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Ecological Study on the Zooplankton Community in the Oyashio Region
During the Spring Phytoplankton Bloom

Yoshiyuki Abe

(Received 26 August 2016, Accepted 17 October 2016)

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Key words: Mesozooplankton, Macrozooplankton, Phytoplankton bloom, Oyashio region

1. Preface

In marine ecosystems, zooplankton play an important role in the transfer production of both the grazing food chain and the microbial food web for higher trophic levels (Raymont, 1983). In addition to the food mediator role, zooplankton accelerate the vertical material flux, termed “Biological pump” (Longhurst and Harrison, 1989; Longhurst, 1991). In high-latitude oceans (Arctic, subarctic, subantarctic and Antarctic), phytoplankton form spring blooms, and nearly half of the primary production is concentrated in a one- to two-month period. In the Oyashio region, western subarctic Pacific, nearly half of the annual primary production occurs from April to May (Saito et al., 2002; Liu et al., 2004; Ikeda et al., 2008). During the same period, zooplankton achieve faster growth (Kobari and Ikeda, 1999, 2001a, 2001b; Shoden et al., 2005). However, evaluation of the accurate growth rate of zooplankton is difficult using the sampling intervals (primarily once per month) usually used in previous studies (cf. Shoden et al., 2005 and references therein). For the evaluation of the accurate growth rate of zooplankton, high-frequency time-series sampling during the spring phytoplankton bloom is essential.

Previously, high-frequency time-series samplings were conducted at St. M in the North Atlantic Norwegian Sea over an 80-day period from March 23 to June 9, 1997 (Irigoin et al., 1998; Meyer-Harms et al., 1999; Niehoff et al., 1999; Hirche et al., 2001; Ohman and Hirche, 2001). In the eastern and western subarctic Pacific, high-frequency time-series samplings of zooplankton were achieved as a part of a series of iron fertilization effect studies (SEEDS I, SEEDS II and SERIES) (Tsuda et al., 2005, 2006, 2007, 2009; Fig. 1A).

Based on high-frequency time-series samplings at St. M in the Norwegian Sea, the egg production rates and composition of adult females of the dominant copepod species Calanus finmarchicus increase from pre-bloom to bloom peak and decrease during the post-bloom period (Niehoff et al., 1999). For C. finmarchicus, short-term changes in various population parameters, including feeding (Irigoin et al., 1998), reproduction (Niehoff et al., 1999), population structure (Hirche et al., 2001) and mortality (Ohman and Hirche, 2001), were evaluated during the spring phytoplankton bloom.

In terms of zooplankton fauna, dominant zooplankton species vary between the North Atlantic and North Pacific (Lalli and Persons, 1998). Although copepods dominate in both oceans, small-sized Calanus spp. (total length ca. 5 mm) dominate in the North Atlantic, and large-sized Neocalanus spp. (7-9 mm), with a 1-2 year generation period, dominate in the North Pacific (Conover, 1988). The utilization patterns of phytoplankton bloom during the spring also vary with oceans. Thus, Calanus spp. in the North Atlantic uses the phytoplankton bloom as an energy source for the reproduction of adults, while the reproduction of Neocalanus spp. in the North Pacific occur at deeper ocean layers without feeding, and these species utilize the phytoplankton bloom as an energy source for the development of newly recruited generations at the surface layer (Fig. 1B, C; Conover, 1988; Parsons and Lalli, 1988). These facts suggest that the zooplankton response to the spring phytoplankton bloom might vary between the North Atlantic and North Pacific.

Based on iron fertilization experiments in the North Pacific, the abundance of early copepodid stages increased in iron fertilization areas (SEEDS I, Tsuda et al., 2005). Conversely, in other experiments, the high abundance of copepods graze down the phytoplankton bloom (SEEDS II, Tsuda et al., 2007, 2009), and upward vertical migrations of subsurface resident copepods were observed for the phytoplankton bloom area (SERIES) (Tsuda et al., 2006). These results are clear responses of zooplankton to the phytoplankton bloom. However, because these zooplankton responses to the artificial bloom are enhanced through iron fertilization, it is likely that zooplankton responses might vary with the natural conditions. To evaluate zooplankton responses to the spring phytoplankton bloom under natural conditions, high-frequency time-series samplings were conducted in the Oyashio region during the spring phytoplankton bloom. This project, known as the “Ocean Ecodynamics Comparison in the Subarctic Pacific” (OECOS), was endorsed through the North Pacific Marine Science Organization (PICES) (Ikeda et al., 2010).
The OECOS project was conducted at station A-5 in the Oyashio region from March 8 to May 1, 2007 using two consecutive cruises (T/S Oshoro-Maru [March] and R/V Hakuho-Maru [April - May]). During these cruises, high-frequency CTD casts, water sampling and various net samplings were conducted. Based on the OECOS project, various aspects of physical, chemical and biological changes during spring bloom were evaluated (Table 1). Within the findings of the OECOS project, three topics were highlighted: firstly, during the spring phytoplankton bloom, three water masses of different geographical origins exchange at the surface layer (Kono and Sato, 2010), and a high phytoplankton density was observed for Coastal Oyashio Water (COW) containing a high iron concentration originating from the Sea of Okhotsk (Nakayama et al., 2010). Secondly, the effects of feeding on the primary production of the two dominant taxa (Neocalanus copepods and euphausiids) were evaluated as 28% of the primary production for Neocalanus copepods (Kobari et al., 2010b) and 4.9% of the primary production for euphausiids (Kim et al., 2010b). Thirdly, diel migrant copepods (Metridia spp., Gaetanus simplex and Pleuromamma scutulata) cease diel vertical migration (DVM) and remain at...
deep ocean layers during the phytoplankton bloom period (Yamaguchi et al., 2010b; Abe et al., 2012).

For these findings, the causes of each issue have been described in the literature. However, synthesis studies addressing the entire plankton community from phytoplankton to macrozooplankton during the OECOS project have not previously been conducted. Thus, the interaction and relative importance of each topic issue remain unclear. Moreover, comparisons of the zooplankton responses to the spring phytoplankton bloom between the OECOS project and other studies (North Atlantic Norwegian Sea St. M: Irigoien et al., 1998; Meyer-Harms et al., 1999; Ohman and Hirche, 2001; North Pacific SEEDS I: Tsuda et al., 2005; SEEDS II: Tsuda et al., 2007, 2009, SERIES: Tsuda et al., 2006) have not been made.

In the present study, short-term changes in phytoplankton (pico-, nano- and micro-size), protozooplankton and various species of meso- and macrozooplankton (abundance, biomass, population structure, vertical distribution, growth rates and feeding ecology) were evaluated during the OECOS period. The aim of the present study was to evaluate lower trophic levels during the spring phytoplankton bloom. To this end, reported and unpublished data were summarized, and new data on the population structure and feeding ecology of macrozooplankton during the OECOS period were added. Furthermore, Dr. Barbara Niehoff (AWI, Germany) and Prof. Atsushi Tsuda (AORI, Japan) provided additional zooplankton data on other high-frequency time-series samplings (SEEDS I, SEEDS II, SERIES and St. M), and comparisons with the OECOS data were achieved. The comparison of five time-series datasets revealed common patterns and different points, and the characteristics of zooplankton responses to the spring phytoplankton bloom were evaluated.

The present study is outlined in the following manner. In chapter 2, field sampling, analysis methods, physical environments, exchanges in water mass and temporal changes in phytoplankton, microzooplankton and mesozooplankton biomass are overviewed. In chapter 3, temporal changes in population structure of dominant meso- and macrozooplankton species are described. In chapter 4, temporal changes in vertical distribution of dominant copepod species are evaluated. In chapter 5, after multiplying individual masses, the abundance data of dominant meso- and macrozooplankton species are converted to carbon units, and subsequently, the growth rates are estimated in carbon units. In chapter 6, the feeding ecology of mesopelagic copepods and macrozooplankton are evaluated, and the zooplankton biomass and production are estimated for each species and compared between pre-bloom (March) and post-bloom (April) periods. In chapter 7, short-term changes in zooplankton during the spring phytoplankton bloom in the present study (OECOS) are compared with those in the other data sets (SEEDS I, SEEDS II, SERIES and St. M). Finally, based on these overviews, recommendations and future study directions are discussed.
2. Materials and Methods and Environmental Changes

2-1. Field sampling

Daily measurements of temperature, salinity and chlorophyll a (chl a) fluorescence data were obtained through CTD casts (SBE-9 plus, Sea Bird Electronics, Washington) at a single station (St. A-5, 42°00'N, 145°15'E, depth 4,000 m, Fig. 2) in the Oyashio region during March 9–14 and April 5–May 1, 2007. The data were averaged every 1 m. Based on temperature and salinity data, the mixture ratios of the three water masses (Coastal Oyashio Water: COW; modified Kuroshio Water: MKW; Oyashio Water: OYW) in the 0-50 m water column were calculated (Kono and Sato, 2010).

To clarify the origin of the water mass at the surface layer of 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, referred to as the Fisheries Research Agency Regional Ocean Model (FRA-ROMS; Fisheries Research Agency of Japan, 2014, http://fin.dc.affrc.go.jp/fra-roms/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) to generate realistic re-analysis products. Lagrangian particle-tracking experiments were conducted using the FRA-ROMS velocity field. The positions of the particles, estimated based on an advection equation, 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 minutes. Through linear interpolation, \((u, v)\) was estimated based on the flow velocity of the FRA-ROMS with a 1/10° horizontal resolution.

We initially released particles at different depths (10, 20, 30, 50, 75, 100, 125, 150 and 200 m) at the sampling station (42°00'N, 145°15'E) and conducted a particle back-tracking experiment for the previous six months. We examined temporal changes at locations of the released particles to determine the origin of the water and evaluated the observed water temperature changes.

The water samples were collected from 11 depths (0, 5, 10, 20, 30, 50, 75, 100, 125 and 150 m) using 12-L Niskin X bottles (General Oceanics) mounted on a CTD-RMS. Each 1-L water sample was filtered through a 20-μm mesh, Millipore polycarbonate membrane filter (2-μm) and a Whatman GF/F filter under low vacuum pressure. After filtration, each filter was immersed in 6 mL of N,N-dimethyl-formamide (DMF) for 6 hours at ~5°C in the dark (Suzuki and Ishimaru, 1990). Subsequently, the chl a concentration was measured using a Turner Designs fluorometer (Turner Designs Co., TD-700) (Kobari et al., 2010a).

Water samples (1–L) collected at 5-m depth during April 6–30, 2007 were preserved in glutaraldehyde at a final concentration of 1% and subsequently settled and concentrated 10–20-fold using a siphon. Appropriate aliquots (1 mL) of the concentrated samples were transferred to glass slides, and diatom species were identified and counted using an inverted microscope. When the identification of diatom species was not possible using an inverted microscope, the samples were cleaned and desalted with DW, and subsequently the samples were filtered through a 0.2-μm Millipore polycarbonate membrane and dried. The dried filter was trimmed and mounted on a stub and subsequently ion-sputtered. The samples were observed using a scanning electron microscope (JMS-840A, JEOL Ltd., Tokyo), and species identification was conducted.

Water samples (200 mL) collected at 5-m depth during April 6-30, 2007 were preserved in Lugol’s solution at a final concentration of 2% and subsequently settled and concentrated to 10 mL using a siphon. Appropriate aliquots (0.5-1 mL) of the concentrated samples were transferred to a counting chamber and microzooplankton (tintinnids, naked ciliates, other ciliates, thecate dinoflagellates, thecate dinoflagellates and diatom feeding dinoflagellates Gyrodinium spp.) were identified and enumerated under an inverted microscope. The species identification of ciliates was based on Montagnes and Lynn (1991) and Strüder-Kypke et al. (2001).

Mesozooplankton net samples were collected 23 times in daytime and 22 times at night using twin NORPAC nets (100-
2-2-1. Zooplankton sample analyses

In the land laboratory, NORPAC net samples (335-μm mesh size) were split using a Motoda splitting device (Motoda, 1957), and another aliquot was used for microscopic analysis. For euphausiids, the three dominant species, E. pacifica, N. plumchrus, and N. flemingeri) were enumerated. For VMPS samples, the species identification and enumeration were achieved for copepodid stages (C1-C6) of major epipelagic copepods (E. bungii, M. pacifica, M. okhotensis, N. cristatus, N. flemingeri and N. plumchrus) and mesopelagic copepods (Gaetanus spp.). Amongst the night NORPAC net (100-μm mesh) samples collected at 0-500-m depth, copepodid C1-C6/F/M stages of Eucalanus bungii, Metridia pacifica, M. okhotensis, Neocalanus cristatus, N. flemingeri and N. plumchrus were enumerated.

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2-2-1. Net sample analyses

In the land laboratory, NORPAC net samples (335-μm mesh) were split using a Motoda splitting device (Motoda, 1957), and another half- aliquot was used to measure the wet mass, and another aliquot was used for microscopic analysis. For the wet mass measurement, the samples were transferred to a weighed 100-μm mesh and aspirated, and subsequently, the wet mass was measured using a microbalance (Mettler PM4000, precision 0.01 g) (Yamaguchi et al., 2010a). The remaining half aliquot of the samples was observed under a stereomicroscope for the identification and enumeration of 15 taxa (amphipods, appendicularians, chaetognaths, cnidarians, copepods, doliolids, euphausiids, mysids, ostracods, polychaetes, pteropods, salps, shellfish, fish and others). Amongst the night NORPAC net (100-μm mesh) samples collected at 0-500-m depth, copepodid C1-C6/F/M stages of Eucalanus bungii, Metridia pacifica, M. okhotensis, Neocalanus cristatus, N. flemingeri and N. plumchrus were enumerated.

From Bongo net samples, macrozooplanktonic euphausiids, amphipods, cnidarians and chaetognaths were quantified. For euphausiids, the three dominant species, Euphausia pacifica, Thysanoessa insipina and T. longipes, were sorted. Eggs and nauplii were not observed in the samples. A few calyptopis larvae were observed, but were not quantified because of the lack of morphological characteristics for the identification of Thysanoessa spp. For furcilia larvae, juveniles, adult males and adult females, species identification was conducted according to Suh et al. (1993) for E.
Pacific and Endo and Komaki (1979) for T. insipinata and T. longipes. The furcilia larvae and juveniles of T. insipinata and T. longipes were sorted to species level based on the position of the carapace lateral denticle: middle margin for T. insipinata and posterior margin for T. longipes (Endo and Komaki, 1979). The adults were separated from juveniles based on the development of external secondary sexual characteristics: petasma for males and thelycum for females (Makarov and Denys, 1981). Adult females with attached spermatophores were also counted separately. The total length (TL, mm), from the tip of the rostrum to the distal end of the telson, was measured to the nearest 0.1 mm using an eyepiece micrometre under a dissecting microscope.

All amphipods detected in the Bongo net samples were sorted and enumerated at the species level. For the most abundant species, Cyphocaris challenger, Primno abyssalis and Themisto pacifica, the 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. challenger) of the straightened body using an eye-piece micrometre with a precision of 0.05 to 0.10 mm. The segments in the first pleopod were counted to determine the instar stage of each amphipod. The specimens were separated into five categories according to the developmental stage and sex (juvenile, immature male, mature male, immature female and mature female) (Yamada and Ikeda, 2000, 2001a, 2001b, 2004; Yamada et al., 2002, 2004).

For cnidarians, the most abundant species Aeglantha digitale were sorted and counted, and the results are expressed as abundance per m². Size measurements were made for bell height (BH) and gonad length (GL). For all individuals, the sizes were measured using an eye-piece micrometre with a precision of 0.5 mm (BH) or 0.05 mm (GL). Based on the ratio of GL to BH, A. digitale were separated into immature (GL/BH was < 10%) and mature (GL/BH was ≥10%) stages (McLaren, 1969).

For chaetognaths, all individuals were sorted and enumerated at the species level from Bongo net samples using a stereomicroscope. The species identification of chaetognaths was conducted according to Nakasawa and Marumo (1976) and Terazaki (1996). Concerning the third dominant chaetognath species (Pseudosagitta scrippsiæ), as the likelihood of P. scrippsei, the body length (BL, mm) was measured using a micrometre calliper or eye-piece micrometre mounted on a stereomicroscope with a precision of 0.05 to 0.10 mm. For the two most abundant species, E. hamata and P. elegans, the specimens were classified into five maturation stages (juvenile and stages I-IV) according to Thomson (1947), Terazaki and Miller (1986) and Johnson and Terazaki (2003).

### 2-2-2. Gut content analyses

For mesopelagic copepods, euphausiids and chaetognaths, gut content analyses were conducted. For mesopelagic copepods, the C6F specimens of G. simplex, G. variabilis, P. scutellata, P. elongata, P. briostrata and H. tanneri were sorted from the night VMPS samples obtained on March 8, and April 11 and 29. The gut was extracted from each preserved sample using a stereomicroscope and dissected on a glass slide. The gut contents were identified and enumerated at the species or genus level using a dissecting microscope. For microplankton cells in the guts, the overall conditions of the cells were classified into three categories depending on the proportion of broken parts: 100% intact, 50-100% fragmented and 0-50% fragmented.

For carnivorous copepods (P. elongata and H. tanneri), most of the gut content was observed as mandible gnathobase (blade). From NORPAC net samples, C1-C6 stages of dominant copepod species (G. simplex, G. variabilis, P. scutellata, P. elongata and H. tanneri) were sorted, the mandible gnathobase was dissected and sketched, and the size of mandible blade (MB) was measured. The length of the mandible blade (MB) was measured at a precision of 1 µm, and the presence length (PL, µm) was estimated from regressions (Dalpadado et al., 2008):

\[
PL = 19.23 MB - 376.3
\]

The morphology of MB significantly varies with species (Arashkevich, 1969; Dalpadado et al., 2008). Based on the morphology and length of MB, species and stage identifications were obtained for each prey when possible.

For euphausiids, gut content analyses were conducted for 15 adult female/male specimens of the two dominant euphausiids, E. pacifica and T. insipinata. The specimens with mean BL at each sampling date were selected for the gut content analysis. Using a stereomicroscope, the gut of each specimen was removed from the carapace and dissected on a glass slide, and subsequently the food items were mounted using a cover glass. Taxonomic accounts of the food items were examined and enumerated using an inverted microscope (Nakagawa et al., 2001). The major copepod body parts in the gut contents were mandible gnathobase (blade). Based on the morphology and size of the gnathobase, the prey of the copepods was identified and enumerated at the species level according to copepodid stages (Dalpadado et al., 2008). The gut fullness was scored into 5 categories according to Nakagawa et al. (2001) (0; empty stomach, I; 25-50% full, II; 50-75% full, III; 75-100% full).

For chaetognaths, gut contents of the three dominant chaetognaths (E. hamata, P. elegans and P. scrippsiæ) were analysed. To avoid the effects of cod-end feeding, the food items observed forward of 1/4 of the gut were not enumerated (Øresland, 1987). For the copepods in the gut contents of chaetognaths, the copepodid stages were identified when poss-
sible. When the swimming legs or urostyle of the copepods were damaged, their stages were estimated based on the PL of the dominant copepods in the Oyashio region (Ueda et al., 2008). The number of prey per chaetognaths (NPC, no. of prey ind. \(^{-1}\), Nagasawa and Marumo, 1972) was calculated for each species at each sampling date.

2-2-3. Biomass

To estimate the biomass of each copepod species, the mean copepodid stage (MCS) was calculated for epi- and mesopelagic copepods (see 2-3-2). Based on the reported values of dry mass (DM) and the carbon: dry mass ratio (C: DM), regressions between the carbon mass \((CM, \mu g)\) and the copepodid stage (CS) were calculated:

\[
\log_{10} CM = a \times CS + b
\]

where \(a\) and \(b\) are fitted constants (Table 2). From these regressions and MCS values, the mean \(CM\) of each species was calculated, and subsequently the total mass was calculated after multiplying the mean \(CM\) by the abundance of each species.

For macrozooplankton taxa (euphausiids, amphipods, cnidarians and chaetognaths), based on the body size data, \(BL (mm)\) or \(BH (mm)\) (see 2-2-1), the wet mass \((WM)\) of amphipods and the DM of euphausiids, cnidarians and chaetognaths were estimated using reported allometric equations, which varied with taxa (Table 2). Subsequently, the carbon biomass was estimated using reported ratios between \(WM\), \(DM\) and \(CM\) (Table 2).

2-3. Data and statistical analyses

2-3-1. Correlation analysis with water mass-mixing ratio

Correlation analyses based on the water mass mixing ratio at 0–50 m (Kono and Sato, 2010) were conducted to determine the abundance (ind. m\(^{-2}\)) and biomass (mg C m\(^{-2}\)) of epipelagic copepods at 0–50 m (\(E. bungii\), \(M. pacifica\), \(M. okhotensis\), \(N. cristatus\), \(N. flemingeri\), \(N. plumchrus\)) mesopelagic copepods at 0–1000 m (\(G. simplex\), \(G. variabilis\), \(P. scutellata\), \(P. elongata\), \(P. birostrata\) and \(H. tanneri\)) and macrozooplankton at 0–200 m (\(E. pacifica\), \(T. inspinata\), \(C. challenger\), \(P. abyssalis\), \(T. pacifica\), \(A. digitale\), \(E. hamata\) and \(P. elegans\)).

Table 2. Regression formulae used for carbon biomass estimation for various zooplankton species in the Oyashio region. \(WM\): wet mass in mg (mg WM ind.\(^{-1}\)) \(DM\): dry mass in mg (mg DM ind.\(^{-1}\)) \(CM\): dry mass in \(\mu g\) (\(\mu g\) DM ind.\(^{-1}\)), \(CS\): copepodid stage, \(BL\): body length (mm), \(BH\): bell height (mm), \(TL\): total length (mm). Regressions first reported in the present study are shown with the coefficient of determination \((r^2)\).

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<th>Taxa / Species</th>
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<tr>
<td><strong>Copepods</strong></td>
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<tr>
<td><em>Eucalanus bungii</em></td>
<td>(\log_{10} CM = 0.3564 \times CS - 0.2050, r^2 = 0.993)</td>
<td>Ueda et al., 2008</td>
</tr>
<tr>
<td><em>Metridia pacifica</em></td>
<td>(\log_{10} CM = 1.2407 \times CS - 5.4079, r^2 = 0.999)</td>
<td>Ueda et al., 2008</td>
</tr>
<tr>
<td><em>Metridia okhotensis</em></td>
<td>(\log_{10} CM = 0.8372 CS - 2.6382, r^2 = 0.999)</td>
<td>Padmavari, 2002; Ikeda et al., 2006</td>
</tr>
<tr>
<td><em>Neocalanus cristatus</em></td>
<td>(\log_{10} CM = 0.4020 CS - 0.3798, r^2 = 0.999)</td>
<td>Ueda et al., 2008</td>
</tr>
<tr>
<td><em>Neocalanus flemingeri</em></td>
<td>(\log_{10} CM = 0.2716 CS - 1.0328, r^2 = 0.729)</td>
<td>Ueda et al., 2008</td>
</tr>
<tr>
<td><em>Neocalanus plumchrus</em></td>
<td>(\log_{10} CM = 0.3974 CS - 0.0306, r^2 = 0.981)</td>
<td>Ueda et al., 2008</td>
</tr>
<tr>
<td><em>Giothanas</em> spp.</td>
<td>(\log_{10} CM = 0.3331 CS - 0.3293, r^2 = 0.882)</td>
<td>Yamaguchi and Ikeda, 2000; Ikeda et al., 2006</td>
</tr>
<tr>
<td><em>Pleuromamma scutellata</em></td>
<td>(\log_{10} CM = 0.6349 CS - 1.7888, r^2 = 0.999)</td>
<td>Yamaguchi and Ikeda, 2000; Ikeda et al., 2006</td>
</tr>
<tr>
<td><em>Paraeuchaeta elongata</em></td>
<td>(\log_{10} CM = 0.3362 CS - 1.0630, r^2 = 0.951)</td>
<td>Yamaguchi and Ikeda, 2002; Ikeda et al., 2006</td>
</tr>
<tr>
<td><em>Paraeuchaeta birostrata</em></td>
<td>(\log_{10} CM = 0.3369 CS - 1.2355, r^2 = 0.995)</td>
<td>Yamaguchi and Ikeda, 2002; Ikeda et al., 2006</td>
</tr>
<tr>
<td><em>Heterorhabdus tanneri</em></td>
<td>(\log_{10} CM = 0.6976 CS - 1.9922, r^2 = 0.999)</td>
<td>Yamaguchi and Ikeda, 2000; Ikeda et al., 2006</td>
</tr>
<tr>
<td><strong>Euphausiids</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Euphausia pacifica</em></td>
<td>(DM = 0.0012BL^{1.737}, CM = 0.3673 DM, TL = 1.292 BL = 0.0762)</td>
<td>Kim et al., 2010a</td>
</tr>
<tr>
<td><em>Thysanoessa insiprata</em></td>
<td>(DM = 0.0043BL^{1.460}, CM = 0.3808 DM, TL = 1.514 BL = 0.575)</td>
<td>Kim et al., 2010a</td>
</tr>
<tr>
<td><strong>Amphipods</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyphocaris challengeri</em></td>
<td>(WM = 0.027 BL^{3.71}, DM = 0.199 WM, CM = 0.368 DM)</td>
<td>Yamada and Ikeda, 2006</td>
</tr>
<tr>
<td><em>Primno abyssalis</em></td>
<td>(WM = 0.025 BL^{2.38}, DM = 0.226 WM, CM = 0.543 DM)</td>
<td>Yamada and Ikeda, 2006</td>
</tr>
<tr>
<td><em>Themisto pacifica</em></td>
<td>(WM = 0.029 BL^{2.20}, DM = 0.228 WM, CM = 0.463 DM)</td>
<td>Yamada and Ikeda, 2006</td>
</tr>
<tr>
<td><strong>Hydrozoons</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aglantha digitale</em></td>
<td>(\log_{10} DM = -0.454(\log_{10} BH)^2 + 1.883\log_{10} BH - 2.402, CM = 0.204 DM)</td>
<td>Takahashi and Ikeda, 2006; Runge et al., 1987</td>
</tr>
<tr>
<td><strong>Chaetognaths</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eukrohnia hamata</em></td>
<td>(\log_{10} DM = -3.80 \log_{10} BL - 0.79, CM = 0.326 DM)</td>
<td>Matsumoto, 2008; Ikeda and Takahashi, 2012</td>
</tr>
<tr>
<td><em>Parasagitta elegans</em></td>
<td>(\log_{10} DM = -2.91 \log_{10} BL - 0.79, CM = 0.477 DM)</td>
<td>Imao, 2005; Omori, 1969</td>
</tr>
</tbody>
</table>
2-3-2. Population structure of copepods

To define the population structure of copepods, the mean copepodid stage (MCS) was calculated using the following equation (Marin, 1987):

\[ \text{MCS} = \frac{\sum (i \times N_i)}{N} \]

where \( N_i \) is the abundance (ind. \( m^{-2} \)) of \( i \)th copepodid stage \((i = 1 \text{ to } 6)\) and \( N \) is the total abundance of copepodid stages. The small and large MCS values indicate the dominance of early and late copepodid stages, respectively.

2-3-3. Cohort analyses in macrozooplankton

For macrozooplankton (euphausiids, amphipods, cnidarians and chaetognaths), cohort analyses were conducted based on the size–frequency histograms of \( BL \) or \( BH \) at each sampling date fitted to normal distribution curves. The length–frequency data were separated into multiple normal distribution curves using the free software “R” with an add-in package “mcmult” (Fraley et al., 2012).

2-3-4. Vertical distribution

For copepods, to clarify the depth distribution of each copepodid stage, the depths containing 50% of the resident population (50% distributed layer: \( D_{50\%} \)) were calculated. Additional calculations of \( D_{25\%} \) and \( D_{75\%} \) were also obtained for all copepodid stages. Day–night differences in the vertical distribution of each copepodid stage were evaluated using two-sample Kolmogorov–Smirnov tests (Sokal and Rohlf, 1995). To avoid errors resulting from small sample sizes in this DVM analysis, comparisons were obtained only for stages with >20 ind. \( m^{-2} \). Notably, the robustness of the Kolmogorov–Smirnov test for evaluating the DVM of zooplankton can be questionable in the case of large differences (>10-fold) in abundance between day and night (Venrick, 1986). However, because the day and night differences in the abundance observed in the present study were less than 5-fold, evaluations of DVM using the Kolmogorov–Smirnov test would be appropriate.

2-3-5. Growth rate

To calculate the mass-specific growth rate \( (g, \text{ day}^{-1}) \), the individual mass \( (CM: \mu g \text{ C ind.}^{-1}) \) was calculated based on the MCM using the regressions listed in Table 2 for the NOR-PAC net sampling date (epipelagic copepods) and the VMPS sampling date (mesopelagic copepods). For the MCS calculation, deep-sea resident stages (C6 stages of \( N. calumus \) spp.) were omitted. For macrozooplankton taxa, based on the mean \( BL \) or \( BH \) of each cohort at each sampling date, individual mass \( (CM: \mu g \text{ C ind.}^{-1}) \) was calculated using the equations listed in Table 2. To clarify the species showing growth during the study period, the linear regression

\[ Y = aX + b, \]

where \( Y \) is log-transformed individual mass \( \log_{10} [CM: \mu g \text{ C ind.}^{-1}] \), \( X \) is Julian day starting on 1 March, and \( a \) and \( b \) are fitted constants, was applied. For species showing significant growth, the mass-specific growth rate was calculated using the following equation (Omrani and Ikeda, 1984):

\[ g = \ln \left( \frac{CM_{x+t}}{CM_x} \right) / t \]

where \( CM_x \) is individual mass (\( \mu g \text{ C ind.}^{-1} \)) at day \( x \), and \( t \) is the interval between sampling date (day).

2-3-6. Production estimation

To estimate the production of each zooplankton species during the OECOS period, the respiration rate \( (R: \mu lO_2 \text{ ind.}^{-1} \text{ h}^{-1}) \) was estimated based on the empirical equation of Ikeda (2014):

\[ \ln R = 23.097 + 0.813 \times \ln CM (\mu g \text{ C ind.}^{-1}) - 6.248 \times 1000 / T - 0.136 \times \ln D + \text{Taxa} \]

where \( CM \) is individual carbon mass (\( \mu g \text{ C ind.}^{-1} \)), \( T \) is temperature at distribution layer of each species (K: absolute temperature), \( D \) is distribution depth (m) and Taxa is a constant number that varies with taxa: 0 for copepods, 0.6 for euphausiids, 0.421 for amphipods, 0.425 for cnidarians and \(-0.345 \) for chaetognaths (Ikeda, 2014). Gross production \( (P_g) \) is expressed as the sum of the net production \( (P_n) \) and respiration \( (R) \):

\[ P_g = P_n + R. \]

Assimilation efficiency \( (A) \) and gross growth efficiency \( (K_i) \) are expressed using the following equations:

\[ A = (P_g + R) / F \text{ and } K_i = P_n / F, \]

where \( (F) \) is the food requirement. For general zooplankton, \( A \) and \( K_i \) are 70% and 30%, respectively (Ikeda and Motoda, 1978). \( P_n \) is expressed as:

\[ P_n = 0.75 \times R. \]

From \( R \), the individual growth rate \((P_g: \text{ mg C ind.}^{-1} \text{ day}^{-1})\) was calculated using the following equation:

\[ P_g = R \times 12/22.4 \times 0.75 \times 24/1000, \]

where 12/22.4 is the carbon mass (12 g) in 1 mol (22.4 L) carbon dioxide, and \( \times 24 \) is the time conversion factor from \( \text{h}^{-1} \) to \( \text{day}^{-1} \) and division by 1,000 is the unit conversion from \( \mu g \) to mg. The daily population production \((\text{mg C m}^{-2} \text{ day}^{-1})\) was estimated after multiplying \( P_g \) by the abundance (ind. \( m^{-2} \)).

2-4. Environmental changes during the OECOS period

2-4-1. Hydrography

Temporal changes in temperature and salinity in the 0–1,000 m water column and the chl \( a \) and water mass composition in the 0–50 m water column from March 8 to May 1, 2007, are shown in Fig. 4. Throughout the study period, the temperature ranged from 2 to 6°C, and the salinity ranged from 33.2 to 34.2 (Fig. 4A, B). The chl \( a \) contents showed three peaks (2–6 mg \( m^{-2} \)) on April 7, 11 and 23 (Fig. 4C). For the water mass mixing ratio in the 0–50 m water column, the OYW and MKW comprised approximately half of the water mass during March. Cold COW was observed in early April, and the
observed timings of COW corresponded with the chl a peaks described above (Fig. 4C, D). For the eleven Bongo net sampling dates, the dominant water masses varied, i.e., COW for April 20 and 25, OYW for March 14 and April 6 and MKW for March 9 and April 8, 10, 12, 15, 17 and 30 (Fig. 4D).

The FRA-ROMS analyses revealed that the estimated origin of each water mass varied. The origin of COW was the Sea of Okhotsk, while the origin of OYW was the east Kamchatka current, which flows along the southern edge of the Kurile chain (Fig. 5). During 2006-2007, clockwise warm water eddies were observed around the Oyashio region, and the origin of MKW was associated with this warm water eddy (Fig. 2B). The experienced water temperatures during the previous six months also significantly varied with the water mass (p < 0.001, one-way ANOVA) (Fig. 5). The estimated temperatures of COW, MKW and OYW were 1.5-6.0°C (4.0±1.4°C: mean ± 1 sd), 3.6-8.1°C (5.8±1.4°C) and 2.2-4.9°C (3.3±0.6°C), respectively.

2-4-2. Phytoplankton community

Temporal changes in the size-fractionated integrated mean chl a in the 0-150 m water column and the diatom cell density and species composition at 5-m depth are shown in Fig. 6. A chl a peak was observed on April 8 and dominated with a large-sized (> 20 µm) fraction after April (Fig. 6A). The HPLC-CHEMTAX analyses revealed that >74% of the chl a content was composed of diatoms in April 2007 (Isada et al., 2010). A diatom cell peak was observed on April 7 and dominated with centric diatoms throughout the study period. The dominant diatom taxa were Thalassiosira spp. before April 20 and subsequently changed to Chaetoceros spp. thereafter (Fig. 6B).

2-4-3. Microzooplankton community

Temporal changes in the microzooplankton abundance and...
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Fig. 5. Results of FRA-ROMS analyses, which back-calculated the origin of each water mass at each sampling date. (A) COW; coastal Oyashio water (25 April), (B) MKW; modified Kuroshio water (12 April), (C) OYW; Oyashio water (6 April). Colours indicate experienced temperatures.

Fig. 6. Temporal changes in the integrated mean values of size-fractionated chlorophyll $a$ in the 0-150 m water column (A) and the diatom cell concentration and taxonomic composition at the 5 m depth (B) in the Oyashio region from March-April 2007. Note that the diatom taxonomic data were only available for April.

Fig. 7. Temporal changes in the abundance (A) and biomass (B) of the microzooplankton community at a 5 m depth in the Oyashio region during March-April 2007. Peaks of microzooplankton abundance were observed on April 7 and 25, and athecate dinoflagellates were abundant (Fig. 7A). In terms of biomass and taxonomic accounts (ciliates, athecate dinoflagellates and thecate dinoflagellates) at 5-m depth from March 8 to April 30, 2007 are shown in Fig. 7. Peaks of microzooplankton abundance were observed on April 7 and 25, and athecate dinoflagellates were abundant (Fig. 7A).
of biomass, microplankton peaked on April 9, and the phagotrophic athecate dinoflagellate *Gyrodinium* sp. (diatom feeder) was dominant in biomass (Fig. 7B).

**2-4-4. Mesozooplankton biomass**

Temporal changes in the day and night mesozooplankton wet mass in the 0-150 m and 0-500 m water columns on March 8 and May 1, 2007 are shown in Fig. 8A (0-150 m) and 8B (0-500 m), respectively. The night: day ratio (N: D ratio) was also calculated. The vertical distribution (0-150 m and 150-500 m) of the zooplankton biomass, evaluated based on differences in the standing stocks (g WM m\(^{-2}\)) of the two sampling layers (i.e., the values at 150-500 m = [values at 0-500 m] - [values at 0-150 m]), is shown in Fig. 8C (day-time) and 8D (night-time). Mesozooplankton biomass of the 0-150 m water column ranged from 7.6 (mean day and night values in March 9) to 147.7 g WM m\(^{-2}\) (April 8). The mesozooplankton wet mass was low during March but increased after April 8 and reached eight- and two-times higher values than those in March in the 0-150 m and 0-500 m water columns, respectively (Fig. 8A, B).

Concerning day-night differences in the 0-150 m water column, the biomass was higher at night than in the daytime in March, while no differences were detected in April (N: D ratio = 1, Fig. 8A). Day-night differences in the mesozooplankton biomass were not observed for the 0-500 m water column during the entire study period (Fig. 8B). Concerning the vertical distribution, most of the mesozooplankton biomass (92±3% [mean ± SD] for daytime, 82±5% for nighttime) was distributed at the 150-500 m layer prior to April 7, and gradually becoming shallower thereafter, while the biomass at 0-150 m exceeded that at the 150-500 m both day and night after April 13 (Fig. 8C, D).

**3. Population Structure of Dominant Species**

**3-1. Results**

**3-1-1. Epipelagic copepods**

Temporal changes in the abundance, biomass and copepodid stage composition of epipelagic copepods (*E. bungii*, *M. pacifica*, *M. okhotensis*, *N. cristatus*, *N. flemingeri* and *N. plumchrus*) in the 0-500 m water column in the Oyashio region from March to April 2007 are shown in Fig. 9. For *E. bungii*, the abundance ranged from 4,369 to 26,654 ind. m\(^{-2}\), the biomass ranged from 129.6 to 575.3 mg C m\(^{-2}\), and the mean biomass was 288.1 ± 91.6 mg C m\(^{-2}\) [mean ± SD] (Fig. 9A). Only late copepodid stages (C3-C6) were observed in March (Fig. 9A). The C3 composition gradually decreased from March to April 10. The C1 stage was
initially observed on April 12 and the total abundance rapidly increased, reaching nearly half of the population by April 25.

The abundance and biomass of *M. pacifica* ranged from 4,384 to 45,364 ind. m$^{-2}$ and 139.1 to 1915.4 mg C m$^{-2}$, respectively (Fig. 9B). The mean biomass of *M. pacifica* was at 529.3 ± 467.1 mg C m$^{-2}$. For the population structure, C6 dominated during early March, while all copepodid stages were observed throughout the study period (Fig. 9B). In April, the C6 composition decreased 12%, and the C1-C3 compositions increased 75%. Among these stages, the C1 stage comprised nearly half of the population in April.

The abundance and biomass of *M. okhotensis* ranged from 1,082 to 15,174 ind. m$^{-2}$ and 5.3 to 120.4 mg C m$^{-2}$, respectively. The mean biomass of *M. okhotensis* was 27.7 ± 26.0 mg C m$^{-2}$, which was extremely lower (ca. 1/20) than that of its congener *M. pacifica* (Fig. 9C). For the population structure, late copepodid stages (C4-C6) were dominant, and the most dominant stage was C5 (35%) followed by C6 (24%). C1 was extremely low throughout the study period, consistent with the findings for *M. pacifica*, as described above.

The abundance and biomass of *N. cristatus* ranged from 861 to 5,088 ind. m$^{-2}$ and 149.2 to 965.8 mg C m$^{-2}$, respectively (Fig. 9D). The mean biomass of *N. cristatus* was 595.9 ± 242.1 mg C m$^{-2}$. For the population structure, C1-C3 were predominant (composing >75%) in March, but decreased from March to late April, composing only 20% by late April. However, the composition of C4-C5 stages increased from March to April, and C4 composed 52% of the population by the end of April.

The abundance and biomass of *N. flemingeri* ranged from 1,931 to 18,300 ind. m$^{-2}$ and 54.6 to 585.7 mg C m$^{-2}$, respectively (Fig. 9E). The mean biomass of *N. flemingeri* was 208.9 ± 134.8 mg C m$^{-2}$. For *N. flemingeri*, all copepodid stages were observed. Throughout the study period, C1-C3 stages composed 65-85% of the population. Among the species, the C1 composition peaked on April 8 (75%), C2 was high on April 18 (53%) and C3 was high on April 25 (45%). Thus, a succession in dominant stages within the C1-C3 stage composition was observed for *N. flemingeri* in April.

The abundance and biomass of *N. plumchrus* ranged from 0 to 6,027 ind. m$^{-2}$ and 0 to 138.2 mg C m$^{-2}$, respectively (Fig. 9F). The mean biomass of *N. plumchrus* was 39.0 ± 42.6 mg C m$^{-2}$. These values were the lowest within the sympatric *Neocalanus* spp. (Fig. 9F). For the population structure of *N. plumchrus* (which commonly occurred after 15 April), C1-C3 stages composed 59-100% and showed slight temporal changes.

### 3–1–2. Mesopelagic copepods

Temporal changes in the abundance, biomass and copepo-
did stage composition (in abundance) of mesopelagic copepods are shown in Fig. 10. These mesopelagic copepod data were computed using day and night vertical stratified samplings through VMPS from 9 strata in the 0-1,000 m water column, and expressed in units per 1-m² water column.

The abundance and biomass of *Gaetanus* spp. ranged from 359 to 910 ind. m⁻² and 66.5 to 166.9 mg C m⁻², respectively (Fig. 10A). The mean biomass of *Gaetanus* spp. was 110.2 ± 29.8 mg C m⁻². *Gaetanus* spp. primarily comprised *G. simplex* and *G. variabilis*, and C4-C6 composed 75-90% of the population throughout the study period.

The abundance and biomass of *Pleuromamma scutullata* was 326-1,031 ind. m⁻² and 23.7 - 58.0 mg C m⁻², respectively (Fig. 10B). The mean biomass of *Pleuromamma scutullata* was 39.2 ± 10.4 mg C m⁻². For the population structure, C5 and C6 dominated, and C6 comprised more than 50% of the population of *Pleuromamma scutullata*, except for the night March 8 (Fig. 10B).

The abundance of *Paraeuchaeta elongata* was 261-771 ind. m⁻² and significantly increased throughout the study period (r=0.90 for correlation between abundance and Julian day, p<0.01, Fig. 10C). The biomass of *Paraeuchaeta elongata* was 53.3 - 249.4 mg C m⁻² with a mean value of 150.2 ± 50.4 mg C m⁻² (Fig. 10C). The population structure of *Paraeuchaeta elongata* primarily comprised C1-C3, particularly dominated with C2 (14-45%).

The abundance and biomass of *Paraeuchaeta birostrata* ranged from 174 to 559 ind. m⁻² and 75.0 to 217.9 mg C m⁻², respectively (Fig. 10D). The mean biomass of *Paraeuchaeta birostrata* was 155.5 ± 42.5 mg C m⁻². The abundance of *Paraeuchaeta birostrata* significantly increased during the study period (r=0.54 correlation with Julian day, p<0.05). The population structure of *Paraeuchaeta birostrata* was similar to that of *Paraeuchaeta elongata* and primarily comprised C1-C3 (52 -69% of total population). Among these stages, C2 was the most abundant (27-49%).

The abundance and biomass of *Heterorhabdus tanneri* ranged from 60 to 138 ind. m⁻² and 5.3 to 22.7 mg C m⁻², respectively (Fig. 10E). The mean biomass of *Heterorhabdus tanneri* was 15.1 ± 4.7 mg C m⁻². For Heterorhabdidae, inter-molt growth was more than 900% in body mass, thus the smallest C1 and C2 of *Heterorhabdus tanneri* are difficult to collect using the ordinary mesh size of the plankton net (Yamaguchi and Ikeda, 2000b). Because early copepodid stages (C1-C2) were not collected in the present study, the population structure was skewed for late copepodids, particularly for the predominance of C6.

3-1-3. Macrozooplankton

The data on macrozooplanktonic taxa (euphausiids, amphipods, cnidarians and chaetognaths) were derived from Bongo
net samplings at night from the 0-200 m water column. For euphausiids, two species, *E. pacifica* (63.3% of total euphausiids species) and *T. inspinata* (33.6%), were dominant. Temporal changes in abundance, biomass and total length (*TL*) histograms are shown in Fig. 11.

The abundance and biomass of *E. pacifica* ranged from 40 to 1,040 ind. m$^{-2}$ (mean ± 1 sd: 335 ± 346 ind. m$^{-2}$) and 116 to 2,330 mg C m$^{-2}$, respectively (Fig. 11A). The mean biomass of *E. pacifica* was 755 ± 796 mg C m$^{-2}$. The abundance of *E. pacifica* peaked from April 7-8, consistent with the timing of the chl $a$ peak. For *E. pacifica*, the *TL* ranged from 5.2 to 25.4 mm. Based on the cohort analyses, two cohorts were identified. The mean *TL* of the large-sized cohort was 13.8 - 17.6 mm, while that of the small-sized cohort was 6.9 - 10.5 mm. Numerically, the large-sized cohort was predominant in the *E. pacifica* population (Fig. 11A). The small-sized cohort primarily comprised juveniles, and the large-sized cohort comprised females, without spermatophores and adult males. After April 17, females with spermatophores were observed in 3.8% - 17.2% of the population. Based on the mean *TL* of each cohort, the daily growth rate in *TL* was calculated as 0.082 mm *TL* day$^{-1}$.

The abundance and biomass of *T. inspinata* ranged from 50 to 186 ind. m$^{-2}$ (mean ± 1 sd: 111 ± 47 ind. m$^{-2}$) and 135 to 576 mg C m$^{-2}$, respectively. The mean biomass of *T. inspinata* was 317 ± 150 mg C m$^{-2}$, ca. 1/2 - 1/3 of that of *E. pacifica* (Fig. 11B). The *TL* of *T. inspinata* ranged from 3.7 to 26.7 mm. Based on the cohort analyses, two size cohorts were recognized. The mean *TL* of the large- and small-sized cohorts was 16.5 - 18.1 mm and 4.9 - 9.3 mm, respectively (Fig. 11B). The large-sized cohort was dominant in population number. The small-sized cohort comprised juveniles, and the large-sized cohort comprised adult males and adult females with spermatophores. Notably, the *TL* s of adult females with spermatophore were consistently larger than those of adult males within the large-sized cohort. Based on the mean *TL* of each cohort, the growth rate of *T. inspinata* was 0.022 mm *TL* day$^{-1}$.

For amphipods, 13 species belonging to 9 genera were observed throughout the sampling period. Among these species, four species, *C. challengeri*, *P. abyssalis* *T. pacifica* and *T. japonica*, were predominant, accounting for 85% of the abundance and 84% of the biomass. For the two numerically dominant amphipod species, *C. challengeri* and *T. paci-
fica, temporal changes in abundance, biomass and body length (BL) histograms are shown in Fig. 12.

The abundance of C. challengeri ranged from 14 to 934 ind. m$^{-2}$ (mean ± SD: 168 ± 248 ind. m$^{-2}$) (Fig. 12A). The biomass ranged from 11.2 to 488.9 mg C m$^{-2}$ with mean biomass at 91.1 ± 129.9 mg C m$^{-2}$. Both the abundance and biomass were low during March, while high values were observed on April 12 and 20. For C. challengeri, the BL ranged from 2.4 - 15.0 mm, and this species was classified into 7 cohorts. Each cohort corresponded with the differences in instar number. Thus, based on smaller sizes, each cohort comprised instar 4, instar 5, instar 6, instar 7, instar 8, instar 9 and instars 10-12, respectively. The minimum BL of mature females and males was 9.81 mm and 13.00 mm, respectively.

The abundance and biomass of T. pacifica ranged from 4 to 216 ind. m$^{-2}$ (mean ± SD: 39.3 ± 39.6 ind. m$^{-2}$) and 0.7 to 37.5 mg C m$^{-2}$ (24.5 ± 23.4 mg C m$^{-2}$), respectively (Fig. 12B). Both the abundance and biomass were low from March to April 10, but was higher on April 20 and 25. For T. pacifica, cohort analyses were conducted with pooled BL data at 5-10 day intervals. The BL of T. pacifica ranged from 2.4 to 15.2 mm, and this species was separated into 3 or 4 cohorts. The smallest BL cohort (mean BL: 1.9 - 2.1 mm) comprised juveniles, while the middle-sized cohort (mean BL: 2.8 - 4.5 mm, note that two cohorts were identified from April 20 - 30) comprised immature females/males, and the large-sized BL cohort (mean BL: 5.1 - 5.5 mm) comprised mature females and males.

The abundance and biomass of cnidarian A. digitale ranged from 16 to 316 ind. m$^{-2}$ (mean ± SD: 115 ± 88 ind. m$^{-2}$) and 4.1 to 81.3 mg C m$^{-2}$ (24.5 ± 23.4 mg C m$^{-2}$), respectively (Fig. 13). Both the abundance and biomass were low in March and high in April. The BH of A. digitale ranged from 4 to 18 mm. Based on the cohort analysis, two cohorts were identified for A. digitale throughout the study period. The mean BH, of the small- and large-sized cohorts was 6.2-9.1 mm and 10.5-13.1 mm, respectively. The composition of the mature specimens in the population ranged from 8% to 49% and was less than 8.3% from March 9 to April 10 but rapidly increased to 30.4% on April 15 and subsequently remained high until end of the study period (14-49%).

Throughout the study period, three chaetognath species belonging to three genera were observed (E. hamata, P. elegans and P. scrippsi). For E. hamata and P. elegans, two numerically dominant chaetognaths (>95% in total chaeto-
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The abundance and biomass of *E. hamata* ranged from 113 to 2,543 ind. m$^{-2}$ (mean ± SD: 1,050 ± 594 ind. m$^{-2}$) and 10.2 to 208.9 mg C m$^{-2}$ (92.2 ± 53.8 mg C m$^{-2}$), respectively (Fig. 14). Both the abundance and biomass were low in March and high after April 8. The BL of *E. hamata* ranged from 5.8 to 23.7 mm. Based on the cohort analyses, the BL at each sampling date was separated into three cohorts. The mean BL of each cohort was 7.9 - 10.7 mm (small-sized cohort), 10.5 - 13.2 mm (middle-sized cohort) and 12.6 - 15.4 mm (large-sized cohort). The small-sized cohort primarily comprised juveniles and stage I individuals, while both the middle- and large-sized cohorts comprised stage I individuals. Juveniles were abundant from March 9-14 and April 12-15.

The abundance and biomass of *P. elegans* ranged from 52.4 to 380.4 ind. m$^{-2}$ (means ± SD: 176.0 ± 92.4 ind. m$^{-2}$) and 45.7 to 471.6 mg C m$^{-2}$ (193.6 ± 123.5 mg C m$^{-2}$), respectively (Fig. 14B). The BL of *P. elegans* ranged from 11.0 to 41.3 mm, and small specimens (< 10 mm) were not observed during the study period. The large body sizes of *P. elegans* were comparable to the occurrences of the small body sizes of *E. hamata*. Because of the large body sizes of *P. elegans*, the abundance of *P. elegans* was lower than that of *E. hamata*, and the total biomass of *P. elegans* was higher than that of *E. hamata* (Fig. 14A, B). Based on the cohort analyses, the BL histogram of *P. elegans* was divided into three cohorts throughout the study period. The mean BL of each cohort ranged from 15.1 - 22.1 mm (small-sized cohort), 21.4 - 28.1 mm (middle-sized cohort) and 26.4 - 31.3 mm (large-sized cohort). The small-, middle- and large-sized cohorts comprised stage I, stage II and stage III individuals, respectively. At end of the study period (April 30), stage IV
(mature specimens) was observed for the large-sized cohort (Fig. 14B).

3-1-4. Correlations with water mass exchanges

The results of the correlation analyses between the mixture ratio of water mass and abundance or the biomass of epipelagic, mesopelagic copepods and macrozooplankton are shown in Table 3. For epipelagic copepods, positive correlations were observed between the COW and the abundance and biomass of N. flemingeri and the biomass of N. plumchrus. Negative correlations were observed between the OYW and the abundance of M. pacifica, N. cristatus, N. flemingeri and N. plumchrus and the biomass of N. cristatus. For MKW, no correlations were detected for any species.

For mesopelagic copepods, a negative correlation was observed between MKW and the abundance of H. tanneri. Except for this interaction, no correlations were detected between the water masses and the abundance/biomass of mesopelagic copepods.

For macrozooplankton, positive correlations were observed between the COW and the abundance and biomass of the amphipod T. pacifica, cnidarian A. digitale and chaetognath P. elegans (except for the biomass of A. digitale). Negative correlations were observed between the MKW and the abundance of the euphausiid T. inspinata and chaetognath E. hamata. Negative correlations were also observed between the OYW and the abundance of the amphipod P. abyssalis and the biomass of the chaetognath E. hamata. For euphausiids or amphipods, correlations with the mixture ratio of the water mass were less than those of the other macrozooplankton taxa.

3-2. Discussion

3-2-1. Population structure of each zooplankton species

Tsuda et al. (2004) and Shoden et al. (2005) studied the life cycles of E. bungii in the Oyashio region. E. bungii has a one generation per year life cycle with diapause at C3-C6 stages. This species ascends from a deep ocean layer to the surface between February and April, and reproduction and growth occur during the spring phytoplankton bloom in the Oyashio region (Shoden et al., 2005). During the OECOS period, the population initially comprised C3-C6 stages, and following the phytoplankton bloom (Fig. 4C), rapid increases of C1 and C2 stages were observed (Fig. 9A). The rapid increases of C1 and C2 stages after April 15 might reflect
Table 3. Correlation coefficient (r) matrix between the mixture ratio of water mass (COW: coastal Oyashio water, MKW: modified Kuroshio water, OY: Okhotsk) and abundance (ind. m$^{-3}$) or biomass (mg C m$^{-3}$) of epipelagic copepods (Eb: Euphausia pacifica, Ga: Gaetanus spp., Mo: Metridia pacifica, Mp: Metridia okhotensis, Nc: Neocalanus cristatus, Nf: N. flemingeri, Np: N. plumchrus) in the Oyashio region during March-April 2007. For details of the mixture ratio of water mass, see Kono and Sato (2010). Significance is marked with asterisks: <0.05, p<0.01.

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<td>Abundance vs. MKW</td>
<td>0.231</td>
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<td>Abundance vs. OY</td>
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<td>0.629</td>
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Concerning the life cycle of *M. pacifica* in the Oyashio region, all copepodid stages occur throughout the year, and there are two pronounced generations: the first generation, characterized by rapid growth during the spring phytoplankton bloom (generation length: 2–3 months), and the second generation, characterized by slow development (9–10 months) with overwintering at C5 in deep ocean layers (up to 1,000–2,000 m) (Padmavati et al., 2004). Because the occurrence of the C1 stage of *M. pacifica* was much earlier than that of *E. bungii* and the dominance of C6F stages were observed from March to April 7 (Fig. 9B), the occurrence of the C1 stages likely reflected reproduction prior to the spring phytoplankton bloom. Based on field observations, a low egg hatching rate was reported for *M. pacifica*, likely reflecting the negative effect of diatom aldehyde on copepod development and growth during the spring phytoplankton bloom (Halsband-Lenk, 2005; Hopcroft et al., 2005). Because diatoms are the primary dominant phytoplankton taxon during the spring phytoplankton bloom in the Oyashio region (Isada et al., 2010), the negative effect of diatoms on copepod development might have occurred for *M. pacifica* during the OECOS period, reflecting the decreasing *M. pacifica* biomass observed during April (Fig. 9B).

For *M. okhotensis*, a two-year generation length was estimated, and this species utilizes the spring phytoplankton bloom during the first year for development to C5 and during the next year for reproduction (Padmavati et al., 2004). Because the composition of early copepodid stages was quite low (Fig. 9C), the reproduction of *M. okhotensis* did not occur in the Oyashio region during the OECOS period. For *M. okhotensis* in the Oyashio region, substantial parts of their population would be transported from the neighbouring Sea of Okhotsk (Padmavati et al., 2004). During the OECOS period, one water mass (COW) was derived from the Sea of Okhotsk (Fig. 5A). While both the abundance and biomass of *M. okhotensis* were positively correlated with coefficients for COW (r = 0.422 for abundance, 0.369 for biomass), and reproduction during the phytoplankton bloom period. During the OECOS period, the additional recruitment of overwintering C3-C4 stages to the C6F population from April 20-30 has been reported (Yamaguchi et al., 2010a). In addition, in the Alaskan Gyre, the maturation of an overwintered *E. bungii* population during the spring phytoplankton bloom has also been reported (Miller et al., 1984). Within the overwintered stages (C3-C6), C5F and C6F stages might utilize the early phase of the phytoplankton bloom at the beginning of April for reproduction, and C3 and C4F stages might utilize the phytoplankton bloom in April as an energy source for growth to C6F and gonad maturation (Yamaguchi et al., 2010a). Consequently, these species could experience extended reproduction throughout the phytoplankton bloom period, reflecting the continuous recruitment of the C6F population.
although these correlations were not significant (Table 3), these findings suggest that the effects of transportation from the Sea of Okhotsk might not be as large as previously expected for *M. okhotensis*.

For *N. cristatus*, reproduction occurs below 500 m from October to December, with a resulting peak of C1 observed at the near-surface layer from January to February. This newly recruited population develops to C5 by the end of June, and subsequently migrates down to a deeper layer for diapause from summer to autumn (Miller et al., 1984; Kobari and Ikeda, 1999; Tsuda et al., 2004). During the OECOS period, the development of this newly recruited population from C1 to C4 stages was observed (Fig. 9D). Details on growth rate of *N. cristatus* are discussed in Chapter 4.

**Neocalanus flemingeri** also undergoes seasonal ontogenetic vertical migration. According to Kobari and Ikeda (2001a), the dominant stages of *N. flemingeri* in the Oyashio region shift seasonally: C1 and C2 in March, C3 and C4 in April and C5 in early June, and subsequently populations enter overwintering at C4 or C6 stages at a deep ocean layer from autumn to winter. During the OECOS period, C1, C2 and C3 stages peaked in population structure on April 9, 18 and 25, respectively (Fig. 9E), reflecting the development of *N. flemingeri* from C1 to C3 stages during the spring phytoplankton bloom of the OECOS period.

For *N. plumchrus*, the surface occurrence timing of copepodid stages of this species is much later than that of the sympatric two *Neocalanus* spp., while reproduction at a deep layer continues ca. eight months from October to May in the Oyashio region (Tsuda et al., 1999; Kobari and Ikeda, 2001b). A recent molecular DNA identification study on nauplii (Fujioaka et al., 2015) reported that the vertical distribution of N1–N2 was > 250 m, while that of the N3 extended from the surface to a deeper layer and that of N4–N6 occurred only at the surface layer. According to Fujioka et al. (2015), the reproduction of *N. plumchrus* occurs at a deep layer and development ceases at N3, thus N3 acts as a mediator of developmental timing after N4, and subsequently, the initiation of development from N3 to N4 is triggered by the onset of the spring phytoplankton bloom. Because the development of *N. plumchrus* from N4 to N6 occurred at the surface layer in April, these individuals might reach the C1 stage near May (Fig. 1B). For the OECOS period, the first occurrence of *N. plumchrus* after April 7 suggested that these individuals undergo naupliar development (N4–N6) prior to April 7 (Fig. 9F).

Both *Gaetanus simplex* and *G. variabilis* are medium-sized copepods (total lengths ca. 4 mm) belonging to Aetideidae and are distributed throughout the mesopelagic zones of the subarctic Pacific Ocean, Bering Sea and Sea of Okhotsk (Brodskii, 1950). The life cycle of *G. variabilis* in the Oyashio region has been reported as two years, with reproduction timing during the spring phytoplankton bloom (Yamaguchi and Ikeda, 2000a). During the OECOS period, *Gaetanus* spp. was predominantly at C4–C6 stages (Fig. 10A), and the occurrence of spermatophore-attached C6F have been reported (Abe et al., 2012). These findings suggest that reproduction of *Gaetanus* spp. might have occurred during the OECOS period. However, as the naupliar development at *in situ* temperature requires 51 days (Yamaguchi and Ikeda, 2000a), the recruitment of C1 stage individuals might not have been detectable in the present study.

*Pleuromamma scutallata* is distributed at approximately 250–500 m, and this species performs nocturnal DVM and functions as a suspension feeder with a one-year generation length, showing peak reproduction during the spring phytoplankton bloom (Yamaguchi and Ikeda, 2000b). The population structure of *P. scutallata* primarily comprised C5 and C6 stages during the OECOS period (Fig. 10B), consistent with the phenomenon observed during the same season of a previous study (Yamaguchi and Ikeda, 2000b). Together with high MCS (Fig. 10B), the dominance of mature specimens in C6F and the occurrence of C6M with spermatophores at 500–750 m during April (Abe et al., 2012) suggest active reproduction for *P. scutallata* in April.

In the Oyashio region, *P. elongata* has a one-year generation length, and reproduction occurs throughout the year, peaking from April–June (Yamaguchi and Ikeda, 2001). The significant increase in abundance, progressive dominance of C1–C3 stages and gradual decrease in MCS (Fig. 10C) suggest the continuous recruitment of C1 stages to the *P. elongata* population during the OECOS period. During the OECOS period, the mean composition of egg-carrying C6F individuals (32%) (Abe et al., 2012) is much higher than the annual mean (4.3%, Yamaguchi and Ikeda, 2001). These findings suggest that *P. elongata* undergoes active reproduction during the OECOS period.

The life cycle of *P. birostrata* was also studied in the Oyashio region. These species have a one-year generation length, and reproduction occurred throughout the year, peaking from in April–June (Yamaguchi and Ikeda, 2001). During the OECOS period, the composition of C1–C3 stages was high for *P. birostrata* (52–69%) (Fig. 10D), and the composition of egg-carrying specimens in the C6F population (54%) (Abe et al., 2012) was much higher than the reported annual mean (mean 5% and range 0–33%, Yamaguchi and Ikeda, 2001). Thus, these findings suggest that reproduction of *P. birostrata* was initiated during the OECOS period.

For *H. tanneri*, the generation length is one year, and spermatophore-attached C6F are observed throughout the year, with peak reproduction in December (Yamaguchi and Ikeda, 2000b). The increased inter molt growth of C3–C4 individuals was observed during the summer when the zooplankton biomass was high. Together with the predominance of C6 in the population (Fig. 10E) and the seasonal developmental timing (C3–C4 in summer), *H. tanneri* undergoes reproduc-
tion and the development of early copepodid stages during the spring phytoplankton bloom.

In the Oyashio region, the euphausiid E. pacifica reproduce twice a year: March to April and August (Kim et al., 2009). In the present study, the continuous occurrence of spermatoaphore-attached females was observed after April 17 (Fig. 11A), suggesting that E. pacifica reproduction occurred in late April. However, the low composition of spermatoaphore-attached females (< 5%) and the faster growth rates (0.082 mm TL day$^{-1}$) than those of T. inspinata (0.022 mm TL day$^{-1}$, Kim et al., 2010a) suggest that E. pacifica utilized the spring phytoplankton bloom for body development and not reproduction.

T. inspinata reproduction occurred throughout the year with a peak from March - May (Kim et al., 2009). Even during the OECOS period, most of the adult females had attached spermatoophores (Fig. 11B), suggesting that the spring phytoplankton bloom was used as an energy source for the reproduction of T. inspinata.

For C. challengeri, the compositions of egg- or juvenile-carrying specimens within mature females increased during April (Abe et al., 2016), and the juvenile composition in the total population rapidly increased in late April (Fig. 12A). This species reproduce throughout the year, peaking from April to July (Yamada and Ikeda, 2000). The population structure and reported reproduction timing suggest active reproduction for C. challengeri during the OECOS period.

T. pacifica in the Oyashio region has four generations per year, with a reproduction peak in early summer, and peaks in both abundance and biomass during the summer (Yamada et al., 2004). During the OECOS period, increases in the composition of egg- and juvenile-carrying females of T. pacifica through April were reported (Abe et al., 2016). These findings suggest that T. pacifica underwent reproduction based on their increased mesozooplankton biomass (Fig. 8A).

The life cycle of A. digitale lasts one year, with a reproduction peak from June to August in the Oyashio region (Takahashi and Ikeda, 2006). Assuming this life cycle schema, two cohort sizes based on the BH were observed, corresponding to those recruited from spring to summer (large-sized BH cohort) and late summer to autumn (small-sized BH cohort) in the previous year. The composition of mature specimens in the large-sized BH cohort increased after April 15 (Fig. 13), suggesting that A. digitale grew and matured during the spring phytoplankton bloom.

For E. hamata, mature specimens are distributed at depths below 250 m in the subarctic Pacific (Terazaki and Miller, 1986). Because the sampling depths in the present study were much shallower (0-200 m), only small-sized juveniles and immature specimens (stage I) were collected for E. hamata. In the Oyashio region, the recruitment of the new generation occurs from spring to summer (Matsumoto, 2008). The high abundance of juveniles in March and mid-April might reflect the recruitment of a new generation of E. hamata (Fig. 14A).

Because the nighttime vertical distribution depths for P. elegans are much shallower than 200 m (Ozawa et al., 2007), the sampling design of the present study may cover the entire population of P. elegans in the Oyashio region. Mature stage IV specimens with BLs of approximately 30 mm, were observed on April 30, 2007 (Fig. 14B). The reproduction of P. elegans peaks from late spring to summer in the Oyashio region (Terazaki, 1998; Kotori, 1999). These findings suggest the initiation of reproduction for P. elegans at end of the April during the OECOS period.

3-2-2. Responses of zooplankton for water mass exchange

As previously described, the geographical origins and temperatures of the three water masses observed during the OECOS period varied (Fig. 5). Within the three water masses, COW showed positive correlations with five species, while MKW showed one positive and two negative correlations with species, and OYW showed a negative correlation with six species (Table 3). These findings suggest high zooplankton abundance and biomass under COW conditions. While OYW also originated from the cold-water mass, the lowest experienced temperature may induce the low zooplankton growth rate in OYW. Because the origin of COW was the Sea of Okhotsk, the high primary production of the marginal sea (note that the Sea of Okhotsk is in the southernmost ice coverage ocean in the northern hemisphere) may support sufficient food conditions for the various zooplankton species examined in the present study (Fig. 5).

Because each chaetognath species showed species-specific temperature and salinity ranges, each species is considered an indicator of the water mass (Russell, 1935; Bieri, 1959). During the OECOS period, P. elegans showed a high positive correlation with COW. Similar water mass correlations between COW and P. elegans were observed for the cnidarian A. digitale (Table 3). Both species (P. elegans and A. digitale) are subarctic/arctic species, with similar geographical distributions and little DVM behaviour (Kotori, 1976; Shiota et al., 2012). However, macrozooplanktonic euphausiids and amphipods showed strong DVM behaviour (Iguchi et al., 1993; Ikeda and Shiga, 1999). The more moderate effects of water-mass exchange on euphausiids and amphipods compared to the other macrozooplankton taxa (Table 3) might reflect the strong DVM behaviours of these individuals, which masked the effects of water-mass exchange at the surface layer.

Because the growth of epipelagic copepods occurred at the surface layer, the surface temperature is considered the most important factor to determine growth and survival during the spring. Within the three water masses, the observed temperature was the lowest for OYW. Thus, it is particularly interesting that most epipelagic copepods showed negative
correlations with OYW (Table 3). The lowest temperature at OYW may induce slower growth and decrease the survival rate of epipelagic copepods in OYW compared with those in the other water masses. However, mesopelagic copepods showed little effect on water-mass exchange (Table 3), likely reflecting the fact that the water mass exchange at the surface layer has less effect on the distribution of mesopelagic copepods.

4. Vertical Distribution of Dominant Copepods

4-1. Results

For epi- and mesopelagic copepods, day and night vertical stratified samplings were collected with a VMPS (60 μm mesh) between 0 and 1,000 m. Diel and ontogenetic changes in the vertical distribution \(D_{50\%}\) of epipelagic copepods (E. bungii, M. pacifica, M. okhotensis, N. cristatus, N. flemingeri and N. plumchrus) and mesopelagic copepods (P. scutullata, P. elongata and P. birostrata) in the Oyashio region are shown in Figs. 15-17.

4-1-1. Epipelagic copepods

Eucalanus bungii had no DVM during all copepodid stages throughout the study period (Kolmogorov-Smirnov test, \(p > 0.05\), Fig. 15A). E. bungii was concentrated at approximately 250-500 m both day and night on March 8, 2007. The vertical distribution ranges of C3-C6 extended (50-750 m) both day and night on April 5. The vertical distribution of C4-C6 reached the surface by April 11, but C3 stayed in the deep layer. During April 23-29, C6F were consistently distributed at the surface layer. Newly recruited C1-C2 were observed at the surface layer on April 29. On April 29, C1-C4 were distributed near the surface layer. No sexual differences in the vertical distribution were observed for C4-C5, while the C6M remained below 150 m both day and night, and C6M never occurred at the surface layer.

For M. pacifica, daytime distribution depths of C1-C3, C4-C5 and C6 on March 8 were at 150-250, 150-500 and 250-500 m, respectively (Fig. 15B). At night, all copepodid stages, except C6M, performed nocturnal ascent and were distributed in the upper 150 m. These strong nocturnal DVMs were observed on April 5 and 11. From April 23-24 and 28-29, DVM was not observed for C1-C5. Only the C6F stage continued a nocturnal ascent on both April 23 and 29. The magnitude of the DVM was 46-359 m (evaluated by day \(D_{50\%}\)-night \(D_{50\%}\)) for C6F. The daytime distribution depths increased with increasing copepodid stages, and the DVM magnitude also increased. The C6M of M. pacifica were distributed at 250-500 m depths both day and night and never occurred at the surface layer, consistent with E. bungii C6M.

For M. okhotensis, adult specimens (C6F/M) did not per-
form DVM on March 8 and remained below 250 m both day and night ($p > 0.05$, Fig. 15C). The nocturnal ascent DVM was observed for C5F/M on April 5 and C5F/M and C6F on April 11. The magnitude of these DVM was 71-358 m. On April 23 and 29, the nocturnal ascent DVM was detected only for C6F. The C6M of *M. okhotensis* was distributed at 250-500 m both day and night throughout the study period. For *N. cristatus*, C1-C4 was distributed in the upper 250 m both day and night throughout the study period (Fig. 16A).

![Fig. 16](image)

**Fig. 16.** Ontogenetic changes in the vertical distribution of *Neocalanus* copepods, *N. cristatus* (A) and *N. flemingeri* / *N. plumchrus* (B), in the Oyashio region during March to April 2007. Open and solid symbols denote $D_{50\%}$ of day and night, respectively. Vertical bars indicate the depth ranges of $D_{25\%}$ to $D_{75\%}$. Note that no diel vertical migration was detected for all species/stages using the Kolmogorov-Smirnov test. Dominant water masses at each date are shown in the parentheses. COW: coastal Oyashio water, MKW: modified Kuroshio water, OYW: Oyashio water.

**Fig. 17.** Ontogenetic changes in vertical distribution of mesopelagic copepods, *Pleuromamma scutullata* (A), *Paraeuchaeta elongata* (B) and *Paraeuchaeta birostrata* (C), in the Oyashio region during March to April 2007. Open and solid symbols denote $D_{50\%}$ of day and night, respectively. Vertical bars indicate depth ranges of $D_{25\%}$ to $D_{75\%}$. Asterisks indicate that the presence of DVM detected using the Kolmogorov-Smirnov test. *: $p<0.05$, **: $p<0.01$. Dominant water masses at each date are shown in the parentheses. COW: coastal Oyashio water, MKW: modified Kuroshio water, OYW: Oyashio water.
m on March 8, but extended to the surface layer after April 5. Throughout the study period, C6 stages occurred below 500 m. No DVM was observed in any copepod stage of *N. cristatus* during the study period (*p* > 0.05, Fig. 16A).

For *N. flemingeri*, C1–C4 were distributed at 50–250 m and were not observed in surface water both day and night on March 8 (Fig. 16B). *N. plamchus* was observed after April 11. The C1–C4 stages of both species were distributed near the surface layer after April 5.

### 4-1-2. Mesopelagic copepods

For *P. scutallata*, C5F/M and C6F showed clear DVM (*p* < 0.01) with a magnitude of 156–171 m on March 8 (Fig. 17A). Nocturnal ascent DVM was observed for C5F/M on April 5 (*p* < 0.01), while no DVM was detected for all copepod stages after April 11 (*p* > 0.05). The OVM of *P. scutallata* was characterized by a developmental ascent with a magnitude of 102–138 m (Fig. 17A).

*Paraeuchaeta elongata* after C4 stages showed clear DVM, characterized by nocturnal ascent with a magnitude of 120–160 m throughout the study period (Fig. 17B). Because C1 and C2 were distributed at the deepest layer, the OVM of *P. elongata* was characterized by developmental ascent with a magnitude of 478–675 m (Fig. 17B).

For *P. bichostrata*, DVM was not detected for most dates (Fig. 17C). Concerning OVM, C1 and C6 of *P. bichostrata* were distributed at the deepest layers, and C4 and C5 were detected at the shallowest layers. Because of these stage-specific vertical distributions, the OVM of *P. bichostrata* comprises a mixture of two patterns: developmental ascent for the early copepod stages (D<sub>100</sub> of C1–C4: 339–357 m) and developmental descent for the late copepod stages (D<sub>100</sub> of C6F–C4: 237–273 m) (Fig. 17C).

### 4-2. Discussion

#### 4-2-1. Epipelagic copepods

The vertical distribution of *E. bungii* showed clear temporal changes. The activation of diapause and the upward migration of overwintered C3–C6F stages were observed on April 5 (Fig. 15A). The timing of upward migration was faster for C6F than for C3–C4 stages, and newly recruited C1–C3 stages were distributed at 0–50 m, while C6M resided at deeper layers throughout the study period (Fig. 15A). The activation of *E. bungii* diapause remains unclear. Based on high-frequency samplings obtained during iron-fertilization experiments in the Gulf of Alaska, the upward migration of *E. bungii* from the subsurface (20–50 m) to the surface layer has been observed during high phytoplankton bloom (Tsuda et al., 2006). During the OECOS period of the present study, the timing of the ascent migration of *E. bungii* corresponded with the timing of the chl a peak. For SEEDS I (the highest chl a recorded iron-fertilization experiment), high standing stocks of early copepodid stages of large grazing copepods likely resulted from the reduced mortality rates of these stages, as suspension feeders feed on large diatoms and less predation pressure on eggs and nauplii (Tsuda et al., 2005). For the OECOS period, the surface distribution of C1–C3 stages might also reflect of abundance of their food phytoplankton and also reflect lower predation pressures.

*Metridia pacifica* has active DVM (Tsuda and Sugisaki, 1994). The daily downward carbon transportation through *M. pacifica* DVM was estimated to be 8.0 mg C m<sup>−2</sup> day<sup>−1</sup>, and the yearly total was 3.0 g C m<sup>−2</sup> year<sup>−1</sup>, accounting for 15% of the total passive sinking POC flux at 150 m (Takahashi et al., 2009). For the OECOS period, active DVM was observed, except for C6M from March 8 to April 11. Interestingly, these DVM were only limited for C6F during April 23–24 and 28–29 (Fig. 15B). The other stages were observed at deep layers throughout the day on these dates. These patterns were also observed for the two mesopelagic copepods (*P. scutallata* and *Gaetanus simplex*), as both species performed DVM during the normal season (Abe et al., 2012). The flexibility of DVM behaviour has been well documented for *Metridia* spp. Thus, within the same stage, only less-lipid accumulated specimens perform DVM in *M. pacifica* (= *M. lucens*) (Hays et al., 2001), and their DVM patterns varied with the presence/absence of visual vertebrate predators (Osgood and Frost, 1994). Seasonally, the magnitude of DVM is smaller during spring than during summer and winter, reflecting seasonal changes in light penetration, which is smaller during the spring because of the phytoplankton bloom (Takahashi et al., 2009). The continuous DVM of C6F stage *M. pacifica* might reflect reproduction at the surface layer during the spring phytoplankton bloom.

For the congener *M. okhotensis*, nocturnal DVM was observed on April 5 and 11–12, but ceased, except for C6F, after April 23. The active DVM of *M. okhotensis* has been previously reported (Hattori, 1989). The seasonally limited DVM pattern observed only in April has also been reported for *M. okhotensis* in the Oyashio region (Padmavati et al., 2004; Takahashi et al., 2008). The continuous DVM behaviour of C6F stages in late April during the OECOS period was similar to that of congener *M. pacifica*. These findings suggest that the DVM patterns of C6F support reproduction at the surface layer.

The vertical distribution of early stages (C1–C3) of *N. cristatus* was at 0–250 m on March 8 and 0–150 m on April 5 and 23, and subsequently a shallower distribution was observed on April 29: 0–25 m for C1–C2 and 50–100 m for C3–C4. These patterns (shallower changes in vertical distribution of early copepodid stages with advances of phytoplankton bloom) were reported during iron-fertilization experiments (SERIES) (Tsuda et al., 2006). Commonly, the C2 stages of *N. cristatus* occurred shallower than the C1 stages (Fig. 16A), likely reflecting the occurrence of reproduction below depths of 1,000 m (Miller et al., 1984; Kobari and Ikeda, 1999). The initial feeding stage is C1 for *N. cristatus*, while other
Neocalanus spp. (N. flemingeri and N. plumchrus) initiate feeding at N4 (Saito and Tsuda, 2000). The first feeding stage of Neocalanus spp. shows a broader vertical distribution range (Fujioika et al., 2015). A deeper distribution of C1 compared to C2 in N. cristatus might reflect this broader vertical distribution.

A comparison of the vertical distribution depths between three Neocalanus spp. and E. bungii during the OECOS period revealed that N. cristatus and E. bungii were distributed deeper than N. flemingeri and N. plumchrus. As for feeding habits, the late copepodid stages of N. cristatus and E. bungii feed on sinking particles or aggregations (Dagg, 1993), while major food items of late copepodid stages of N. flemingeri and N. plumchrus are phytoplankton (Sato et al., 2011). These differences in food preference may contribute to the deeper distribution of N. cristatus and E. bungii compared to N. flemingeri and N. plumchrus. The vertical separation of these species pairs was observed: large body-sized N. cristatus and E. bungii were distributed below 50 m and small body-sized N. flemingeri and N. plumchrus distributed at the surface layer in the eastern subarctic Pacific during the spring (Mackas et al., 1993). In the Oyashio region, species-specific vertical separation was reported for these four species, from shallow to deep in the following order, N. plumchrus, N. flemingeri, E. bungii and N. cristatus, and these vertical segregations contribute to the niche separation of large grazing copepods during the growing season (Sato et al., 2011; Tsuda et al., 2014).

For N. flemingeri, the vertical distribution was broader (25–100 m) on March 8, but concentrated at 0–50 m after April 5, similar to the temporal changes observed for N. cristatus. Iron-fertilization experiments revealed the upward migration from the sub-surface layer for the C3-C5 stages of N. plumchrus (Yamaguchi and Ikeda, 2002a). The distribution depths of N. plumchrus were distributed at relatively shallow depths within the mesopelagic copepods, their OVM might show a developmental descent pattern (r-selection) (Yamaguchi et al., 2004a).

The upward migration of N. flemingeri during the spring phytoplankton bloom may also reduce the mortality and high survival rate of early copepodid stages.

For N. plumchrus, N1–N2 are distributed from deeper layers to 250 m, and N3 was observed at broader depths from deeper layers to the surface layer; the development from N4 to N6 has been observed at the surface layer in April (Fujioika et al., 2015). The observation of copepodid stages of N. plumchrus on April 5 might reflect development from N4 to N6 during the spring phytoplankton bloom.

4-2-2. Mesopelagic copepods

The DVM magnitude of P. scutullata during the OECOS period was 156–188 m (Fig. 17A). These values are within the range of the reported values for this species in the Oyashio region (20–249 m, Yamaguchi and Ikeda, 2000b). The ceased DVM was also observed for P. scutullata, but it occurred earlier (from 11 April) than in M. pacifica (after April 23, Fig. 15B). The earlier cessation in P. scutullata suggests that mesopelagic P. scutullata might sensitively respond to increases in passive sinking POC flux. The developmental descent of the OVM was observed for P. scutullata throughout the study period (Fig. 17A). Yamaguchi et al. (2004a) examined the OVM patterns of mesopelagic copepods and found that within the mesopelagic copepods, OVM characterized by developmental descent was common for shallower resident species (<1,000 m), while developmental ascent was the common OVM for deeper species (>1,000 m). These shifts in OVM patterns in mesopelagic copepods are consistent with the lifetime fecundity of this species, i.e., shallower resident species have high fecundity with small-sized eggs (r-selection), while deeper resident species have lower fecundity with large-sized eggs (K-selection). To reduce mortality, the shallower species of early stages tend to be distributed at shallower depths, characterized by high temperatures to achieve faster growth (r-selection). For deeper resident species, to avoid predation, early stages occur at deeper depths (K-selection) (Yamaguchi et al., 2004a). Because P. scutullata were distributed at relatively shallow depths within mesopelagic copepods, their OVM might show a developmental descent pattern (r-selection).

In the Oyashio region, vertical separation within the genus has been reported for the three Paraeuchaeta spp. (P. elongata, P. birostrata and P. rubra), and P. elongata distributed at the shallowest depths, with a distribution centre at 310 m (Yamaguchi and Ikeda, 2002a). The distribution depths of P. elongata in the present study are consistent with these depths. However, P. birostrata occurs at deeper depths of approximately 800 m (Yamaguchi and Ikeda, 2002a). In the present study, P. birostrata was distributed between 500 and 1,000 m, thus vertical separation within Paraeuchaeta species was also observed in the present study (Fig. 17B, C). The vertical separations within the congner species might reduce food competition in the food-limited mesopelagic realm (Yamaguchi and Ikeda, 2002a).

Nocturnal ascent DVM was observed for carnivorous P. elongata throughout the study period, except on April 5 and 23–24 (Fig. 17B). As previously described, the ceased DVM reflected particle feeders inhabiting the epipelagic (M. pacifica) and mesopelagic (P. scutullata) layers after April 11 or 23 during the OECOS period (Abe et al., 2012; Figs. 15B, 17A). However, the ceased DVM was not observed for P. elongata. While results of the ceased DVM of suspension feeders in the epipelagic and mesopelagic layers might result from the increasing POC flux after the spring phytoplankton bloom in mid-April, such effects may be limited for carnivorous P. elongata, as this species performs continuous DVM, even after the spring phytoplankton bloom.

For P. birostrata, the OVM pattern greatly varied from that of P. elongata. The OVM pattern of P. birostrata reflected a mixture of developmental ascent at early copepodid stages and developmental descent at late copepodid stages (Fig.
17C). For *P. birostrata*, C4 is the shallowest stage throughout the year, and C1 and C6 are the deepest (Yamaguchi and Ikeda, 2002a). This combined OVM pattern is consistent with the findings of the present study. The OVM patterns of *Paraechueta* spp. are associated with the magnitude of the inter-molt growth of each developmental stage, and the shallowest stage shows the highest inter-molt growth within the species (Yamaguchi and Ikeda, 2002b).

5. Growth of Dominant Copepods and Macrozooplankton

5-1. Results

As previously described (chapter 3), various zooplankton species achieved growth and reproduction in the Oyashio region during the spring phytoplankton bloom. To conduct species-specific comparisons, the growth of each species was calculated according to the standardized carbon-mass specific growth rate ($g$) (see 2-3-5).

For the epipelagic *E. bungii*, the composition of C3 showed a rapid decrease on April 25 (Fig. 9A). Two cohorts were recognized for *E. bungii*: overwintered C3 and C4-C5 populations prior to April 25, and newly recruited C1-C2 and C3 populations after April 25 (Fig. 9A). Each cohort was referred to as large-sized (C3-C5) and small-sized (C1-C3) cohorts, respectively. Significant growth was observed for each cohort (Fig. 18, $p < 0.05$). The growth rate ($g$) (mean ± sd) of both small- (Eb1) and large-sized (Eb2) cohorts was 0.061±0.440 and 0.029±0.074 day$^{-1}$, respectively.

The individual biomass of *M. pacifica* was high (3.0 μg C ind.$^{-1}$) on March 8, but low thereafter. For *M. okhotensis*, the individual biomass was high on April 5 (83.2 μg C ind.$^{-1}$), but low and highly variable for the other sampling dates. The individual carbon mass of *N. cristatus* ranged from 26.3 to 201.1 μg C ind.$^{-1}$ (except for C6) and showed significant growth throughout the OECOS period (Nc: $p < 0.05$). The mean growth rate ($g$) of this cohort was 0.064±0.179 day$^{-1}$.

5-1-1. Dominant copepods

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chrus, except C6, ranged from 25.9 to 93.0 and 2.68 to 16.19 μg C ind. −1, respectively. No significant growth was detected for N. flemingeri, while significant growth was observed for N. plumchrus (Fig. 18, p < 0.05). The mean growth rate (g) of this cohort was 0.039±0.492 day −1.

No mesopelagic copepods examined in the present study showed significant growth during the OECOS period. The individual carbon masses of mesopelagic copepods were 55.2-100.8 μg C ind. −1 for Gaetanus spp., 11.8-51.6 μg C ind. −1 for P. scutullata, 89.6-283.7 μg C ind. −1 for P. elongata, 189.7-258.7 μg C ind. −1 for P. birostrata and 41.5-156.1 μg C ind. −1 for H. tanneri (Fig. 19).

5-1-2. Macrozooplankton
For macrozooplankton, temporal changes in the individual carbon mass were analysed based on the body length (BL or BH) of each cohort along the sampling date. The results for euphausiids and amphipods are shown in Fig. 20, and the results for cnidarians and chaetognaths are shown in Fig. 21.
For the euphausiid E. pacifica, individual carbon masses of small and large cohorts were 280-1,310 and 3,091-7,024 μg C ind. −1, respectively. Significant growth was observed for both cohorts (p < 0.05), and the mean growth rate (g) was 0.033±0.041 day −1. For T. inspinata, the individual carbon mass of the small and large cohorts was 0-3,928 and 22,662-30,074 μg C ind. −1, respectively. Significant growth was observed for the large-sized cohort (p < 0.05), with a mean growth rate (g) of 0.022±0.021 day −1.
For all amphipod species, no significant growth was detected for all cohorts throughout the study period. For C. challenger, the individual mean carbon mass for each cohort was 40.7, 85.4, 171.6, 364.7, 754.1 and 1,274.2 μg C ind. −1 (ordered from small to large body size). For P. abyssalis, the individual mean carbon mass for each cohort was 19.5, 47.6, 78.7 and 700.9 μg C ind. −1. For T. pacifica, the individual mean carbon biomass for each cohort was 21.5, 64.8, 189.9 and 326.0 μg C ind. −1.
For the cnidarian A. digitale, small- and large-sized cohorts were identified, and no significant growth changes were
detected. The individual mean carbon mass of small- and large-sized cohorts was 47.6–134.2 and 200.5–381.6 μg C ind.\(^{-1}\), respectively (Fig. 21).

For chaetognaths, the individual mean carbon mass of small- (Eh1), middle- (Eh2) and large-sized (Eh3) cohorts in *E. hamata* ranged from 16.3 to 48.0, 44.0 to 98.5 and 83.8 to 173.0 μg C ind.\(^{-1}\), respectively. Significant growth was detected for all cohorts (\(p < 0.05\)), and the mean growth rate (\(g\)) of Eh1, Eh2 and Eh3 was 0.081±0.094 (Eh1), 0.100±0.095 (Eh2) and 0.041±0.059 (Eh3) day\(^{-1}\), respectively (Fig. 21). The individual mean carbon mass of small-, middle- and large-sized cohorts of *P. elegans* ranged from 208 to 634, 577 to 1273 and 1,065 to 1,745 μg C ind.\(^{-1}\), respectively. Significant growth was observed for middle- (Pe1) and large-sized (Pe2) cohorts (\(p < 0.05\)), and the mean growth rate (\(g\)) of Pe1 and Pe2 was 0.071±0.085 and 0.049±0.041 day\(^{-1}\), respectively (Fig. 21). The growth rates for the body length were 0.039–0.050 mm day\(^{-1}\) for *E. hamata* and 0.042–0.101 mm day\(^{-1}\) for *P. elegans* (Table 4).

Throughout the OECOS period, significant growth in individual carbon mass was observed for the following taxa/species: copepods (*E. bungii, N. cristatus* and *N. plumchrus*), euphausiids (*E. pacifica* and *T. inspinata*) and chaetognaths (*E. hamata* and *P. elegans*). Inter- and intra-species (between cohort) differences were examined using one-way ANOVA, and the results revealed no significant differences in the growth rates for various zooplankton species and taxa during the OECOS period (\(p = 0.99\), Table 5).

### 5-2. Discussion

In the present study, significant growth was observed for copepods (*E. bungii, N. cristatus* and *N. plumchrus*), euphausiids (*E. pacifica* and *T. inspinata*) and chaetognaths (*E. hamata* and *P. elegans*). Although various copepod species were examined in the present study (eleven species), only three species showed significant growth with time, partly reflecting the morphological characteristics of this taxon. Because copepods have six morphologically different cope-
Podid stages, the population structure was divided into six categories. The low resolutions in population structure of copepods may prevent detailed cohort analysis of this taxon. However, fine-scaled body length divisions of macrozooplankton taxa were achieved, facilitating the separation of cohorts for macrozooplankton taxa (Figs. 11–14). These advantages in the population structure analysis (body length measurement) facilitated the detection of significant growth for two dominant macrozooplankton taxa (euphausiids and chaetognaths) in the present study.

5-2-1. Growth rate of copepods

Analyses based on the mean copepodid stage (MCS), the growth rates (g) of small (C1–C3 population) and large (C3–C5 population) cohorts of E. bungii, N. cristatus and N. plumchrus were 0.061±0.440, 0.029±0.074, 0.064±0.179 and 0.039±0.492 day⁻¹, respectively. The body size (copepodid stage), temperature and food (chl a) affect the growth rate (g) of copepods, which increases with increasing temperature, younger copepodid stages and increasing ambient chl a concentration under laboratory conditions (Liu and Hopcroft, 2006a, 2006b). During the OECOS period, although the differences were insignificant, the growth rate of the small-sized cohort was higher than that of large-sized cohort within E. bungii.

During the OECOS period, Kobari et al. (2010c) estimated the stage duration and growth rates of the four dominant copepods (E. bungii, N. cristatus, N. flemingeri and N. plumchrus) using on-board rearing experiments. The growth rate of E. bungii C2 was 0.04 day⁻¹ based on laboratory rearing (Kobari et al., 2010c). This value was slightly lower than that of the small-sized cohort of E. bungii based on the cohort analysis evaluated in the present study (0.061 day⁻¹). From laboratory rearing, the growth rate of N. cristatus was 0.06 day⁻¹ (Kobari et al., 2010c). From natural cohort analysis, the g of N. cristatus was 0.067 day⁻¹ in the Bering Sea shelf (Vidal and Smith, 1986). The estimated value obtained from the cohort analysis during the OECOS period (0.064 day⁻¹) was between these two values. Interestingly, within the same OECOS period, the g derived from laboratory rearing (Kobari et al., 2010c) was slightly lower than that using the natural cohort method (the present study). Because of the presence of predators under natural conditions, the predation removal at late copepodid stages may reflect the dominance of early copepodid stages, characterized by a high g (Liu and Hopcroft, 2006a, 2006b). To confirm these hypotheses in copepods, additional data accumulation on g is required using both laboratory rearing and natural cohort methods in the future.

5-2-2. Growth rate of macrozooplankton

During the OECOS period, the mean growth rates (g) of large-sized cohorts of the euphausiids E. pacifica and T. inspinata were 0.033 and 0.022 day⁻¹, respectively (Fig. 20). For E. pacifica, the g at the Oregon coast and Gulf of Alaska (at 5°C) was 0.0089-0.0135 day⁻¹ and 0.0025 day⁻¹, respectively (Pinchuk and Hopcroft, 2007; Shaw et al., 2010). The g of E. pacifica in the present study was higher than these values. For euphausiids, the g showed an exponentially negative relationship with body mass under constant temperature and a positive relationship with temperature (Ross, 1982; Shaw et al., 2010). Because the mean body mass was higher for T. inspinata (Fig. 20), the g of T. inspinata may be lower than that of E. pacifica. Concerning the horizontal distribu-

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A positive correlation with the chl. a concentration was observed for the g of T. inermis (a species having wax ester that mainly feeds on phytoplankton), while no correlation with chl. a was observed for E. pacifica, which has high g during the phytoplankton bloom period (Pinchuk and Hopcroft, 2007). In the present study, as the food concentration was high around the annual peak (spring phytoplankton bloom), the g is expected to be high around the bloom, which explains why the g value obtained in the present study is higher than the annual data in the eastern North Pacific (Shaw et al., 2010).

For chaetognaths, the growth rate of this taxon is commonly expressed by increases in body length rather than body mass. The specific growth rates of the chaetognath body length from various locations are summarized in Table 4. In the Oyashio region, the growth rate of the chaetognath E. hamata body length showed seasonal changes and was higher from the spring to the summer, and lower during the winter (Matsumoto, 2008). In the present study, the growth rates of each E. hamata cohort ranged from 39 to 50 μm day⁻¹. These values were higher than those obtained on an annual basis in the Oyashio region (6-20 μm day⁻¹; Nishiuchi, 1999; Matsumoto, 2008), but lower than the values in the eastern subarctic Pacific (83–100 μm day⁻¹; Terazaki and Miller, 1986).

A comparison on growth rates of two sympatric chaetognaths in the present study showed that the growth rate of P. elegans (42–101 μm day⁻¹) was faster than those of E. hamata (39-50 μm day⁻¹). In the eastern subarctic Pacific, the growth rate of mesopelagic E. hamata (83–100 μm day⁻¹) was slower than that of epipelagic P. elegans (167–200 μm day⁻¹) (Table 4).

Because the vertical distribution of E. hamata is deeper than that of P. elegans (Ozawa et al., 2007), the temperature of E. hamata was lower than that of P. elegans. Within chaetognath species (P. elegans), the growth rate increases with increasing habitat temperature (Sameoto, 1971). In addition, the abundance and biomass of mesozooplankton and copepods, the major prey of chaetognaths, are high at the surface layer and exponentially decrease with increasing depth in the Oyashio region (Yamaguchi et al., 2002, 2004b). Based on the habitat temperature and food availability, the growth rates of mesopelagic chaetognaths were slower than those of epipelagic species.

### Table 4. Growth rates in the body length of Eukrohnia hamata and Parasagitta elegans from various oceans.

<table>
<thead>
<tr>
<th>Chaetognath species</th>
<th>Growth rate (μm day⁻¹)</th>
<th>Location</th>
<th>Habitat temperature (°C) and depth</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td>Eukrohnia hamata</td>
<td>6-20</td>
<td>Site H, Western North Pacific</td>
<td>2-17</td>
<td>Nishiuchi, 1999</td>
</tr>
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<td></td>
<td>15</td>
<td>Site H, Western North Pacific</td>
<td>2.3-2.9 (≥250 m)</td>
<td>Matsumoto, 2008</td>
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<tr>
<td></td>
<td>39-50</td>
<td>St. A-5, Western North Pacific</td>
<td>1-6 (0-200 m)</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>83-100</td>
<td>Station P, Eastern North Pacific</td>
<td>3.8-6.0 (100-500 m)</td>
<td>Terazaki and Miller, 1986</td>
</tr>
<tr>
<td>Parasagitta elegans</td>
<td>14-44</td>
<td>High-Arctic fjord, Svalbard</td>
<td>−1.7-4</td>
<td>Grigor et al., 2014</td>
</tr>
<tr>
<td></td>
<td>20-70</td>
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<td>2-17</td>
<td>Nishiuchi, 1999</td>
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<tr>
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<td>Saito and Kiørboe, 2001</td>
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<td>This study</td>
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<td>Choe and Deibel, 2000</td>
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<td>7.8-17.1</td>
<td>Conway and Williams, 1986</td>
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<tr>
<td></td>
<td>150</td>
<td>Oslofjord, southern Norway</td>
<td></td>
<td>Jakobsen, 1971</td>
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<tr>
<td></td>
<td>167-200</td>
<td>Station P, Eastern North Pacific</td>
<td>6.0-13.8 (Surface)</td>
<td>Terazaki and Miller, 1986</td>
</tr>
</tbody>
</table>

### Table 5. Results of one-way ANOVA for the mass-specific growth rate (g) of various zooplankton species (cf. Figs. 18-21) in the Oyashio region during March and April in 2007. For one-way ANOVA, the species were applied as independent variables. df: degree of freedom, SS: sum of squares.

<table>
<thead>
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<th>Parameter</th>
<th>df</th>
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<td>Species</td>
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<tr>
<td>Error</td>
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</table>
6-1-1. Feeding ecology

Within mesopelagic copepods, the gut contents of the suspension feeders, C6F of *G. simplex*, *G. variabilis* and *P. scutullata*, are shown in Table 6. The results of the gut content analyses of suspension feeding copepods, diatoms (mainly *Thalassiosira* spp.), dinoflagellates, cyanophytes, foraminifers, radiolarians and tintinnids are also shown. Similar results for all three species of protozooplankton (foraminifers, radiolarians and tintinnids) were observed on March 8, prior to the spring phytoplankton bloom, but not on April 11.

**Table 6.** Gut contents of mesopelagic suspension feeding copepods (*Gaetanus simplex*, *G. variabilis* and *Pleuromamma scutullata*) in the Oyashio region on March 8, and April 11 and 29, 2007. Gut contents were examined for C6F specimens collected from the most abundant depth layer at night. The numbers of examined specimen are shown in the parentheses. For each cell condition, three categories (intact [100%], fragment [50-100%] and broken [0-50%]) were scored. (R.S.): resting spore.

<table>
<thead>
<tr>
<th>Species / taxa</th>
<th>Gaetanus simplex</th>
<th>Gaetanus variabilis</th>
<th>Pleuromamma scutullata</th>
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<td>Diatoms</td>
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</tr>
<tr>
<td><em>Actinocyclus</em> spp.</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Arpetia tabularis</em></td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Coscinodiscus</em> spp.</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Neodenticula</em> seminae</td>
<td>5</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Odontella aurita</em></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><em>Thalassiosira</em> spp.</td>
<td>15</td>
<td>22</td>
<td>20</td>
</tr>
<tr>
<td><em>Unidentified</em> pennate diatoms</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>Chaetoceros</em> furcellatus (R.S.)</td>
<td>2</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceratium</em> fusus</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Unidentified</em> dinoflagellates</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Dinoflagellate cyst</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Cyanophytes</td>
<td>9</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Foraminifers</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Radiolarians</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Tintinnids</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Intact (100%)</td>
<td>10</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Fragment (50-100%)</td>
<td>6</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Broken (0-50%)</td>
<td>19</td>
<td>10</td>
<td>7</td>
</tr>
</tbody>
</table>

**Table 7.** Gut contents of mesopelagic carnivorous copepods (*Paraeuchaeta elongata* and *Heterorhabdus tanneri*) in the Oyashio region during spring 2007. Note that only amorphous materials for the other species and dates were observed, and these results were not included in this table. For comparison, although prey calanoid copepods observed only as mandible blade (MB), their prosome and total lengths (PL and TL) were calculated using the described equations (Dalpadado et al., 2008 for MB-PL, Yamaguchi unpublished for PL-TL).

<table>
<thead>
<tr>
<th>Species / taxa and stage</th>
<th>Length (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MB</td>
</tr>
<tr>
<td><em>Paraeuchaeta elongata</em> C6F (29 April)</td>
<td></td>
</tr>
<tr>
<td><em>Metridia pacifica</em> C2</td>
<td>48</td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>-</td>
</tr>
<tr>
<td><em>Neocalanus cristatus</em> C1 or <em>N. plumchrus</em> C2</td>
<td>70</td>
</tr>
<tr>
<td><em>Trictonia borealis</em> C6M</td>
<td>-</td>
</tr>
<tr>
<td><em>Heterorhabdus tanneri</em> C6F (29 April)</td>
<td></td>
</tr>
<tr>
<td><em>Metridia pacifica</em> C4</td>
<td>75</td>
</tr>
</tbody>
</table>
during the spring phytoplankton bloom. From all species, the resting spores of *Chaetoceros furcellatus* with intact cell conditions were observed on April 29. The cell conditions of the food items also varied with copepod species. The proportion of intact cells was highest for *P. scutullata* (33-68%), followed by *G. simplex* (29-62%), and the least proportion of intact cells was for *G. variabilis* (17-43%). The proportion of broken (0-50%) cell showed the opposite pattern: the proportion was lowest in *P. scutullata* (13-33%), higher in *G. simplex* (27-54%), and highest in *G. variabilis* (51-80%).

For carnivorous mesopelagic copepods, most of the gut contents were amorphous materials, and species identification from these materials was possible only for *P. elongata* and *H. tanneri* on April 29, 2007 (Table 7). As for the prey items of *P. elongata* C6F, early copepodid stages (C1–C2) of dominant epipelagic copepods (*M. pacifica* and *Neocalanus* spp.), nauplii and poecilostomatoid copepods were also observed. From the gut contents of *H. tanneri* C6F, the mandible blade of *M. pacifica* C4 was observed. Notably, the total length (*TL*) of the prey organisms was smaller in *P. elongata* C6F (118-1,131 µm) than in *H. tanneri* C6F (1,780 µm) (Table 7).

The gut contents of two euphausiid species (*E. pacifica* and *T. inspinata*) on March 9, April 8, and April 29 are shown in Fig. 22. Within the food items, the dominant taxa of *E. pacifica* were diatoms on March 9 and tintinnids on April 8 and 29 (Fig. 22A, B). Numerically, diatoms were dominant in *Chaetoceros* spp. and *Thalassiosira* spp., tintinnids were
dominant in *Psychoclyis obtusa* throughout the study period (Table 8). For *T. inspinata*, diatoms were the dominant food items on March 9 and April 29, while tintinnids were the dominant food on April 8 (Fig. 22C, D). No sexual differences in the food items were detected for both species. As for special characteristics of food items of *T. inspinata*, the proportion of copepods in all food items was high: 13.9% (mature female) and 2.3% (mature male) on March 9.

Because these proportions were based on number, when evaluating the proportions in mass, the importance of crustaceans might be more evident. Copepods (*Metridia* spp., *Neocalanus* spp. and *Oithona* spp.), chaetognaths and euphausiids were observed in the gut contents of *T. inspinata* (Table 8), and *T. inspinata* fed on larger-sized food items compared with those of *E. pacifica*. For the copepod prey of *E. pacifica*, only small-sized *Metridia* spp. and *Oithona* spp. showed...
small compositions.

The gut contents of three chaetognaths (*Eukrohnia hamata*, *Parasagitta elegans* and *Pseudosagitta scrippsae*) in the Oyashio region from March-April in 2007. NPC: number of prey per chaetognath.

<table>
<thead>
<tr>
<th>Food item (%)</th>
<th>E. hamata</th>
<th>P. elegans</th>
<th>P. scrippsae</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Copepods</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucalanus bungii -</td>
<td>12.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Eucalanus bungii C2 -</td>
<td>-</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Eucalanus bungii C3 -</td>
<td>-</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Eucalanus bungii C5F -</td>
<td>1.1</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>Eucalanus bungii C6F -</td>
<td>10.2</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Neocalanus cristatus -</td>
<td>1.1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Neocalanus cristatus C4 -</td>
<td>2.3</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Neocalanus sp. -</td>
<td>1.1</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Metridia pacifica -</td>
<td>-</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Metridia pacifica C5F -</td>
<td>-</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Metridia pacifica C6F -</td>
<td>-</td>
<td>12.5</td>
<td></td>
</tr>
<tr>
<td>Pleuronema scutellata C6F -</td>
<td>-</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Pseudocalanus sp. -</td>
<td>-</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Unidentified copepods</td>
<td>26.7</td>
<td>50.0</td>
<td>16.7</td>
</tr>
<tr>
<td><strong>Chaetognaths</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eukrohnia coppepods</td>
<td>6.7</td>
<td>-</td>
<td>8.3</td>
</tr>
<tr>
<td>Parasagitta elegans</td>
<td>-</td>
<td>-</td>
<td>4.2</td>
</tr>
<tr>
<td>Appendicularians</td>
<td>6.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Unidentified organisms</td>
<td>60.0</td>
<td>21.6</td>
<td>31.3</td>
</tr>
<tr>
<td>Number of individual food containing (n)</td>
<td>1,938</td>
<td>1,301</td>
<td>143</td>
</tr>
<tr>
<td>Number of total individual examined (n)</td>
<td>0.008</td>
<td>0.068</td>
<td>0.336</td>
</tr>
</tbody>
</table>

**6-1-2. Biomass and production**

The monthly mean biomass of epipelagic copepods and macrozooplankton species in March (prior to the spring phytoplankton bloom) and April (phytoplankton bloom period) are shown in Fig. 23. The biomass of whole zooplankton community was 2,692 mg C m⁻² in March. Within the species examined in the present study, the highest biomass (1,131 mg C m⁻²) was recorded for *M. pacifica* in March, corresponding to 46% of all net zooplankton biomass (Fig. 23). Following *M. pacifica*, *N. cristatus* and *E. bungii* were also abundant, accounting for 354 mg C m⁻² (12%) and 312 mg C m⁻² (11%), respectively in March. However, the composition of mesopelagic copepods and macrozooplankton in the total zooplankton biomass was low in March.

In April, the total zooplankton biomass slightly increased to 3,807 mg C m⁻², which was 30% higher than in March (Fig. 23). The dominant species in April greatly varied with those in March. The biomass of *M. pacifica* decreased to 337 mg C m⁻² (one-fourth of that in March), and the biomass of epipelagic copepod *N. cristatus*, mesopelagic copepods *P. elongata* and *P. birostrata* and macrozooplanktonic euphausiid *E. pacifica* and *T. inspinata* and chaetognath *P. elegans* increased. Among these species, the biomass of *E. pacifica* was 896 mg C m⁻² (= 4.6 times higher than in March), composing the highest proportion (24%) of the total zooplankton biomass in April (Fig. 23).

Production showed a similar species-composition pattern...
with that in biomass, but compositions of carnivores were less (Fig. 24). The total zooplankton production was 42.3 mg C m$^{-2}$ day$^{-1}$ in March, comprising 48% (20.5 mg C m$^{-2}$ day$^{-1}$) M. pacifica. Following M. pacifica, N. cristatus and E. bungii produced 5.1 and 4.5 mg C m$^{-2}$ day$^{-1}$, respectively, accounting for 12.0% and 10.6% of the total production, respectively. The total zooplankton production in April was 43.3 mg C m$^{-2}$ day$^{-1}$, with similar values in March. In addition, the species composition significantly varied, and the composition of M. pacifica decreased 12.3% in April. However, the compositions of the two dominant euphausiids increased, accounting for 25.0% of the total zooplankton production for E. pacifica and 10.3% for T. inspinata.

6-2. Discussion

6-2-1. Feeding ecology

Concerning the feeding ecology of mesopelagic suspension feeding copepods, the protozooplankton in the gut contents in March might reflect the relatively small sinking flux of phytoplankton to deeper layers before the initiation of the spring phytoplankton bloom. However, the occurrence of resting diatom spores on April 29 might reflect changes in food items, which respond quickly to the changes in sinking particles from the surface layer. The species-specific differences in cell conditions regarding food items might reflect the species-specific vertical distribution of each species. Thus, the distribution depths were in the order of P. scutullata < G. simplex < G. variabilis (Abe et al., 2012), consistent with the proportion of intact cells detected in their guts, i.e., highest for shallower living P. scutullata (33–68%), followed by the intermediate–depth inhabiting G. simplex (29–62%) and smallest for the deep inhabiting G. variabilis (17–43%) (Table 6). The results of the gut content analysis revealed that the taxonomic accounts of food items were similar for mesopelagic suspension feeding copepods; however, increases in the proportion of broken cells with increasing depths might reflect the coprophagy and repacking of suspension feeding copepods in overlaying layers (Sasaki et al., 1988; Yamaguchi et al., 2002).

For mesopelagic suspension feeding copepods, the food
requirements were estimated from empirical metabolic models calculated based on habitat temperature and body mass (for detailed method, see Yamaguchi et al., 2010b). Thus, the estimated ingestion rate of mesopelagic suspension feeding copepods (20.6 mg C m\(^{-2}\) day\(^{-1}\)) was lower than the carbon mass flux at a depth of 500 m (approximately 100 mg C m\(^{-2}\) day\(^{-1}\) estimated from primary production), accounting for approximately 20% of the available particle carbon mass flux per depth (Abe et al., 2012). These findings suggest that mesopelagic suspension feeding copepods could obtain a sufficient amount of food at 500 m in April without any DVM. Thus, the ceased DVM observed for mesopelagic suspension feeding copepods after mid-April (Fig. 17A) might reflect increasing food availability at lower depths, resulting from the initiation of the spring phytoplankton bloom in early April (Fig. 6A).

For carnivorous copepods, the size of the prey animal is associated with the body size of the predator. According to Hansen et al. (1994), the mean ratio in body size between predator: prey is 18:1, ranging from 10:1 to 30:1. Based on these ratios, the sizes of the prey items of C6F of *P. elongata* (*PL*: 4.95 mm, Yamaguchi and Ikeda, 2002b) and *H. tanneri* (*PL*: 2.92 mm, Yamaguchi and Ikeda, 2000b) were 165-495 and 97-292 µm, respectively. These values roughly correspond to the observed values for *P. elongata* (118-1,176 µm), while the food item size of *H. tanneri* (1,780 µm) is 6-19 times (=1,780 / 92 or 1,780 / 292) larger than the predicted prey animal sizes (Table 7). The anomalous large food item of *H. tanneri* might be associated with its specialized feeding mode (injecting venom or anaesthetic into the prey) (Nishida and Ohtsuka, 1996). The mandible blade of *Heterorhabdus* spp. has evolved to inject venom or anaesthetic into prey (Nishida and Ohtsuka, 1996); thus, the feeding mode and prey animals of Heterorhabdidae were significantly different from those of Euchaetidae. The inter-moult growth of *Heterorhabdus* spp. is higher than 900% in body mass (Yamaguchi and Ikeda, 2000b). However, the inter-moult growth of sympatric carnivorous Euchaetidae is approximately 400% in

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Fig. 24. Monthly mean production of various meso- / macrozooplankton species in the Oyashio region during March (before bloom) and April (after bloom) 2007. The sizes of the circles are the mean production (mg C m\(^{-2}\) day\(^{-1}\)) of each species in each month. Grey and black circles indicate suspension feeders (grey) or carnivores (black), respectively. Species were arranged in the order of the mean individual biomass (cf. Figs. 18-21) within the each functional group (epipelagic, mesopelagic copepods and macrozooplankton). Note that the quantified depth ranges varied with groups.

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Abe: Zooplankton Community in the Oyashio Region

Based on the results of the gut content analyses, euphausiids were also found to feed on various zooplankton taxa, even during the spring phytoplankton boom (Table 8). For food items of *E. pacifica* from Sanriku, Nakagawa et al. (2001, 2002) reported that diatoms were dominant, while heterotrophs, particularly copepods, were important regarding carbon mass. In the present study, the compositions of the copepods in food items were low (0–1.0% for *E. pacifica*, 0–15.5% for *T. inspinata*, Table 8, Fig. 22); however, based on mass, the compositions increased, reflecting the large body size of copepods. The intensity of the carnivores varied with species and occurrence of large-sized zooplankton in the gut of *T. inspinata* (Table 8, Fig. 22). These results might reflect the larger body sizes of *T. inspinata* compared with those of *E. pacifica* (Fig. 20) and their predatory morphology, that is, the second thoracic legs of *T. inspinata* were extremely elongated and developed. Because the major food items of *T.
**inspinata** showed increased temporal changes (Fig. 22), they may have flexibility in feeding, that is, they may feed on large-sized crustaceans, such as copepods, before the bloom and shift to numerous diatoms and tintinnids after the bloom.

For chaetognaths, the mean NPC (no. prey ind.−1) was highest for *P. scrippsae* (0.336), followed by *P. elegans* (0.068) and *E. hamata* (0.008) (Table 9). Because these NPC values reflect species differences in BL, to obtain accurate species comparisons, standardization of NPC values based on BL is needed. Comparison of the NPC, standardized using a 10-mm BL interval, showed that the NPC increased with increasing BL, except for the 30-40 mm BL of *P. elegans* (Fig. 25A). Highly significant correlations were observed between the BL and head width (*HW*) for all chaetognath species (*p < 0.05*, Fig. 25B). These findings suggest that wider body-sized organisms are available as food for larger BL chaetognath specimens. Increases in the composition of large-sized food items with increasing BL have been reported for *P. elegans* in the Gulf of Alaska and North Sea (Brodeur and Terazaki, 1999; Saito and Kiorboe, 2001). The highest NPC of *P. scrippsae* observed in the present study (Table 9) might be associated with the largest BL of this species. The large BL of *P. scrippsae* might have enabled the ingestion of a wide-size range of prey during the study period. Notably, the gut passage-time of the large BL *P. scrippsae* was longer than that for other species and thus might increase the NPC of this species.

As remarkable characteristics of food items, the most important food organisms (25.1%) of *P. scrippsae* were the copepods *Metridia* spp. (Table 9). However, for the sympatric chaetognath species, no *M. pacifica* was observed in the food items of the smaller body-sized *E. hamata* (BL: 5.8 - 23.7 mm) and *P. elegans* (11.0 - 41.3 mm) (Table 9). The swimming behaviour of *Metridia* spp. is continuously cruising, and its swimming speed is 2.3-5.4 mm sec−1 (Wong, 1988). *Metridia* spp. performs strong DVM (Takahashi et al., 2009; Yamaguchi et al., 2010b), and the speed of the DVM behaviour is 6.4-9.2 mm sec−1 (Hattori, 1989). While the swimming speed is faster for *Metridia* spp., the large body sized of *P. scrippsae* (BL: 12.0 - 55.0 mm) might enable feeding on *Metridia* spp.

### 6-2-2. Biomass and Production

For the biomass composition of species, the highest biomass was observed for the small-sized copepod of *M. pacifica* in March (46%, Fig. 23). These findings suggest that the abundance of *M. pacifica* was extremely high (Fig. 9B) prior to the initiation of the spring phytoplankton bloom in the Oyashio region. The composition of C6F was high for *M. pacifica* in March (Fig. 9B), and the dominance of large-sized C6F in the population might also reflect the high biomass observed in March. In April, the abundance of *M. pacifica* remained at the same level as that in March and the population primarily comprised small-sized early copepodid stages (Fig. 9B); thus, the overall biomass decreased in April (Fig. 23).

Most species, that showed increased biomass from March to April (i.e., the epipelagic copepod *N. cristata*, mesopelagic copepods *P. elongata* and *P. birostrata*, euphausiids *E. pacifica* and *T. inspinata* and chaetognath *P. elegans*), exhibited significant growth during the OECOS period (Figs. 18-21), suggesting that the increases in biomass might reflect increases in growth, but not increases in reproductive activities.

Notably, increases in the zooplankton biomass from March to April in the Oyashio region were not explained only by internal growth. Particularly in April, various macrozooplankton species had high abundance and biomass (Figs. 11-14). These results reflected the dominance of each species in COW, which was not observed in March (Table 3). Thus, the total zooplankton biomass in the Oyashio region was similar between March and April, while the species composition significantly varied, i.e., the copepod *M. pacifica* was dominant in March and the euphausiid *E. pacifica* was dominant in April (Fig. 23). Because ecological information on euphausiids is limited and there is even less information for copepods, additional information is required for future studies.

Production estimation in the present study was achieved using physiological metabolic methods based on empirical models (Ikeda and Motoda, 1978). The metabolic rates were estimated according to Ikeda (2014), applying four independent variables (body mass, temperature, distribution depth and taxa), while previous formulae applied only two independent variables (only body mass and temperature) (Ikeda, 1985; Ikeda et al., 2001). Although applying four independent variables in the new calculation resulted in a high biomass for mesopelagic copepods in April (Fig. 23), production in this species was estimated to be lower, reflecting deeper distribution depths (Fig. 24). For chaetognaths, although a high biomass was recorded in April (Fig. 23), lower production might reflect an independent variable (taxa) (Fig. 24). Thus, the estimation of a more accurate metabolic rate on zooplankton might be achieved using a Global-Bathymetric Model (Ikeda, 2014), adding two independent variables (depth and taxa) to the formula. For parameters governing zooplankton production, the estimation methods for metabolic rates have advanced over the past four decades. To estimate the feeding rates (food requirements) from the metabolic rates, two parameters, gross growth efficiency (*K^m_/, production / feeding*) and assimilation efficiency (*A^m_/, assimilation / feeding*), are needed. While the estimation of both parameters by laboratory experiments is difficult, the assimilation efficiency could be estimated using the ratio method (Conover, 1966a, 1966b) based on measurements of the organic matter contents in food and faecal pellets. In the Oyashio region, the assimilation efficiency
of the two dominant copepods (Neocalanus spp. and E. bungii) ranged from 34 to 66%, with phytoplankton as food and showed a significantly negative relationship with the ash content of the phytoplankton ($r^2 = 0.79 - 0.87$, $p < 0.001$, Abe et al., 2013). Because the phytoplankton species composition temporally varied during the spring phytoplankton bloom (Fig. 6B), a changing effect on the assimilation efficiency might have occurred during the OECOS period. In future studies, the development of a convenient method for the estimation of the gross growth efficiency ($K_1$) is also needed to accurately estimate zooplankton production.

### 7. Synthesis

In this chapter, the responses of each zooplankton species on the spring phytoplankton bloom in the Oyashio region are described. For epipelagic copepods for which data sets are available for other oceanic locations (North Atlantic and North Pacific), the responses to phytoplankton blooms are compared between locations. Moreover, I further discuss the issues highlighted and remaining points in the present study and propose directions for future studies.

#### 7-1. Responses of zooplankton on a phytoplankton bloom during OECOS period

Temporal changes in chl $a$ and microzooplankton biomass and the responses of each zooplankton species during the OECOS period are summarized in Fig. 26.

Concerning hydrography, three water masses (COW, MKW and OYW) were exchanged in the short-term during the spring phytoplankton bloom. Because of the intrusions of COW, sufficient nutrients originated from the Sea of Okhotsk, and phytoplankton peaked on April 7-8 and 23. Microzooplankton showed peaks one day after chl $a$ peaks, and the biomasses paralleled the temporal changes in chl $a$ (Fig. 26).

For the zooplankton population structure, the development of the copepod *N. cristatus* from C1 to C4 and the growth of two euphausiids (*E. pacifica* and *T. inspinata*) and two chaetognaths (*E. hamata* and *P. elegans*) are shown (Figs. 18-21). The mass-specific growth rate ($g$) showed no significant differences between species (Table 5). These results suggest that there were no food limitations for various feeding modes of zooplankton during the spring phytoplankton bloom period.

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**Fig. 26.** Schematic diagram showing ecological responses (population structure, vertical distribution, reproduction, feeding and community structure) of meso- / macrozooplankton in the Oyashio region during the spring phytoplankton bloom of 2007.
From the vertical distribution of copepods, temporal changes in the vertical distribution were observed for *E. bungii*, *M. pacifica* and *P. scutulata* (Figs. 15, 17). For *E. bungii*, upward migration through activation from resting depths was observed on April 5. Ceased DVM was observed for *M. pacifica* and *P. scutulata* after phytoplankton bloom. *P. scutulata* ceased DVM before *M. pacifica* did, and the epipelagic *M. pacifica* C6F continued DVM. The continuous DVM of *M. pacifica* C6F might reflect reproduction at the surface layer. The mesopelagic carnivorous copepod *P. elongata* performed DVM throughout the study period.

For the reproduction of zooplankton, arousal from diapause was observed for *E. bungii* on April 5, and reproduction was initiated with the phytoplankton bloom peak (April 7-8), and subsequently, the newly recruited population peaked on April 12 (Fig. 9A). For various mesopelagic copepods, the composition of spermatophore-attached C6F increased in April and reproduction likely started in April (Abe et al., 2012). Because the highest composition of mature females with attached-spermatophores was observed in the *T. inspinata* population (more than 40% of the population), their reproduction might have occurred during the study period (Fig. 11B). For amphipods, the occurrence of egg-carrying females might reflect reproduction of *C. challengeri* and *T. pacifica* in April.

Concerning the feeding ecology, mesopelagic suspension feeding copepods fed on protozooplankton species prior to the phytoplankton bloom and on diatom resting spores after the bloom. Based on the cell condition, repacking and coprophagy were observed (Table 6). Species-specific differences in feeding modes were recognized for carnivorous copepods, euphausiids and chaetognaths during the study period (Tables 6-9).

For the total zooplankton biomass, the small-sized copepod *M. pacifica* dominated in March (Fig. 23). Both the biomass and production values in April were similar to those in March, while the species composition significantly varied; the composition of *M. pacifica* decreased, and a high composition of the macrozooplanktonic euphausiid *E. pacifica* was observed in April.

### 7-2. Comparison with other locations

High-frequency samplings of zooplankton during the spring phytoplankton bloom were conducted in the North Atlantic Norwegian Sea (St. M) and the North Pacific (SEEDI, SEEDII, SERIES), and comparative population data on copepods were available for each location (Fig. 1A).

The feeding, growth and reproduction of the dominant copepod *Calanus finmarchicus* have been reported based on high-frequency samplings (continued for approximately 80 days) from March 23 to June 9, 1997, in the Norwegian Sea (Irigoin et al., 1998; Meyer-Harms et al., 1999; Niehoff et al., 1999; Hirche et al., 2001; Olmnan and Hirche, 2001). A significant difference in the ecology between *C. finmarchicus* in the North Atlantic and *Neocalanus* spp. in the North Pacific shows that the former reproduces at the surface layer during the phytoplankton bloom (Fig. 1C). Temporal changes in the abundance, population structure and individual mass at each location are shown in Fig. 27.

The abundance of *C. finmarchicus* in the Norwegian Sea was approximately 10 times higher than that of two dominant copepods (*E. bungii* and *N. cristatus*) in the Oyashio region (Fig. 27A), partly reflecting the quantitative abundance of *C. finmarchicus*, based not only on copepodid stages but also on eggs and nauplii (Niehoff et al., 1999; Hirche et al., 2001). However, a high abundance of *C. finmarchicus* was also observed during the late post bloom period when copepodid stages dominated; thus, the differences in copepod abundances might reflect inter-oceanic differences. Differences in copepod body size (smaller for *C. finmarchicus* in the North Atlantic) might reflect inter-oceanic differences in quantitative abundance.

The population structure of *C. finmarchicus* was dominated by eggs, nauplii and adults before the bloom, but the composition of these components gradually decreased after the bloom and the composition of the copepodid stages increased (Fig. 27B). Based on population structure data, the MCS of *C. finmarchicus* was also calculated, and minimum MCS values were observed on May 5. Thus, the significant recruitment of a new generation likely occurred on May 5, and their populations were divided into two cohorts: the N1-C3 cohort prior to May 5 and the C1-C5 cohort after May 5. The MCS of each cohort was calculated, and the individual mass was also calculated from the MCS using the formula:

$$ Y = 0.0463 \times e^{0.794X} $$

where $X$ indicates the developmental stage from N1 as 1, and $Y$ is the individual mass (µg C ind.$^{-1}$). This formula was developed based on individual carbon mass data on *C. finmarchicus* according to Hirche et al. (2001). Significant positive increases were observed for *C. finmarchicus*. Within the species, the slope (growth rates) of the early copepodid stages that develop during the phytoplankton bloom was higher than that for the later copepodid stage (Fig. 27C).

Temporal changes in the abundance, population structure and individual carbon mass of *E. bungii* and *N. cristatus* during the OECOS and three iron-fertilization experiments in the subarctic Pacific (SEEDS I, SEEDS II, SERIES) are shown in Fig. 28. For the temporal changes of individual carbon mass are shown in Fig. 28E, and the $X$-axis (date) shows the peak of bloom (chl $a$) as occurring on the same Julian day. The highest chl $a$ content was observed in SEEDS I (~18.0 mg m$^{-3}$), and moderate values were observed in the OECOS (0.2-7.3 mg m$^{-3}$) and SERIES (1.4-6.0 mg m$^{-3}$), while the lowest value was observed in SEEDS II (0.8-2.5 mg m$^{-3}$). The results of iron-fertilization experiments showed high abundances of copepods during SEEDS II (biomass was
approximately 3–5 times higher than those of SEEDS I) (Tsuda et al., 2009). Compared with the results of these oceanic iron fertilization experiments, the copepod abundance in the Oyashio region during the OECOS was substantially high. Thus, the abundance of *E. bungii* and *N. cristatus* during the OECOS was approximately 2–4 times higher than that recorded in the three iron-fertilization projects (Fig. 28A).

The mass-specific growth rate (\( g \)) of epipelagic copepods, evaluated using high-frequency samplings, is summarized in Table 10. For *E. bungii*, newly recruited C1 stage individuals were observed for studies in the western subarctic Pacific (OECOS, SEEDS I and SEEDS II). For SERIES in the eastern subarctic Pacific, the composition of *E. bungii* C1–C3 decreased and that of C5 increased after phytoplankton bloom (Fig. 28D). For several locations, growth of C1–C2 stages (OECOS) or C1–C3 stages (SEEDS II) was observed (Fig. 28E), and the mass-specific growth rates (\( g \)) were higher for newly recruited younger generations (Table 10).
For *N. cristatus*, significant increases in MCS were observed for all locations, except SEEDS II, and a significant increase in individual carbon mass was observed for the OECOS period (Fig. 28E). Concerning the $g$ of the *N. cristatus* C1-C5 cohort, the lowest value was observed for OECOS (0.064±0.179 day$^{-1}$), followed by SERIES (0.080±0.275 day$^{-1}$), and the highest value was observed for SEEDS I (0.116±0.172 day$^{-1}$), characterized by high chl $a$ values (Table 10).

The $g$ values of epipelagic copepods during the spring phytoplankton bloom varied from 0.002 (*N. cristatus* in SEEDS II, Tsuda et al., 2009) to 0.210 (*C. finmarchicus* egg-C3 natural cohort at St. M, Niehoff et al., 1999) (Table 10). Within the four species examined, *C. finmarchicus* and *E. bungii* showed arousal from diapause, migration to the surface layer and reproduction at the surface layer. Because of these life
cycle patterns, the growth and maturation of adult cohorts and growth of newly recruited cohorts can be traced within the same time frame (Fig. 27C). Common for both species, the growth and maturation of adult cohorts and newly recruited cohorts were consistent with the cycle patterns according to laboratory experiments (Liu and Hopcroft, 2006). Within the chl a, the growth and maturation of adult cohorts and newly recruited cohorts were higher than that of the adult cohorts (Table 10). Within the copepods, E. bungii showed ceased DVM during the spring phytoplankton bloom period (Fig. 26). The ceased DVM reflected the effect of the spring phytoplankton bloom on the mesopelagic ecosystem.

As a feature of the present study, the responses to the spring phytoplankton bloom and water mass exchanges of various macrozooplankton species were evaluated. Particularly, the macrozooplanktonic euphausiid E. pacifica was shown to be the most dominant zooplankton species in biomass and production in April (Figs. 23, 24). Previously, zooplankton studies in the Oyashio region primarily focused on mesozooplankton, such as copepods, which are relatively easy to collect (Ikeda et al., 2008). Because the present study revealed the importance of macrozooplankton or micronekton, samplings using large-mouth devices, such as Bongo nets, MOCNESS and MOHT, are required in future studies.

As a future direction, the development of methods to accurately measure the gross growth efficiency (\( K_\gamma \)) of zooplankton is important. The lack of available \( K_\gamma \) data hinders the accurate estimation of zooplankton production using physiological methods. As a solution for these issues, the RNA:

### Table 10. Comparison of the mean mass-specific growth rate (\( \gamma \)) of dominant copepods: (Calanus finmarchicus in the North Atlantic, Eucalanus bungii, Neocalanus cristatus and N. plumchrus in the North Pacific) during the phytoplankton bloom.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cohort stage</th>
<th>Mass-specific growth rate (( \gamma ))</th>
<th>Method</th>
<th>Study period</th>
<th>Location</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calanus finmarchicus</td>
<td>C1-C5</td>
<td>0.044±0.253</td>
<td>Natural cohort</td>
<td>May-June</td>
<td>Norwegian Sea, St. M</td>
<td>Niehoff et al., 1999</td>
</tr>
<tr>
<td></td>
<td>C1-C5</td>
<td>0.210±1.058</td>
<td>Natural cohort</td>
<td>May-June</td>
<td>Norwegian Sea, St. M</td>
<td>Niehoff et al., 1999</td>
</tr>
<tr>
<td>Eucalanus bungii</td>
<td>C4-C6</td>
<td>0.013±0.059</td>
<td>Natural cohort</td>
<td>July</td>
<td>western subarctic Pacific, SEEDSII</td>
<td>Tsuda et al., 2005</td>
</tr>
<tr>
<td></td>
<td>C3-C5</td>
<td>0.020±0.041</td>
<td>Natural cohort</td>
<td>July-Aug.</td>
<td>western subarctic Pacific, SEEDSII</td>
<td>Tsuda et al., 2009</td>
</tr>
<tr>
<td></td>
<td>C3-C5</td>
<td>0.029±0.074</td>
<td>Natural cohort</td>
<td>Mar.-Apr.</td>
<td>Oyashio region, OECOS</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>C4</td>
<td>0.04</td>
<td>Incubation</td>
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<td>Kobari et al., 2010c</td>
</tr>
<tr>
<td></td>
<td>C4</td>
<td>0.041±0.137</td>
<td>Natural cohort</td>
<td>July-Aug.</td>
<td>western subarctic Pacific, SEEDSII</td>
<td>Tsuda et al., 2009</td>
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<tr>
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<td>C1-C2</td>
<td>0.061±0.440</td>
<td>Natural cohort</td>
<td>Mar.-Apr.</td>
<td>Oyashio region, OECOS</td>
<td>This study</td>
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<td></td>
<td>C1-C6</td>
<td>0.072±0.081</td>
<td>Natural cohort</td>
<td>July-Aug.</td>
<td>eastern subarctic Pacific, SERIES</td>
<td>Tsuda et al., 2006</td>
</tr>
<tr>
<td>Neocalanus cristatus</td>
<td>C1-C5</td>
<td>0.002±0.292</td>
<td>Natural cohort</td>
<td>July-Aug.</td>
<td>western subarctic Pacific, SEEDSII</td>
<td>Tsuda et al., 2009</td>
</tr>
<tr>
<td></td>
<td>C5</td>
<td>0.05</td>
<td>Natural cohort</td>
<td>Mar.-June</td>
<td>Bering Sea shelf</td>
<td>Vidal and Smith, 1986</td>
</tr>
<tr>
<td></td>
<td>C3</td>
<td>0.06</td>
<td>Incubation</td>
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<td></td>
<td>C4</td>
<td>0.07</td>
<td>Natural cohort</td>
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<td></td>
<td>C2</td>
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<tr>
<td></td>
<td>C1-C5</td>
<td>0.080±0.275</td>
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<td>July</td>
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<td>Tsuda et al., 2006</td>
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<tr>
<td></td>
<td>C1-C5</td>
<td>0.116±0.172</td>
<td>Natural cohort</td>
<td>July</td>
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<td>Tsuda et al., 2005</td>
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<td>Neocalanus plumchrus</td>
<td>C4</td>
<td>0.02</td>
<td>Incubation</td>
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<td>0.039±0.492</td>
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<td>Mar.-Apr.</td>
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<td>This study</td>
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<td>C5</td>
<td>0.04</td>
<td>Natural cohort</td>
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<td></td>
<td>C4</td>
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<td></td>
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<td>Mar.-May</td>
<td>Gulf of Alaska</td>
<td>Liu and Hopcroft, 2006a</td>
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<td>0.11</td>
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<td>C1</td>
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<td>Incubation</td>
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<td>Liu and Hopcroft, 2006a</td>
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<td>Natural cohort</td>
<td>Mar.-June</td>
<td>Bering Sea shelf</td>
<td>Vidal and Smith, 1986</td>
</tr>
</tbody>
</table>
DNA ratio, amount of hormones and enzyme activities were measured, but the precision of these measurements was relatively low; thus, these issues are still problematic (Runge and Roff, 2000).

From high-frequency samplings, such as those obtained in the present study, temporal resolution was improved. However, the analytical levels of spatial- and vertical-resolutions remain low. In the OECOS, large temporal changes in the vertical distribution of epi- and mesopelagic copepods were evaluated using high-frequency samplings by VMPS. Notably, the minimum sampling depth interval of VMPS was 25 m in the present study. Because there is such a low vertical resolution, the problem of a low spatial and vertical resolution remains when attempting to obtain adequate comparisons with high-resolution CTD data commonly collected at an interval of 1 m.

To obtain high spatial-resolution zooplankton data, traditional plankton net towing can be used. Indeed, VPR (Video Plankton Recorder) or UVP (Underwater Video Profiler), which obtain zooplankton visual data with fine spatial and vertical resolutions, is a solution to this problem. Because VPR could obtain zooplankton data with no physical damage, small-scale distributions of various doliolid generations have been reported in the Oyashio-Kuroshio frontal region (Takahashi et al., 2013, 2015) and the ecology of small plociostomatoid copepods (Oncaea spp.) attached on appendicularian houses (Nishibie et al., 2015).

In a Norwegian fjord and the Greenland Sea, zooplankton responses to the spring phytoplankton bloom have been evaluated by VPR (Norrbin et al., 2009; Sainmont et al., 2014). Because large body-sized copepods, such as Neocalanus spp. and E. bungii, were dominant in the Oyashio region, VPR analysis might be suitable for zooplankton studies in this region. From VPR samplings, we obtained temperature and depth data as well as zooplankton individual size data (= biomass) within the same time frame. These findings suggest that we could obtain all four of the independent variables (body mass, temperature, distribution depth and taxa) required for calculating the metabolic rate using the Global Bathymetric Model (Ikeda, 2014) within one VPR cast.

Combining image analysis methods, such as VPR, with physiological production estimation methods (Ikeda and Motoda, 1978; Ikeda, 2014) will enable the accurate estimation and mapping of zooplankton secondary production. From such analyses, zooplankton production estimations are possible at high resolution (e.g., 1 m interval), such as physical oceanographic CTD data. Today, nearly 150 years have passed since the German scientist Dr. Victor Hensen (Taniguchi, 1994) initiated modern plankton studies (ca. 1870). However, the method for plankton net sampling and the microscopic analysis of the net samples have changed little from that time. From a historical perspective, we are in a transitional period of zooplankton quantification methods from the use of plankton net samplings to visual analysing methods that cause no physical damage to zooplankton with high spatial and vertical resolutions. Thus, high-frequency samplings using imaging instruments, such as VPR or UVP, might provide spatial and temporal high-resolution zooplankton data as well as provide new insights into the zooplankton realm in future studies.

### 8. Summary

In marine ecosystems, zooplankton play an important role in the transfer production of both the grazing food chain and microbial food web for higher trophic revels. In addition to a food mediators role, zooplankton accelerate the vertical material flux, termed the “Biological pump”. In the Oyashio region, western subarctic Pacific, nearly half of the annual primary production occurs from April to May. During this same period, zooplankton grow faster. However, it is difficult to generate an accurate evaluation of zooplankton growth rates using the ordinary sampling interval (once per month) from previous studies. For an accurate evaluation of the growth rates of zooplankton, high frequency time-series samplings during the spring phytoplankton bloom are needed. The OECOS is an international research programme for the evaluation of zooplankton responses to the spring phytoplankton bloom using high-frequency time-series samplings.

During the OECOS period, high frequency oceanographic observations, including CTD casts (approximately every day), water samplings and various net samplings, were conducted at St. A–5 in the Oyashio region from March 8 to May 1, 2007. In the present study, short-term changes in phytoplankton, protozooplankton and meso- and macrozooplankton abundance, biomass, population structure, vertical distribution, growth rates and feeding ecology were studied during the OECOS period. Based on these phenological descriptions, the present study aimed to evaluate the lower trophic levels during the spring phytoplankton bloom in the Oyashio region. For comparison, copepod data collected from other high-frequency time-series samplings during the phytoplankton bloom (SEEDS I, SEEDS II, SERIES and St. M) were gathered and compared with those of the OECOS. A thorough comparison of the five time-series data and characteristics of zooplankton responses to the phytoplankton bloom were conducted.

Throughout the OECOS period, three dominant water masses (COW, MKW and OYW) occurred at the surface layer (0–50 m) over a short period of time. Because the COW contains sufficient nutrients originating from the Sea of Okhotsk, phytoplankton peaks were observed at the COW on April 7–8 and 23. The composition of diatoms was more than 74% of the chl a content during April, and centric diatoms predominated throughout the study period. The domi-
significant differences between species. These findings sug-

mestic copepods, increases in the composition of sper-

the arousal from diapause and upward migration to the sur-

was low in March, but increased after April 8.

For the zooplankton population structure, the copepod N.

For the reproduction of zooplankton, reproduction of the

epelagic copepod E. bungii was initiated in response to the

phytoplankton bloom peak on April 7–8, and newly recruited

early copepodid stages were observed on April 12. For

mesopelagic copepods, increases in the composition of sper-

matophore-attached C6F in April suggested the initiation of

reproduction. Throughout the study period, most adult

females of T. inspinata had spermatophores, and the high pro-

portion of attached-spermatophore females to the total popu-

lation (>40%) suggested that spawning had occurred. For

amphipods, the reproduction of C. challengeri and T. pacifica

was initiated in April.

In response to water masses, various species showed high

abundance and biomass under COW-dominated conditions

and low abundance and biomass under OYW-dominated

conditions. Few species showed any correlations with

MKW. Zooplanktonic responses to high abundance under

COW and low abundance under OYW might reflect the dif-

ferent characteristics of each water mass. The results of

FRA-ROCS analyses revealed that the temperature of OYW

was lowest and induced low zooplankton growth rates.

However, the geographical origin of COW is the Sea of

Okhotsk, a marginal sea with high primary productivity, pro-

duce dinoflagellates dominated in the microzooplankton com-

munity. The mesozooplankton wet mass at 0–150 m ranged

approximately 5 times higher than that of the adult cohort.

The highest g of N. cristatus was observed for SEEDS I, char-

acterized by the highest chl a, suggesting that the g values

increased with increasing chl a within the observed chl a range (~18 mg m⁻³).

As a feature of the present study, the response to the spring

phytoplankton bloom and water masses on macrozooplank-

ton, with limited ecological information taxa, was evaluated.

Particularly, the euphausiid E. pacifica was the most dominant

zooplankton species in biomass and production after the

spring phytoplankton bloom. Previous zooplankton studies

in the Oyashio region primarily focused on mesozooplankton,
such as copepods. However, because of their importance,
studies on macrozooplankton and micronekton are needed in
the future. From high-frequency time-series sampling, such as
the OECOS project, the time-resolution analysis was signif-
iciently improved, but the problems of low analytical levels
of spatial- and vertical-resolution remain. Thus, the applica-
tion of visual imaging instruments, such as VPR (Video
Plankton Recorder) and UVP (Underwater Video Profiler),
which collect zooplankton data continuously, has been sug-
gested as a solution for increasing the spatial- and vertical
resolution of zooplankton data analysis in future studies.
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10. References


