 2012). Thus, northward shifts and species composition changes in the zooplankton community have been reported in the western Arctic Ocean (Matsuno et al., 2011; Nelson et al., 2014; Ershova et al., 2015a).

Calanoid copepod *Calanus glacialis* is a highly dominant zooplankton species and is a key species in the shelf region of the Arctic Ocean (Hopcroft et al., 2010; Matsuno et al., 2012). This species is known to be distributed across the Arctic Ocean, the Bering Sea and the Okhotsk Sea (Conover, 1988). The species grazes on ice-algae and reproduces under sea ice during the spring (Daase

et al., 2013). Recent molecular analysis revealed that populations of *C. glacialis* have different haplotypes between the Arctic Ocean and Bering Sea (Nelson et al., 2009). While the population of the Bering Sea is believed to be transported to the Arctic Ocean through the Bering Strait, it is thought that they may not successfully reproduce in the Arctic Ocean (Nelson et al., 2009).

Because *C. glacialis* is a key species in the Arctic ecosystem, evaluation of the effects of climate change on this species is of special importance. From modelling studies, it is expected that the abundance of *C. glacialis* will decrease in the Arctic Ocean, and their main geographical distribution will be shifted from the Atlantic sector to the Pacific sector until 2099 (Wassmann et al., 2015). From long-term observations in the Chukchi Sea from 1945 to 2012, Ershova et al. (2015b) reported that *C. glacialis* was abundant under the conditions of negative Pacific Decadal Oscillation (PDO) and positive Arctic Oscillation (AO) indices. However, the changing mechanisms of *C. glacialis* population structure (abundance, biomass and development stage) remain unknown, and the effects of environmental factors on their population are still unclear.

In the present study, we evaluated the population structure of *C. glacialis* in the western Arctic Ocean during the summers

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(July–October) of 1991–2014. Their population parameters (abundance, biomass, mean copepodid stage [MCS] and lipid contents of copepodid 5 stage [C5]) were analysed for correlations to various environmental parameters (year, Julian day, latitude, depth, temperature, salinity and chlorophyll *a*) by applying structural equation modelling (SEM). To evaluate regional patterns, these analyses were conducted in three sub-regions separated by latitude in the western Arctic Ocean.

2. Materials and methods

2.1. Field sampling

Zooplankton samplings were conducted at 371 stations, located between 65°39'N–78°52'N latitude and 174°45'E–133°38'W longitude, in the western Arctic Ocean from 7 July to 13 October of 1991, 1992, 2007, 2008, 2010, 2012, 2013 and 2014 (22–63 stations in each year) (Fig. 1). Zooplankton samples were collected by vertical hauls of a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm) from a 150 m depth (for stations where bottom depth was deeper than 150 m) or 5 m above of sea bottom (for stations where bottom depth was shallower than 150 m). The volume of water filtered through the net was calculated using a flowmeter mounted at the mouth ring of the net. Zooplankton samples were immediately preserved with 5% v/v borax-buffered formalin.

At each sampling station, temperature and salinity were measured by a CTD sensor (Neil Brown Mark 3B in 1991 and 1992, Sea-Bird Electronics Inc., SBE 911 Plus after 2007). After 2007, water samples were collected for chlorophyll *a* (Chl. *a*) concentration from 4 to 9 depths (0, 5, 10, 20, 30, 50, 75, 100, 125 and 150 m, which varied depending on the bottom depth) by a bucket and rosette multi-Niskin samplers mounted on the CTD. The water samples

were filtered through GF/F filters and Chl. *a* was extracted with *N,N*-dimethylformamide and measured by a fluorometer (Turner Designs, Inc., 10-AU-005) using the non-acidified method (Welschmeyer, 1994).

2.2. Samples and data analysis

In the laboratory, *C. glacialis* populations were enumerated by copepodid stage level (C1–C6F/M). For species identification, we referred to Frost (1974). For the C5 stage, the lipid reserves (the lipid length [LL] relative to the prosome length [PL]) were classified into three categories: I (LL is 0–4% of PL), II (LL is 4–40% of PL) and III (LL is >40% of PL). The mean copepodid stage (MCS) of *C. glacialis* was calculated using the following equation:

$$MCS = \frac{\sum_{i=1}^6 i \times A_i}{\sum_{i=1}^6 A_i}$$

where *i* (1–6 indicates C1–C6) is the copepodid stage, and *A_i* (ind. m⁻²) is the abundance of the *i*th copepodid stage. Using the individual wet mass of each copepodid stage (μg wet mass [WM] ind.⁻¹, Matsumo et al., 2012), population biomass (g WM m⁻²) was calculated by multiplying individual wet mass and abundance of each copepodid stage, then summing the whole population of *C. glacialis* (C1–C6).

To evaluate regional differences, the study area was divided into three latitudinal regions: region I (RI, 65–69°N), region II (RII, 69–71°N), region III (RIII, 71–79°N) (Fig. 1). As determined from topography, RI and RII were located in the shelf region, and RIII covered from the slope to the basin regions in the western Arctic Ocean. These three regions correspond to the geographical distribution of water masses. Thus, RI is characterised by warm Pacific

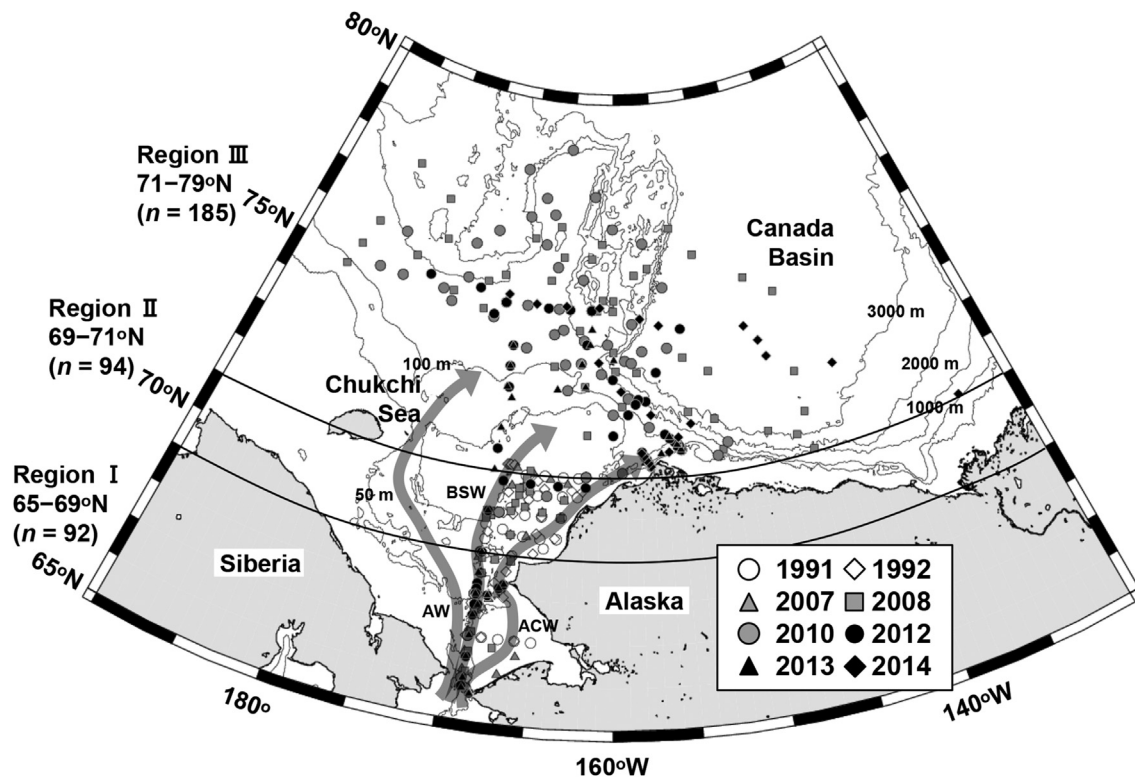


Fig. 1. Location of the sampling stations in the western Arctic Ocean during the summers of 1991–2014. Symbols denote stations where samplings were conducted. Depth contours (50, 100, 1000, 2000 and 3000 m) are superimposed. Latitudinally, stations were separated into three regions: I, II and III. The numbers in parentheses indicate the number of stations contained in each region. Arrows indicate directions of ocean currents. ACW: Alaskan Coastal Water, AW: Anadyr Water, BSW: Bering Shelf Water.

water inflow from the Pacific Ocean through the Bering Strait (Woodgate et al., 2010). RII is located at a branch of three currents: Alaskan coastal water, Anadyr water and Bering shelf water, and their positions vary with wind force and direction (Weingartner et al., 2005). RIII is characterised by deep depths (30–3863 m, mean: 1004 m), while the other regions are shallow (21–60 m, with means of 42–48 m). RIII is dominated by ice-melt water at the surface layer, and eddy formation at the slope region (Nikolopoulos et al., 2009).

To evaluate temporal changes, correlation analyses of environmental parameters (temperature, salinity and Chl. *a*) and *C. glacialis* population parameters (abundance, biomass, MCS and mean lipid accumulation for C5) with Julian day were conducted at each region. To clarify which factors (temporal or spatial) are important for changing the MCS, an analysis of covariance (ANCOVA) with Julian day and region as independent variables was conducted. Correlation analyses and ANCOVA were performed using StatView v5 (SAS Institute Inc., Cary, NC, USA).

To evaluate the environmental factors controlling the changes in the *C. glacialis* population, we applied Structural Equation Model (SEM) analysis (Stomp et al., 2011). For the SEM analysis, environmental parameters (sampling year, latitude, Julian day, bottom depth, integrated mean temperature, salinity and Chl. *a*), *C. glacialis* population parameters (abundance, biomass, MCS and mean lipid accumulation) were normalised (average = 0, standard deviations = 1), and regressions among all parameters were calculated. For the path analysis, we set the parameters three

category levels (1: sampling year, latitude, Julian day and bottom depth, 2: temperature, salinity and Chl. *a*, 3: population parameters of *C. glacialis*). Subsequently, the insignificant relations ($p > 0.05$) between the parameters were removed from the final model. The overall fit of the final model was evaluated by the goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI). The standardized path coefficients were independent variables, which indicate the relative contributions of the different paths within the SEM (Stomp et al., 2011). The SEM analysis was performed using add-in software for MS-Excel (<http://www.ohmsha.co.jp/data/link/978-4-274-06925-3/>).

3. Results

3.1. Temporal changes in hydrography

Throughout the study area, integrated mean temperature at net towed depth (0–150 m) ranged between -1.4 and 10.6 °C (Fig. 2). In terms of temporal changes in temperature during July to October, significant increases and decreases were observed for RII and RIII, respectively, while no relation was recognized for RI. Integrated mean salinity ranged from 28.4 to 33.2, and a significant decrease was only observed in RI (Fig. 2). Integrated Chl. *a* ranged between 7 and 856 mg m⁻². Temporally significant decreases were observed in Chl. *a* at all three regions, but the decreasing rates were faster in RI (Fig. 2).

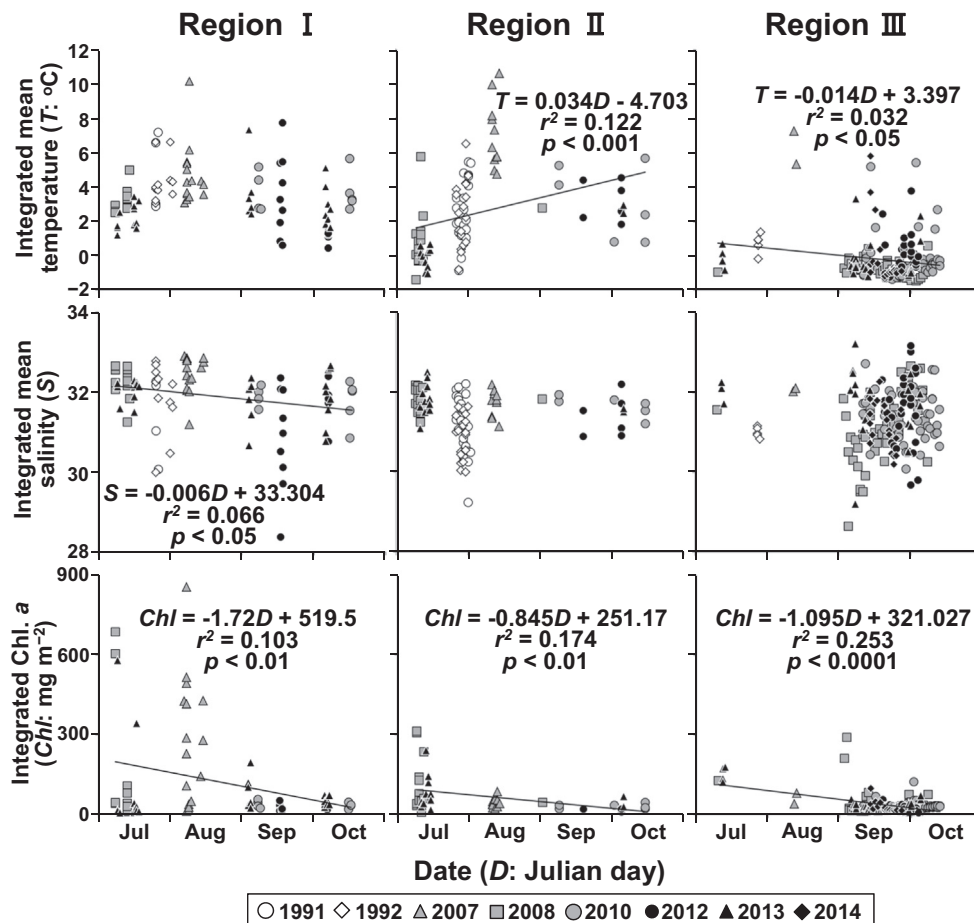


Fig. 2. Temporal changes in integrated mean temperature, integrated mean salinity, and integrated Chl. *a* in three regions (region I, II and III) in the western Arctic Ocean during the summers of 1991–2014. Symbols varied by year.

3.2. Temporal changes in *Calanus glacialis*

Throughout the study period, abundance of *C. glacialis* in the western Arctic Ocean ranged from 58 to 80,317 ind. m⁻². A significant decrease and increase in abundance from July to October was detected for RI and RII, respectively (Fig. 3). The zooplankton biomass was 0.04–72 g WM m⁻², and significant increases were observed in RII and RIII. MCS ranged from 1.6 to 5.2, and significantly increased from July to October in all three regions. Mean values of abundance, biomass and MCS at each region are summarized in Table 1. The ANCOVA showed that Julian day ($p < 0.0001$) was a more important environmental parameter influencing the change in MCS than region ($p < 0.05$) (Table 2). The interaction between Julian day and region also had a significant relationship with MCS ($p < 0.05$). In terms of lipid accumulation, no significant relationship was detected in any region (Fig. 3).

Spatially and temporally changing patterns of *C. glacialis* population structure varied between the abundance and biomass

(Fig. 4). High abundance values were observed in two region and seasons: i.e., RI during July and RIII during September. Furthermore, high biomass values were observed only in RIII during September. MCS also showed differences between abundance and biomass. Thus, MCS was low (ca. 2 MCS) at high abundance stations, while MCS was high (ca. 4 MCS) at high biomass stations. RII showed notably low values for both abundance and biomass throughout the study period.

3.3. SEM analysis

The SEM analysis of this study resulted in fairly high GFI (0.94–0.97) and AGFI (0.94–0.97) for all three regions (Fig. 5). The structure of the factors controlling *C. glacialis* population varied with region: the structure was complicated for RI, while simpler for the other regions (Fig. 5). Throughout the three regions, four relationships were commonly observed: three positive relationships between abundance and biomass (path coefficients: $pc = 0.62$ to

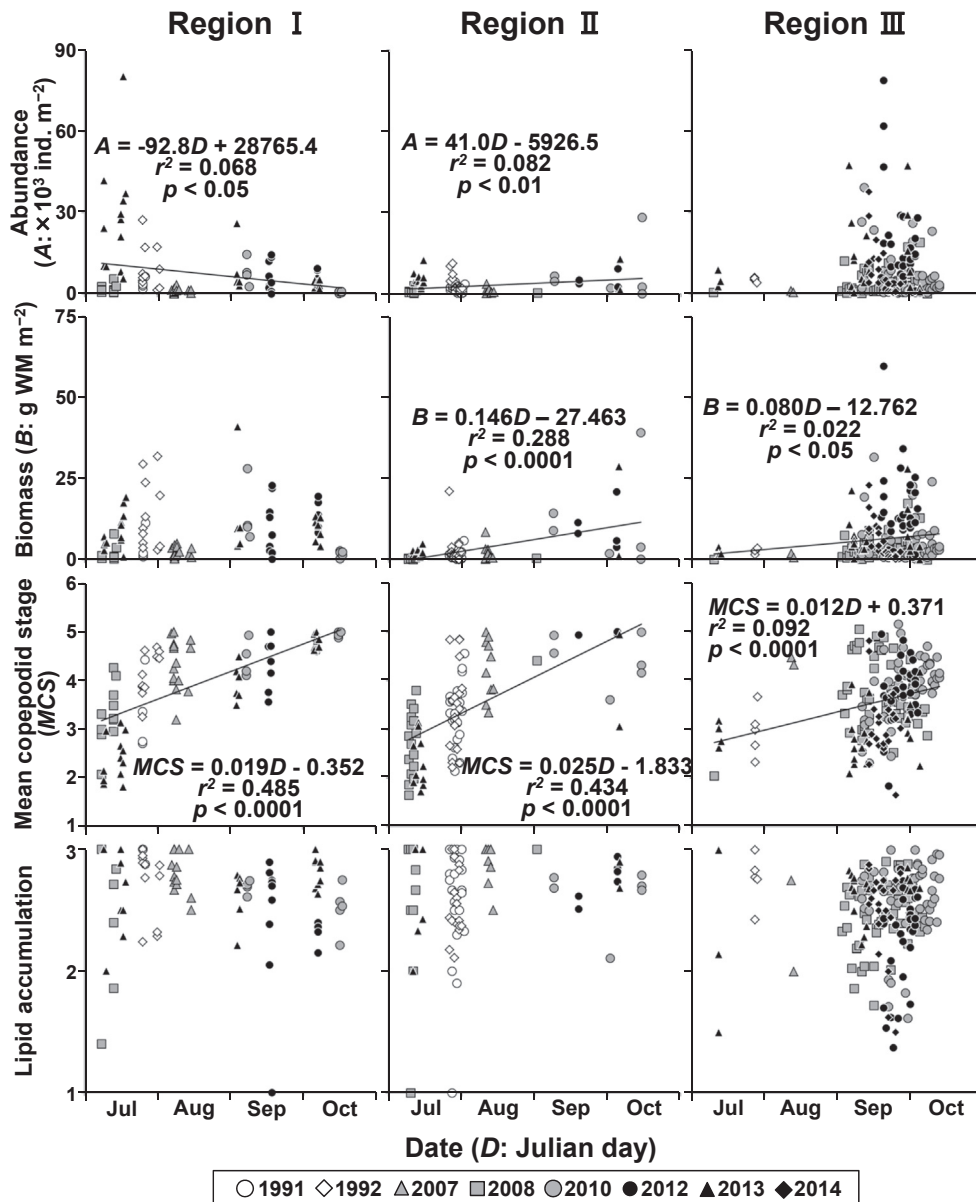


Fig. 3. Temporal changes in abundance, biomass, mean copepodid stage (MCS), and lipid accumulation (C5 stage) of *C. glacialis* in three regions (region I, II and III) in the western Arctic Ocean during the summers of 1991–2014. Symbols varied by year.

Table 1Ranges of abundance, biomass and mean copepodid stage (MCS) in each region (RI–RIII, cf. Fig. 1). Values in parenthesis indicate mean \pm standard deviation.

	RI	RII	RIII
Abundance (ind. m ⁻²)	58–80,309 (7528 \pm 11,679)	64–28,141 (2856 \pm 3760)	85–78,698 (8439 \pm 11,354)
Abundance (ind. m ⁻³)	2–1673 (154 \pm 237)	1–625 (66 \pm 83)	1–934 (80 \pm 126)
Biomass (g WM m ⁻²)	0.16–41.04 (7.68 \pm 8.01)	0.04–37.04 (3.68 \pm 7.12)	0.07–71.74 (7.83 \pm 9.48)
Biomass (g WM m ⁻³)	0.004–0.76 (0.16 \pm 0.15)	0.002–1.05 (0.08 \pm 0.15)	0.001–1.18 (0.07 \pm 0.12)
MCS	1.82–5.00 (3.97 \pm 0.89)	1.65–5.01 (3.44 \pm 0.98)	1.65–5.17 (3.60 \pm 0.73)

0.89), Julian day and MCS (pc = 0.31 to 0.90), and temperature and MCS (pc = 0.38 to 0.52); and one negative relationship between MCS and abundance (pc = –0.53 to –0.40).

4. Discussion

4.1. Spatial and temporal changes in population structure

Calanus glacialis is mainly distributed in the shelf region of the Arctic Ocean (Conover, 1988). The generation length of the species is known to be 1–3 years and varies with region (Falk-Petersen et al., 2009). In the western Arctic Ocean, abundance and biomass of *C. glacialis* are known to vary spatially: high in the shelf region, while low in the basin region (Lane et al., 2008; Hopcroft et al., 2010). Population structure of *C. glacialis* in the western Arctic Ocean during the summer also varies spatially: early copepodid stages dominate the shelf region, while late copepodid stages dominate the basin region (Matsuno et al., 2012).

In this study, areas with low MCS and high abundance showed spatial and temporal patterns similar to those observed in RI during July and RIII during September (Fig. 4). Because low MCS indicates dominance of the early copepodid stages, the spatial and temporal changes in low-MCS and high-abundance areas suggest that there are regional differences in reproductive timing (Fig. 4). Because *C. glacialis* achieves the reproduction stage by grazing on ice-algae in the surface layer, their reproduction timing is known to match to the peak of primary production in each region (Hirche and Kwasiński, 1997; Daase et al., 2013). The regional patterns in timing of the low-MCS period may be a reflection of the regional differences in the timing of the peak of primary production.

From spring to summer, *C. glacialis* in the Chukchi Sea is reported to have more active reproduction on the shelf than in the basin (Plourde et al., 2005). During open water season, nutrients provided by Pacific water result in high primary production on the shelf (Hill and Cota, 2005). Due to this high primary production, it is possible for *C. glacialis* to actively reproduce in the shelf region (Plourde et al., 2005). On the other hand, molecular analysis on *C. glacialis* revealed that there are two haplotypes in the Bering Sea and the Arctic Ocean (Nelson et al., 2009). From long-term observations (1945–2012), the population in the shelf region is considered to be the Bering Sea population, which is transported from the Bering Sea (Ershova et al., 2015a). These facts suggest that the population in RI is the same one transported from the Bering

Sea. These regional differences in population origin may induce the regional differences in population structure observed in this study.

In RII, it was notable that both abundance and biomass were extremely low and few early copepodid stages occurred throughout the summer (Fig. 4). These results suggest that *C. glacialis* reproduction was inactive in RII. In RII, approximately 70% of the population of *C. glacialis* consists of the Bering Sea haplotype (Nelson et al., 2009). To complete one generation, *C. glacialis* requires sufficient depth (≥ 200 m) in which to spend the diapause phase (Hirche, 1991; Ashjian et al., 2003). However, shallower depths (ca. 50 m) of the Chukchi Sea shelf may prevent their overwintering, and *C. glacialis* may fail to maintain their population on the Chukchi Sea shelf (Nelson et al., 2009; Ershova et al., 2015a). This finding would be the reason for the low abundance and biomass of *C. glacialis* in RII.

Table 2

Result of ANCOVA on mean copepodid stage (MCS), with the Julian day and region (cf. Fig. 1) applied as independent variables.

Parameters	d.f.	SS	F-value	p-value
Julian day	1	73.19	150.02	***
Region	2	2.99	3.06	*
Julian day*Region	2	4.53	4.64	*
Error	365	178.08	–	–

d.f., degree of freedom; SS, sum of squares.

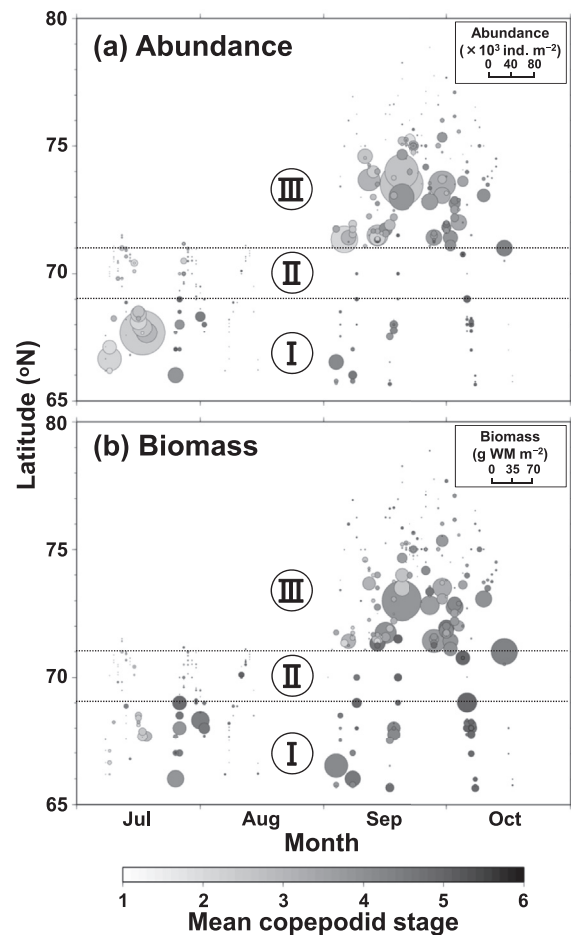
*: $p < 0.05$, ***: $p < 0.0001$.

Fig. 4. Temporal and latitudinal distributions of abundance (a) and biomass (b) for *C. glacialis* in the western Arctic Ocean during the summers of 1991–2014. The symbol size and colour indicate the abundance/biomass and mean copepodid stage, respectively. Circled I, II and III symbols mean regions I, II and III, respectively.

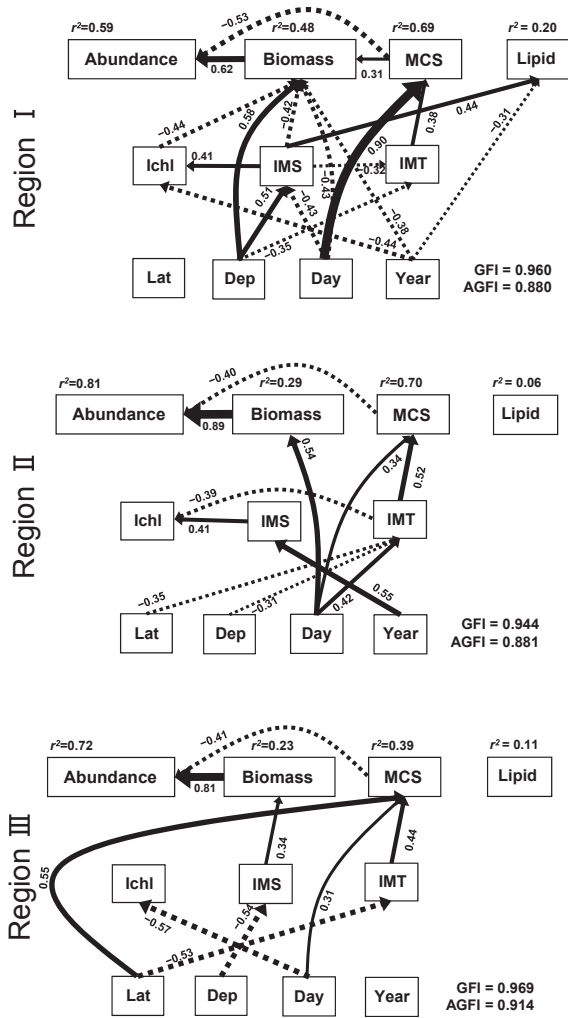


Fig. 5. Results of structural equation models (SEM) for *C. glacialis* population parameters (abundance, biomass, mean copepodid stage and lipid accumulation) with environmental factors. The values along the pathways represent standardized path coefficients. Arrows with solid or dashed lines indicate positive or negative effects. Thickness of arrows varied with path coefficient values. Only the >0.3 path coefficients and arrows are shown. For all significant path coefficients, see supplemental Fig. 1. The overall fit of the model was evaluated using the goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI). MCS: mean copepodid stage, Lipid: lipid accumulation index, IMT: integrated mean salinity, IMS: integrated mean salinity, Ichl: integrated chlorophyll, Lat: latitude, Dep: bottom depth, Day: Julian day, Year: sampling year.

As determined from the regional distribution of genetic haplotypes, RI–RIII of this study were divided into different populations (Nelson et al., 2009). The high abundance in RI may be a result of the populations transported from the Bering Sea. The other population is located in oceanic regions with sufficient depths (≥ 200 m), and long periods of ice cover (RIII). Due to the inadequate depths in RII (ca. 50 m), *C. glacialis* may not complete their life cycle. Throughout the three regions, their population origin was varied and induced regional differences in abundance, biomass and population structure.

4.2. Factors controlling population structure

Throughout the three regions, four relationships (positive relationships between abundance and biomass, Julian day and MCS, temperature and MCS, as well as a negative relationship between

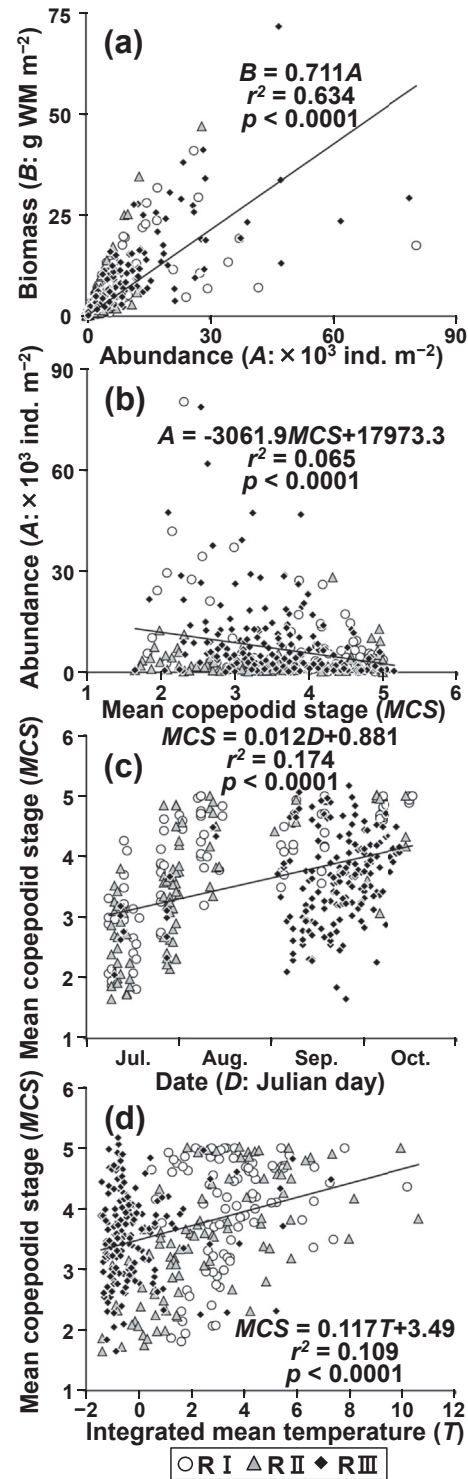


Fig. 6. *Calanus glacialis*: Relationships between biomass and abundance (a), abundance and mean copepodid stage (MCS) (b), MCS and Julian day (c), and MCS and integrated mean temperature (d) in the western Arctic Ocean during the summers of 1991–2014. Symbols varied with region: RI, RII and RIII mean region I, II and III, respectively.

MCS and abundance) were commonly detected by SEM analysis (Fig. 5). Scatter plots for each relationship are shown in Fig. 6. In this study, we applied seven environmental parameters (year, Julian day, latitude, depth, temperature, salinity and Chl. a) in the SEM analysis, but only two parameters, Julian day and temperature, were selected as effective parameters with significant relationships

with the population parameters. The effect of Julian day (D) on *C. glacialis* population in the western Arctic Ocean is that the MCS of the population increased with time ($MCS = 0.012D + 0.881$, Fig. 6c). On the other hand, abundance (A) decreased with increasing MCS ($A = -3061.9 MCS + 17,973.3$, Fig. 6b). From these relationships, it is suggested that 83 days are required for increasing 1 MCS, while abundance decreases 3062 ind. m^{-2} simultaneously. These seasonal decreases in abundance and growth are considered to be caused by natural mortality (Tande, 1988) or predation by predators such as medusae and fish (e.g., polar cod) (Purcell et al., 2010; Rand et al., 2013).

The effect of temperature on population, an increase of copepod growth rate with increasing temperature in their habitat, is well-known (cf. Corkett and McLaren, 1978). In this study, a positive relationship between MCS and temperature was detected (Fig. 6d). This suggests that growth of the *C. glacialis* population is accelerated by higher temperatures in the western Arctic Ocean from July–October. In the other marginal region of the Arctic Ocean, temperature is reported to have a clear influence on biomass of *C. glacialis* in the northern Barents Sea (Dvoretzky, 2011; Dvoretzky and Dvoretzky, 2009). In the Norwegian Sea, temperature was the environmental variable that explained most of the total variation in the abundance and distribution of *Calanus* species (Broms et al., 2009). The mesozooplankton community was found to be strongly related to longitude, temperature, bottom depth, Chl. a , and salinity in late summer in the waters of Iceland (Gislason and Silva, 2012). The information included in this study suggests that the sensitivity of Arctic copepods to environmental changes is primarily related to temperature.

5. Conclusion

Calanus glacialis in the western Arctic Ocean during the summer shows clear seasonal changes in growth (increase of MCS) and abundance (decrease) with temperature being the most important environmental driver. As a future prospect, the *C. glacialis* population transported from the Bering Sea is of special interest. Presently, the transported population is considered to be unable to reproduce in the Arctic Ocean (Nelson et al., 2009). However, recent warming conditions provide a long open water period and the occurrence of autumn phytoplankton blooms has been reported in the western Arctic Ocean (Nishino et al., 2015). During autumn blooms, *C. glacialis* feed on the phytoplankton and obtain energy for diapause (Matsuno et al., 2015). Additionally, during autumn blooms, frequent occurrences of high temperature eddies that transport *C. glacialis* from the shelf to the basin have been reported (Llinás et al., 2009; Watanabe et al., 2014). In the future, warming conditions may provide long open water periods; frequent eddies to transport the *C. glacialis* population from the Bering Sea; and occurrences of autumn phytoplankton blooms. Under such conditions, it seems that *C. glacialis* may increase in abundance in the Arctic Ocean in the near future.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.polar.2016.09.001>.

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