



Short-term changes in abundance and population structure of dominant pelagic amphipod species in the Oyashio region during the spring phytoplankton bloom



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HIGHLIGHTS

- The dynamics of four dominant amphipods in the Oyashio region were studied during the spring.
- The utilization of the spring bloom was varied by species, specific for amphipod species.
- Three dominant amphipods achieved growth, maturation and reproduction during the spring.
- Species-specific utilization of the spring bloom may be related to life-cycle phenology.
- Less effect of water mass change on amphipods may be caused by their strong DVM.

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ABSTRACT

Short-term changes in the population structure of dominant amphipods in the Oyashio region during the spring bloom were studied and discussed from the perspective of the effect of water mass change and the utilization of a phytoplankton bloom. Throughout the sampling period, amphipods belonging to 9 genera and 13 species were found. Among them, three amphipods (*Cyphocaris challengeri*, *Primno abyssalis* and *Themisto pacifica*) accounted for 89% of the total amphipod abundance and 92% of the biomass. For *C. challengeri*, the compositions of egg- and juvenile-carrying specimens within mature females were increased through April; juveniles exhibited a drastic increase in late April. These facts suggest that *C. challengeri* primarily achieved reproduction during the spring phytoplankton bloom. For *P. abyssalis*, growth of the mean body length was observed for each juvenile cohort. Thus, *P. abyssalis* achieved juvenile growth during the spring phytoplankton bloom. For *T. pacifica*, the compositions of egg- and juvenile-carrying females increased through April. These facts suggest that *T. pacifica* achieved maturation during the spring phytoplankton bloom. The effect of the water mass exchange on the amphipod population was more moderate than that observed on the other macrozooplankton taxa. This finding may be a result of a strong diel vertical migration behavior, which functions to maintain the population position. The species-specific differences in the amphipods in the utilization of spring phytoplankton may be related to the species-specific life cycle timing (phenology) in this region.

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1. Introduction

Pelagic amphipods are widely distributed among zooplankton communities in the world's oceans (Raymont, 1983), and at least 67 species occur in the western subarctic Pacific Ocean and neighboring seas (Yoo, 1970). The three species reported as the

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dominant amphipods in the Oyashio region are the following: 2 hyperiids (*Primno abyssalis* Bowman and *Themisto pacifica* Bowman) and 1 gammarid (*Cyphocaris challengeri* Stebbing) (Yamada and Ikeda, 2006). Amphipods prey on other zooplankton (calanoid copepods, mysids, chaetognaths and euphausiids) (Pakhomov and Perissinotto, 1996; Froneman et al., 2000; Auel et al., 2002; Marion et al., 2008; Kraft et al., 2013), while they are preyed upon by marine birds (Rosing-Asvid et al., 2013), demersal fishes (Dempson et al., 2002; Walkusz et al., 2013), seals (Nielsen et al., 1995) and whales (Lowry and Frost, 1984). Thus, in a marine ecosystem, pelagic amphipods play a vital role in connecting between secondary production and higher trophic production. Because of their importance, various studies have been conducted on their ecology, such as diel vertical migration (DVM), life cycle and diet (Marion et al., 2008; Kraft et al., 2013; Semenova, 1974; Ikeda, 1995; Ikeda and Shiga, 1999; Harvey et al., 2009; Olsen et al., 2014). In the Oyashio region, the life cycle and population structure of three dominant amphipod species have been reported (Yamada and Ikeda, 2006, 2000, 2003; Yamada et al., 2002, 2004). However, all of these studies were based on samples that were collected in monthly or bimonthly intervals, and no information is available for short-term changes in the amphipod community or population structure.

In the Oyashio region, during the spring, dominant water masses characterized by different temperatures are known to change drastically at the surface layer within a short time period (Kono and Sato, 2010). Simultaneously, a large phytoplankton bloom is known to occur at the surface layer, and approximately half of the annual primary production is concentrated during the spring (Saito et al., 2002; Liu et al., 2004; Ikeda et al., 2008). Because amphipods are reported to reproduce and grow during the spring bloom (Yamada and Ikeda, 2006), evaluation of the effects of the water mass exchange and primary production on the amphipod community and population dynamics is of special interest. To evaluate the biological responses to the spring phytoplankton bloom, high-frequency samplings were conducted at a fixed station in the Oyashio region. This project, known as the “Ocean Ecodynamics Comparison in the Subarctic Pacific” (OECOS), is endorsed by the North Pacific Marine Science Organizations (PICES). Through the OECOS project, short-term changes in various taxa have been evaluated, e.g., epi- and mesopelagic copepods (Yamaguchi et al., 2010a,b; Abe et al., 2012), euphausiids (Kim et al., 2010a,b) and hydromedusae (Abe et al., 2014); however, no information is available for the dynamics of amphipods during the same period.

As part of the OECOS project, this study aimed to evaluate short-term changes in the population structure of the three dominant amphipods (*C. challengeri*, *P. abyssalis* and *T. pacifica*) in the Oyashio region during March and April 2007. We analyzed the three dominant amphipods based on the Bongo net samples that were collected between 0 and 200 m with 4- to 5-day intervals and evaluated the effects of water mass changes and phytoplankton blooms on their population. Species-specific differences in the responses to these environmental changes were discussed from the viewpoint of their ecology (e.g., DVM, life cycle and phenology).

2. Materials and methods

2.1. Field sampling

Macrozooplankton samples were collected at a single station (42°00'N, 145°15'E, depth approx. 4000 m) in the Oyashio region of the western subarctic Pacific at night (20:00–21:00 local time) on the 9th and 14th of March and the 6th, 8th, 10th, 12th, 15th, 17th, 20th, 25th and 30th of April 2007 (Fig. 1). Bongo nets (70-cm mouth diameter, 315- μ m mesh size) were obliquely towed from a 200-m depth to the surface (400-m wire with 60°

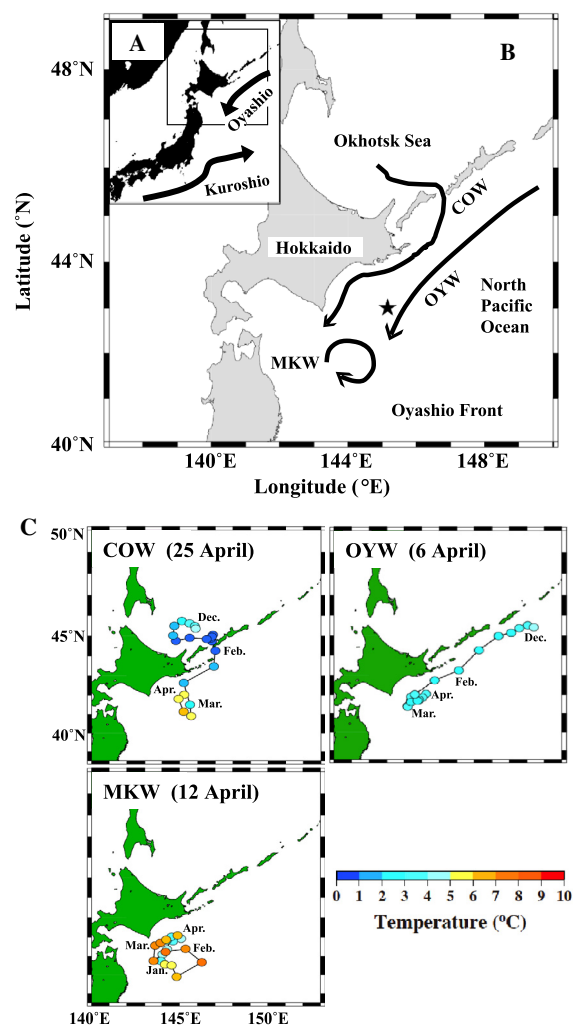


Fig. 1. Location of the Oyashio region (A) and sampling station (star) in the Oyashio region (B). For A and B, the approximate current flows are shown. The lower three panels are the results from the FRA-ROMS analyses, which back-calculated the origin of the water masses at each sampling date (C). COW: coastal Oyashio water (25 April); MKW: mixed Kuroshio water (12 April); OYW: Oyashio water (6 April).

wire angle) at a speed of 2 knots. Because of the limitation of shipping time, only one net tow was made on each occasion. After collection, the samples were immediately preserved with v/v 5% borax-buffered formalin-seawater. The filtered water volumes were estimated from the readings of a flow-meter (Rigoshia Co. Ltd., Tokyo) mounted on a net ring.

The environmental parameters of temperature, salinity and chlorophyll *a* (Chl. *a*) fluorescence were measured with a CTD (SBE-9 plus, Sea Bird Electronics, Washington) cast at each sampling. Based on the temperature and salinity data, the mixture ratios of the three water masses (Coastal Oyashio Water: COW; Oyashio Water: OYW; modified Kuroshio Water: MKW) in the 0–50 m water column were calculated (Kono and Sato, 2010). Regarding food conditions, the mesozooplankton wet mass (g WM m^{-2}) data, collected with twin-NORPAC nets (100- and 315- μ m mesh sizes, 45-cm diameter) from 0–150 m during the nights of March 9–14 and April 6 to May 1, were analyzed (Yamaguchi et al., 2010a). Samples collected by two mesh sizes were used for different purposes: species identification for fine-mesh samples and wet mass estimation for coarse-mesh samples. Because the results of both mesh sizes (WM in course-mesh samples and biovolume in fine-mesh samples) were highly correlated ($r^2 = 0.92$, $p < 0.0001$), temporal changes in both mesh net samples were confirmed to be similar (Yamaguchi et al., 2010a).

2.2. Enumeration and measurement

All samples were examined in the land laboratory. All amphipods in the samples were sorted and enumerated by species. Identifications were made based on Nagata (Nagata, 1997); for juveniles, identifications were made based on several relevant references in this region (Yamada et al., 2004; Yamada and Ikeda, 2001a,b). For the three most abundant species, namely *C. challengerii*, *P. abyssalis* and *T. pacifica*, body length (BL, mm) was measured as the maximal distance between the tip of the head and the distal end of the uropod (or telson for *C. challengerii*) of the straightened body with an eye-piece micrometer with a precision of 0.05–0.10 mm. The number of segments in the first pleopod was counted to determine the instar stage of each amphipod. Specimens were separated into 5 categories according to the developmental stage and sex (juvenile, immature male, mature male, immature female and mature female) (Yamada and Ikeda, 2000; Yamada et al., 2002, 2004; Yamada and Ikeda, 2001a,b, 2004). Wet mass (WM, mg ind.⁻¹) was estimated from the BL by the following equations that varied by species (Yamada and Ikeda, 2000):

$$C. challengerii: WM = 0.027 BL^{2.71}$$

$$P. abyssalis: WM = 0.023 BL^{2.88}$$

$$T. pacifica: WM = 0.029 BL^{2.82}$$

The estimated WM was converted to dry mass (DM, mg ind.⁻¹) using the reported water content of each species (*C. challengerii*: 80.1%, *P. abyssalis*: 77.4% and *T. pacifica*: 77.2% Yamada and Ikeda, 2003). For the other amphipod species, the WM was directly measured using an electric balance (precision of 10 mg; Mettler Toledo) with the aid of a pre-weighed mesh. The WM data were converted to DM using an equation (Kotori, 1976) ($DM = 0.12 WM$). For *C. challengerii* and *T. pacifica* mature females, additional identification was determined for the specimen condition: egg- or juvenile-carrying and presence or absence of parasitic ellobiopsis (*Thalassomyces marsupii*) within the marsupium (Kane, 1964; Wing, 1975).

2.3. Data analysis

2.3.1. Analysis on the origin of a water mass

To clarify the origin of the water mass at the surface layer (depths of 10, 20, 30, 50, 75, 100, 125, 150 and 200 m) on each sampling date, re-analyses of the hydrographic data (temperature, salinity, sea surface height and geostrophic velocity) were performed using a 1/10° grid high-resolution ocean model known as the Fisheries Research Agency Regional Ocean Model (FRA-ROMS; Fisheries Research Agency of Japan, 2014, <http://fm.dc.affrc.go.jp/fra/T1\ndashroms/index.html>). FRA-ROMS is a ROMS (Rutgers University and UCLA, <http://myroms.org/index.php>) based on an ocean model that assimilates satellite sea surface heights and temperatures and field study data in the North Pacific via a three-dimensional variation method that uses an empirical orthogonal function (EOF) joint mode (Fujii and Kamachi, 2003) and then generates the realistic re-analysis products. Lagrangian particle-tracking experiments were conducted using the FRA-ROMS velocity field. The positions of the particles were estimated by calculating an advection equation, which were inversely related to time:

$$\frac{dx}{dt} = -u(x, y, t), \quad \frac{dy}{dt} = -v(x, y, t),$$

where $(x(t), y(t))$ is the position of a particle at time t and (u, v) is the velocity at the position (x, y) at time t . For this calculation, the time resolution was applied at 80 min. By linear interpolation, (u, v) was estimated using a flow velocity of the FRA-ROMS

with a 1/10° horizontal resolution. We initially released particles at the sampling station (42°00'N, 145°15'E) and conducted a particle backtracking experiment for the past six months. We examined the temporal change in the locations of the released particles to determine the origin of the water and evaluated the observed water temperature changes.

2.3.2. Cohort analysis on body length

For the three most dominant amphipods (*C. challengerii*, *P. abyssalis* and *T. pacifica*), cohorts were analyzed based on BL frequency distribution data of each sampling date fitted to normal distribution curves. Length-frequency data were separated into multiple normal distribution curves by the aid of the free software “R” with an add-on package “mclust” (Fraley et al., 2012).

2.3.3. Correlation analysis with environmental parameters

For the three dominant amphipod species (*C. challengerii*, *P. abyssalis* and *T. pacifica*), the abundance (ind. m⁻²) and biomass (mg DM m⁻²) of each species were quantified for each sampling date. Then, a correlation analysis with environmental parameters (e.g., Julian day from 1 March, integrated mean temperature, salinity, Chl. *a*, water mass mixing ratio in the 0–50 m water column and zooplankton biomass in the 0–150 m water column) was performed.

3. Results

3.1. Hydrography

Temporal changes in the temperature, salinity, Chl. *a*, water mass mixing ratio and mesozooplankton biomass from 9 March to 1 May 2007 are shown in Fig. 2. During this period, the temperature and salinity varied between 2 and 6 °C and 33.2 and 34.2, respectively (Fig. 2, A, B). Chl. *a* had three peaks (1–6 mg m⁻³) on the 7, 11 and 23 of April (Fig. 2(C)). For the water mass mixture ratio in the 0–50 m water column, the OYW and MKW composed approximately half of the water mass during March. Cold COW occurred in early April, and the timing of its occurrence corresponded with the timing of the Chl. *a* peaks that were mentioned above. For the 11 Bongo net sampling dates, the dominant water masses were COW for the 20 and 25 of April, OYW for 14 March and 6 April and MKW for 9 March and 8, 10, 12, 15, 17 and 30 April (Fig. 2(D)).

From the Lagrangian particle-tracking experiments using FRA-ROMS, the origin of the water mass was estimated to be varied. The origin of COW was estimated to be in the Okhotsk Sea, whereas the origin of OYW was estimated to be the east Kamchatka current that flows along the southern edge of the Kuril Islands (Fig. 1(C)). During the OECOS sampling period, clockwise warm water eddies were observed around the sampling station, and the origin of MKW was associated with that warm water eddy (Fig. 1(C)). The observed water temperature during the past six months also varied with the water masses. The measured temperatures of COW, OYW and MKW were 1.49–5.98 °C (3.95 ± 1.37 °C: mean \pm 1 sd), 2.24–4.86 °C (3.29 ± 0.63 °C) and 3.58–8.10 °C (5.80 ± 1.37 °C), respectively. The observed water temperature significantly varied with the water mass ($p < 0.001$, one-way ANOVA) (Fig. 1(C)). The mesozooplankton biomass varied between 8.3 and 93.9 g WM m⁻² (mean \pm 1 sd: 66.2 ± 29.1 g WM m⁻²), was lower during March, and increased 7-fold after 10 April (Fig. 2(E)).

3.2. Abundance and biomass

Throughout the sampling period, amphipods belonging to 9 genera and 13 species were observed (Table 1). Among these, three

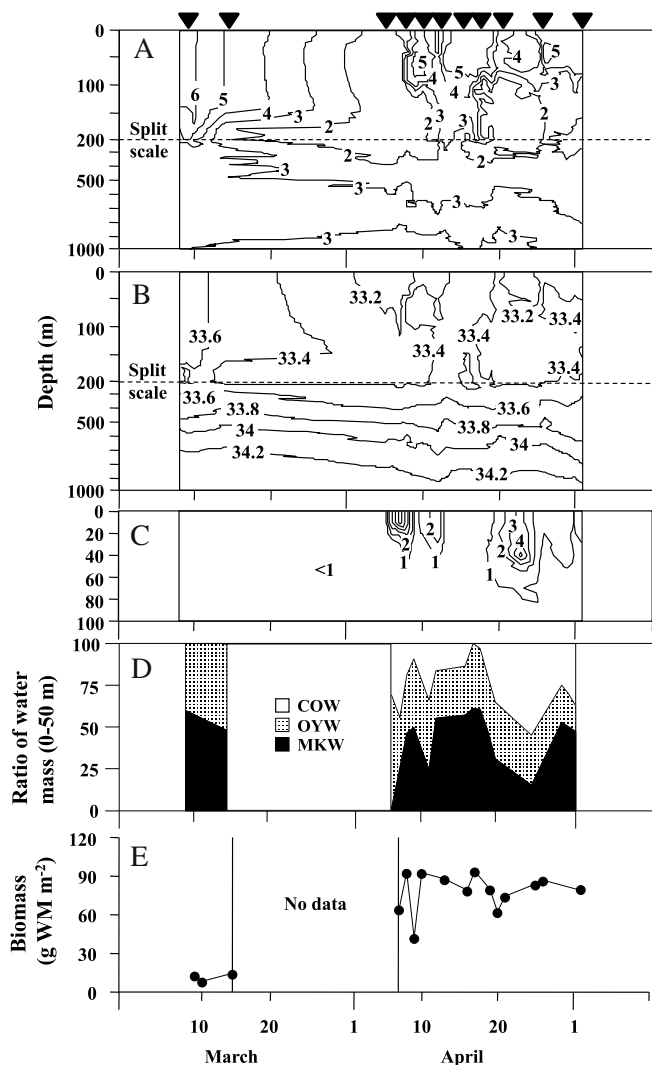


Fig. 2. Temporal changes in temperature (A, °C), salinity (B), chlorophyll *a* (C, mg m^{-3}), the ratio of water mass at 0–50 m (D, %) and mesozooplankton wet mass at 0–150 m (E, g WM m^{-2}) in the Oyashio region between 9 March to 1 May 2007. Data in D and E are from Kono and Sato (2010) and Yamaguchi et al. (2010a), respectively. COW: coastal Oyashio water; OYW: Oyashio water; MKW: modified Kuroshio water.

amphipods (*C. challengerii*, *P. abyssalis* and *T. pacifica*) dominated and accounted for 89% of the total amphipod abundance and 92% of the total biomass.

The abundance of *C. challengerii* varied between 14 and 934 ind. m^{-2} (mean \pm 1 sd: $167.5 \pm 247.9 \text{ ind. m}^{-2}$) during the sampling period (Fig. 3). The biomass of *C. challengerii* varied between 0.03 and 1.32 g DM m^{-2} (mean \pm 1 sd: $247.48 \pm 353.05 \text{ mg DM m}^{-2}$). Both the abundance and biomass were low during March but increased from April onward.

The abundance of *P. abyssalis* was 0.7–74.5 ind. m^{-2} (mean \pm 1 sd: $27.9 \pm 21.5 \text{ ind. m}^{-2}$) during the sampling period (Fig. 3). Their biomass ranged between 0.05 and 22.74 mg DM m^{-2} (mean \pm 1 sd: $10.49 \pm 7.24 \text{ mg DM m}^{-2}$). Significant increases in the abundance and biomass were detected across the sampling dates (Table 2, Fig. 3). *Primno abyssalis* juveniles composed more than 50% of the population throughout the sampling period (Fig. 3).

The abundance of *T. pacifica* varied between 4 and 216 ind. m^{-2} (mean \pm 1 sd: $39.3 \pm 39.6 \text{ ind. m}^{-2}$) (Fig. 3). Their biomass varied between 1.54 and 81.07 mg DM m^{-2} (mean \pm 1 sd: $13.72 \pm 18.61 \text{ mg DM m}^{-2}$). Both the abundance and biomass were

Table 1

Mean abundance and biomass of planktonic amphipods in the 0–200 m water column in the Oyashio region during March–April 2007. Values in parentheses indicate percentage compositions relative to the total amphipod community. Species are arranged in order of quantitative biomass.

Species	Abundance (ind. m^{-2})		Biomass (mg DM m^{-2})	
<i>Cyphocaris challengerii</i>	167.60	(63.19)	247.48	(83.98)
<i>Themisto pacifica</i>	39.34	(14.83)	13.77	(4.67)
<i>Primno abyssalis</i>	27.90	(10.52)	10.49	(3.56)
<i>Themisto japonica</i>	23.27	(8.77)	9.79	(3.32)
<i>Phronima sedentaria</i>	0.32	(0.12)	5.89	(2.00)
<i>Phronima atlantica</i>	2.29	(0.86)	4.65	(1.58)
<i>Hyperia medusarum</i>	0.26	(0.10)	1.22	(0.41)
<i>Scina borealis</i>	3.96	(1.49)	1.00	(0.34)
<i>Scina crassicomis</i>	0.07	(0.03)	0.13	(0.05)
<i>Vibilia gibbosa</i>	0.03	(0.01)	0.11	(0.04)
<i>Paraphronima gracilis</i>	0.05	(0.02)	0.10	(0.04)
<i>Scina spp.</i>	0.03	(0.01)	0.04	(0.01)
<i>Scina curvicaudata</i>	0.08	(0.03)	0.02	(0.01)
<i>Mimonectes diomedea</i>	0.05	(0.02)	0.01	(0.00)

low from March to 10 April but increased after 12 April and peaked on 25 April.

3.3. Body length and cohort

The BL of the three most dominant amphipods, namely *C. challengerii*, *P. abyssalis* and *T. pacifica*, ranged from 2.4–15.0 mm, 1.4–6.8 mm and 1.4–9.2 mm, respectively (Fig. 4). A cohort analysis identified 7 cohorts for *C. challengerii*, 3–5 cohorts for *P. abyssalis* and 4 cohorts for *T. pacifica* throughout the sampling period. The separation of each cohort corresponded to the differences in the instar number (Fig. 5). Concerning the temporal changes in the mean BL of each cohort, an increase in BL occurred for the mean BL of each cohort of *P. abyssalis*, whereas a decrease in BL occurred in *C. challengerii*, which was caused by the new recruitment of juveniles in the population (Fig. 5). No apparent temporal changes were detected for the mean BL of each *T. pacifica* cohort during the study period.

3.4. Egg- and juvenile-carrying and parasite occurrence

Among the *C. challengerii* females, the compositions of the egg- or juvenile-carrying mature females increased, whereas those that were not egg-carrying decreased during early April (Fig. 6(A)). Parasitized mature females with ellobiopsids appeared in April, and their composition increased and reached 14.3% of the total female population. For *T. pacifica*, the composition of egg- or juvenile-carrying mature females increased during April (Fig. 6(B)). No parasitic infection of ellobiopsids was observed for *T. pacifica* in this study.

3.5. Correlations with environmental parameters

From the correlation analysis between the amphipod abundance or biomass and the environmental parameters, significant correlations were observed for five parameters (Table 2). Positive correlations were observed between the Julian day and the abundance or biomass of *P. abyssalis* and the mixing ratio of COW and the abundance or biomass of *T. pacifica*. A negative correlation was observed between the OYW ratio and the abundance of *P. abyssalis*. Common among the three dominant amphipods, both the abundance and biomass had positive trends with the Julian day, COW ratio, Chl. *a* and mesozooplankton, whereas abundance and biomass had negative trends with salinity and the OYW ratio (Table 2).

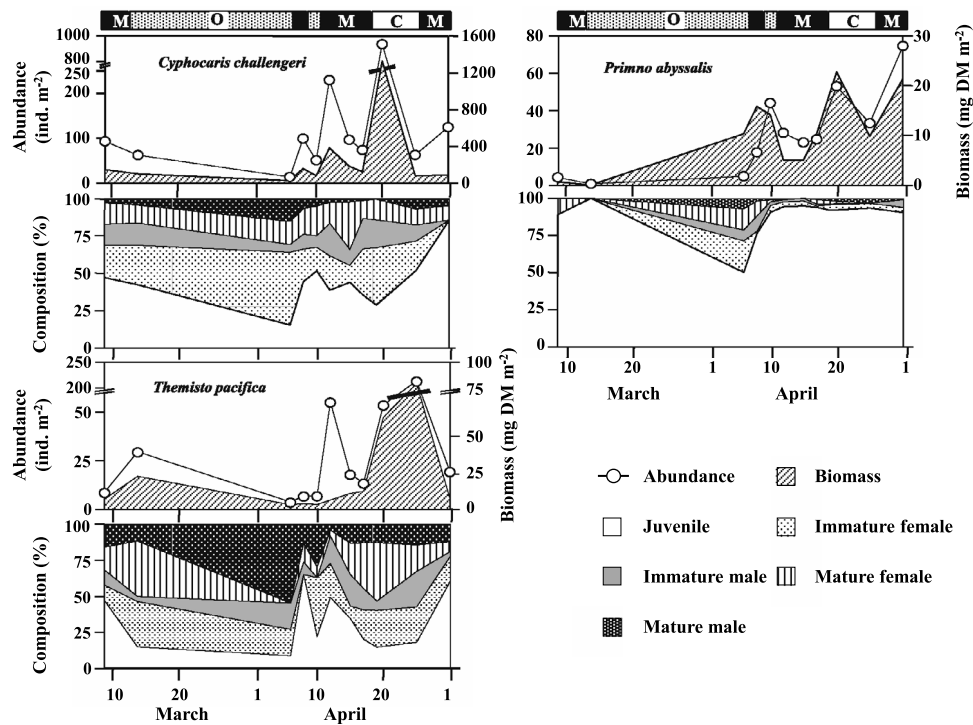


Fig. 3. Temporal changes in abundance, biomass and population structure (immature/mature male/female and juvenile composition in abundance) of *Cyphocaris challengereri*, *Primno abyssalis* and *Themisto pacifica* in the Oyashio region from 9 March to 30 April 2007. The dominant water masses at each sampling date are shown by the upper bars. C: coastal Oyashio water; M: mixed Kuroshio water; O: Oyashio water.

Table 2
Correlation coefficients (r) between environmental parameters (Julian day, integrated mean temperature, salinity, mixing ratio of water mass, chlorophyll a and mesozooplankton wet weight) and abundance and biomass of the three dominant amphipods, *Chyphocaris challengereri* (Cc), *Primno abyssalis* (Pa) and *Themisto pacifica* (Tp), in the Oyashio region from March to April 2007. For details of the mixture ratio of water mass, see [Kono and Sato \(2010\)](#).

Environmental parameter	Abundance (0–200 m)			Biomass (0–200 m)		
	Cc	Pa	Tp	Cc	Pa	Tp
Julian day	0.247	0.781**	0.365	0.208	0.721*	0.349
Temperature (0–50 m)	–0.113	0.053	–0.329	–0.121	–0.277	–0.280
Salinity (0–50 m)	–0.163	–0.128	–0.414	–0.163	–0.407	–0.357
COW ratio of water mass (0–50 m)	0.218	0.539	0.626	0.179	0.583	0.646
OYW ratio of water mass (0–50 m)	–0.238	–0.679	–0.299	–0.211	–0.324	–0.221
MKW ratio of water mass (0–50 m)	0.042	–0.044	–0.362	0.024	–0.310	–0.431
Chl. a (0–150 m)	0.272	0.12	0.478	0.282	0.455	0.490
Mesozooplankton wet weight (0–150 m)	0.038	0.417	0.175	0.034	0.393	0.097

* $p < 0.05$.

** $p < 0.01$.

4. Discussion

4.1. Effect of water mass exchange

During the spring in the Oyashio region, the dominant water masses at the surface layer varied temporally and a high concentration of Chl. a appeared during the COW-dominant period ([Kono and Sato, 2010](#)). Changes in the pico- and nano-phytoplankton dominant species and the size compositions were reported to also vary with the water masses ([Sato and Furuya, 2010](#)). For the macrozooplankton taxa, a significantly high abundance of euphausiids under low temperatures ([Kim et al., 2010a](#)) and a high abundance and biomass of hydromedusa *Aglantha digitale* under COW conditions were reported ([Abe et al., 2014](#)). In this study, a significant positive correlation between the COW ratio and the abundance and biomass of *T. pacifica* were also detected ([Table 2](#)). Common to the other two species, the correlation coefficients with the COW ratio were positive both in their abundance and biomass ([Table 2](#)).

Three water masses observed in this study had a different geographical origin and relative temperature. The origin of the COW was the Okhotsk Sea, and its relative water temperature was in the middle of the three water masses ([Fig. 1\(C\)](#)). The middle temperature of the COW suggests that the amphipod abundance and biomass could not be explained by a simple temperature effect alone. As an alternative explanation, the geographical origin of the water masses, which varied from others, should be considered. The Okhotsk Sea, the origin of the COW, is the southernmost ice-covered ocean in the Northern Hemisphere. In the Okhotsk Sea, the ice-melt fresh water near the surface layer becomes warmer during the summer (e.g., low density water with warmer, less-saline characteristics), and strong pycnocline develops between the dense saline cold intermediate water in the deep layer ([Zenkevitch, 1963](#)). Because of these special hydrographic characteristics (ice-covered in winter and strong pycnocline in summer), large-sized amphipods with a strong DVM are known to be dominant for zooplankton communities in the Okhotsk Sea ([Volkov, 2008](#)). Thus, the high amphipod abundance in the COW is considered to be

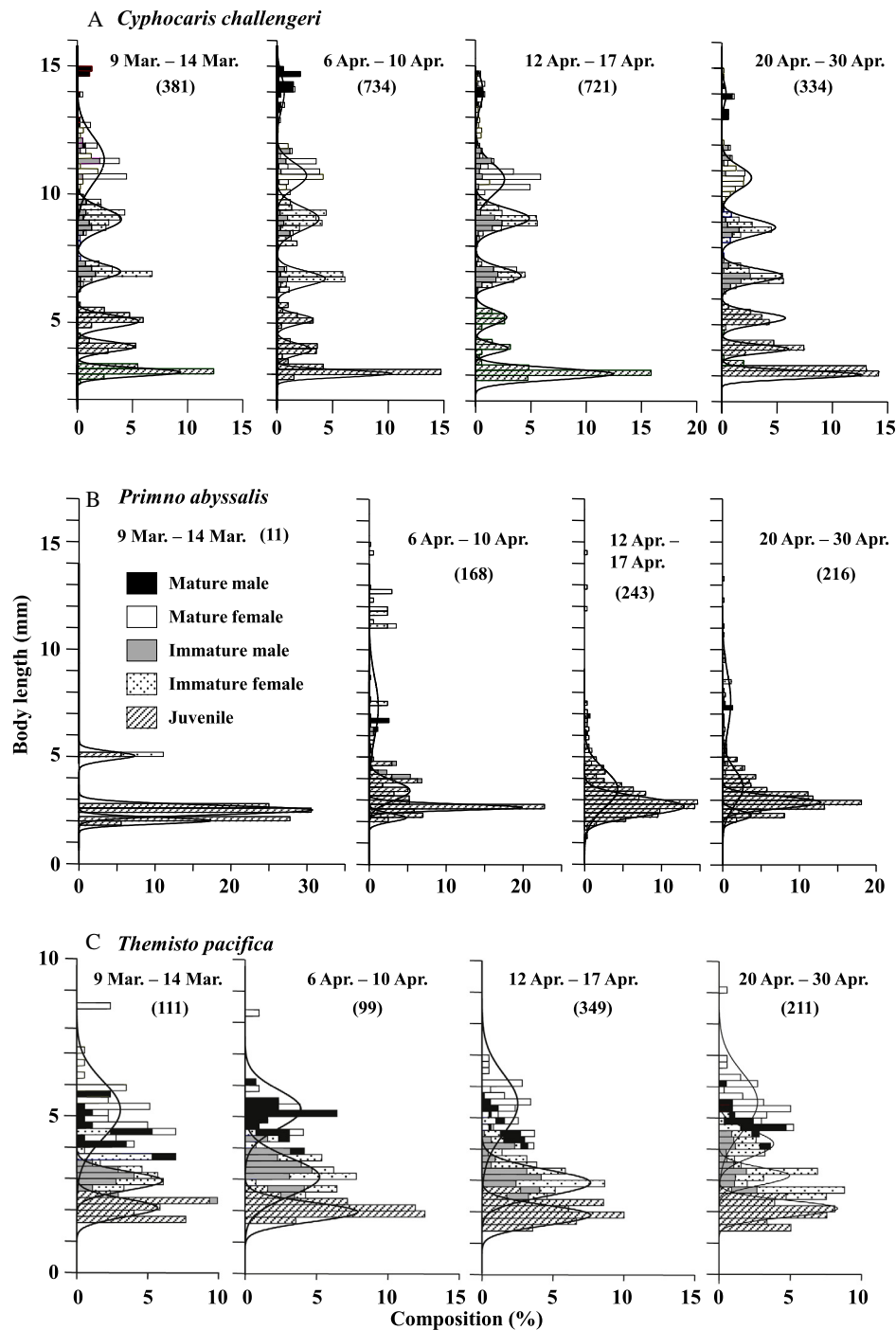


Fig. 4. Temporal changes in the body length of *Cyphocaris challengerii* (A), *Primno abyssalis* (B) and *Themisto pacifica* (C) in the Oyashio region from 9 March to 30 April 2007. To create each panel, the length data were integrated with 2–3 sampling dates. The numbers in parentheses are individual measurements. Smooth curves indicate the results of a cohort analysis.

caused by the geographical origin of the water mass (Okhotsk Sea).

During the OECOS period, other macrozooplankton taxa (euphausiids and hydromedusae) are reported to be affected by the water mass exchange (Kim et al., 2010a,b). Compared with these taxa, the amphipods in this study have less association with the water masses. Because of a lesser effect on the surface water mass exchange on amphipods, the strong DVM of this taxon should be considered. A nocturnal ascent DVM was observed for three abundant amphipods in this study (*C. challengerii*, *P. abyssalis* and *T. pacifica*) (Yoo, 1970; Semenova, 1974; Ikeda, 1995; Thurston, 1976;

Wing, 1976). During September, when the sea surface temperature reached 18 °C and a strong thermocline developed in the Oyashio region, the magnitude of the DVM was reported to be 262 m and 280 m for *C. challengerii* juveniles and females, 252 m and 48 m for *P. abyssalis* juveniles and females, and 354 m and 134 m for *T. pacifica* juveniles and females, respectively (Yamada et al., 2004; Yamada, 2002). These large magnitudes of DVM may function to maintain their population position because they reside at deep layers during the daytime. A lesser effect of the water mass exchange on the amphipod community and population, compared with the other

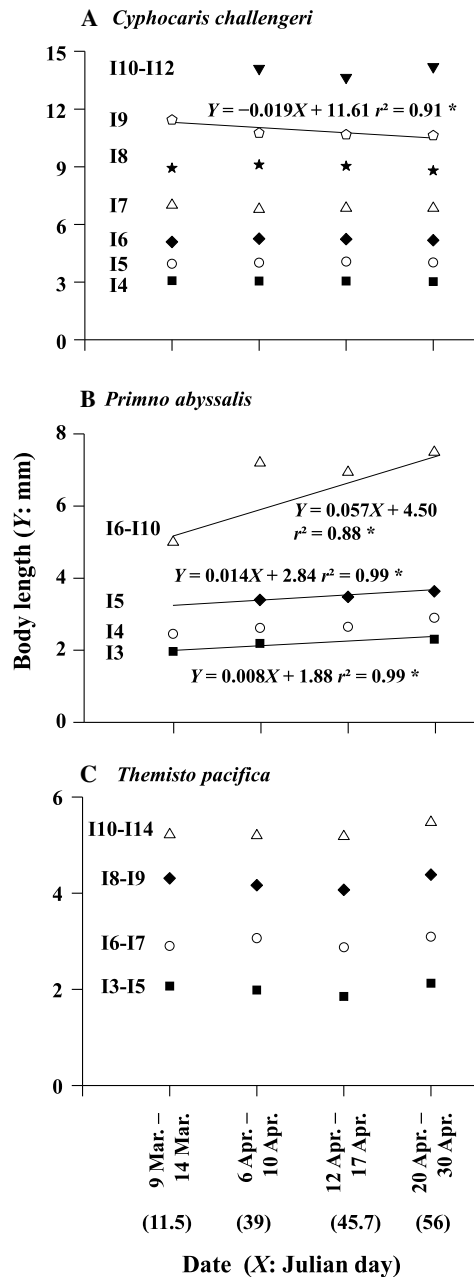


Fig. 5. Temporal changes in the mean body length of each cohort of *Cyphocaris challengereri* (A), *Primno abyssalis* (B) and *Themisto pacifica* (C) identified from Fig. 4. Regression lines indicate temporal changes in the mean body length of each cohort (Y: mm), exhibiting a significant relationship with the sampling dates (X: Julian day). Instar numbers included in each cohort are shown in the panels. *: $p < 0.05$.

macrozooplankton taxa, might be a reflection of the strong DVM behavior of the three dominant amphipods in this region.

4.2. Growth and reproduction

Because factors controlling amphipod abundance and biomass add to the external water mass exchange, their internal growth and reproduction may also be important. Actually, both the abundance and biomass of all three dominant species had a positive correlation coefficient with the Julian day (Table 2). These facts suggest that the amphipods achieve growth (increase in biomass) and reproduction (increase in abundance) during the study period.

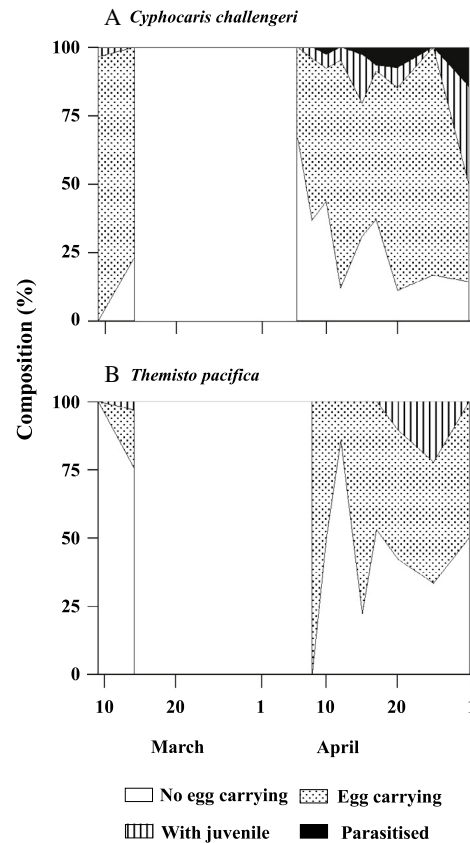


Fig. 6. Temporal changes in the population characteristics of females (not egg carrying, egg carrying, with juveniles and parasitized) of *Cyphocaris challengereri* (A) and *Themisto pacifica* (B) in the Oyashio region from 9 March to 30 April 2007.

For *C. challengereri*, compositions of egg- or juvenile-carrying specimens within the mature females increased during April (Fig. 6(A)) and the juvenile composition of the total population increased rapidly during late April (Fig. 3). This species is known to reproduce throughout the year, with a peak from April to July (Yamada and Ikeda, 2000); active reproduction is expected to be in late April in this study. From the BL cohort analysis, a significant decrease in the mean BL of instar 4 along with the Julian day was observed (Fig. 5(A)). Considering the increase in juvenile-carrying females within the same period (Fig. 6(A)), released juveniles from the marsupium of mature females may be recruited to instar 4 as new populations. Thus, *C. challengereri* primarily achieved reproduction during the spring phytoplankton bloom. For mature females, the composition of parasite-infected specimens increased during April (Fig. 6(A)). The observed prevalence (14.3% of female) in this study may be comparable to the highest value that is reported in southeastern Alaska (range between 0% and 15%; grand mean of two years, 1.5%) (Wing, 1975).

For *P. abyssalis*, the abundance of this study (mean 28 ind. m^{-2} , 0–200 m) is similar to the reported values in this region during March and April 1997/1998 (10–40 ind. m^{-2} , 0–500 m Yamada et al., 2002). Concerning biomass, the present results (0.01 g DM m^{-2} , Table 1) are much lower than the reported values in March and April 1997 (0.1–0.2 g DM m^{-2} Yamada et al., 2002). This large discrepancy may be caused by the vertical distribution. The night vertical distribution depths of this species were reported to be 200–400 m (southern Japan Sea Ikeda, 1995) or 150–500 m (western subarctic Pacific Yamada, 2002). Considering such a deep distribution of this species, the sampling depth of this study (0–200 m) may have failed to collect the main population of this

species. This is why the population structure of this species was strongly skewed to juveniles (Fig. 3). The dominance of juveniles, which was caused by the shallower sampling of this study, may yield a lower biomass for this study than the reported value in the previous study in this region (Yamada et al., 2002). In the Oyashio region, the reproduction peak of this species is considered to be during early summer (Yamada et al., 2002). Thus, *P. abyssalis* is expected to grow during the sampling period. From the cohort analysis on the BL of this species, the growth of the mean BL was observed for each cohort (Fig. 5(B)). The regression formulae between BL (Y : mm) and the Julian day (X : day) were $Y = 0.008X + 2.33$, $Y = 0.009X + 2.72$, and $Y = 0.017X + 2.72$, for I3, I4 and I5, respectively ($p < 0.05$ for all results). These daily growth rates (0.008–0.017) correspond well with the reported value in the Oyashio region ($Y = 0.014X + 0.52$ Yamada et al., 2002). Thus, *P. abyssalis* may achieve juvenile growth during the spring phytoplankton bloom.

The *T. pacifica* population in the Oyashio region is reported to have four generations per year with a reproductive peak in early summer and both the abundance and biomass peaks in the summer (Yamada et al., 2004). In this study, the composition of egg- and juvenile-carrying females of *T. pacifica* increased through April (Fig. 6(B)). These facts suggest that *T. pacifica* achieved maturation during the spring phytoplankton bloom. *Themisto pacifica* has been reported as a host of ellobiosid *T. marsupii* in southeastern Alaska (Wing, 1975). No infected specimens were observed in the Oyashio region (Fig. 5). It may be partly caused by the low prevalence of *T. marsupii* on *T. pacifica*. As a comparable value, 0.7% infection (2 infections in 275 specimens) has been reported in southeastern Alaska (Wing, 1975).

4.3. Conclusions

For the three dominant amphipod species (*C. challengerii*, *P. abyssalis* and *T. pacifica*) in the Oyashio region, the abundance and biomass peaks were in the summer and reproduction was during spring to summer (*C. challengerii*) or summer (*P. abyssalis* and *T. pacifica*) (Yamada et al., 2002). From this study, the adaptation to and utilization of the spring phytoplankton bloom varied among amphipod species in terms of growth for *P. abyssalis*, maturation for *T. pacifica* and reproduction for *C. challengerii*. These species-specific differences in utilization of the spring phytoplankton may be related to the species-specific life cycle timing (phenology) of the amphipods in this region.

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References

Abe, Y., Ishii, K., Yamaguchi, A., Imai, I., 2012. Short-term changes in population structure and vertical distribution of mesopelagic copepods during the spring phytoplankton bloom in the Oyashio region. *Deep-Sea Res.* 1 65, 100–112.

Abe, Y., Yamaguchi, A., Matsuno, K., Kono, T., Imai, I., 2014. Short-term changes in population structure of *Hydromedusa Aglantha digitale* during the spring phytoplankton bloom in the Oyashio region. *Bull. Fish. Sci. Hokkaido Univ.* 64, 71–81.

Auel, H., Harjes, M., Rocha, D.R., Stübing, D., Hagen, W., 2002. Lipid biomarkers indicate different ecological niches and trophic relationships of the arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biol.* 25, 374–383.

Dempson, J.B., Shears, M., Bloom, M., 2002. Spatial and temporal variability in the diet of anadromous arctic charr, *Salvelinus alpinus*, in northern Labrador, Development. *Environ. Biol. Fishes* 22, 49–62.

Fraley, C., Raftery, A.E., Murphy, T.B., Scrucca, L., 2012. mclust Version 4 for R: Normal mixture modeling for model-based clustering, classification, and density estimation, Technical Report No. 597. Department of Statistics, University of Washington.

Froneman, P.W., Pakhomov, E.A., Treasure, A., 2000. Trophic importance of the hyperiid amphipod, *Themisto gaudichaudi*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. *Polar Biol.* 23, 429–436.

Fujii, Y., Kamachi, M., 2003. Three-dimensional analysis of temperature and salinity in the equatorial Pacific using a variational method with vertical coupled temperature-salinity empirical orthogonal function modes. *J. Geophys. Res.* 108, <http://dx.doi.org/10.1029/2002JC001745>.

Harvey, M., Galbraith, P.S., Descroix, A., 2009. Vertical distribution and diel migration of macrozooplankton in the St. Lawrence marine system (Canada) in relation with the cold intermediate layer thermal properties. *Prog. Oceanogr.* 80, 1–21.

Ikeda, T., 1995. Distribution, growth and life cycle of the mesopelagic amphipod *Primno abyssalis* (Hyperidea: Phrosinidae) in the southern Japan Sea. *Mar. Biol.* 123, 789–798.

Ikeda, T., Shiga, N., 1999. Production, metabolism and production/biomass (P/B) ratio of *Themisto japonica* (Crustacea: Amphipoda) in Toyama Bay, southern Japan Sea. *J. Plankton Res.* 21, 299–308.

Ikeda, T., Shiga, N., Yamaguchi, A., 2008. Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific. *J. Oceanogr.* 64, 339–354.

Kane, J.E., 1964. *Thalassomyces marsupii*, a new species of ellobiosid parasite on the hyperiid amphipod *Parathemisto gaudichaudii* (Guér.). *N.Z. J. Sci.* 7, 289–303.

Kim, H.S., Yamaguchi, A., Ikeda, T., 2010a. Metabolism and elemental composition of the euphausiids *Euphausia pacifica* and *Thysanoessa inopinata* during the phytoplankton bloom season in the Oyashio region, western subarctic Pacific Ocean. *Deep-Sea Res.* II 57, 1733–1741.

Kim, H.S., Yamaguchi, A., Ikeda, T., 2010b. Population dynamics of the euphausiids *Euphausia pacifica* and *Thysanoessa inopinata* in the Oyashio region during the 2007 spring phytoplankton bloom. *Deep-Sea Res.* II 57, 1727–1732.

Kono, T., Sato, M., 2010. A mixing analysis of surface water in the Oyashio region: Its implications and application to variations of the spring bloom. *Deep-Sea Res.* II 57, 1595–1607.

Kotori, M., 1976. The biology of chaetognaths in the Bering Sea and the north-western North Pacific Ocean, with emphasis on *Sagitta elegans*. *Mem. Fac. Fish. Hokkaido Univ.* 23, 95–183.

Kraft, A., Berge, J., Varpe, Ø., Falk-Petersen, S., 2013. Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*. *Mar. Biol.* 160, 241–248.

Liu, H., Suzuki, K., Saito, H., 2004. Community structure and dynamics of phytoplankton in the western subarctic Pacific Ocean: A synthesis. *J. Oceanogr.* 60, 119–137.

Lowry, L.F., Frost, K.J., 1984. Foods and feeding of bowhead whales in western and northern Alaska. *Sci. Rep. Cetacean Res.* 35, 1–16.

Marion, A., Harvey, M., Chabot, D., Brêthes, J.C., 2008. Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. *Mar. Ecol. Prog. Ser.* 373, 53–70.

Nagata, K., 1997. Order amphipoda. In: Chihara, M., Murano, N. (Eds.), *An Illustrated Guide to Marine Plankton in Japan*. Tokai Univ. Press, Tokyo, pp. 1131–1203.

Nielsen, K.T., Haug, T., Potelov, V., Timoshenko, Y.K., 1995. Feeding habits of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. *Polar Biol.* 15, 485–493.

Olsen, B.R., Troedsson, C., Hadziavdic, K., Pedersen, R.B., Rapp, H.T., 2014. A molecular gut content study of *Themisto abyssorum* (Amphipoda) from Arctic hydrothermal vent and cold seep systems. *Mol. Ecol.* 23, 3877–3889.

Pakhomov, E.A., Perissinotto, R., 1996. Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. *Mar. Ecol. Prog. Ser.* 134, 91–100.

Raymont, J.E.G., 1983. Plankton and Productivity in the Oceans. *Zooplankton*. Vol. 2, second ed. Pergamon Press, Oxford.

Rosing-Asvid, A., Hedeholm, R., Arendt, K.E., Fort, J., Robertson, G.J., 2013. Winter diet of the little auk (*Alle alle*) in the Northwest Atlantic. *Polar Biol.* 36, 1601–1608.

Saito, H., Tsuda, A., Kasai, H., 2002. Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res.* II 49, 5463–5486.

Sato, M., Furuya, K., 2010. Pico- and nanophytoplankton dynamics during the decline phase of the spring bloom in the Oyashio region. *Deep-Sea Res.* II 57, 1643–1652.

Semenova, T.N., 1974. Diurnal vertical migration of *Parathemisto japonica* Bov. (Hyperidea) in the Sea of Japan. *Oceanology* 14, 272–276.

Thurston, M.H., 1976. The vertical distribution and diurnal migration of the crustacean amphipoda collected during the Sond Cruise, 1965 I. The Gammaridea. *J. Mar. Biol. Ass. UK* 56, 359–382.

Volkov, A.F., 2008. Mean annual characteristics of zooplankton in the sea of Okhotsk, Bering Sea and Northwestern Pacific (annual and seasonal biomass values and predominance). *Russ. J. Mar. Biol.* 34, 437–451.

Walkusz, W., Majewski, A., Reist, J.D., 2013. Distribution and diet of the bottom dwelling Arctic cod in the Canadian Beaufort Sea. *J. Mar. Syst.* 127, 65–75.

Wing, B.L., 1975. New records of Ellobiosidae (Protista (*Incertae sedis*)) from the North Pacific with a description of *Thalassomyces albatrossi* n.sp., a parasite of the mysid *Stilomysis major*. *Fish. Bull.* 73, 169–185.

- Wing, B.L., 1976. Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan coastal waters (Ph.D. thesis), University of Rhode Island, Kingston.
- Yamada, Y., 2002. Life history, metabolism and production of four pelagic amphipods in the Oyashio region, western subarctic Pacific (Ph.D. thesis), Hokkaido University, Hokkaido.
- Yamada, Y., Ikeda, T., 2001a. Notes on early development and secondary sexual characteristics of the mesopelagic amphipod *Cyphocaris challengeri* (Gammaridea; Lysianassidae). Bull. Fish. Sci. Hokkaido Univ. 52, 55–59.
- Yamada, Y., Ikeda, T., 2001b. Notes on early development and secondary sexual characteristics of the mesopelagic amphipod *Primno abyssalis* (Hyperiidea: Phrosinidae). Bull. Fac. Fish. Hokkaido Univ. 52, 61–65.
- Yamada, Y., Ikeda, T., 2003. Metabolism and chemical composition of four pelagic amphipods in the Oyashio region, western subarctic Pacific Ocean. Mar. Ecol. Prog. Ser. 253, 233–241.
- Yamada, Y., Ikeda, T., 2004. Some diagnostic characters for the classification of two sympatric hyperiid amphipods, *Themisto pacifica* and *T. japonica*, in the western North Pacific. Bull. Fish. Sci. Hokkaido Univ. 54, 59–65.
- Yamada, Y., Ikeda, T., 2006. Production, metabolism and trophic importance of four pelagic amphipods in the Oyashio region, western subarctic Pacific. Mar. Ecol. Prog. Ser. 308, 155–163.
- Yamada, Y., Ikeda, T., 2000. Development, maturation, brood size and generation length of the mesopelagic amphipod *Cyphocaris challengeri* (Gammaridea: Lysianassidae) off southwest Hokkaido, Japan. Mar. Biol. 137, 933–942.
- Yamada, Y., Ikeda, T., Tsuda, A., 2002. Abundance, growth and life cycle of the mesopelagic amphipod *Primno abyssalis* (Hyperiidea: Phrosinidae) in the Oyashio region, western subarctic Pacific. Mar. Biol. 141, 333–341.
- Yamada, Y., Ikeda, T., Tsuda, A., 2004. Comparative life-history study on sympatric hyperiid amphipods (*Themisto pacifica* and *T. japonica*) in the Oyashio region, western North Pacific. Mar. Biol. 145, 515–527.
- Yamaguchi, A., Onishi, Y., Omata, A., Kawai, M., Kaneda, M., Ikeda, T., 2010a. Population structure, egg production and gut content pigment of large grazing copepods during the spring phytoplankton bloom in the Oyashio region. Deep-Sea Res. II 57, 1679–1690.
- Yamaguchi, A., Onishi, Y., Omata, A., Kawai, M., Kaneda, M., Ikeda, T., 2010b. Diel and ontogenetic variations in vertical distributions of large grazing copepods during the spring phytoplankton bloom in the Oyashio region. Deep-Sea Res. II 57, 1691–1702.
- Yoo, K.I., 1970. Ecological studies on pelagic amphipods in the western North Pacific (Ph.D. thesis), University of Tokyo, Tokyo, (in Japanese).
- Zenkevitch, L., 1963. Biology of the Seas of the USSR. George Allen and Unwin Ltd., London, p. 955.