



Seasonal phenology of four dominant copepods in the Pacific sector of the Arctic Ocean: Insights from statistical analyses of sediment trap data



Koki Tokuhiro^{a,*}, Yoshiyuki Abe^{a,b}, Kohei Matsuno^a, Jonaotaro Onodera^c, Amane Fujiwara^c, Naomi Harada^c, Toru Hirawake^{a,b}, Atsushi Yamaguchi^{a,b}

^a Graduate School of Fisheries Science, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, 041-8611, Japan

^b Arctic Research Center, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Japan, 001-0021, Japan

^c Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa, 237-0061, Japan

ARTICLE INFO

Keywords:

Generalized additive models

Calanus hyperboreus

Metridia longa

Paraeuchaeta glacialis

Heterorhabdus norvegicus

ABSTRACT

In recent years, marine ecosystems have changed due to the drastic sea ice reduction in the Arctic Ocean, but the relationship between copepod phenology and environmental drivers is unclear. To reveal the relationship, seasonal changes in the flux (abundance of swimmers), population structure, lipid accumulation and gonad maturation of four dominant copepods (*Calanus hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) were studied using a sediment trap deployed at a depth of 222 m in the Pacific-Arctic sector from October 2010 to September 2013. *C. hyperboreus*, mostly comprising copepodid stage 6 females (C6F), exhibited several peaks in flux in spring and autumn. *C. hyperboreus* C6Fs were dominated by lipid-rich specimens year-round, and gonad development was observed in these samples from February to April. The *M. longa* flux showed no clear seasonality. Gonad maturation of *M. longa* C6Fs occurred from February to September. *P. glacialis* flux exhibited two peaks in autumn of 2011 and 2012. In contrast to the former two species, lipid-rich, mature *P. glacialis* C6Fs occurred year-round. *H. norvegicus* copepodid stage 6 males (C6Ms) also occurred throughout the year, likely because *H. norvegicus* has functional feeding appendages, even in C6Ms. From generalized additive models, *C. hyperboreus*, *M. longa* and *P. glacialis* showed relationships with daytime length and/or sea ice concentrations, but the relationship patterns were different. These findings suggest that the response (e.g., vertical migration) to the environmental parameters could vary with species and the drastic sea ice reductions may affect the copepod phenology in the Pacific-Arctic sector.

1. Introduction

In recent years, drastic sea ice reductions have been observed in the Pacific sector of the Arctic Ocean (Markus et al., 2009). Because of the reductions of sea ice and the effect of resultant temperature increases, lower trophic levels of the marine ecosystem structure are reported to be changing in the Pacific-Arctic sector (Grebmeier, 2012).

In the marine ecosystem of the Arctic Ocean, planktonic copepods are important secondary producers and food sources for fish and marine mammals (Lowry et al., 2004; Wassmann et al., 2006). However, ice coverage in the Pacific-Arctic sector throughout much of the year precludes access and high-frequency zooplankton sampling using ordinary ship observations. Sediment traps that collect sinking particles offer a powerful tool for collecting seasonal samples, even in oceanic areas that are difficult to access (Buesseler et al., 2007). Zooplankton collected via sediment traps are called “swimmers” and are excluded from the

sinking particle analysis. Although plankton-net sampling reveals the vertical distribution of the zooplankton community, swimmer samples collected by a sediment trap give us only limited information about the zooplankton community near a deployed depth (Seiler and Brandt, 1997). However, by collecting zooplankton over an annual cycle, seasonal changes in the zooplankton community can be evaluated semi-quantitatively using swimmer samples from sediment traps (Ota et al., 2008; Kraft et al., 2012; Makabe et al., 2016).

In the Arctic Ocean, zooplankton swimmers from sediment traps have been frequently analysed, especially in the Canadian Arctic. For example, the life cycle of *Metridia longa* (Makabe et al., 2010), seasonal changes in the flux of nauplii and adults of *Calanus hyperboreus* (Ota et al., 2008), and high numbers of copepod carcasses in the sinking flux (Sampei et al., 2012) have been reported. These studies are important for elucidating seasonal changes in the zooplankton copepod community. However, the seasonal changes in copepod phenology and

* Corresponding author..

E-mail address: k.tokuhiro0319@fish.hokudai.ac.jp (K. Tokuhiro).

<https://doi.org/10.1016/j.polar.2018.08.006>

Received 1 March 2018; Received in revised form 27 July 2018; Accepted 24 August 2018

Available online 28 August 2018

1873-9652/ © 2018 Elsevier B.V. and NIPR. All rights reserved.

environmental parameters vary within the Arctic region (Conover, 1988; Falk-Petersen et al., 2009), so more regional studies are needed.

Within the Arctic Ocean, the greatest reduction of sea ice has been reported in the Chukchi Sea (Perovich, 2011). Since 2010, sediment trap moorings have been used at the Station Northwind Abyssal Plain trap (St. NAPt) in the Pacific sector of the Arctic Ocean (Harada, 2016). Based on the sediment trap at NAPt, seasonal changes in diatom, dinoflagellate, silicoflagellate and radiolaria fluxes (Onodera et al., 2015, 2016; Ikenoue et al., 2015) are revealed. For mesozooplankton, the population structures and fluxes of large dominant copepods (*C. hyperboreus*, *M. longa*, *P. glacialis*, *H. norvegicus*) and small dominant copepods (*Oncaea parila*) have been reported (Matsuno et al., 2015). Analyses of faecal pellets collected by the sediment trap at St. NAPt showed massive feeding activity of amphipods (*Themisto libellula*) during the open water period (Matsuno et al., 2016). According to Matsuno et al. (2014), the peak season of the fluxes of the dominant four copepods relates to the timing of their active vertical migration, and their reproduction timing varies with the feeding mode of each species. While this information is important to clarify the general seasonal pattern of change (phenology) of the copepods, the relationship between environmental parameters and copepod phenology was not quantitatively evaluated because the dataset was insufficient for the application of the statistical analysis. Thus, the use of three years of subsequent data (from 2010 to 2013) may provide more robust insights than previously available (e.g., Matsuno et al., 2014, 2015). Based on multiple and consecutive years of data now available, the complex relationships between environmental parameters and copepod phenology could be assessed statistically (i.e., generalized additive models [GAMs]).

In the present study, we assessed the seasonal changes in zooplankton swimmer flux, population structure, lipid accumulation and gonad maturation of four dominant copepods (*C. hyperboreus*, *M. longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) based on samples collected over three years by a sediment trap moored in the Chukchi Sea. For adult females, body length and biomass (wet, dry and ash-free dry masses) were measured, and their seasonal patterns of change were evaluated. These results were compared with environmental parameters by GAMs to clarify which environmental factors exert effects on

the seasonal timing of copepod population parameters.

2. Materials and methods

2.1. Field sampling

A time-series sediment trap (SMD26 S-6000, open mouth area 0.5 m², Nichiyu Giken Kogyo, Co. Ltd.) was moored at St. NAPt (75°00'N, 162°00'W, 1975 m depth) of the Northwind Abyssal Plain of the Pacific-Arctic sector (Fig. 1) from 4 October 2010 to 18 September 2013. The deployed depth was 181–319 m (mean: 222 m), which was monitored by a pressure sensor mounted on the sediment trap. Because the mooring sites were slightly different among the years due to sea ice coverage and bathymetry at the station, the mean depths in each sampling period were changed: 188 m in the 1st year (from 4 October 2010 to 28 September 2011), 261 m in the 2nd year (from 4 October 2011 to 18 September 2012), and 222 m in the 3rd year (from 4 October 2012 to 18 September 2013). The cups of the sediment trap were automatically rotated and replaced at 10- to 15-day intervals. The trap mooring was fastened to the sea floor by a rope. The sample cups were filled with 5% buffered formalin seawater before the sediment trap was deployed. After the trap was retrieved, each of the samples ($n = 78$) was gently filtered with a 1-mm mesh net, and the organisms retained on the mesh net (> 1 mm size) were treated as zooplankton swimmers and preserved in 5% buffered formalin seawater. For the smaller (< 1 mm) fractions, the samples were dried, and the total mass flux (mg dry mass [DM] m⁻² day⁻¹) was quantified.

Time-series data of the weekly average ice coverage near St. NAPt during the mooring period were calculated from the sea ice concentration dataset (http://iridl.ldeo.columbia.edu/SOURCES/.IGOS-S/.nmc/.Reyn_Smith_Oiv2/, cf. Reynolds et al., 2002). MODIS/Aqua Level 3 binned chlorophyll-*a* data (reprocessing version 2012.0) were downloaded from the Distributed Active Archive Center (DAAC) of the Goddard Space Flight Center (GSFC), NASA. We used daily data at a 9-km resolution composited to a running mean of 9 days. Daytime hours at St. NAPt were calculated according to the Casio advanced calculation (<http://keisan.casio.jp/exec/system/1184726771>).

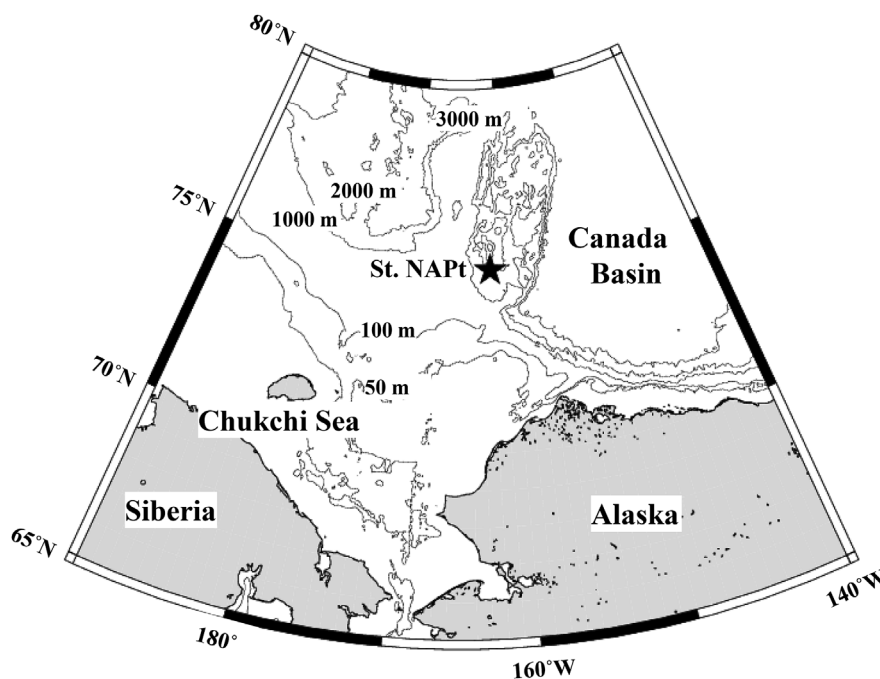


Fig. 1. Location of the moored sediment trap station (St. NAPt, solid star) in the Pacific-Arctic sector.

2.2. Sample analysis

In the present study, swimmers were defined as zooplankton in the > 1 mm samples. Four numerically dominant large copepod species (*C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus*) were selected from the sample and counted according to their development stages under a microscope, as previously described by Matsuno et al. (2014, 2015). The early copepodid stages of *M. longa* are smaller than 1 mm (Sampei et al., 2009) and 81% of C1–C3 *M. longa* have been observed to pass through this mesh (Tokuhira, unpublished data), potentially resulting in an underestimation of abundance for this species.

C. hyperboreus, *M. longa* and *P. glacialis* contain an oil sac in their prosome. To evaluate the seasonal variation in lipid storage of C6Fs, the oil sac length (OSL) relative to the prosome length (PL) was scored into three categories: I) OSL was 0–4% of PL, II) OSL was 4–40% of PL, and III) OSL was > 40% of PL (Matsuno et al., 2014). For these three species, the gonad maturation of C6Fs was evaluated according to Hirche and Niehoff (1996) (*C. hyperboreus*) and Tande and Grønvik (1983) (*M. longa* and *P. glacialis*). The gonads were classed into three categories: I) immature, II) small oocytes in the ovary or oviduct, and III) large opaque eggs in the oviduct. Among the dominant species, *H. norvegicus* were not distinguishable by lipid accumulation, nor by gonad maturation because these organisms accumulated lipids in the form of many small oil droplets, and their gonads were difficult to observe without dissection.

The flux (F , individuals $m^{-2} day^{-1}$) of zooplankton swimmers was calculated using the following equation:

$$F = N \times \frac{1}{0.5} \times \frac{1}{d}$$

where N is the number of individuals, 0.5 is the mouth area (m^2) of the sediment trap and d is the sampling interval (days).

2.3. Body length and biomass

Seasonal changes in the body length and biomass of dominant copepod C6Fs (*C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus*) were evaluated. Six specimens of C6F were randomly selected from each sample, and the prosome lengths (PL) were measured using an ocular micrometre under a stereomicroscope, with precision of 0.05–0.1 mm. After desalting with distilled water and removing body surface water using tissue paper, specimens were placed in a pre-weighed aluminium dish, and the wet mass (WM) was measured with a precision of 10 μg using an electronic balance (METTLER TOLEDO AT261). After drying in an oven at 60 °C for 5 h and cooling, the dry mass (DM) was measured with a precision of 1 μg using a microbalance (METTLER TOLEDO XP6V) as per Yamaguchi et al. (2010). After the DM measurement, the specimens were combusted at 480 °C for 5 h in a muffle furnace, and after cooling, the ash (Ash) was measured with a precision of 1 μg using a microbalance.

Seasonal changes in PL, WM, DM and ash-free dry mass (AFDM = DM–Ash) of stage C6F of the dominant copepods were tested using a one-way ANOVA. The definition of seasons is as follows: Spring is from April to June, summer is from July to September, autumn is from October to December, and winter is from January to March.

2.4. Comparison with environmental parameters

Before performing the statistical modelling, the multi-collinearity of all continuous explanatory variables was evaluated using variance inflation factors (VIFs). All VIF values were below 5, indicating that no collinearity was assumed in this study (Zuur et al., 2009). GAMs were fitted to the copepod parameters (the flux of total copepodid stages, prosome length, wet mass, dry mass, ash free dry mass, lipid accumulation and gonad maturation for C6Fs) of the dominant copepods (*C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus*), and the

environmental variables. The stage composition of the four copepods were not tested by this modelling because of an underestimation of the abundance for the early copepodid stages for some species (e.g., *M. longa*) (Sampei et al., 2009), as mentioned above. For the environmental variables, daytime length (which range 0–1, 0: polar night, 1: midnight sun), sea ice concentration (SIC), mean trap depth during each sampling period (D_{ave} , m), mean temperature at the trap depth during each sampling period (T_{ave} , °C), total mass flux (TMF, $mg DM m^{-2} day^{-1}$) were included in the GAMs as explanatory variables. To evaluate the inter-annual changes, the sampling year (i.e., 1st, 2nd, and 3rd sampling years) was also used as a nominal variable in the GAMs. The definition of the sampling year was as follows: 1st year) 4 October 2010–28 September 2011, 2nd year) 4 October 2011–18 September 2012), and 3rd year) 4 October 2012–18 September 2013. It should be noted that lipid and gonad maturation scores for *H. norvegicus* were not used in this modelling because of the difficulties in assigning scoring categories previously mentioned. Chl. *a* could not be included in GAMs because of the low temporal coverage of the data. All statistical analyses were carried out in the R software with the package “mgcv” (version 3.4.3, R Development Core Team, 2017).

3. Results

3.1. Hydrography

The sea ice concentration around St. NAPt showed clear seasonal changes, with over 90% coverage from mid-November to mid-June, rapidly decreasing from mid-June to mid-August, completely melting from mid-August to mid-October and then increasing again from mid-October to early November (Fig. 2a). Chlorophyll *a* at the surface ranged between 0.05 and 0.28 $mg m^{-2}$. The temperature at the deployed depth was -1.6 to 0.1 °C (-0.9 ± 0.2 °C, data not shown). The total particle mass flux ranged from 0.1 to 263 $mg DM m^{-2} day^{-1}$ and was highest from November to December in 2010 and 2011, when the ice coverage started to increase, and in July 2013, during the sea ice melting season. Polar night occurred from November to January, and the midnight sun was observed from May to July (Fig. 2b). Day and night contrast within one day occurred from February to April and again from August to October, with daytime hours increasing during the former and decreasing during the latter.

3.2. Population structure

The *C. hyperboreus* flux showed four peaks in the spring and one peak in the autumn of 2012; the first peak was in May 2011, the second and third peaks were in April and June 2012, the fourth peak was in October 2012 and the fifth peak was in May 2013 (Fig. 3a). Throughout the year, the stage structure of *C. hyperboreus* was dominated by C6Fs (mean \pm sd: $94 \pm 5\%$).

The *M. longa* flux exhibited a large fluctuation and no clear seasonality (Fig. 3b). Adult females (C6F) comprised $\sim 70\%$ of the *M. longa* flux in February of each year. C1 and C2 mainly occurred from September to October.

The flux of *P. glacialis* was higher from August to October in 2011 and from July to August in 2012 (Fig. 3c). During the later period, the ratio of C3 in the population was higher compared with the other periods.

The flux of *H. norvegicus* showed one peak through the sampling period and no clear seasonal changes (Fig. 3d). The contribution of C6Ms was high for the *H. norvegicus* population throughout the year. C6Fs contributed 26–52% of the adults. The annual mean sex ratio was skewed towards males (C6F:C6M = 0.66:1).

3.3. Lipid accumulation and gonad maturation

C6Fs of *C. hyperboreus* with high lipid contents occurred throughout

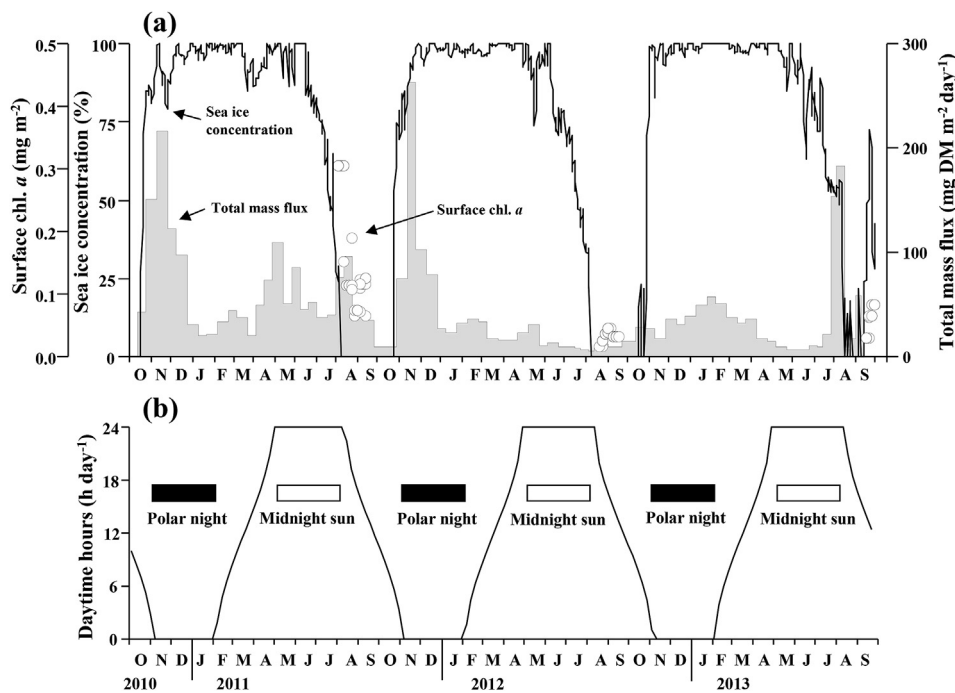


Fig. 2. Seasonal changes in the sea ice concentration (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_Smith_OIv2/, data from Reynolds et al., 2002), total mass flux (<math>< 1 \text{ mm}</math> size fraction), surface chlorophyll *a* from satellite (a) and in daytime hours (b) at St. NAPt in the Pacific-Arctic sector from October 2010 to September 2013.

the year, with a mean of 38% ($\pm 8\%$) of the population being categorized as lipid accumulation III, i.e., the OSL was $> 40\%$ of PL. Lipid accumulation in *C. hyperboreus* C6Fs showed little seasonal changes, but the proportion of the high lipid individuals was likely to decrease with the year (Fig. 4a). C6F lipid accumulation exhibited clear seasonal changes for *M. longa*. Low lipid accumulation was observed from May to August, whereas high lipid accumulation occurred from November to February (Fig. 4b). *P. glacialis* C6F was dominated by lipid-rich specimens (lipid accumulation III) throughout the year (mean \pm sd: $54 \pm 10\%$ of C6F population) and showed little seasonal patterns (Fig. 4c).

Most C6Fs of *C. hyperboreus* had immature gonads throughout the year, and mature and spawning specimens occurred from February to April (Fig. 5a). For *M. longa*, gonad maturation I individuals dominated most of the year, whereas mature specimens occurred from February to November (Fig. 5b). For *P. glacialis*, specimens with mature gonads occurred throughout the year, in contrast to those of the other two species. The percentage of mature specimens was high from October to April, and the percentage reached approximately 100% from February to April in 2013 (Fig. 5c).

3.4. Body length and biomass

Seasonal changes in PL, WM, DM and AFDM of C6Fs were observed for all four dominant copepods (Table 1). Within these copepods, significant seasonal changes for all four parameters were observed for *M. longa* and *P. glacialis* ($p < 0.001$, Table 1). Significant negative correlations were also observed between the water content and AFDM compositions in *C. hyperboreus* and *P. glacialis* ($p < 0.001$, Fig. 6).

3.5. Comparison with environmental parameters

From GAMs, the *C. hyperboreus* flux had significant positive relationships with daytime length (> 0.3), SIC (> 0.9), T_{ave} (> -0.6) and TMF (< 50) (Table 2, Fig. 7). The significant relationships of the *P. glacialis* flux were similar to those of *C. hyperboreus* without T_{ave} , and the positive relationships were observed with daytime length (> 0.7), SIC (< 0.8), TMF (< 50). The fluxes of *M. longa* and *H. norvegicus*

showed one significant relationship with SIC (> 0.5) and D_{ave} (< 220), respectively (Fig. 7). With regard to the lipid accumulation, *C. hyperboreus* showed significant positive relationships with D_{ave} (> 230), T_{ave} (> -0.7) and TMF (> 100), while *M. longa* with daytime length (< 0.6) and SIC (< 0.05 or > 0.95) (Fig. A5). The lipid accumulation of *P. glacialis* exhibited no significant relationship with any environmental parameters (Table 2). For gonad maturation, *C. hyperboreus* showed significant positive relationships with daytime length (0.2–0.8), SIC (> 0.9) and T_{ave} (> -0.9) (Fig. A6). The gonad maturation of *M. longa* was affected by daytime length, and an inter-annual change was also detected (Table 2). *P. glacialis* had significant positive relationships with daytime length (< 0.5) and SIC (< 0.8) (Fig. A6). Inter-annual changes in these copepod parameters were detected only for the individual body size and weight (i.e., PL, WM, DM and AFDM) with the exception of gonad maturation for *M. longa* (Table 2).

4. Discussion

4.1. Zooplankton collected by sediment trap

Plankton-net sampling allows us to know the spatial distribution of the zooplankton community, while swimmer samples collected by a sediment trap give us only limited information about the zooplankton community at the deployed depth (Seiler and Brandt, 1997). Although there are various disadvantages (e.g., semi-quantitative collection at a fixed depth), analyses on year-round zooplankton samples using a sediment trap are a powerful tool, especially for ice-covered oceans, to reveal seasonal changes in the zooplankton community and copepod phenology (Ota et al., 2008; Kraft et al., 2012; Matsuno et al., 2014; Makabe et al., 2016).

Zooplankton collected by a sediment trap could be influenced not only by zooplankton abundance around the deployed depths but also by zooplankton behaviour. Since active zooplankton swimmers represented by copepodid stages and adults have their own specific downward or upward movements, these vertical migrants might only be collected periodically using sediment traps (Ota et al., 2008). However, our limited knowledge of the behaviour of zooplankton on encountering a sediment trap are important impediments to

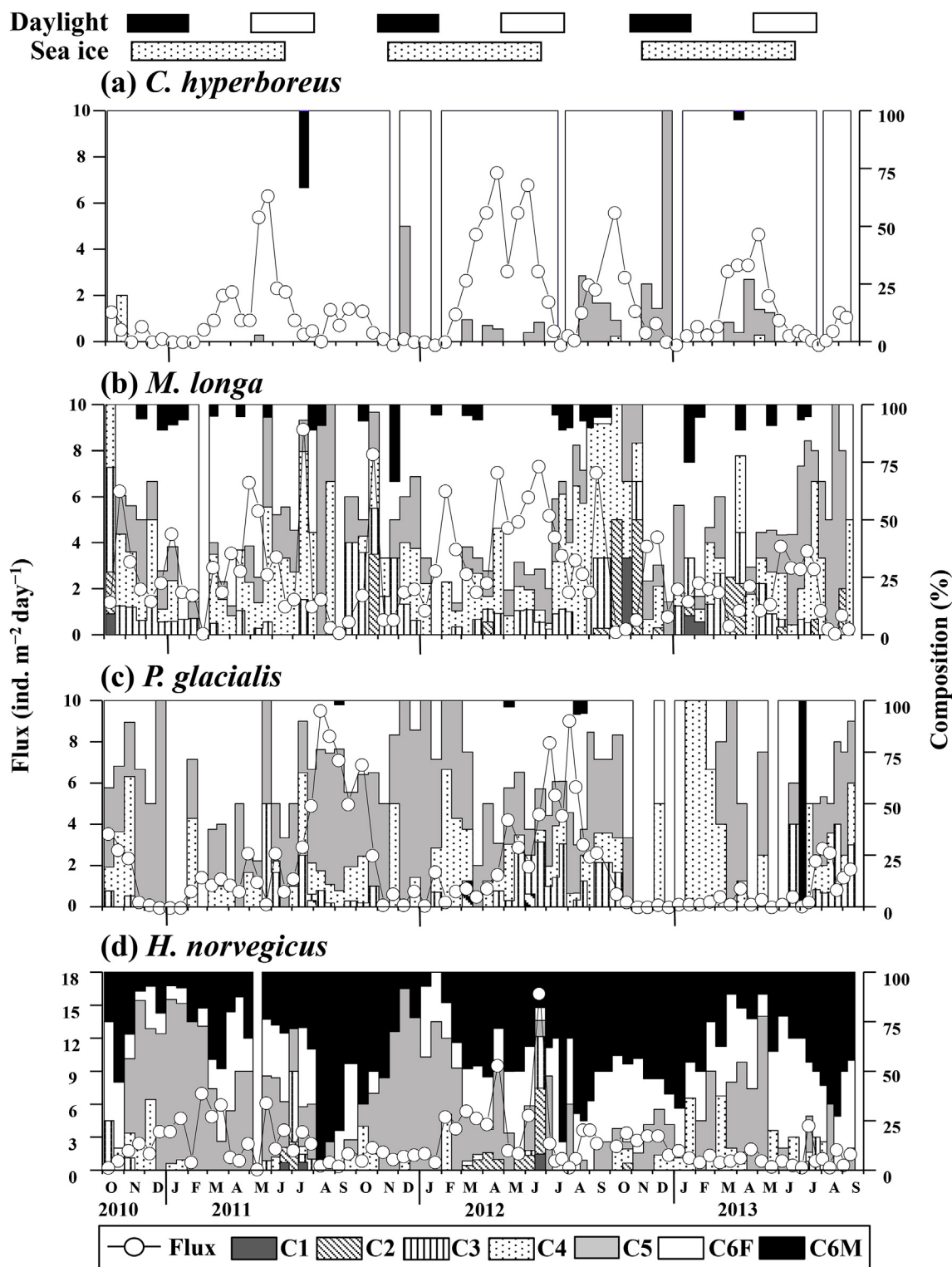


Fig. 3. Seasonal changes in the flux and copepodid stage composition of the four large calanoid copepods, *Calanus hyperboreus* (a), *Metridia longa* (b), *Paraeuchaeta glacialis* (c) and *Heterorhabdus norvegicus* (d), collected by deployed sediment trap at depths of 181–319 m of St. NAPt in the Pacific-Arctic sector from October 2010 to September 2013. For comparison, seasonal timings of midnight sun (open), polar night (solid) and ice cover (dotted, > 90% sea ice concentration, cf. Fig. 2) are shown by the bars atop the abscissa.

understanding the contribution of such zooplankton (Steinberg et al., 1998). For this reason, it is not easy to compare the abundance data from sediment traps with samples collected by plankton nets (Seiler and Brandt, 1997).

4.2. *C. hyperboreus*

C. hyperboreus is widely distributed in the Arctic Ocean. This species undergoes a seasonal vertical migration to the deep sea in winter

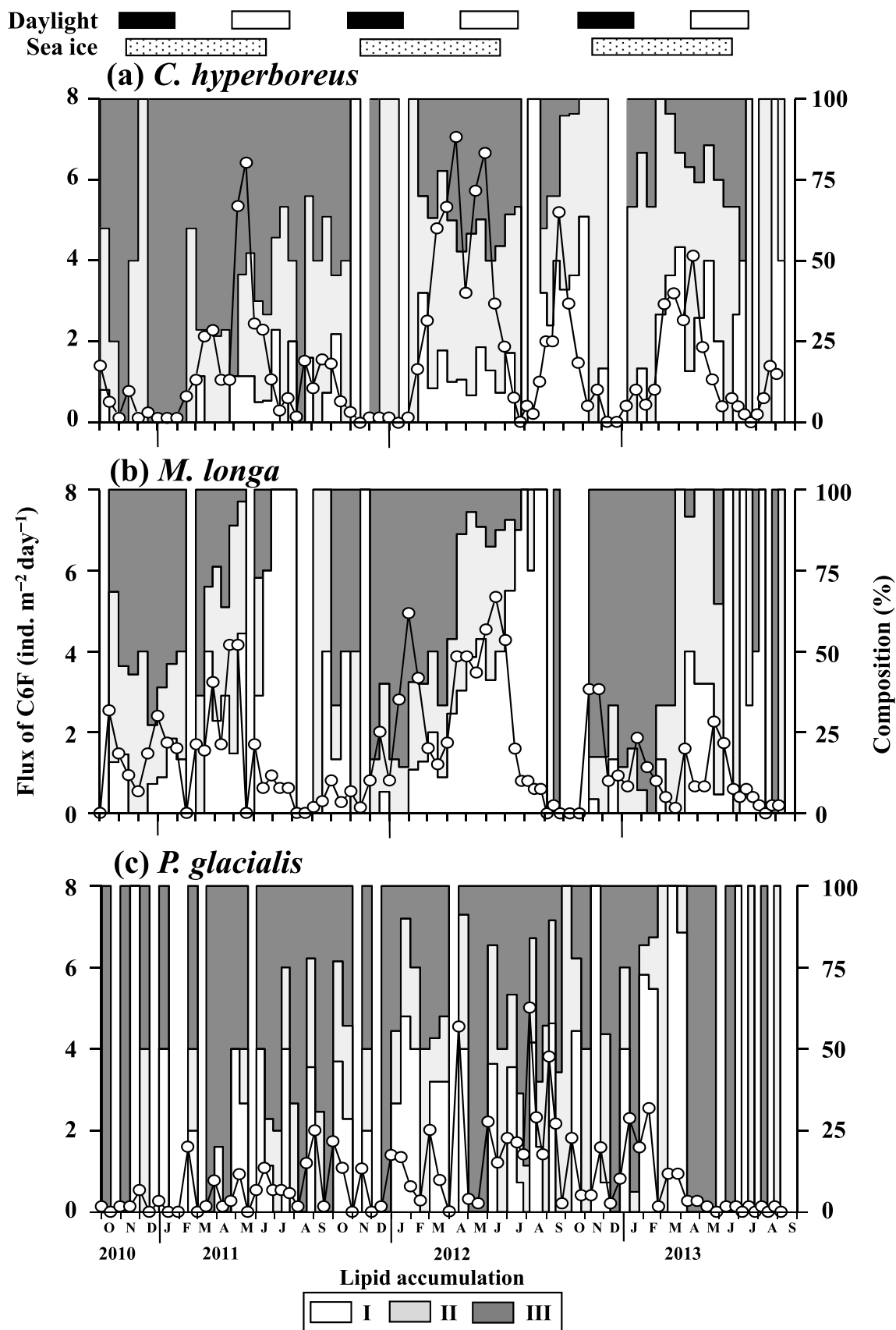


Fig. 4. Seasonal changes in the flux of adult females (C6F), in lipid accumulation composition (I–III) of *Calanus hyperboreus* (a), *Metridia longa* (b) and *Paraeuchaeta glacialis* (c) at depths of 181–319 m of St. NAPt in the Pacific-Arctic sector. For comparison, the seasonal timings of midnight sun (open), polar night (solid) and ice cover (dotted, > 90% sea ice concentration, cf. Fig. 2) are shown by the bars atop the abscissa.

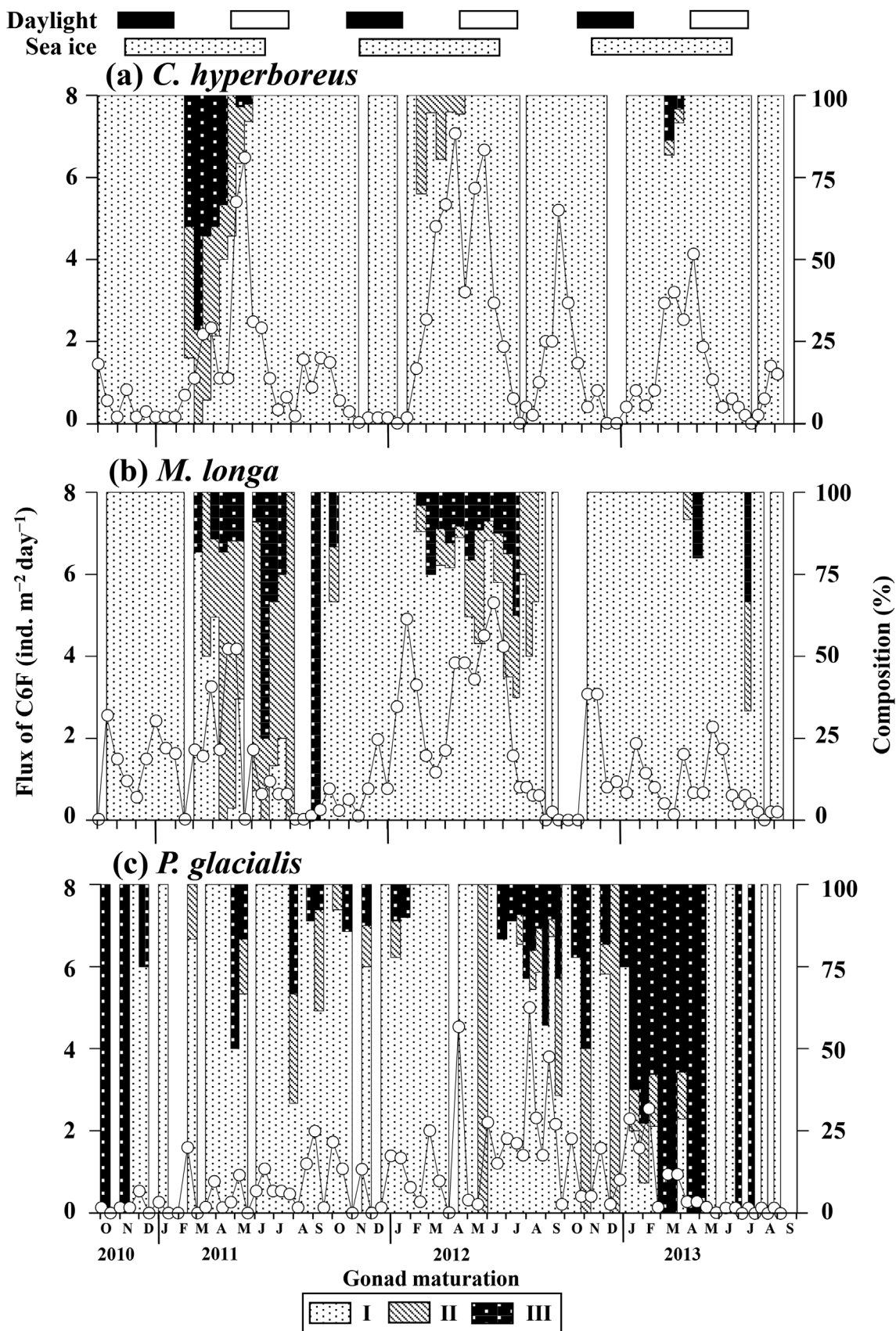


Fig. 5. Seasonal changes in the flux of adult females (C6F), in gonad maturation composition (I–III) of *Calanus hyperboreus* (a), *Metridia longa* (b) and *Paraeuchaeta glacialis* (c) at depths of 181–319 m of St. NAPt in the Pacific-Arctic sector. For comparison, the seasonal timings of midnight sun (open), polar night (solid) and ice cover (dotted, > 90% sea ice concentration, cf. Fig. 2) are shown by the bars atop the abscissa.

Table 1

Test for seasonal differences (one-way ANOVA) in the prosome length (PL), wet mass (WM), dry mass (DM) and ash free dry mass (AFDM) within C6Fs of *Calanus hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*. Samples were collected in a sediment trap at depths of 181–319 m of St. NAPt in the Pacific-Arctic sector from October 2010 to September 2013. *: $p < 0.05$, ***: $p < 0.001$, NS: not significant.

Species	Parameter	df	SS	F	p-value
<i>C. hyperboreus</i>	PL	71	4.740	1.042	NS
	WM	71	1280	2.494	***
	DM	71	60.9	1.423	*
	AFDM	71	52.5	1.36	NS
<i>M. longa</i>	PL	68	1.447	2.862	***
	WM	68	25.8	7.563	***
	DM	68	0.933	5.325	***
	AFDM	68	0.608	4.202	***
<i>P. glacialis</i>	PL	62	13.096	2.677	***
	WM	62	2002	4.154	***
	DM	62	289	5.178	***
	AFDM	62	249	4.704	***
<i>H. norvegicus</i>	PL	66	0.917	2.089	***
	WM	66	65.0	3.669	***
	DM	66	0.667	1.168	NS
	AFDM	66	0.498	1.007	NS

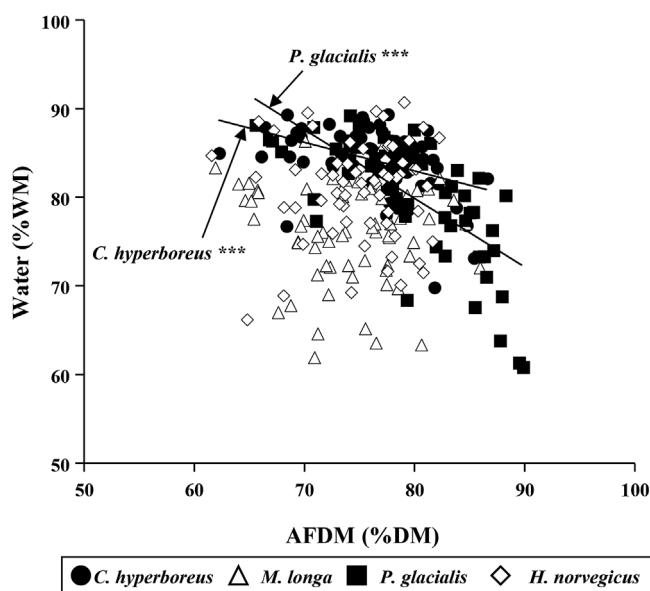


Fig. 6. Relationships between the water composition (% wet mass, WM) and AFDM composition (% dry mass, DM) for C6Fs of *C. hyperboreus*, *M. longa*, *P. glacialis* and *H. norvegicus* at depths of 181–319 m of St. NAPt in the Pacific-Arctic sector from October 2010 to September 2013. For significant relationships, regression lines are shown. ***: $p < 0.001$.

(Hirche, 1997) and an upward migration in April in the Greenland Sea (Hirche and Niehoff, 1996). Dawson (1978) reported that the early copepodid stage of *C. hyperboreus* moved upward during spring to summer and downward after the summer in the central Arctic Ocean. Auel and Hagen (2002) showed that the summer distribution of *C. hyperboreus* was mainly restricted to epipelagic water (0–200 m) in the central Arctic Ocean. In the present study, *C. hyperboreus* was dominated by C6Fs throughout the year at a depth of 181–319 m (mean: 222 m) at St NAP (Fig. 3a). Near the NAPt, adult females of *C. hyperboreus* were mainly distributed at approximately 200 m in depth from November to June and in the surface layer during the summer over the Northwind Ridge and Chukchi Plateau (Ashjian et al., 2003). Thus, the

population structure corresponds well to the depth distribution of C6Fs in *C. hyperboreus*, which could occur in the surface layer throughout an annual cycle (Dawson, 1978; Hirche, 1997; Ashjian et al., 2003).

Falk-Petersen et al. (2009) reported that lifespans from 1 to 2 years and up to 4–6 years are possible for *C. hyperboreus* depending on geographical region and food availability. While there is regional variability in the life cycle of *C. hyperboreus*, a three-year generation time is generally assumed in the Arctic Ocean, with reproduction occurring from November–March, growth to C3 occurring during the first summer, growth to C4 occurring during the second summer, adult overwintering occurring during the third year and reproduction occurring the following spring (Dawson, 1978; Conover, 1988; Hirche and Niehoff, 1996). If the population of *C. hyperboreus* in the Pacific-Arctic sector has a similar life cycle as mentioned above, the early copepodid stage is expected to be collected by the sediment trap. However, the youngest stage was stage four in this study, which suggests the early copepodid stages were distributed mainly in the upper layer (e.g., 0–100 m) above the deployed depth of the trap (181–319 m) in the Pacific sector of the Arctic Ocean (Ashjian et al., 2003).

Gonad maturation of *C. hyperboreus* was observed from February to April (Fig. 5a). Gonad development and maturation and egg production in *C. hyperboreus* are facilitated in the absence of feeding by using stored lipids (wax esters) accumulated in the body as an energy source during winter, when food is scarce (Conover, 1962, 1967; Lee, 1974; Conover and Siferd, 1993; Hirche, 1996; Hirche and Niehoff, 1996). In the Arctic Ocean, reproduction of *C. hyperboreus* begins in winter and is finished prior to the start of the spring phytoplankton bloom (Wiborg, 1954; Hirche, 1991; Conover and Siferd, 1993; Melle and Skjoldal, 1998; Niehoff et al., 2002). At St. NAPt, in the present study, a phytoplankton bloom started as an ice-edge bloom in early August when the sea ice melted (Fig. 2a). Since reproduction of *C. hyperboreus* occurred much earlier than that of the phytoplankton bloom, the energy requirements of the resulting juvenile copepodid stage could be met with a sufficient phytoplankton bloom (Conover, 1965; Hirche and Niehoff, 1996). Thus, this life-cycle pattern of *C. hyperboreus* may have an advantage in that the newly recruited generation is timed to encounter a sufficient phytoplankton bloom (Conover, 1965; Hirche and Niehoff, 1996).

C. hyperboreus showed five peaks in flux, and the peaks occurred in the spring and autumn. The high flux of copepods in the sediment trap samples would reflect the active vertical migration among the trap depth, resulting in the collection of swimmers (Matsuno et al., 2014, 2015; Makabe et al., 2016). From this viewpoint, these peaks of *C. hyperboreus* may be the result of their seasonal and/or diel vertical migration (Hays, 1995; Hirche and Niehoff, 1996). Considering the seasonal vertical migration, adult females of *C. hyperboreus* were mainly distributed at ~200 m depth from November to February, at ~300 m depth from February to June, and in the surface layer during summer over the Northwind Ridge and Chukchi Plateau (Ashjian et al., 2003). Therefore, the flux peak could be related to variation in the preferred depth occupied by the species over the season. However, the occurrence of the peak differed among the sampling years in this study. Hays (1995) noted that late copepodid stages of *C. hyperboreus* exhibited a diel vertical migration in near-surface layers at temperate latitudes, although not in the Arctic during midnight sun in the summer. On the other hand, Fortier et al. (2001) reported that *C. hyperboreus* perform a diel vertical migration in the midnight sun under the sea ice. From GAMs in this study, the flux of *C. hyperboreus* had a strong relationship with daytime length, and the effect of the daytime length was positive when the daytime length was more than 0.3 (Fig. 7). This indicates that light intensity restricts the vertical distribution of *C. hyperboreus*, and the diel vertical migration for the species did not cease during the midnight sun (Fortier et al., 2001). Some *Calanus* spp. are very sensitive to light and can respond to irradiance from the night sky, moonlight and aurora down to depths of 70–170 m, and thus are able to perform diel vertical migration during the polar night (Bâtnes et al., 2015).

Table 2

Result of generalized additive models (GAMs) based on the flux of total copepodid stages, prosome length (PL), wet mass (WM), dry mass (DM) ash free dry mass (AFDM), lipid accumulation and gonad maturation for C6F of the dominant copepods (*Calanus hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis* and *Heterorhabdus norvegicus*) with environmental parameters. Int.: intercept, Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Species	Parameters	Int.	Daytime	SIC	D_ave	T_ave	TMF	Year
<i>C. hyperboreus</i>	Flux (ind. m ⁻² day ⁻¹)		***	**		*	*	
	PL	***						*
	WM	***	*	**				
	DM	***						**
	AFDM	***						**
	Lipid accumulation	**				*	*	*
<i>M. longa</i>	Gonad maturation	***	**	***		***		
	Flux (ind. m ⁻² day ⁻¹)			*				
	PL	***		*		*	**	**
	WM		*	**		*		
	DM	***	***	***		*		
	AFDM		*	***	***	*	***	*
<i>P. glacialis</i>	Lipid accumulation	***	***	**				
	Gonad maturation	***	***					*
	Flux (ind. m ⁻² day ⁻¹)		***	***			*	
	PL	***					**	*
	WM	*	*	**		*		
	DM	**	*	***	***	***		*
<i>H. norvegicus</i>	AFDM		*	***	*			
	Lipid accumulation	***						
	Gonad maturation	**	***	**				
	Flux (ind. m ⁻² day ⁻¹)	***			**			
	PL	***		**				
	WM	***	***	*			*	
	DM	***	*			**		
	AFDM	***				**		*

However, since the negative trend in flux was observed when the daytime length was less than 0.3 in GAMs, the diel vertical migration of *C. hyperboreus* might be weakened during the polar night in the Pacific sector of the Arctic Ocean.

4.3. *M. longa*

M. longa is omnivorous, distributed mainly in deep layers, and performs a diel vertical migration (Conover and Huntley, 1991; Ashjian et al., 2003). This species does not exhibit a seasonal vertical migration or resting at depths (Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984). C6Fs in this species accumulate lipids in their prosomes (Lee, 1975), with the proportion of lipid-rich specimens highest in February, decreasing gradually over the summer (Fig. 4b). Considering the seasonality of the lipid accumulation, nauplii and eggs of *C. hyperboreus* (and other copepods) could provide an important food resource under the sea ice (Conover and Huntley, 1991). That food condition in the winter might be a reason that lipid-rich specimens were observed at a high level in February in this study.

M. longa does not have a diapause phase, but C6Fs perform overwintering by reducing their physiological activity in the winter (Tande and Grønvik, 1983; Båmstedt and Ervik, 1984; Grønvik and Hopkins, 1984; Båmstedt, 1985). The gonad maturation timing of overwintered *M. longa* C6F is thought to be controlled by various environmental parameters that allow them to reproduce at different times (Tande and Grønvik, 1983). In the present study, opposite seasonal timings were observed for lipid accumulation and gonad development, which suggested that gonad maturation may be achieved by accumulated lipids as an energy source. Gonad development in mature individuals occurred during seasons with daytime, centring on periods with midnight sun, while high proportions of specimens with accumulated lipids were observed during polar night (Fig. 4b). Thus, the presence of daytime

hours is a potential cue for the commencement of gonad maturation in *M. longa*.

Falkenhaus et al. (1997) showed that *Metridia* spp. exhibited a tendency to avoid the surface during the day and to perform a diel vertical migration during the midnight sun period in the Arctic Ocean. Berge et al. (2009) also reported that the diel vertical migration of zooplankton is regulated by the diel variation in solar and lunar illuminations during the polar night in Svalbard. In our study, *M. longa* showed large fluctuations and no clear seasonality (Fig. 3b). Based on the results of GAMs, the flux of this species related to the SIC, not daytime length, and the positive effect by the SIC was observed when SIC was greater than 50% (Fig. 7). The diel vertical migration for *M. longa* was not clear from the sediment trap sampling, but the sea ice concentration could be an important factor that restricts the vertical distribution or behaviour of this species. Berge et al. (2009) reported that diel vertical migration in the winter is stronger in open water than in ice-covered waters for this species, but this was not supported by our findings (i.e., high flux in high sea ice coverage).

Older stages of *M. longa* spend the winter close to the surface and migrate into deeper layers for the summer, whereas young stages remain at greater depths for most of the year (Hirche and Mumm, 1992). A similar distribution pattern is observed over the Northwind Ridge and Chukchi Plateau (Ashjian et al., 2003). In the present study, the flux of C6Fs was low from August to September (Fig. 4b), perhaps because *M. longa* C6Fs remained near the surface layer. For the reproductive period, mature specimens occurred from February to November (Fig. 5b). This reproductive activity resulted in increases of early copepodid stages from September to October (Fig. 3b). *M. longa* in Balsfjorden has an annual life cycle, with spawning probably occurring at the beginning of May and overwintering (October to March) occurring first as C5 and adults, then favouring adults in the late winter (Grønvik and Hopkins, 1984). Therefore, the seasonal life-cycle pattern

Flux

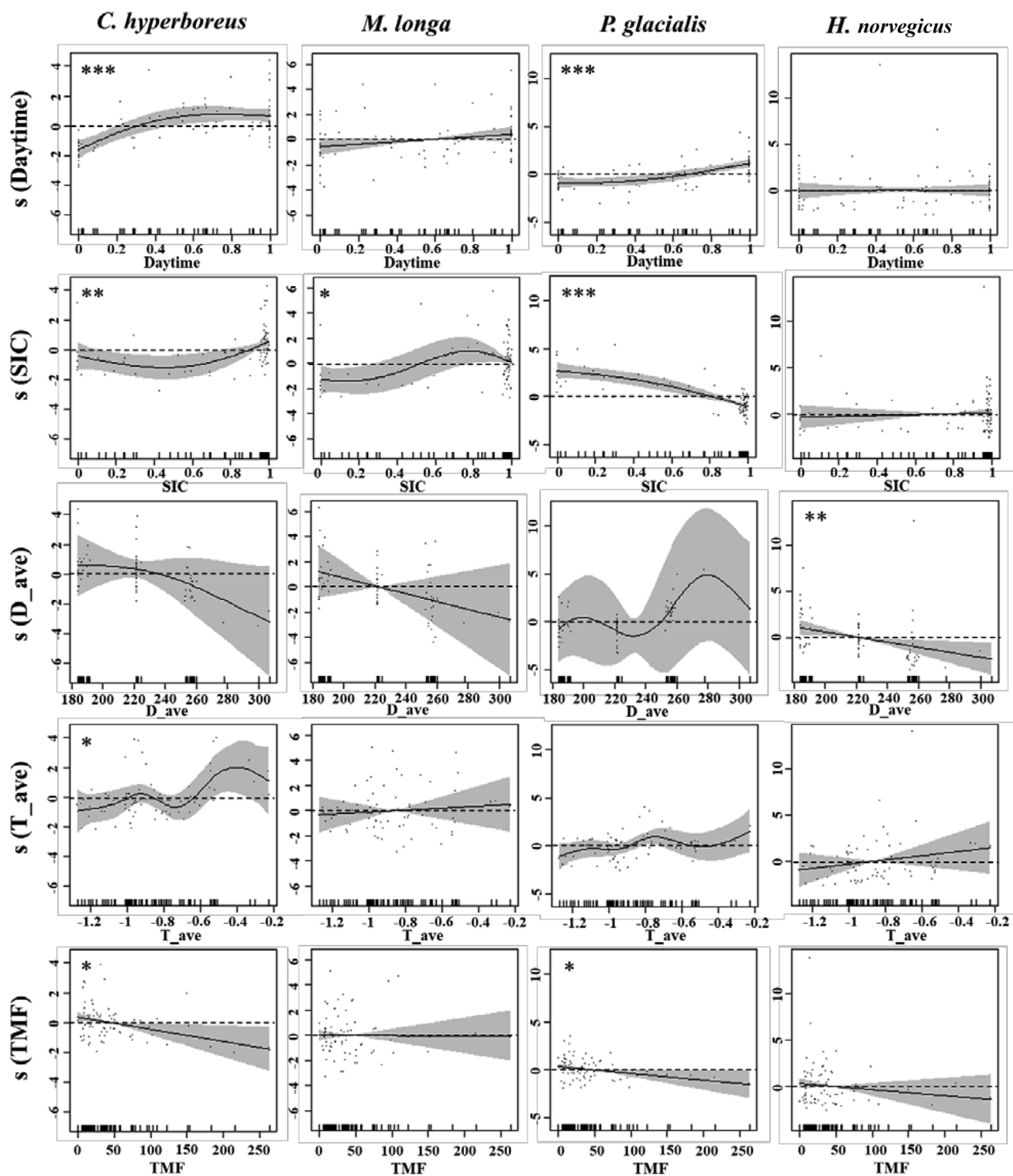


Fig. 7. Result of GAMs based on the flux of total copepodid stages for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

of *M. longa* in this area is summarized as follows: C6Fs that accumulate lipids in February develop their gonads from April to August (Fig. 4b); then, C6Fs engage in reproduction in the surface layer from August to September, and consequently, newly recruited C1 to C2 stages are abundant from September to November (Fig. 3b); then, they grow to C3–C5 in the deep layer.

4.4. *P. glacialis*

P. glacialis is distributed at a depth of 0–500 m in the Arctic Ocean, similar to *P. norvegica* (Grainger, 1989; Auel, 1999, 2004). *P. norvegica*, which is an Atlantic congener species of *P. glacialis*, is known to perform diel vertical migration during autumn (Kaartvedt et al., 2002), but ceases diel vertical migration during the midnight sun and polar night (Fleddum et al., 2001). The flux of *P. glacialis* showed two peaks during the autumn in 2011 and 2012 (Fig. 3c), and the flux had significant relationships with daytime length, SIC and TMF (Table 2). Thus, if *P. glacialis* exhibits a similar diel vertical migration to *P. norvegica*, the flux showed a peak in diel vertical migration in autumn in this study. From GAMs, low SIC (i.e., open water) and low TMF could increase the flux of *P. glacialis* (Fig. 7), and this suggests that the species actively swims searching prey or mating during the open water period (August–October). That is a potential interpretation of why the peaks of *P. glacialis* were observed only during the autumn.

In the present study, *P. glacialis* exhibited high lipid accumulation, and mature individuals occurred throughout the year (Figs. 4c and 5c). These facts may reflect that food for carnivorous *Paraeuchaeta* spp. is available throughout the year and that they experience no resting phase during their life cycle (Båmstedt, 1979; Øresland, 1991; Scott et al., 1999). In the Arctic Kara Sea, phytoplankton blooms occur when ice retreats in late June to early July (Hirche et al., 2006). Early copepodid stages of herbivorous copepods are abundant in mid-July, and the reproduction of carnivorous *P. glacialis* begins in June and peaks in July (Dvoretsky and Dvoretsky, 2015). In this study, early copepodid stages of *P. glacialis* occurred in the summer (Fig. 3c). Considering these seasonal phenomena, *P. glacialis* in the Pacific-Arctic sector may also perform raptorial feeding on herbivorous copepods and reproduce during the ice retreat season when phytoplankton blooms are present.

4.5. *H. norvegicus*

H. norvegicus showed no clear seasonal changes in flux or population structure, while only average depth was selected as a potential factor to influence the flux in GAMs, and the flux was increased in the upper layer (~220 m depth) (Fig. 7). In the central Arctic Ocean, this species is distributed from surface to 1500 m, and the highest abundance is observed during 50–200 m depth (Auel and Hagen, 2002). According to the GAMs results, the main population of *H. norvegicus* may be distributed in the upper layer (~220 m) in the study region. In contrast to the other 3 species studied here, the population structure of *H. norvegicus* is distinguished by the occurrence of C6Ms throughout the year (Fig. 3d). *Heterorhabdus* spp. are typical carnivores (Arashkevich, 1969; Minoda, 1971; Nishida and Ohtsuka, 1996) and feed on copepods, polychaetes and other zooplankton (Harding, 1974; Hopkins, 1985; Nishida and Ohtsuka, 1996). The feeding mode and maintenance of functional feeding structures in *H. norvegicus* is likely to be an important factor in the dominance of C6Ms. The degeneration of feeding appendages is known to be a famous phenomenon for C6Ms and reduces the lifespan of C6Ms in calanoid copepods (Michels and Schnack-Schiel, 2005). For *Calanus* and *Paraeuchaeta* spp., the shorter lifespans of C6Ms may be responsible for the lower composition of C6Ms in their population structures (see *C. hyperboreus* and *P. glacialis* in the present study, Fig. 3a, c), noting the semi-quantitative nature of our sediment trap samples in this study. In contrast, C6Ms of *Heterorhabdus* spp. have

functional feeding appendages (Ohtsuka and Huys, 2001), and maintenance of functional feeding appendages in C6Ms may be a key factor for the dominance of C6Ms in the population structure of *H. norvegicus* throughout the year. Additionally, their active swimming for mating may be an important factor in the high abundance in the trap (Matthews and Bakke, 1997).

4.6. Comparison with environmental parameters

To evaluate the inter-annual changes in copepod parameters, we applied the sampling year as a nominal variable in GAMs. Almost all the inter-annual effects were detected for the individual body size and weight (i.e., PL, WM, DM and AFDM) of the dominant species. As the life-cycles of the dominant copepods are known to be from one to several years (Grønvik and Hopkins, 1984; Falk-Petersen et al., 2009), the specimens collected in each year may reflect a population from different generations, exposed to different environmental conditions. Thus, the inter-annual differences on body size and weight were likely caused by differences in the generation for the species between years, even at a similar sampling location and depth.

In contrast to body size and weight, the flux, lipid accumulation and gonad maturation did not show a significant effect from year to year, except for gonad maturation in *M. longa*. According to Matsuno et al. (2014), the zooplankton flux and reproduction timing of the dominant copepods are believed to be related to the feeding modes (i.e., herbivore, omnivore and carnivore) for each copepod. However, at least one environmental parameter affected the copepods phenology (flux, lipid accumulation and gonad maturation). Of these environmental factors, changes in daytime hours and sea ice concentrations were the most influential on the life cycle of the copepods investigated in this study because the number of times the selected parameters in GAMs were higher than the other ones in the copepod phenology (Table 2). These environmental parameters could directly or indirectly affect the seasonal or diel vertical migration of *C. hyperboreus*, *M. longa* and *P. glacialis*. Among the species, however, the responses by the environmental parameters are thought to be different based on GAMs (Fig. 7). Daytime length showed a strong relationship with *C. hyperboreus* and *P. glacialis*, but the threshold value varied with the species (0.3 vs 0.7, respectively). SIC also exhibited different patterns of influence among the three species. Considering the response of copepods to light intensity, the different copepodid stages for *Calanus* spp. display different sensitivities to irradiance (Båtnes et al., 2015). For the effect of sea ice, the intensity of the diel vertical migration for *P. glacialis* in the winter changed depending on whether sea ice coverage was present or not (Berge et al., 2009). Therefore, these facts imply that the response (e.g., vertical migration) with the environmental parameters (i.e., light intensity and sea ice concentration) could vary with the species, and the drastic sea ice reductions would affect the copepod phenology in the Pacific-Arctic sector.

Acknowledgements

The authors would like to thank Prof. Ichiro Imai, Hokkaido University, for his kind advice and critical reading of the manuscript. The authors would also like to thank Dr. Makoto Sampei, Hokkaido University for permitting the use of the microbalance. We also express our sincere thanks to Dr. Ruth Eriksen (CSIRO) for correcting the English of this manuscript. Part of the present study was financially supported through a Grant-in-Aid for Scientific Research 17H01483 (A), 16H02947 (B), 15KK0268 (Joint International Research) and 18K14506 (Young Scientists) from the Japanese Society for Promotion of Science (JSPS). The present study was partially conducted for the Arctic Challenge for Sustainability (ArCS) project.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.polar.2018.08.006>.

Prosome length

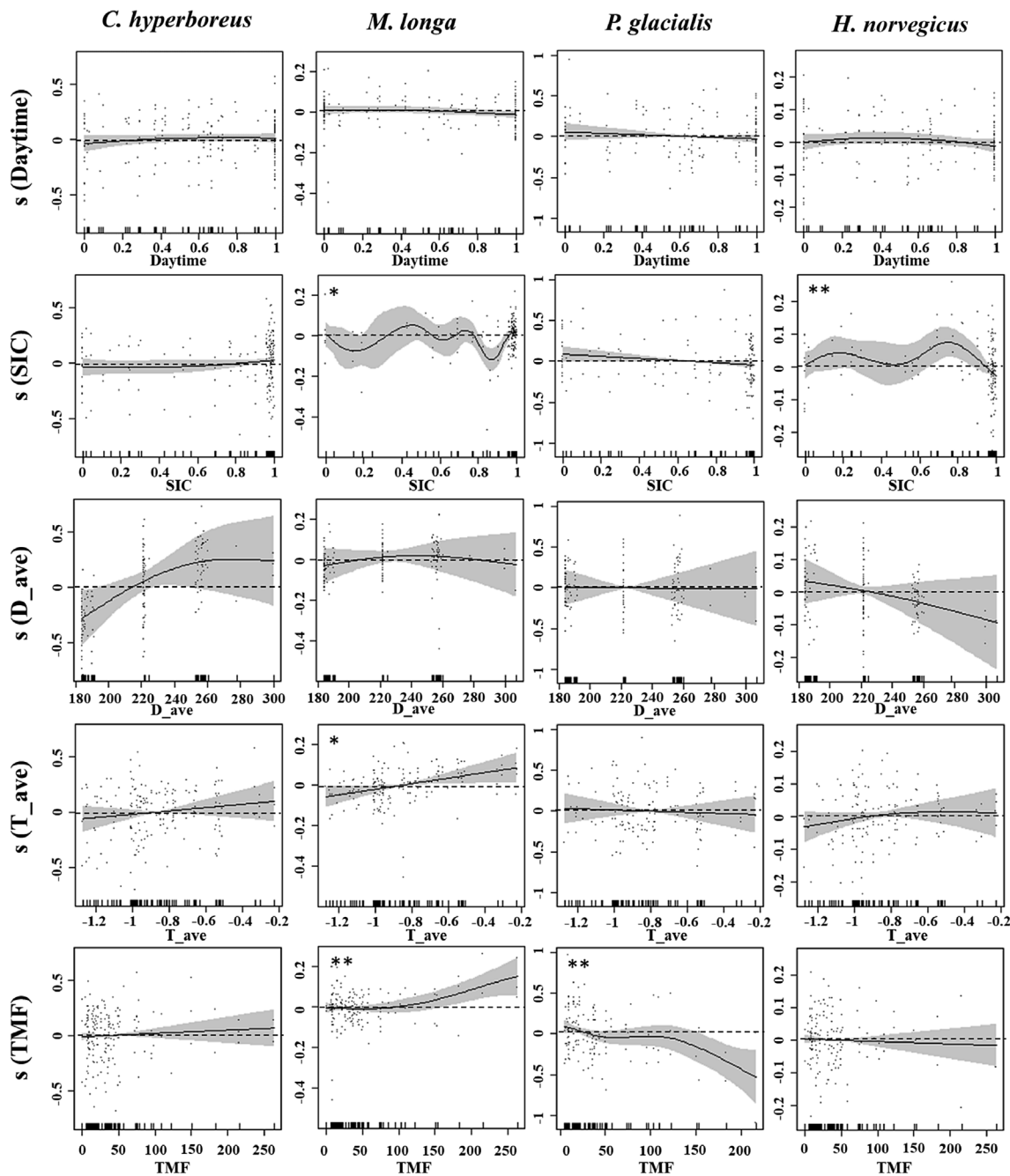


Fig. A.1. Result of GAMs based on the prosome length of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Wet mass

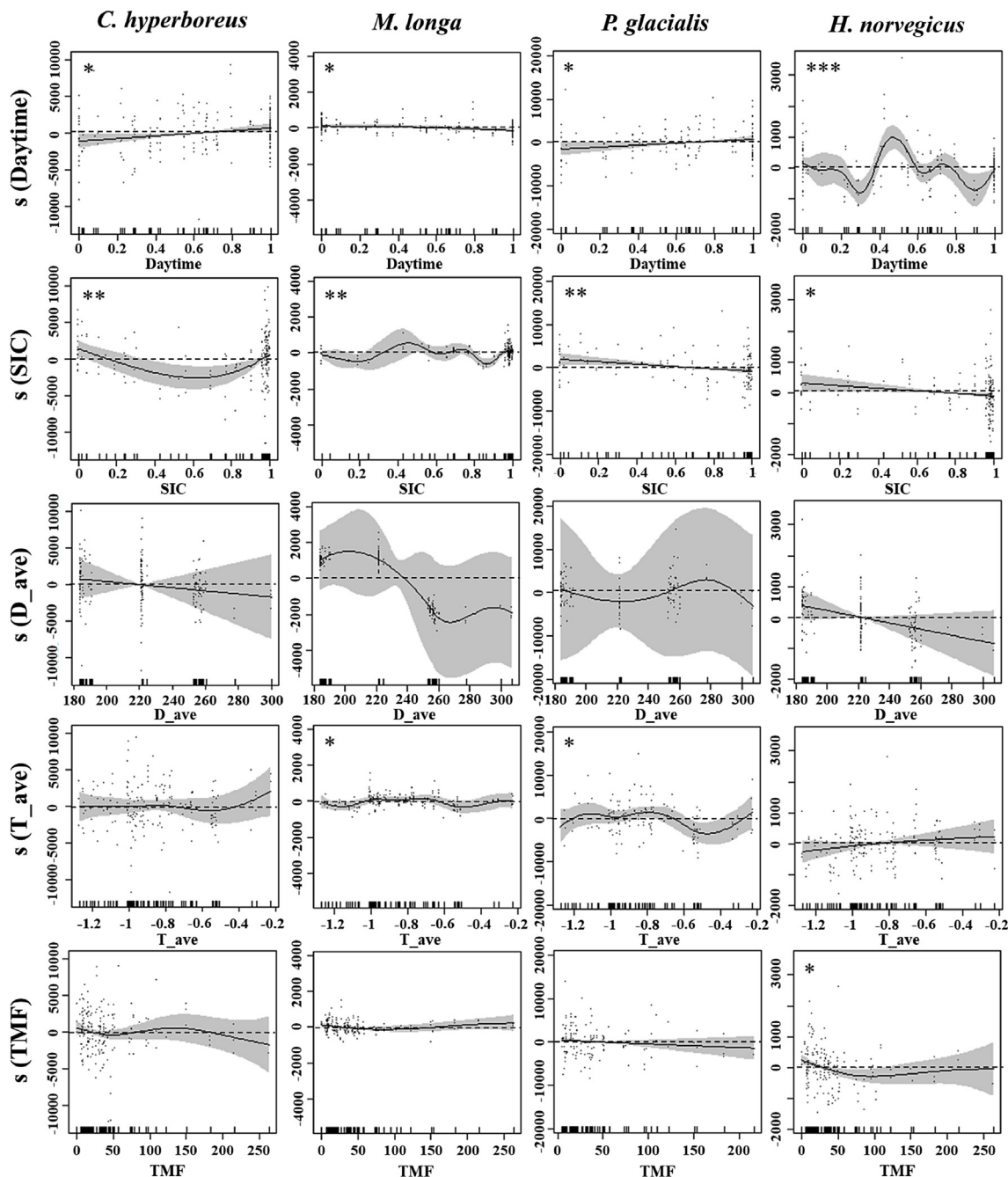


Fig. A.2. Result of GAMs based on the wet mass of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Dry mass

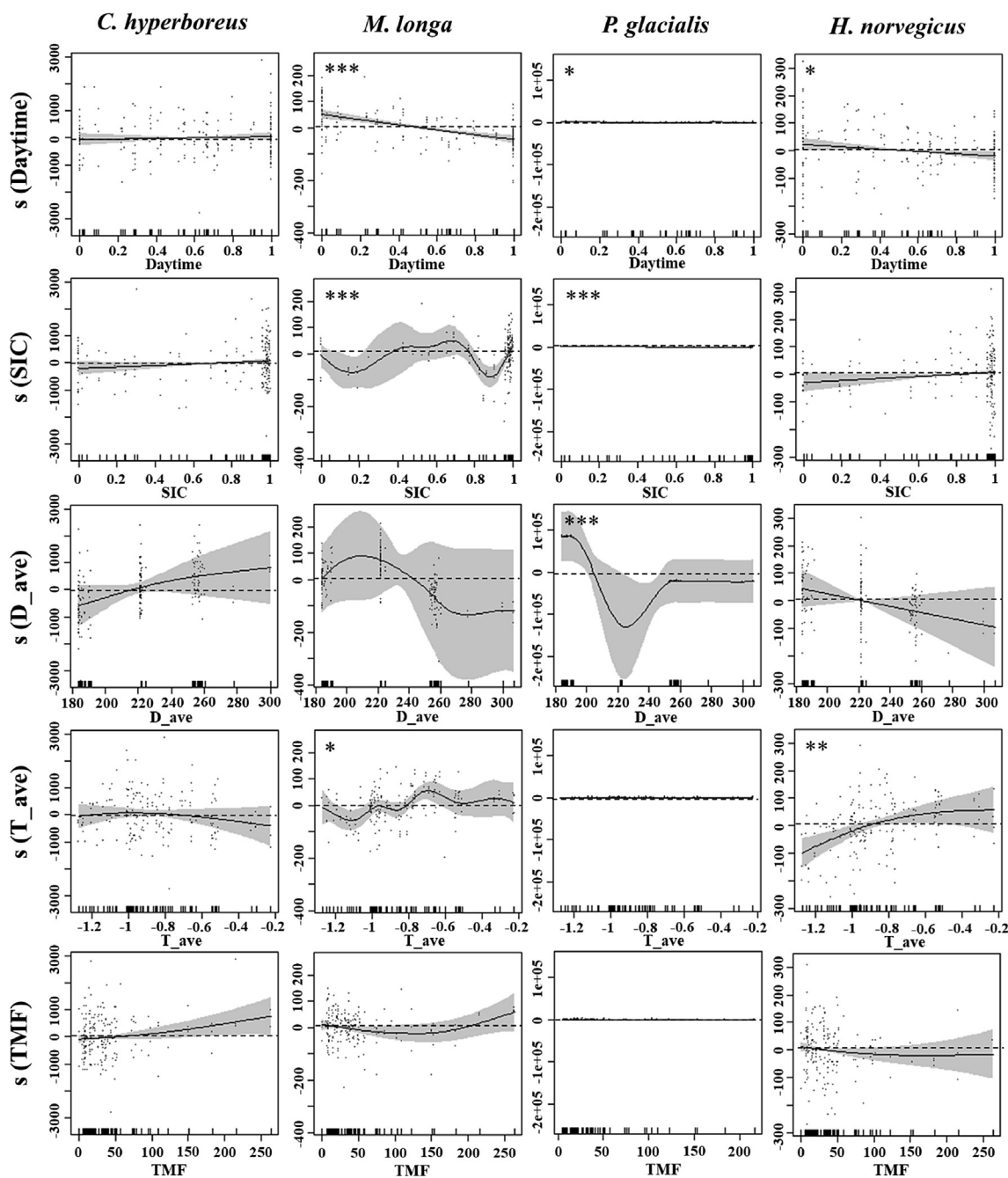


Fig. A.3. Result of GAMs based on the dry mass of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

AFDM

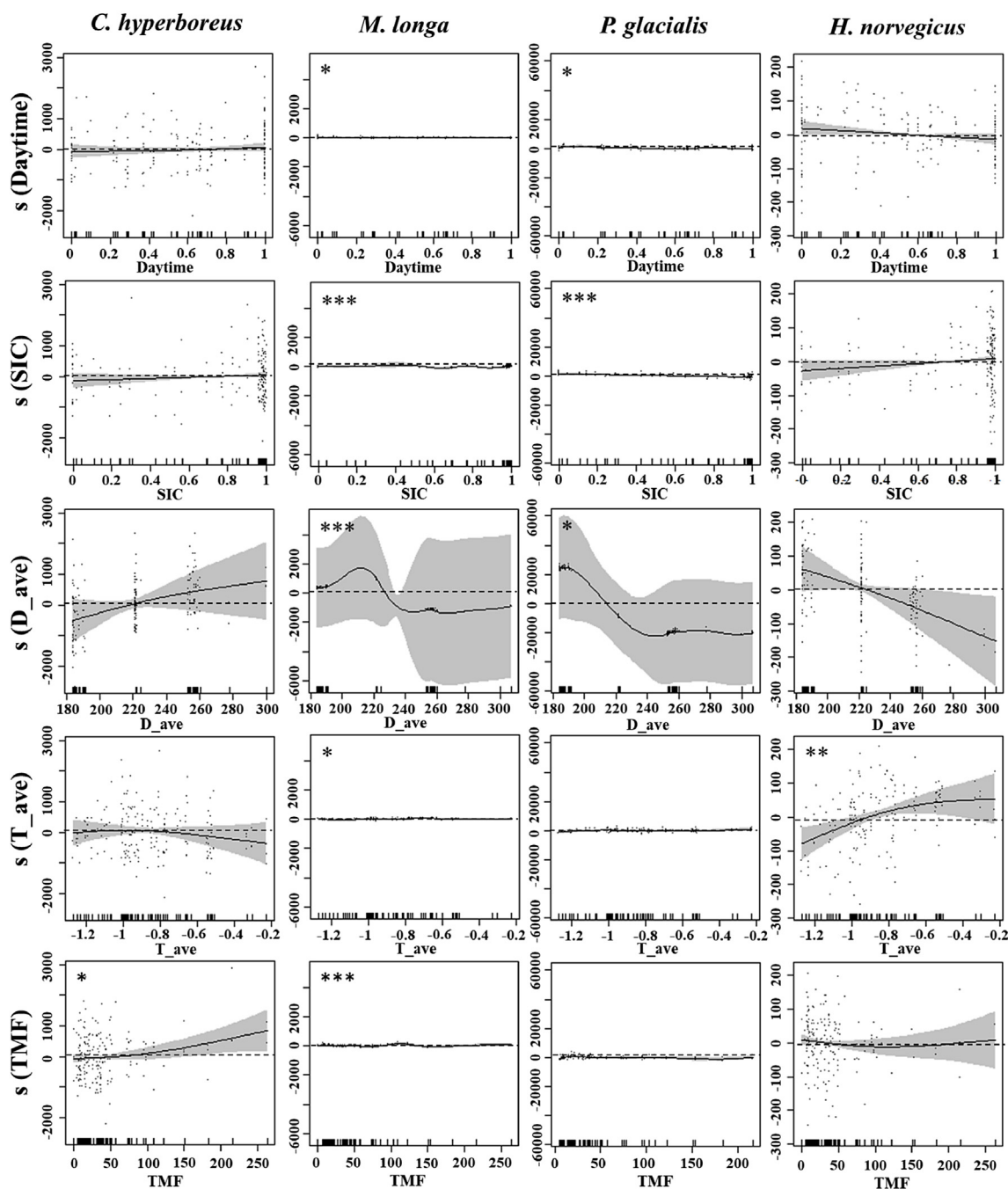


Fig. A.4. Result of GAMs based on the ash-free dry mass of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Lipid accumulation

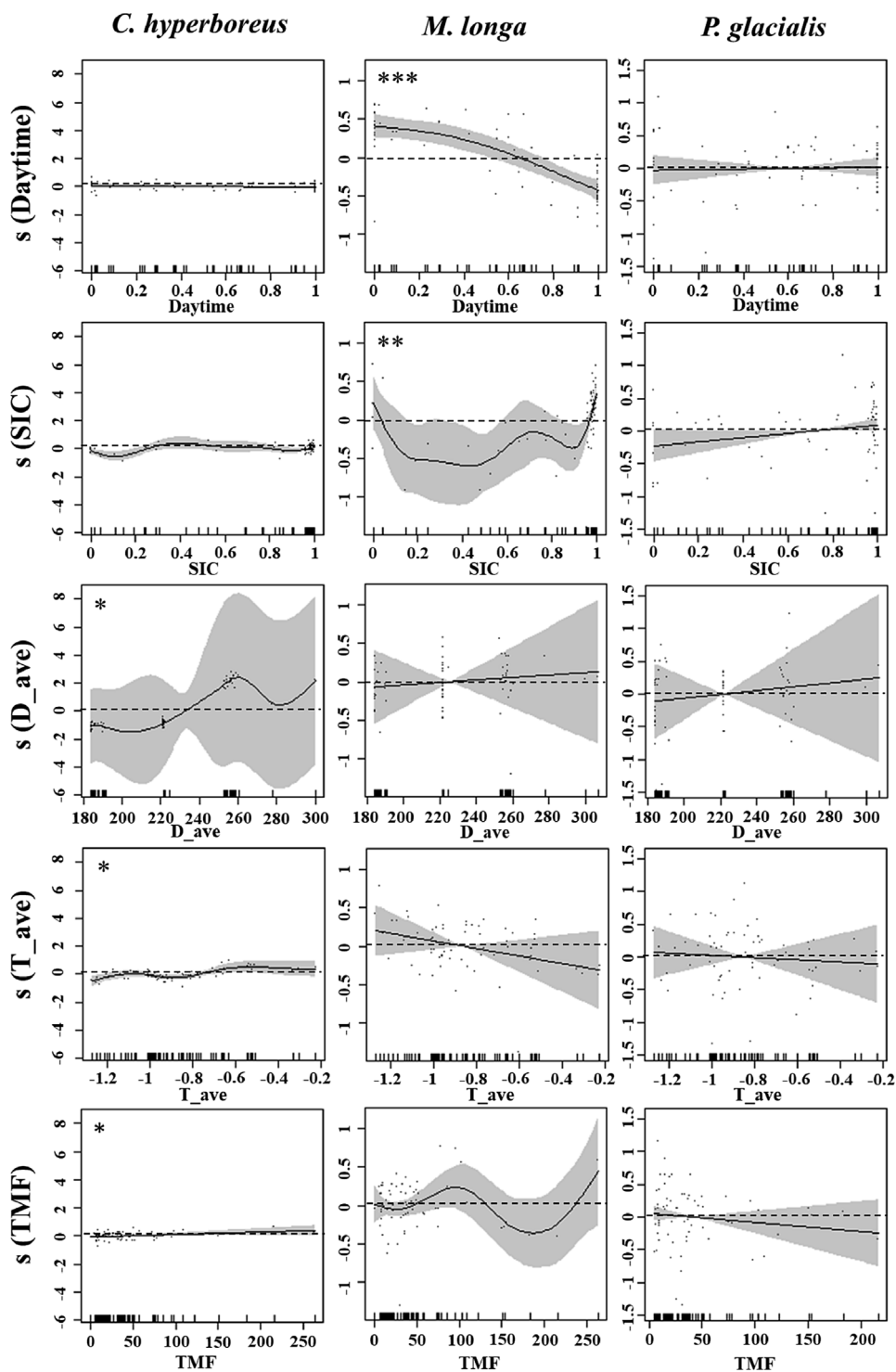


Fig. A.5. Result of GAMs based on the lipid accumulation of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_ave: mean trap depth during each sampling period, T_ave: mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Gonad maturation

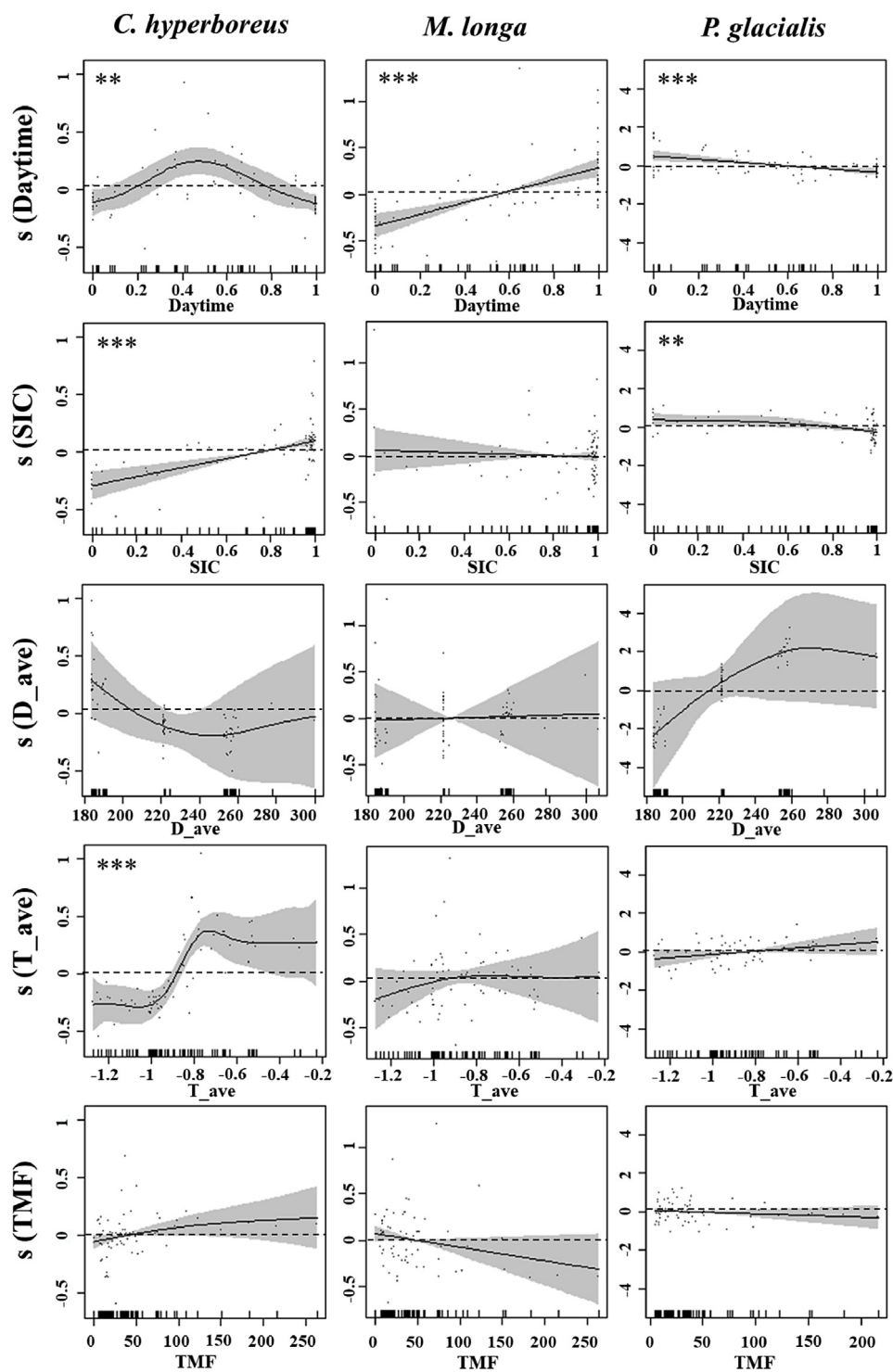


Fig. A.6. Result of GAMs based on the gonad maturation of adult female for the dominant copepods with environmental parameters. Daytime: daytime length, SIC: sea ice concentration, D_{ave} : mean trap depth during each sampling period, T_{ave} : mean temperature at the trap depth during each sampling period, TMF: total mass flux, Year: 1st, 2nd, and 3rd sampling periods as a nominal variable. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

References

Arashkevich, Y.G., 1969. The food and feeding of copepods in the northwestern Pacific. *Oceanology* 9, 695–705.

Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Keuren, D.V., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep-Sea Res.* 1 50, 1235–1261.

Auel, H., 1999. The ecology of Arctic deep-sea copepods (Euchaetidae and Actetidae). Aspects of their distribution, trophodynamics and effect on the carbon flux. *Ber. Polarforsch.* 319, 1–97.

Auel, H., 2004. Egg size and reproductive adaptations among Arctic deep-sea copepods

- (Calanoida, *Paraeuchaeta*). Helgol. Mar. Res. 58, 147–153.
- Auel, H., Hagen, W., 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Mar. Biol. 140, 1013–1021.
- Båmstedt, U., 1979. Reproduction bioenergetics within the summer and winter generations of *Euchaeta norvegica* (Copepoda). Mar. Biol. 54, 135–142.
- Båmstedt, U., 1985. Spring-bloom dynamics in Kosterfjorden, western Sweden: variation in phytoplankton production and macrozooplankton characteristics. Sarsia 70, 69–82.
- Båmstedt, U., Ervik, A., 1984. Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. J. Plankton Res. 6, 843–857.
- Båtnes, A.S., Miljeteig, C., Berge, J., Greenacre, M., Johnsen, G., 2015. Quantifying the light sensitivity of *Calanus* spp. during the polar night: potential for orchestrated migrations conducted by ambient light from the sun, moon, or aurora borealis? Polar Biol. 38, 51–65.
- Berge, J., Cottier, F., Last, K.S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygard, H., Vogedes, D., Griffiths, C., Johnsen, G., Lorentzen, D., Brierley, A.S., 2009. Diel vertical migration of Arctic zooplankton during the polar night. Biol. Lett. 5, 69–72.
- Buesseler, K.O., Antia, A.N., Chen, M., Fowler, S.W., Gardner, W.D., Gustafsson, O., Harada, K., Michaels, A.F., Rutgers, V.D.L.M., Sarin, M., Steinberg, D.K., Trull, T., 2007. An assessment of the use of sediment traps for estimating upper ocean particle fluxes. J. Mar. Res. 65, 345–416.
- Conover, R.J., 1962. Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. Rapp. P.-v. Cons. Int. Explor. Mer. 153, 190–197.
- Conover, R.J., 1965. Notes on the molting cycle, development of sexual characters and sex ratio in *Calanus hyperboreus*. Crustaceana 8, 308–320.
- Conover, R.J., 1967. Reproduction cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*. Crustaceana 13, 61–72.
- Conover, R.J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168, 127–142.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas – distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J. Mar. Syst. 2, 1–41.
- Conover, R.J., Siferd, T.D., 1993. Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. Arctic 46, 303–311.
- Dawson, J.K., 1978. Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. Limnol. Oceanogr. 23, 950–957.
- Dvoretzky, V.G., Dvoretzky, A.G., 2015. Summer population structure of the copepods *Paraeuchaeta* spp. in the Kara Sea. J. Sea Res. 96, 18–22.
- Falkenhang, T., Tande, K.S., Semenova, T., 1997. Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. Mar. Ecol. Prog. Ser. 149, 105–119.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., Sargent, J.R., 2009. Lipids and life strategy of Arctic *Calanus*. Mar. Biol. Res. 5, 18–39.
- Fleddum, A., Kaartvedt, S., Ellertsen, B., 2001. Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. Mar. Biol. 139, 719–726.
- Fortier, M., Fortier, L., Hattori, H., Saito, H., Legendre, L., 2001. Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. J. Plankton Res. 23, 1263–1278.
- Grainger, E.H., 1989. Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey, L., Alexander, V. (Eds.), Proceeding of the Sixth Conference Comité Arctique Int, vol. 1985. Brill Leiden, pp. 48–60.
- Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annu. Rev. Mar. Sci. 4, 63–78.
- Grønvik, S., Hopkins, C.C.E., 1984. Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). J. Exp. Mar. Biol. Ecol. 80, 93–107.
- Harada, N., 2016. Review: potential catastrophic reduction of sea ice in the western Arctic Ocean: its impact on biogeochemical cycles and marine ecosystems. Global Planet. Change 136, 1–17.
- Harding, G.C.H., 1974. The food of deep-sea copepods. J. Mar. Biol. Assoc. U. K. 54, 141–155.
- Hays, G.C., 1995. Diel vertical migration behavior of *Calanus hyperboreus* at temperature latitudes. Mar. Ecol. Prog. Ser. 127, 301–304.
- Hirche, H.J., 1991. Distribution of dominant calanoid species in the Greenland Sea during late fall. Polar Biol. 11, 351–362.
- Hirche, H.J., 1996. The reproductive biology of the marine copepod, *Calanus finmarchicus*-a review. Ophelia 44, 111–128.
- Hirche, H.J., 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar. Biol. 128, 607–618.
- Hirche, H.J., Kosobokova, K.N., Gaye-Haake, B., Harms, I., Meon, B., Nöthing, E.M., 2006. Structure and function of contemporary food webs on Arctic shelves: a panarctic comparison: the pelagic system of the Kara Sea-communities and components of carbon flow. Prog. Oceanogr. 71, 288–313.
- Hirche, H.J., Mumm, N., 1992. Distribution of dominant copepods in the Nansen basin, Arctic Ocean, in summer. Deep-Sea Res. 39, 485–505.
- Hirche, H.J., Niehoff, B., 1996. Reproduction of the Arctic copepods *Calanus hyperboreus* in the Greenland sea-field and laboratory observations. Polar Biol. 16, 209–219.
- Hopkins, T.L., 1985. Food web of an Antarctic midwater ecosystem. Mar. Biol. 89, 197–212.
- Ikenoue, T., Bjørklund, K.R., Onodera, J., Kimoto, K., Harada, N., 2015. Flux variation and vertical distribution of siliceous Rhizaria (Radiolaria and Phaeodaria) in the western Arctic Ocean: indices of environmental changes. Biogeosciences 12, 2019–2046.
- Kaartvedt, S., Dale, T., Bagøien, E., Viken, T., 2002. Bi-modal vertical distribution of the carnivorous copepod *Paraeuchaeta norvegica*. J. Plankton Res. 24, 155–158.
- Kraft, A., Bauerfeind, E., Nöthing, E.V., Bathmann, U.V., 2012. Size structure and life cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. J. Mar. Syst. 95, 1–15.
- Lee, R.F., 1974. Lipid composition of the copepod *Calanus hyperboreus* from the Arctic Ocean. Changes with depth and with season. Mar. Biol. 26, 313–318.
- Lee, R.F., 1975. Lipid of arctic zooplankton. Comp. Biochem. Physiol. 51B, 263–266.
- Lowry, L.F., Sheffield, G., George, C., 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. J. Cetacean Res. Manag. 6, 215–223.
- Makabe, R., Hattori, H., Sampei, M., Ota, Y., Fukuchi, M., Fortier, L., Sasaki, H., 2010. Regional and seasonal variability of zooplankton collected using sediment trap in the southeastern Beaufort Sea. Canadian Arctic. Polar Biol. 33, 257–270.
- Makabe, R., Hattori, H., Sampei, M., Darnis, G., Fortier, L., Sasaki, H., 2016. Can sediment trap-collected zooplankton be used for ecological studies? Polar Biol. 39, 2335–2346.
- Markus, T., Stroeve, J.C., Miller, J., 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. J. Geophys. Res. 114, C12024. <https://doi.org/10.1029/2009JC005436>.
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Imai, I., Chiba, S., Harada, N., Kikuchi, T., 2014. Seasonal changes in mesozooplankton swimmers collected by sediment trap moored at a single station on the Northwind Abyssal Plain in the western Arctic Ocean. J. Plankton Res. 36, 490–502.
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Harada, N., Kikuchi, T., 2015. Seasonal changes in the population structure of dominant planktonic copepods collected using a sediment trap moored in the western Arctic Ocean. J. Nat. Hist. 49, 2711–2726.
- Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Harada, N., Kikuchi, T., 2016. Seasonal changes in mesozooplankton swimmer community and fecal pellets collected by sediment trap moored at the Northwind Abyssal Plain in the western Arctic Ocean. Bull. Fish. Sci. Hokkaido Univ. 66, 77–85.
- Matthews, J.B.E., Bakke, J.L.W., 1997. Ecological studies on the deep-water pelagic community of Korsfjorden (western Norway). Helgol. Wiss. Meeresunters. 30, 47–61.
- Melle, W., Skjoldal, H.R., 1998. Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. Mar. Ecol. Prog. Ser. 169, 211–228.
- Michels, J., Schnack-Schiel, S.B., 2005. Feeding in dominant Antarctic copepods-does the morphology of the mandibular gnathobases relate to diet? Mar. Biol. 146, 483–495.
- Minoda, T., 1971. Pelagic Copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. Mem. Fac. Fish Hokkaido Univ. 18, 1–74.
- Niehoff, B., Madsen, S.D., Hansen, B.W., Nielsen, T.G., 2002. Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. Mar. Biol. 140, 567–576.
- Nishida, S., Ohtsuka, S., 1996. Specialized feeding mechanism in the pelagic copepod genus *Heterorhabdus* (Clanoida: Heterorhabdidae) with special reference to the mandibular tooth and labral glands. Mar. Biol. 126, 619–632.
- Ohtsuka, S., Huys, R., 2001. Sexual dimorphism in calanoid copepods: morphology and function. Hydrobiologia 453/454, 441–466.
- Onodera, J., Watanabe, E., Harada, N., Honda, M.C., 2015. Diatom flux reflects water-mass conditions on the southern Northwind Abyssal Plain, Arctic Ocean. Biogeosciences 12, 1373–1385.
- Onodera, J., Watanabe, E., Nishino, S., Harada, N., 2016. Distribution and vertical fluxes of silicoflagellates, ebridians, and the endoskeletal dinoflagellate *Actiniscus* in the western Arctic Ocean. Polar Biol. 39, 327–341.
- Øresland, V., 1991. Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. Mar. Ecol. Prog. Ser. 78, 41–47.
- Ota, Y., Hattori, H., Makabe, R., Sampei, M., Tanimura, A., Sasaki, H., 2008. Seasonal changes in nauplii and adults of *Calanus hyperboreus* (Copepoda) captured in sediment trap, Amundsen Gulf, Canadian Arctic. Pol. Sci. 2, 215–222.
- Perovich, D.K., 2011. The changing arctic sea ice cover. Oceanography 24, 162–173.
- Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C., Wang, W., 2002. An improved in situ and satellite SST analysis for climate. J. Clim. 15, 1609–1625.
- Sampei, M., Forest, A., Sasaki, H., Hattori, H., Makabe, R., Fukuchi, M., Fortier, L., 2009. Attention of the vertical flux of copepod fecal pellets under Arctic sea ice: evidence for an active detrital food web in winter. Polar Biol. 32, 225–232.
- Sampei, M., Sasaki, H., Forest, A., Fortier, L., 2012. A substantial export flux of particulate organic carbon linked to sinking dead copepods during winter 2007–2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean). Limnol. Oceanogr. 57, 90–96.
- Scott, C.L., Falk-Petersen, S., Sargent, J.R., Hop, H., Lønne, O.J., Poltermann, M., 1999. Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biol. 21, 65–70.
- Seiler, D., Brandt, A., 1997. Seasonal occurrence of plankton Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biol. 17, 337–349.
- Steinberg, D.K., Pilskaln, C.H., Silver, M.W., 1998. Contribution of zooplankton associated with detritus to sediment trap 'swimmer' carbon in Monterey Bay, California, USA. Mar. Ecol. Prog. Ser. 164, 157–166.
- Tande, K.S., Grønvik, S., 1983. Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: sex ratio and gonad maturation cycle in the copepod *Metridia longa* (Lubbock). J. Exp. Mar. Biol. Ecol. 71, 43–54.
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O., 2006. Food webs and carbon flux in the Barents Sea. Prog. Oceanogr. 71, 232–287.
- Wiborg, K.F., 1954. Investigations on zooplankton in coastal and offshore waters of western and north-western Norway. Rep. Norw. Fish Invest. 11, 1–246.
- Yamaguchi, A., Onishi, Y., Omata, A., Kawai, M., Kaneda, M., Ikeda, T., 2010. Population structure, egg production and gut content pigment of large grazing copepods during the spring bloom in the Oyashio region. Deep-sea Res. II 57, 1679–1690.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.