Short-term changes in population structure and vertical distribution of mesopelagic copepods during the spring phytoplankton bloom in the Oyashio region

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ABSTRACT

To evaluate the responses to the spring phytoplankton bloom, short-term changes in population structure and vertical distribution of mesopelagic copepods (*Gaetanus simplex*, *Gaidius variabilis*, *Pleuromamma scutullata*, *Paraeuchaeta elongata*, *P. birostrata*, *Heterorhabdus tanneri* and *Heterostylites major*) were studied in the Oyashio region. Samples were collected with a 60 μm mesh VMPS from 9 strata between 0 and 1000 m both day and night on five occasions during March–April 2007. All the species except Heterorhabdidae species performed reproduction during the spring phytoplankton bloom, while no recruitment to copepodid stages was detected because the newly born individuals were eggs or nauplii. The shallower-living species, *G. simplex*, *P. scutullata* and *P. elongata* had nocturnal ascent diel vertical migration (DVM). While suspension feeding copepods cease DVM after 11 April (*P. scutullata*) or 23 April (*G. simplex*), carnivorous *P. elongata* continued DVM over the study period. Since the gut contents of *G. simplex* showed a nocturnal increment even in the period of no DVM (23 and 29 April), they might be feeding at depth without DVM. Thus, the cessation of DVM in mesopelagic suspension feeding copepods would be induced by the increase of sinking particles (e.g. food for suspension feeders) during the spring phytoplankton bloom.

1. Introduction

Copepods are the most dominant component in terms of zooplankton abundance and biomass throughout the water column of world oceans. While the biomass decreases with depth, the species diversity of copepods is known to have a maximum in the mesopelagic layer (Roe, 1972; Böttger-Schnack, 1996; Yamaguchi et al., 2002; Kuriyama and Nishida, 2006). Mesopelagic copepods transport material by diel vertical migration (DVM) and accelerate passive flux by egesting fecal pellets, therefore, have an important role as a biological pump in the ocean (Yamaguchi et al., 2002; Koppelmann et al., 2004). Since 20–40% of the particulate organic carbon (POC) flux to the mesopelagic layer is consumed by copepods (Sasaki et al., 1988; Yamaguchi et al., 2002; Koppelmann et al., 2004), mesopelagic copepods have an important role in mineralization of organic materials and carbon cycling in the ocean (Hernández-León and Ikeda, 2005a,2005b; Ikeda et al., 2006).

In the Oyashio region located in the western subarctic Pacific, intensive studies have been made on the life cycles of

mesopelagic copepods. The life cycles of various mesopelagic copepods (*Pleuromamma scutullata*, *Heterorhabdus tanneri*, *Gaidius variabilis*, *Paraeuchaeta elongata*, *P. birostrata* and *P. rubra*) have been evaluated (Yamaguchi and Ikeda, 2000a,2000b,2001). In the Oyashio region, the large phytoplankton bloom is known to occur in the surface layer during spring, and about half of annual primary production occurs during this period (Saito et al., 2002; Liu et al., 2004). Since the settling passive flux to deep layers has a peak during this spring phytoplankton bloom (Honda et al., 2002; Onodera et al., 2005), the population structure and vertical distribution of mesopelagic copepods are expected to be influenced by it. However, the long sampling interval (monthly) and low vertical resolution (five layers between 0–2000 m) in previous studies may prevent sufficient evaluation of the short-term changes in population structure and vertical distribution of mesopelagic copepods during the spring phytoplankton bloom.

From the North Pacific Marine Science Organizations project OECOS (Ocean Ecodynamics comparison in the Subarctic Pacific) (Miller and Ikeda, 2006), short-term changes in population structure and vertical distribution of epipelagic large grazing copepods during the spring phytoplankton bloom were evaluated in the Oyashio region during March–May 2007 (Yamaguchi et al., 2010a, 2010b). There were short-term changes in vertical distribution during this

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period; *E. bungii* arouse from diapause in the mesoperagic layer and migrate up into the epipelagic layer, *Metridia pacifica* and *M. okhotensis* perform DVM but this ceases, except in C6F by the end of April (Yamaguchi et al., 2010b). Because of the increase in POC flux during this period, juvenile stages of *Metridia* spp. are estimated to be able to obtain enough food in the mesoperagic layer without DVM, while the C6F continue DVM to enable reproduction in the surface layer (Yamaguchi et al., 2010b). Thus, epipelagic copepods are known to have clear short-term changes in population structure and vertical distribution in response to the spring phytoplankton bloom. The responses of mesopelagic copepods to the spring phytoplankton bloom during the same period, however, remain unknown.

As a part of the OECOS project, this study aims to evaluate how and why mesopelagic copepods respond (or do not respond) phytoplankton bloom over the several trophic cascades. Short-term changes in population structure and vertical distribution of mesope-lagic copepods (*Gaetanus simplex*, *G. variabilis*, *P. scutullata*, *P. elongata*, *P. birostrata*, *H. tanneri* and *Heterostylites major*) during the spring phytoplankton bloom in the Oyashio region were observed. Results are discussed in the light of comparisons with the epipelagic copepods (*Neocalanus* spp., *E. bungii* and *Metridia* spp.) (Yamaguchi et al., 2010a,2010b). Within the mesopelagic copepods, differences in responses between feeding modes; suspension feeders (*G. simplex*, *G. variabilis* and *P. scutullata*) or carnivores (*P. elongata*, *P. birostrata*, *H. tanneri* and *H. major*) are also discussed.

2. Materials and methods

2.1. Field sampling

Sampling were conducted at St. A-5 (42°00′N, 145°15′E) in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007 (Fig. 1). Day and night vertical stratified samplings with a Vertical Multiple Plankton Sampler (VMPS: 60 μm mesh, 0.25 m² mouth opening; Terazaki and Tomatsu, 1997) were made from 9 strata between 0 and 1000 m (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–500, 500–750 and 750–1000 m) (Table 1). Volume of filtered water ranged between 4.3 and 58.9 m³. After the net was retrieved, samples were immediately preserved with 5% borax-buffered formalin. Temperature and salinity were measured by Sea-Bird CTD casts near-daily frequency from 8 to 15
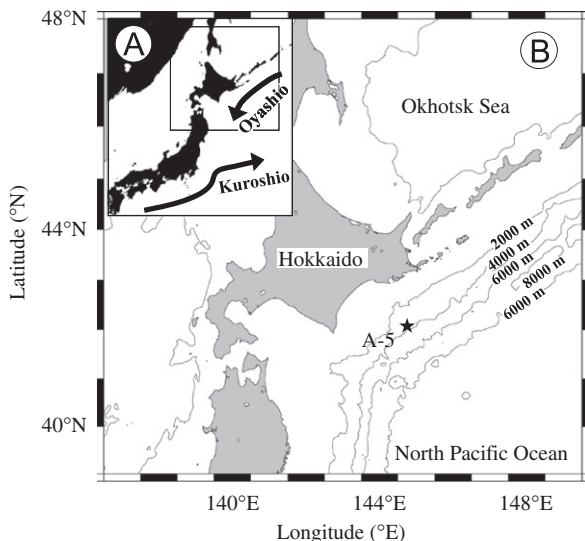
Table 1

Sampling data for VMPS hauls in the Oyashio region during 8 March, 5, 11, 23 and 29 April 2007. (D): Day, (N): night.

Date	Local time
8 March (D)	12:17–13:23
8 March (N)	23:42–0:51
5 April (D)	13:48–15:12
5 April (N)	1:57–3:15
11 April (D)	13:35–14:57
11 April (N)	22:28–0:01
23 April (D)	7:51–9:19
23 April (N)	22:41–0:13
29 April (D)	12:45–14:17
29 April (N)	2:33–3:59

March and from 5 April to 1 May 2007. Details of hydrography during the sampling period are published elsewhere (Kono and Sato, 2010). Water samples for chlorophyll-*a* (chl. *a*) were collected from 0, 5, 10, 20, 30, 40, 50, 75 and 100 m, then filtered through Whatman GF/F filters, and measured fluorometrically after extraction with N, N-dimethyl-formamide (Suzuki and Ishimaru, 1990). Based on depth-integrated primary production data (*IPP*) during the study period (Isada et al., 2010), the downward particle flux to 500 m was estimated from an equation suggested by Suess (1980); $C_{flux} = IPP/(0.0238Z + 0.212)$, where *IPP* is primary production (mg C m^{-2} day^{-1}), and C_{flux} is carbon flux (mg C m^{-2} day^{-1}) at a given depth (*Z*: m).

2.2. Identification and enumeration

Identification and enumeration were made for copepodid stages (C1–C6) of major mesopelagic copepods: *G. simplex*, *G. variabilis*, *P. scutullata*. *P. elongata*, *P. birostrata*, *H. tanneri* and *H. major*. Because of the difficulty in species identification of juvenile stages of *Gaetanus* and *Gaidius* species, C1–C4 individuals of *Gaetanus* spp. and *Gaidius* spp. were counted as C1–C4 individuals of *Gaetanus-Gaidius* spp.

For C6F of *G. simplex* and *G. variabilis*, gut content was scored as one of 4 categories: empty, foregut filled, hindgut filled and fullgut filled (Yamaguchi et al., 2007). For C6F *P. scutullata*, gonad maturation was separated into 3 categories: immature, development and mature (Batchelder, 1986). For C6F *Paraeuchaeta* spp., attachment of spermatophores and egg carrying were also recorded.

To evaluate feeding habits of mesopelagic copepods, gut contents of the major mesopelagic copepods (*G. simplex*, *G. variabilis*, *P. scutullata*. *P. elongata*, *P. birostrata*, *H. tanneri* and *H. major*) were examined. All C6F specimens were sorted from the most numerous layers at night from three sampling dates (8 March, 11 April and 29 April 2007). Their hindguts were carefully removed from the prosome with a pair of fine needles under a dissecting microscope. After removing all remains of the gut wall by means of a pair of tweezers, all gut contents were picked up with a fine pipette and mounted on a slide glass, examined under a compound microscope. Microplankton cells found in the guts were identified to species or genus level and the overall condition of the cells was classified into three categories depending on the proportion of broken cells in the total (100% intact, 50–100% fragment and 0–50% fragment).

For carnivorous copepods, most gut contents especially prey calanoid copepods were only observed as mandible gnathobase (blade). Length of mandible blade (*MB*) was measured with the precision of 1 μm, and their prosome lengths (*PL*, μm) were estimated from regressions: $PL = 19.23\ MB - 376.3$ (Dalpadado et al., 2008). Morphology of *MB* is known to vary with species greatly (Arashkevich, 1969; Dalpadado et al., 2008). Based on

Fig. 1. Location of the Oyashio region in the western subarctic Pacific (A) and sampling station (A-5; star) in the Oyashio region (B). Depth contours (2000, 4000, 6000 and 8000 m) are also shown in (B).

morphology and length of MB, species and stage identification was made for each prey if possible.

2.3. Data processing

To define the population structure, the mean stage ($\bar{S}$, Marin, 1987) was calculated from following equation:

$$\bar{S} = \sum (i \times Ni)/N$$

where Ni is the abundance (ind. m^{-2}) of ith copepodid stage ($i=1$ to 6) and N is the total copepodid abundance of the species. The smaller and larger $\bar{S}$ indicates dominance of early and late copepodid stages, respectively.

To clarify the depth distribution of each stage, depths where 50% of the population resided (50% distributed layer: $D_{50\%}$, Pennak, 1943) were calculated. Additional calculation of $D_{25\%}$ and $D_{75\%}$ were also made for all copepodid stages. Day–night differences in vertical distribution of each copepodid stage were evaluated by two-sample Kolmogorov–Smirnov tests (Sokal and Rohlf, 1995). To avoid errors due to small sample sizes in this DVM analysis, comparisons were made only for stages with > 20 ind. m^{-2}. While the robustness of Kolmogorov–Smirnov test for evaluating DVM of zooplankton can be questioned in the case of the great differences (> 10-fold) in abundance between day and night (Venrick, 1986). Since day and night differences in abundance of this study were less than 5-fold, evaluations of DVM by Kolmogorov–Smirnov test may appropriate.
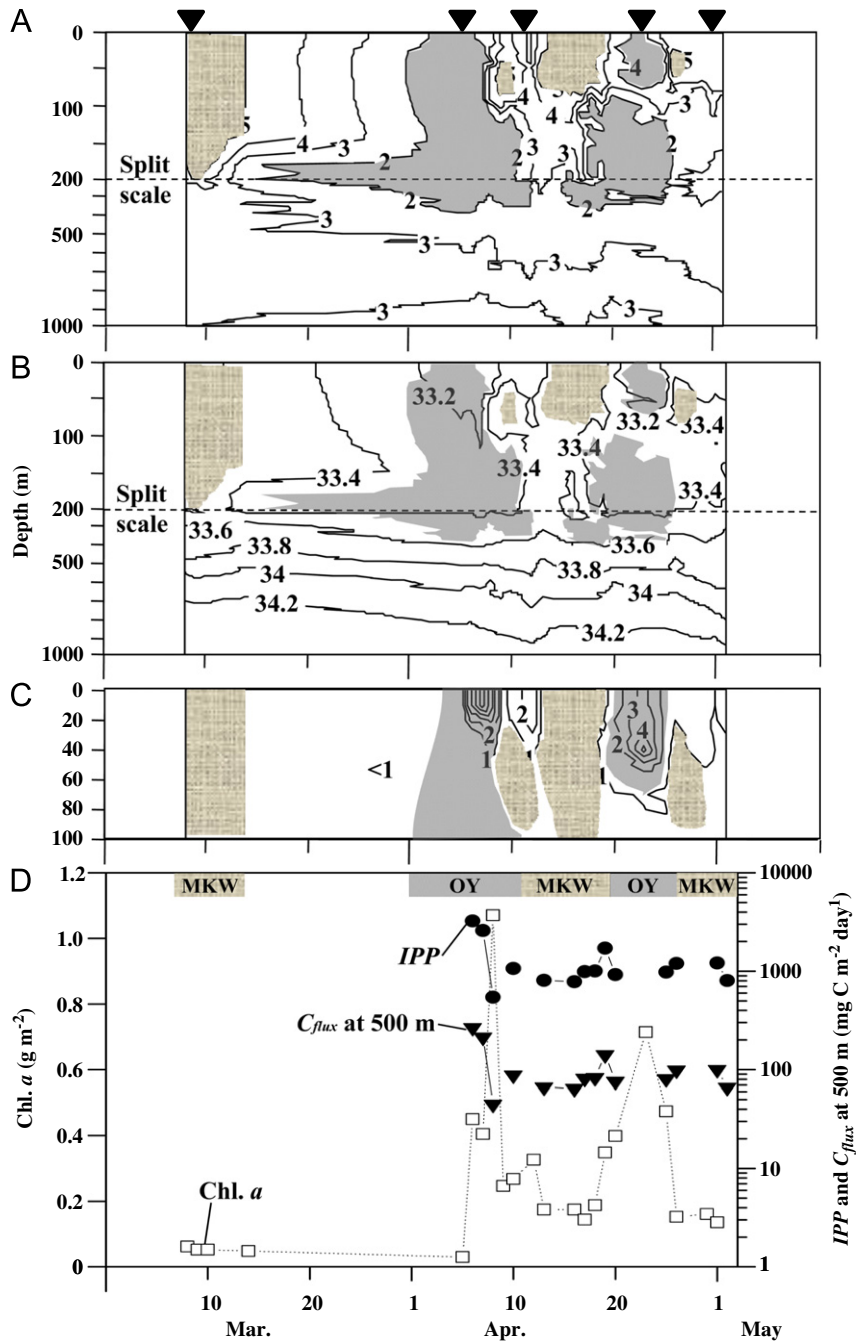

Fig. 2. Vertical and temporal changes in temperature (A), salinity (B), chl. a (C) and depth-integrated chl. a, primary production (IPP) and carbon flux (C_{flux}) at 500 m (D) in the Oyashio region during March to April 2007. Triangles in the top panel indicate sampling dates of VMPS. Note that the depth scales were different among the panels. Horizontal dashed lines in the upper two panels indicate split scales. Shades indicate positions of water masses. MKW: modified Kuroshio water, OY: Oyashio water.

3. Results

3.1. Hydrography

Temporal and vertical changes in temperature, salinity and chl. *a*, IPP, C_{flux} at 500 m and water masses during 8 March to 1 May 2007 are shown in Fig. 2. Temperature of the upper 200 m varied from 2 to 6 °C and was the lowest on 5 April and the highest on 8 March of the five occasions of VMPS samplings (Fig. 2A). Temporal changes in temperature below 200 m depth were small and settled at 2–3 °C. Salinity varied from 33.2 to 34.2, and increased with increasing depth (Fig. 2B). Chl. *a* had peaks (1–6 mg m^{-3}) in the upper 50 m on 7, 11 and 23 April (Fig. 2C). IPP and C_{flux} at 500 m fluctuated around 1000 and 100 mg C m^{-2} day^{-1}, respectively (Fig. 2D). Low chl. *a* during March indicated that the pre-bloom condition, while high chl. *a*, IPP and C_{flux} after 5 April showed that the bloom started, and their magnitude was the greater during Oyashio water dominated (1–10, 20–25 April, Fig. 2D) (cf. Isada et al., 2010).

3.2. Population structure

Abundance of total copepodid stages of C1–C4 of *Gaetanus* and *Gaidius* spp. varied between 221 and 611 ind. m^{-2} (Fig. 3A). C4 was the dominant stage throughout the study period. Abundance of C5–C6 of *G. simplex* and *G. variabilis* varied between 90 and 405 ind. m^{-2} and 177 and 496 ind. m^{-2}, respectively (Fig. 3B, C). Their stage composition showed little temporal change.

Abundance of total copepodid stages of *P. scutullata* varied between 326 and 1031 ind. m^{-2} (Fig. 3D). C5 and C6 comprised more than 50% of the population for *P. scutullata* except at night on 8 March. The $\bar{S}$ was at 4.5 and 5.5, and showed little temporal change.

Abundance of total copepodid stages of *P. elongata* varied between 261 and 771 ind. m^{-2}, and it increased significantly during the study period ($r = 0.94$ for correlation between abundance and Julian day, $p < 0.01$) (Fig. 4A). The population structure of *P. elongata* changed with the proportion of C1–C3 increasing gradually during the study period. The $\bar{S}$ of *P. elongata* gradually decreased, from 4.1 to 3.1 during study period.

Abundance of total copepodid stages of *P. birostrata* varied between 174 and 559 ind. m^{-2}, and was greater in April than in March (Fig. 4B) and significantly increased during the study period ($r = 0.74$ correlation with Julian day, $p < 0.05$). Population structure of *P. birostrata* was composed mainly of C1–C3 (50–80% of total population). The $\bar{S}$ of *P. birostrata* ranged between 3.1 and 3.5, and had little temporal changes.

Abundance of total copepodid stages of *H. tanneri* varied between 60 and 138 ind. m^{-2} (Fig. 4C). Population structure of *H. tanneri* was predominantly C6, and no C1 or C2 stages were observed. The $\bar{S}$ of *H. tanneri* ranged between 5.2 and 6.0, and remained high during the study period.

Abundance of total copepodid stages of *H. major* varied between 13 and 55 ind. m^{-2} (Fig. 4D). C1 and C2 of *H. major* did not occur and their population structure was mainly composed of C5 and C6. The $\bar{S}$ of *H. major* ranged between 4.7 and 5.9 and had little temporal changes during the study period.

3.3. Vertical distribution

C1–C4 of *Gaetanus* and *Gaidius* spp. distributed below 50 m both day and night throughout the study period (Fig. 5). While they sometimes showed bimodal distribution, day and night differences were not detected.

C5 and C6 of *G. simplex* were mainly distributed between 150 and 500 m both day and night during the study period (Fig. 6A). C5 and C6 showed nocturnal ascent migration during 8 March to
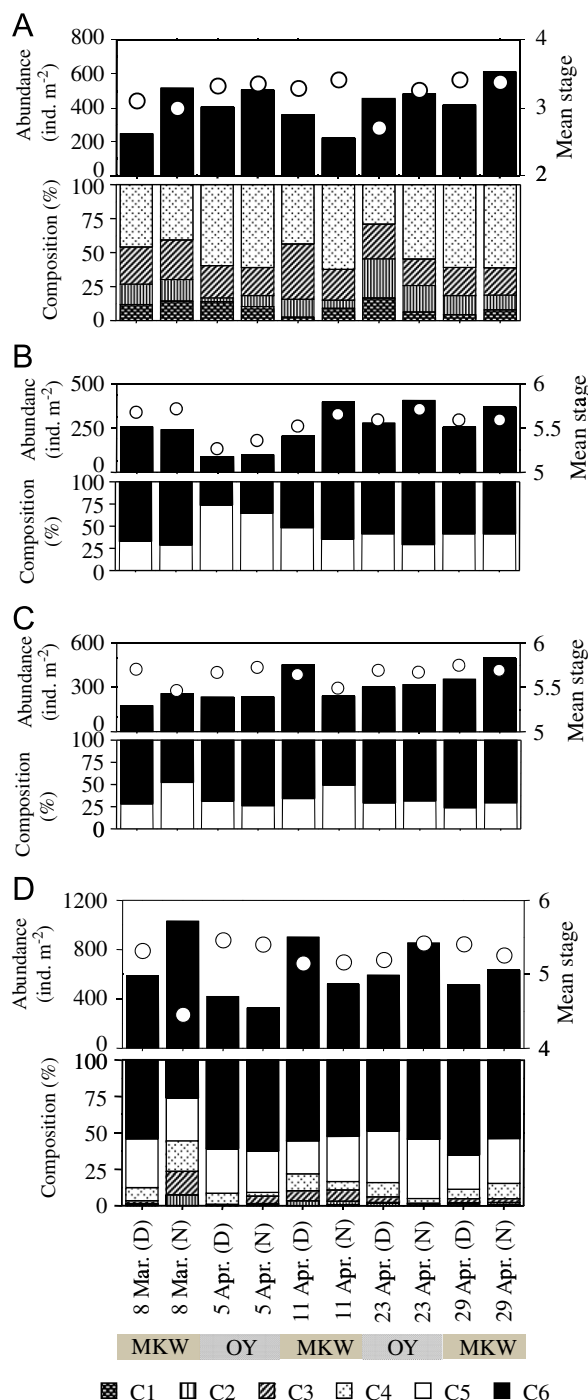

Fig. 3. Temporal changes in abundance (histograms), mean copepodid stage (symbols) and copepodid stage composition of mesopelagic suspension feeding copepods: C1–C4 of *Gaetanus* and *Gaidius* spp. (A), C5 and C6 of *Gaetanus simplex* (B), C5 and C6 of *Gaidius variabilis* (C) and *Pleuromamma scutullata* (D) in the Oyashio region during March to April 2007. (D): Day, (N): night. Bottom column of the panel indicates dominant water masses in the epipelagic depths. MKW: modified Kuroshio water, OY: Oyashio water.

11 April, while they stayed mesopelagic layer throughout the day during 23–29 April (Fig. 6A). C5 and C6 of *G. variabilis* distributed mainly between 250 and 750 m both day and night, and day and night differences were not detected for this species (Fig. 6B).

C1–C3 of *P. scutullata* were distributed around 150–500 m both day and night throughout the study period (Fig. 7). C4–C6F of *P. scutullata* had maximum distribution around 250–500 m in daytime, and centered on 150–250 m at night during 8 March
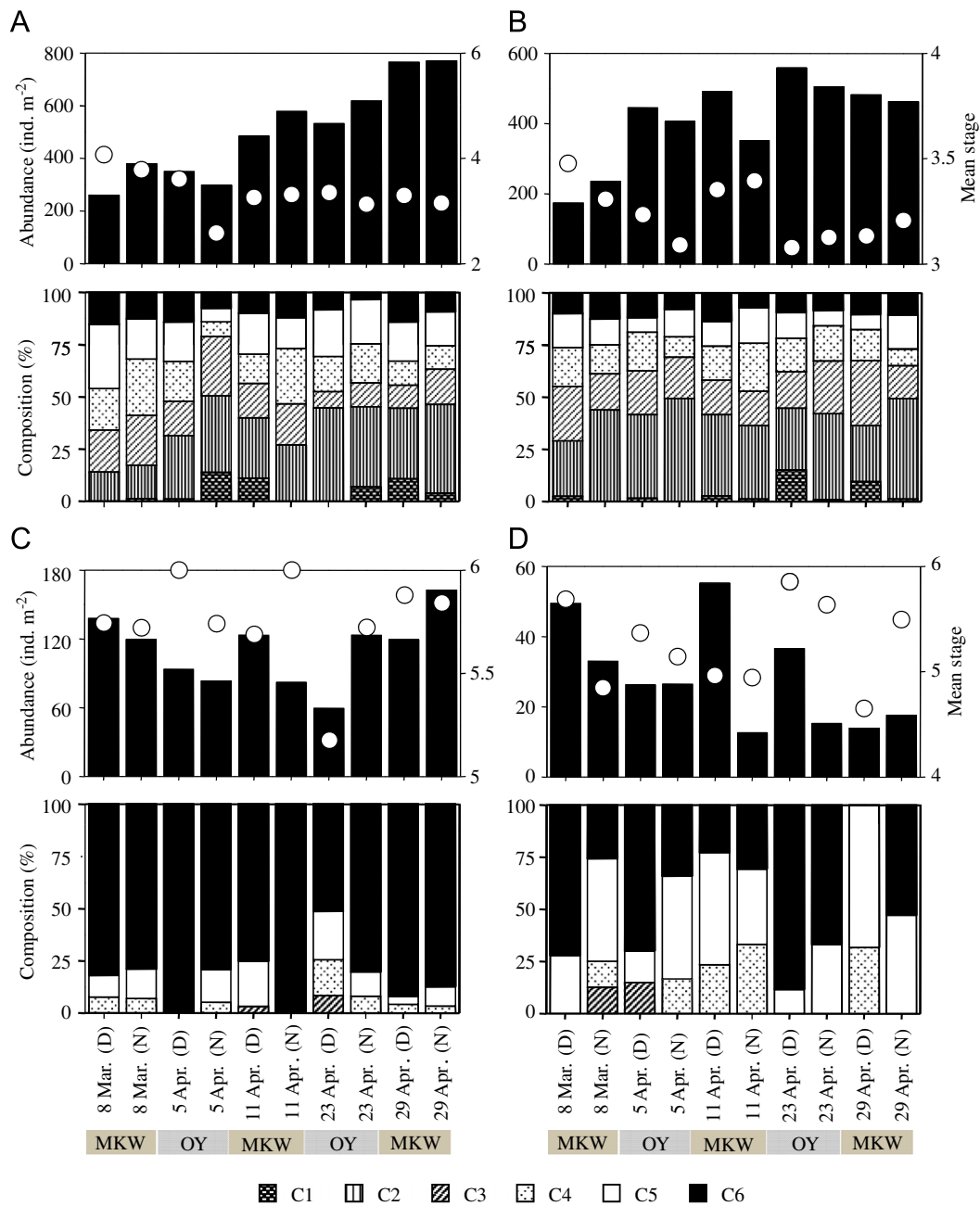
Fig. 4. Temporal changes in abundance (histograms), mean copepodid stage (symbols) and copepodid stage composition of mesopelagic carnivorous copepods: *Paraeuchaeta elongata* (A), *Paraeuchaeta birostrata* (B), *Heterorhabdus tanneri* (C) and *Heterostylites major* (D) in the Oyashio region between March and April 2007. (D): Day, (N): night. Bottom column of the panel indicates dominant water masses in the epipelagic depths. MKW: modified Kuroshio water, OY: Oyashio water.

and 5 April. After mid-April, C4–C6F were distributed around 150–500 m both day and night without DVM on 11, 23 and 29 April. Concerning C6M, they stayed around 250–500 m depth both day and night throughout the study period.

During both day and night, C1, C2 and C3 of *P. elongata* were distributed around 750–1000 m, 250–500 m, and 75–250 m, respectively (Fig. 8). On the other hand, C4–C6 were distributed around 150–500m during daytime and 25–250 m at night on 8 March, and 5, 11 and 29 April. This upward migration at night was also observed on 23 April but to a limited extent.

C1 of *P. birostrata* were distributed mainly between 750 and 1000 m both day and night throughout the study period (Fig. 9). C2 and C3 were distributed widely between 250 and 1000 m and

had maximum abundance around 500–750 m both day and night (Fig. 9). The distribution maximum of C4 and C5 was at 250–750 m and that of C6 was at 750–1000 m both day and night.

C3–C5 of *H. tanneri* were widely distributed around 150–1000 m both day and night, and their distribution center fluctuated within this layer (Fig. 10A). C6 were distributed around 150–500 m both day and night during the study period.

C3–C5 of *H. major* were distributed between 250–750 m both day and night during the study period (Fig. 10B). However, the distribution layer of C6 varied with the sexes: C6F were distributed between 500 and 1000 m and C6M were distributed shallower, between 150–750 m both day and night throughout the study period.
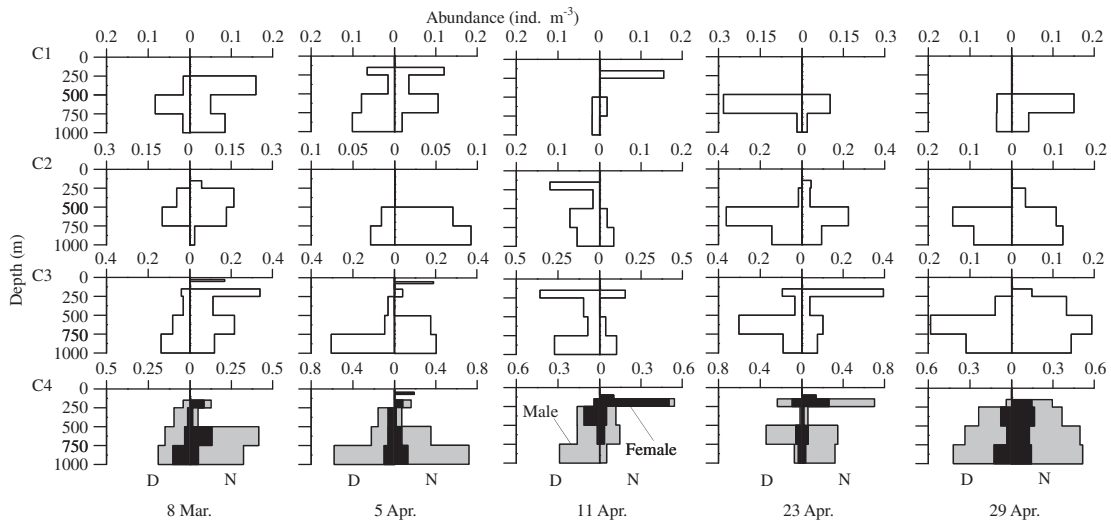
Fig. 5. Day–night vertical distribution of each copepodid stage of C1–C4 of *Gaetanus* and *Gaidius* spp. in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Female and male were identified for C4.
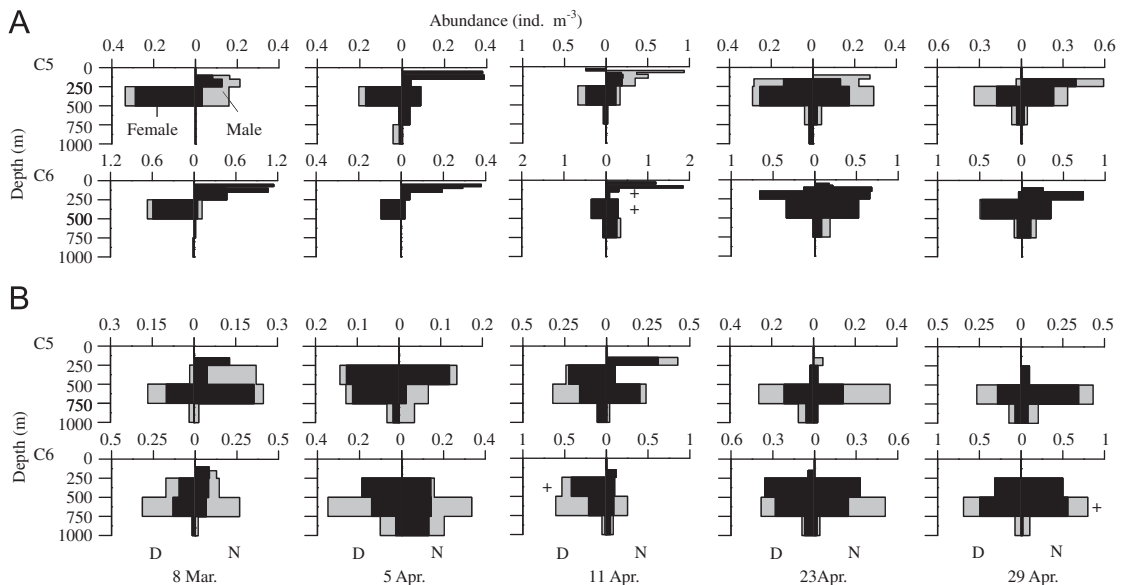

Fig. 6. Day–night vertical distribution of each copepodid stage of C5 and C6 of *Gaetanus simplex* (A) and *Gaidius variabilis* (B) in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Female and male were identified for C5 and C6. +indicates occurrence of spermatophore attached C6F at the layer.

3.4. Diel and ontogenetic vertical migration

Because of the limitation of the several species (i.e. mixture identification of C1–C4 for *Gaetanus* and *Gaidius* spp., no occurrence of C1–C2 for *H. tanneri* and *H. major*), we treated DVM and OVM only for three species: *P. scutullata, P. elongata* and *P. birostrata* (Fig. 11).

C5F/M and C6F of *P. scutullata* had clear DVM with a magnitude of 156–171 m on 8 March (Fig. 11A). This nocturnal ascent DVM was detected for C5F/M on 5 April, while no DVM was detected for all copepodid stages after 11 April. OVM of *P. scutullata* was characterized by a developmental descent with the magnitude of 102–138 m (Fig. 11A).

C4–C6 of *P. elongata* had clear DVM characterized by nocturnal ascent of magnitude 120–160 m throughout the study period (Fig. 11B). It was notable that even the C6M of *P. elongata* had nocturnal ascent DVM with a magnitude of 200 m on 29 April. Since C1 and C2 were distributed in the deepest layer, OVM of

P. elongata was characterized by a developmental ascent with the magnitude of 478–675 m (Fig. 11B).

While the DVM of *P. birostrata* was detected in several occasions (C4F/M in 11 and 29 April, Fig. 11C), *P. birostrata* did not perform DVM in general. Concerning OVM; C1 and C6 of *P. birostrata* were distributed in the deepest layer and C4 and C5 in the shallowest layer. Because of these stage-specific vertical distributions, OVM of *P. birostrata* was estimated to be a mixture of two patterns: developmental ascent during the early copepodid stages ($D_{50\%}$ of C1—C4: 339–357 m) and developmental descent during the late copepodid stages ($D_{50\%}$ of C6F—C4: 237–273 m) (Fig. 11C).

3.5. Population structure indices

Population structure indices for C6F of mesopelagic copepods gut content results of *G. simplex* and *G. variabilis*, gonad maturation of *P. scutullata* and composition of spermatophore-attached
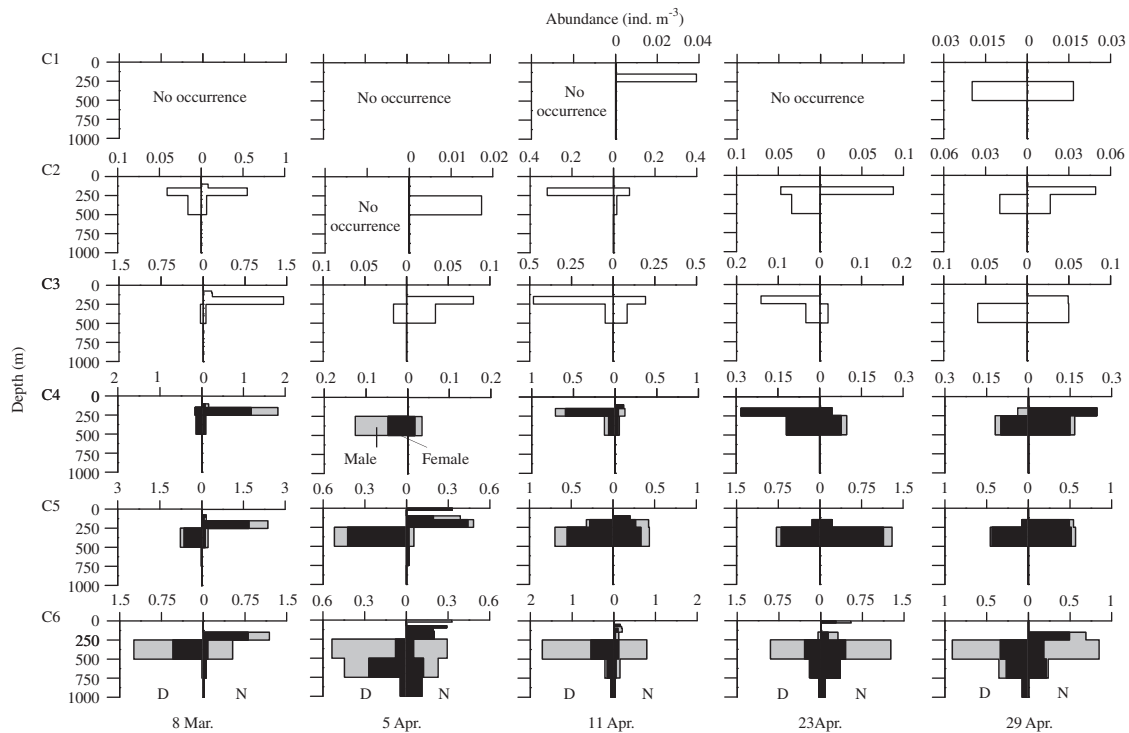
Fig. 7. Day–night vertical distribution of each copepodid stage of *Pleuromamma scutullata* in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Female and male were identified from C4 onward.
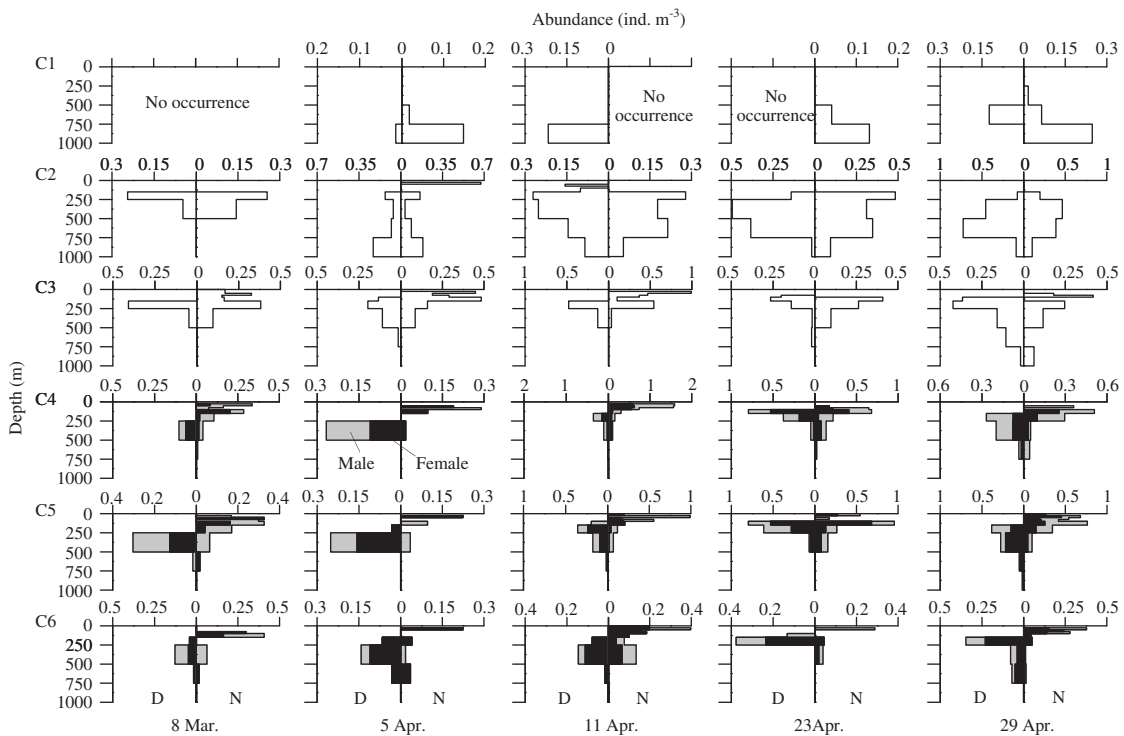

Fig. 8. Day–night vertical distribution of each copepodid stage of *Paraeuchaeta elongata* in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Female and male were identified from C4 onward.

and egg-carrying specimens of *P. elongata* and *P. birostrata* are shown in Fig. 12.

Throughout the study period, the gut content scores of *G. simplex* were higher at night than those at daytime, and the day–night differences were greater on 8 March and 5 April, was

and smaller between 11 and 29 April (Fig. 12A). On the other hand, the gut content scores of *G. variabilis* showed small differences between day and night, and were characterized by the dominance of hindgut or fullgut filled specimens throughout the day (Fig. 12B).
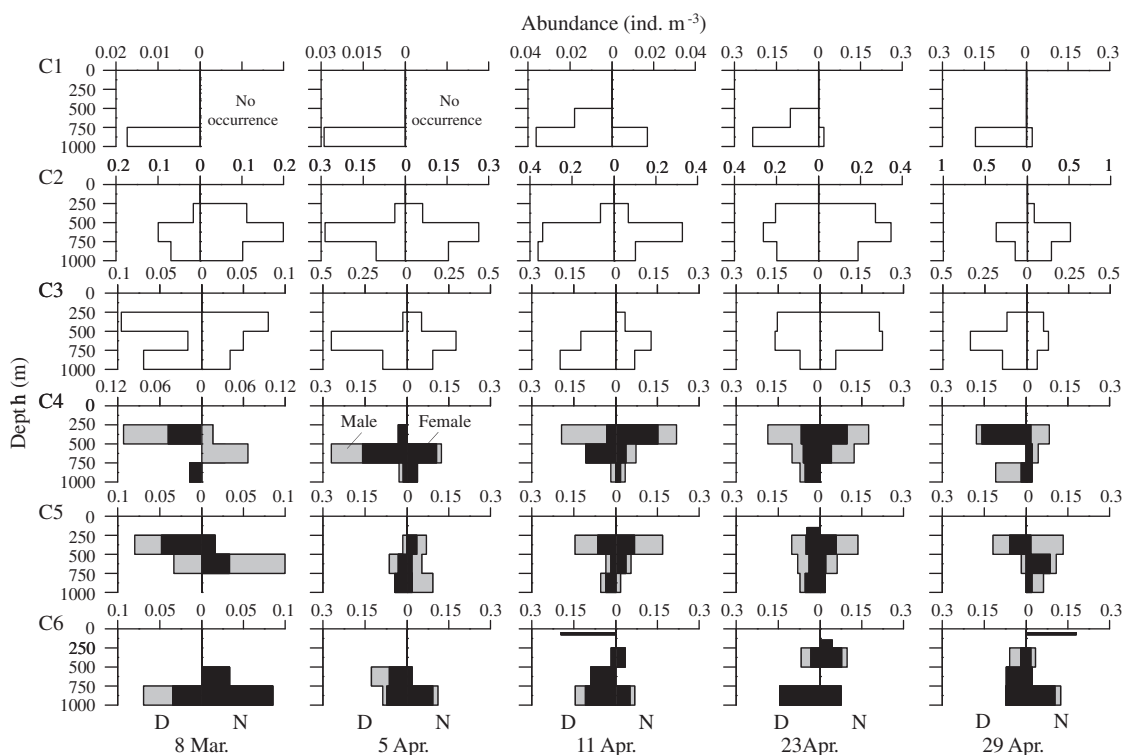
Fig. 9. Day–night vertical distribution of each copepodid stage of *Paraeuchaeta birostrata* in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Female and male were identified from C4 onward.
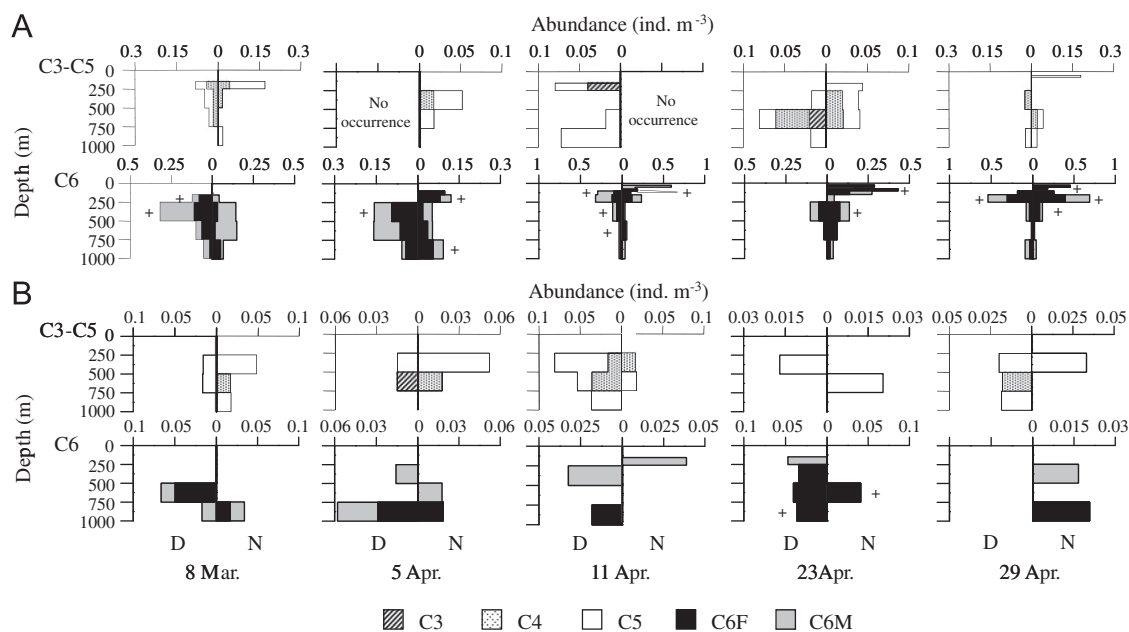

Fig. 10. Day–night vertical distribution of C3–C5 and C6 of *Heterorhabdus tanneri* (A) and *Heterostylites major* (B) in the Oyashio region on 8 March, 5, 11, 23 and 29 April 2007. D: Day, N: night. Note that C1 and C2 of these species did not occur in this study. +indicates occurrence of spermatophore-attached C6F in the layer.

Study of the gonad maturation of *P. scutullata* showed immature specimens dominating during daytime of 8 March, while mature specimens comprised more than 40% on the other sampling dates. Thus, there were no clear temporal changes in gonad maturation composition of C6F *P. scutullata* (Fig. 12C).

Neither spermatophore-attached nor egg-carrying specimens of *P. elongata* occurred on 8 March, while egg-carrying specimens comprised about 30% of C6F between 5 and 29 April (Fig. 12D). Spermatophore-attached and egg-carrying specimens also

occurred in *P. birostrata* (Fig. 12E). While the variability was large, the proportion of egg-carrying individuals of *P. birostrata* ($54 \pm 29\%$: mean $\pm$ sd) was significantly higher than that of *P. elongata* ($32 \pm 19\%$) ($p < 0.05$, U-test).

3.6. Gut contents

Based on gut content analysis, diatoms (mainly *Thalassiosira* spp.), dinoflagellates, cyanophytes, Foraminifera, Radiolaria and Tintinnina
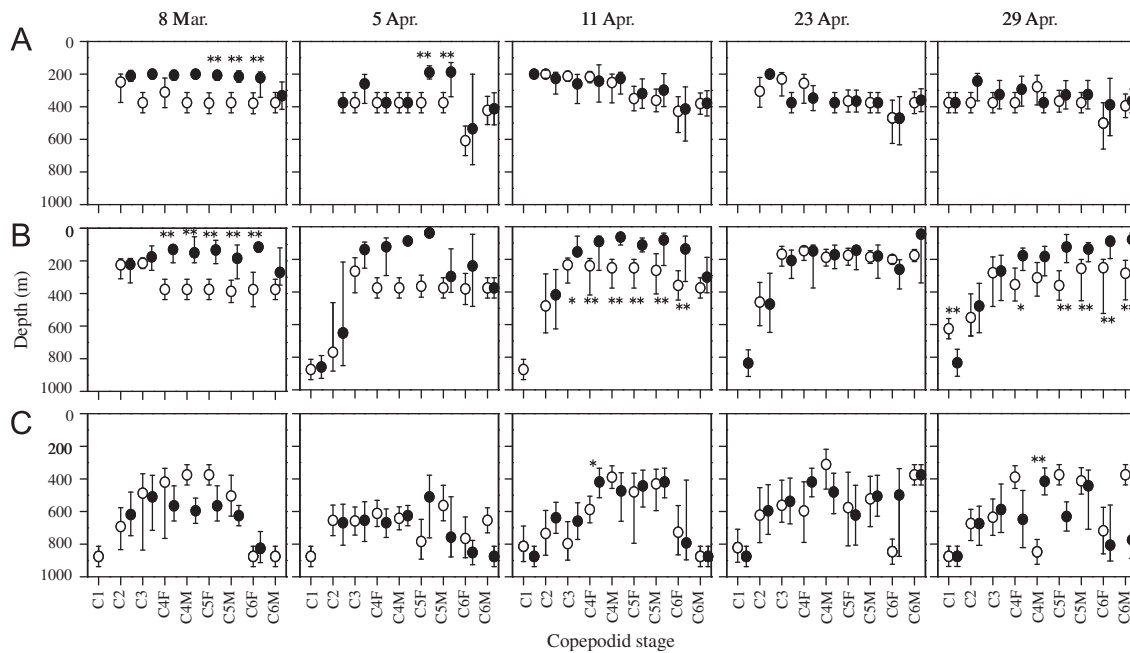
Fig. 11. Ontogenetic changes in vertical distribution of mesopelagic suspension feeding copepod *Pleuromamma scutullata* (A), mesopelagic carnivorous copepods *Paraeuchaeta elongata* (B) and *Paraeuchaeta birostrata* (C) in the Oyashio region during March to April 2007. Open and solid symbols denote $D_{50\%}$ of day and night, respectively. Vertical bars indicate depth ranges of $D_{25\%}$ to $D_{75\%}$. Asterisks indicate that the presence of DVM which detected by Kolmogorov–Smirnov test. *: $p < 0.05$, **: $p < 0.01$.

were observed as food for suspension feeding copepods (Table 2). Protozooplankton (Foraminifera, Radiolaria and Tintinnina) was mainly observed at 8 March when the spring phytoplankton bloom was not initiated (cf. Fig. 2C, D). Resting spore of *Chaetoceros furcellatus* was observed for all species at 29 April in the end of spring bloom (Table 2). It should be noted that cell condition of most of the resting spore of *C. furcellatus* was intact (100%). Proportion of intact (100%) cell was the highest for *P. scutullata* (33–68%), followed by *G. simplex* (29–62%) and least for *G. variabilis* (17–43%). While proportion of broken (0–50%) cell showed reverse pattern: thus the least for *P. scutullata* (13–33%), followed by *G. simplex* (27–54%) and highest for *G. variabilis* (51–80%) (Table 2).

For carnivorous copepods, most of the gut contents were amorphous materials and materials with species identification possible were only observed for *P. elongata* and *H. tanneri* at 29 April 2007 (Table 3). As prey item of *P. elongata* C6F, early copepodid stages (C1–C2) of dominant epipelagic copepods (*M. pacifica* and *Neocalanus* spp.), nauplii and poecilostomatoid copepods were observed. From gut contents of *H. tanneri* C6F, *MB* of *M. pacifica* C4 was only observed. It should be noted that the total length (*TL*) of prey was smaller for *P. elongata* C6F (118–1131 μm) than that of *H. tanneri* C6F (1780 μm) (Table 3).

4. Discussion

4.1. Effect of water mass exchange

During the study period, there observed sequential temporal changes in water masses in the upper 300 m (Fig. 2A, B). These temporal changes may have effect on temporal changes in abundance and population structure of mesopelagic copepods which inhabiting especially upper mesopelagic layer (i.e. *P. scutullata* for suspension feeder and *P. elongata* for carnivores, Fig. 11A, B). However, abundance and population structure of both species showed no relationship between temporal changes in water masses (cf. Fig. 3D, Fig. 4A).

4.2. Population structure

Both *G. simplex* and *G. variabilis* are medium-sized copepods (total length ca. 4 mm) belonging to Aetideidae, known to be distributed in mesopelagic zones of the subarctic Pacific, Bering Sea, Okhotsk Sea and Japan Sea (Brodskii, 1950). The life cycle of *G. variabilis* in the Oyashio region has been reported to have a two-year generation length and to reproduce during the spring phytoplankton bloom (Yamaguchi and Ikeda, 2000a). No previous information was available for the life cycle of *G. simplex*. While C1–C4 were presented for mixture of *Gaetanus* and *Gaidius* spp., abundance and population structure showed little temporal change during the study period (Fig. 3A–C).

Development time of *G. variabilis* from egg to C1 in laboratory experiments has been reported, and 51 days are expected to be needed for egg-C1 development under in situ temperatures (Yamaguchi and Ikeda, 2000a). Because of this long development time, the newly-born generation in this spring bloom would likely be eggs or nauplii during the study period. Since only copepodid stages are treated in this study, recruitment of the new generation to C1 will be difficult to observe. The newly-born generation in this spring bloom would likely be eggs or nauplii is why the copepodid stage structure of both species showed little temporal change in this study (Fig. 3A–C). Since the spermatophore attached C6F were observed for both *G. simplex* and *G. variabilis* (Fig. 6), they seemed to have active reproduction during the study period.

In the Oyashio region, *P. scutullata* is known to be distributed around 250–500 m, perform normal DVM, and is a suspension feeder having 1 year generation length with reproduction during the spring phytoplankton broom (Yamaguchi and Ikeda, 2000b). Predominance of C5 and C6 in the population (Fig. 3D) corresponds with the same season of the previous study (Yamaguchi and Ikeda, 2000b). The high SS and dominance of mature specimens of C6F during April, suggested that active reproduction was expected in the case of *P. scutullata*. While no spermatophore attached specimens were observed for C6F of this species, C6M having spermatophores were observed in 500–750 m on 29 April.
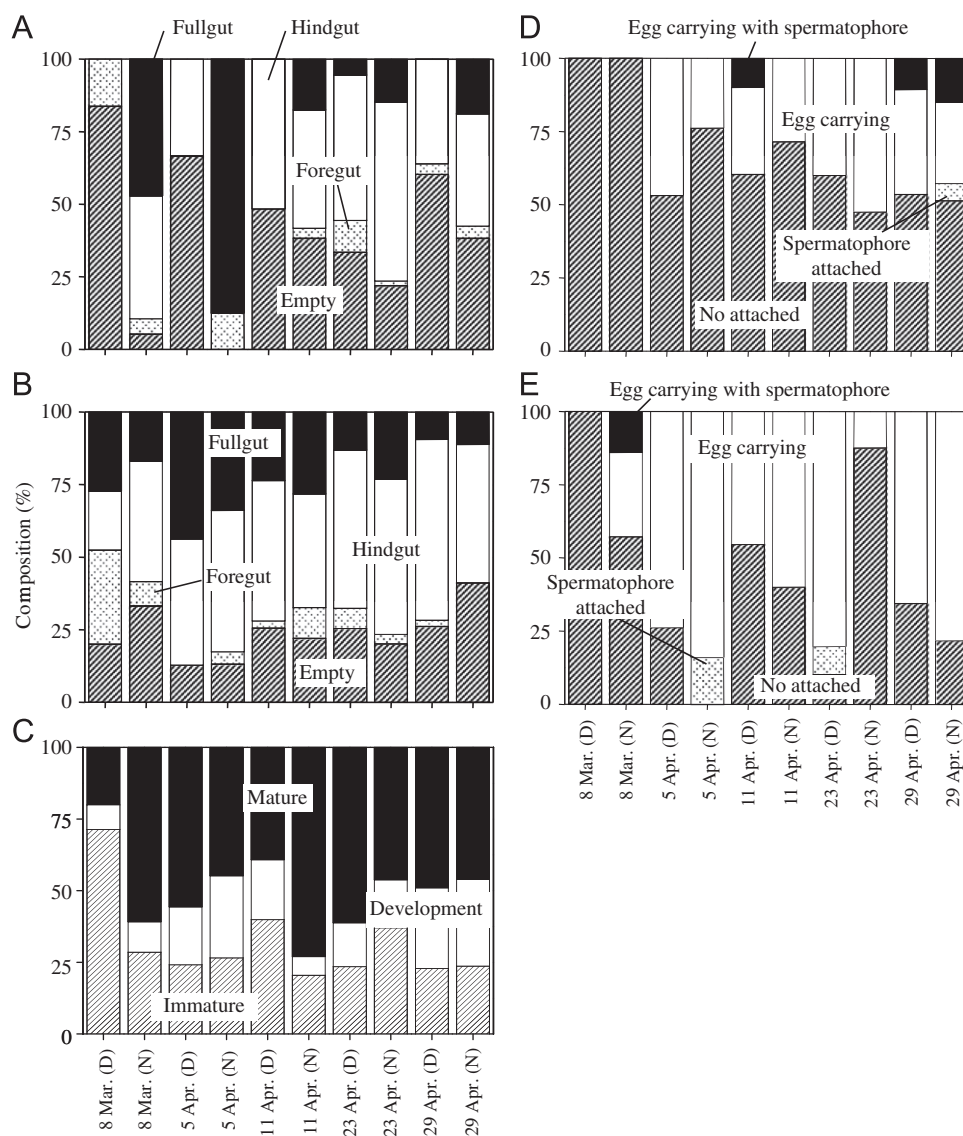
Fig. 12. Temporal changes in some population parameters of mesopelagic copepods in the Oyashio region during March to April 2007. Gut content scores of C6F *Gaetanus simplex* (A) and *Gaidius variabilis* (B), gonad maturation of C6F *Pleuromamma scutullata* (C), composition of egg-carrying and spermatophore-attached C6F *Paraeuchaeta elongata* (D) and *P. birostrata* (E). Gut content scores were separated into four (empty, foregut, hindgut and fullgut). Gonad maturation was separated into three (immature, development and mature).

For suspension feeding copepods, temporal changes in food item were observed: thus protozooplankton (Foraminifera, Radiolaria and Tintinnina) abundant before spring phytoplankton bloom (8 March), while resting spore of *Chaetoceros* were observed at end of the spring phytoplankton bloom (29 April) (Table 2). These temporal changes in food item of suspension feeders might be caused by the temporal changes in taxonomic composition of the micro-sized particle. Concerning *Chaetoceros* resting spore, dominance of 100% intact cell condition in copepod gut is unique feature.

It has been reported that *P. elongata* has a one year generation length, and their reproduction continues throughout the year with a peak during April and June in the Oyashio region (Yamaguchi and Ikeda, 2001). Abundance of *P. elongata* in this study (261 to 771 ind. m^{-2}, 0–1000 m) corresponds well with the reported values (597 $\pm$ 200 ind. m^{-2} [annual mean $\pm$ sd], 0–2000 m; Yamaguchi and Ikeda, 2001). Since distribution of *P. elongata* concentrated < 1000 m, direct comparison on abundance (standing stock) between 0–1000 m and 0–2000 m may possible. Significant increase in abundance, progressive

dominance of C1–C3 and the gradual decrease in *SS* (Fig. 4A) indicate that the recruitment to C1 of *P. elongata* began during the study period. Average composition of egg-carrying C6F individuals in this study (32%, Fig. 12D) is much higher than the annual mean (4.3%, Yamaguchi and Ikeda, 2001). It also suggests that *P. elongata* had active reproduction during the study period. Since their habitat temperature is low, around 2–3 °C (Fig. 2A), development time from egg to C1 is estimated to be 64 day based on laboratory rearing (Ozaki and Ikeda, 1997,1998). Slight increase in proportion of early copepodid stages and decreasing in mean stage during the study period (Fig. 4A) may be the result of recruitment of newly-born population into early copepodid stages.

The life cycle of *P. birostrata* was also studied in the Oyashio region. They have one year generation length and reproduction throughout the year with a peak in April–June (Yamaguchi and Ikeda, 2001). In the present study, greater abundance of *P. birostrata* occurred in April rather than March (Fig. 4B) and the higher composition of spermatophore-attached and egg-carrying C6F individuals (Fig. 12E) suggest that reproduction of

Table 2
Gut content of mesopelagic suspension feeding copepods in the Oyshgio region during 8 March, 11 and 29 April 2007. Gut contents were examined for C6F collected from most abundant depth layer at night. Number of examined specimen was shown in the parentheses. For cell condition, three categories (intact [100%], fragment [50–100%] and broken [0–50%]) were scored. (R.S.): Resting spore.

Species/taxa	Gaetanus simplex			Gaidius variabilis			Pleuromamma scutullata		
	08 March (8)	11 April (12)	29 April (15)	08 March (5)	11 April (10)	29 April (15)	08 March (15)	11 April (7)	29 April (8)
Actinocyclus spp.	1						1		
Azpeitia tabularis	1								
Coscinodiscus spp.	1								1
Neodenticula seminae		5							1
Odontella aurita		1	2			3		6	14
Thalassiosira spp.	15	22	20	5	4	30	4	5	56
Unidentified pennate diatoms		1	1	2	1	2	1		1
Chaetoceros furcellatus (R.S.)		2	2			10			3
Ceratium fusus	1								
Unidentified dinoflagellates								1	
Dinoflagellate cyst			1						
Cyanophytes	5	2							
Foraminifera	9						1		
Radiolaria	2								
Tintinnina						2	1		
Intact (100%)	10	16	16	3	1	8	4	4	52
Fragment (50–100%)	6	7	3			15	3	4	10
Broken (0–50%)	19	10	7	4	4	24	1	4	14

Table 3
Gut contents of mesopelagic carnivorous copepods (*Paraeuchaeta elongata* and *Heterorhabdus tanneri*) in the Oyashio region during spring 2007. Note that there observed only amorphous materials for the other species and dates, thus not included in this table. For comparison, while prey calanoid copepods observed only as mandible blade (*MB*), their prosome and total length (*PL* and *TL*) were calculated using equations (Dalpadado et al., 2008 for *MB*–*PL*, Yamaguchi unpublished for *PL*–*TL*).

Species/taxa and stage	Length (μm)		
	MB	*PL*	*TL*
Paraeuchaeta elongata C6F (29 April)			
Metridia pacifica C2	48	547	913
Nauplii	–	–	118
Neocalanus cristatus C1 or	70	970	1131
Neocalanus plumchrus C2			
	72	1008	1176
Triconia borealis C6M	–	325	415
Heterorhabdus tanneri C6F (29 April)			
Metridia pacifica C4	75	1066	1780

P. birostrata had started in April. The average composition of egg-carrying specimens of C6F in this study (54%, Fig. 12E) was much higher than the reported annual mean (5%, Yamaguchi and Ikeda, 2001). It suggests that *P. birostrata* had started reproduction during the study period.

The inter-molt growth of Heterorhabdidae is reported to be greater than 900% in body mass (Yamaguchi and Ikeda, 2000b). Because of such high inter-molt growth, the body lengths of C1 and C2 of *H. tanneri* would be smaller than mesh openings of the net used in the present study (Yamaguchi and Ikeda, 2000b). Because of the absence of early copepodid stages, the population structure of *H. tanneri* was predominantly C6, and *SS* was high throughout the study period (Fig. 4C). Generation length of *H. tanneri* is reported to be one year, spermatophore-attached C6F occurred throughout the year and their reproduction peak was estimated to be in December (Yamaguchi and Ikeda, 2000b). In this study, spermatophore-attached C6F occurred in limited numbers throughout the study period (Fig. 10A). The life cycle of *H. tanneri* is characterized by the large inter-molt growth of C3

and C4 in summer when the biomass of zooplankton prey has its annual maximum (Yamaguchi and Ikeda, 2000b). Because of this life cycle seasonality, reproduction of *H. tanneri* may be in December and not in the spring of this study.

As the other Heterorhabdidae (*H. major*), their C1 and C2 were also not recorded, and C5 and C6 were the predominant stages in population structure, and *SS* showed high values (Fig. 4D). These contrasting population structures of Heterorhabdidae to those of Euchaetidae suggest that the life cycle pattern and ecology varies widely between families even within the carnivorous species. For instance, the mandible blade of *Heterorhabdus* spp. has evolved to put venom or anesthetic into the prey (Nishida and Ohtsuka, 1996), thus the feeding mode and the prey animals of Heterorhabdidae are expected to be greatly varied to those of Euchaetidae.

For carnivorous copepods, size of prey animal is reported to be a function of body size of predator. Hansen et al. (1994) reported that the average ratio of the size of the predatory copepod to that of its prey was 18:1, ranging from 10:1 to 30:1. From these ratio, sizes of prey item of C6F *P. elongata* (*PL*: 4.95 mm, Yamaguchi and Ikeda, 2002b) and *H. tanneri* (*PL*: 2.92 mm, Yamaguchi and Ikeda, 2000b) are estimated to be 165–495 and 97–292 μm, respectively. These values are roughly corresponded with the observed values for *P. elongata* (118–1176 μm), while the food item size of *H. tanneri* (1780 μm) is anomalously larger than the prediction (Table 3). This anomalous large food item of *H. tanneri* may be related with their specialized feeding modes (put venom or anesthetic into the prey) (Nishida and Ohtsuka, 1996). This specialized feeding mode of Heterorhabdidae may allow them to capture large-sized prey, and also provide anomalously greater inter-molt growth of this family (Yamaguchi and Ikeda, 2000b).

4.3. Vertical distribution

Distribution depth of *G. simplex* was at 150–500 m, and was shallower than that of *G. variabilis* throughout the study period (Fig. 6). Vertical distribution of *G. variabilis* (250–750 m, Fig. 6B) corresponds well with the previous study (Yamaguchi and Ikeda, 2000a).

For *G. simplex*, DVM was observed for C5F/M and C6F during 8 March to 11 April, while no DVM was detected during 23–29 April (Fig. 6A). During the same period, the cessation of DVM was reported for epipelagic *M. pacifica* during 23–29 April, and is considered to be related to the increase of POC flux during the spring phytoplankton bloom (they are estimated to be able to obtain enough food without DVM) (Yamaguchi et al., 2010b). Gut content scores of *G. simplex* were higher at night than those at daytime. These day–night differences were remarkable for 8 March and 5 April when they perform clear DVM (Fig. 12A). These facts suggest that active feeding of diel migrant *G. simplex* takes place in nighttime. The day–night differences were detected for gut content scores on 23 and 29 April when they ceased DVM (Fig. 12A). These results indicate that they feed on POC during nighttime at upper mesopelagic depths where they stayed throughout the day without DVM. The increased POC flux from the surface bloom to the mesopelagic layer may provide enough food for deep-sea copepods during the study period (Yamaguchi et al., 2010b).

For evaluation of food condition of mesopelagic copepods, we have estimate ingestion rates of them (for detailed method, see Yamaguchi et al., 2010b). The estimated mesopelagic suspension feeding copepod stock ingestion rate (20.6 mg C m^{-2} day^{-1}) was less than the carbon flux to 500 m (ca. 100 mg C m^{-2} day^{-1}), about 20% of the supply rate. Thus the estimates show that mesopelagic suspension feeding copepods could likely meet its energetic requirements at 500 m in April without DVM, as was suggested by Hattori (1989). From gut content analysis, increment of proportion of broken cell with increasing depth (Table 2) may reflect of repacking effect (Sasaki et al., 1988; Yamaguchi et al., 2002). Thus, mesopelagic suspension feeding copepods may feed on similar taxonomic components, but their cell condition is varied with depth (Table 2) because of the effect of repacking by copepods in the overlaying layer.

For *G. variabilis*, reverse DVM (nocturnal descent) has been reported (Yamaguchi and Ikeda, 2000a), however a constant DVM pattern was not observed for this species (Fig. 6B). The low DVM intensity of *G. variabilis* may be related to the low day–night differences in gut content scores (Fig. 12B). Throughout the study period the gut fullness of *G. variabilis* was clearly higher than that of *G. simplex*. This may reflect the long gut passage time of deep-living *G. variabilis*. It is well known that deep-sea copepods have longer guts (looped gut) to provide higher assimilation efficiency under food limited conditions (Vinogradov, 1968; Nishida et al., 1991; Kosobokova et al., 2002). The little day–night differences in gut content scores and higher composition of hind gut or full gut filled individuals of *G. variabilis* (Fig. 12B) may reflect the longer digestive time of *G. variabilis*.

The observed magnitude of DVM for *P. scutullata* (156–188 m) (Fig. 7) corresponded well with reported values (20–249 m, Yamaguchi and Ikeda, 2000b). The cessation of DVM (from 11 April) was also observed for this species and this timing was faster than that of *G. simplex* (after 23 April). The faster timing of the cessation of DVM in *P. scutullata* may be related to their distribution depths. Since *P. scutullata* was distributed shallower than the *G. simplex* (Figs. 6B, 7), the response to the temporal changes in amounts of POC flux will be expected to be faster for the shallower-living *P. scutullata*.

Species separation by vertical distribution is reported for three mesopelagic *Paraeuchaeta* spp. (*P. elongata*, *P. birostrata* and *P. rubra*) in the Oyashio region, and *P. elongata* is known to be at the shallowest depth at 310 m (Yamaguchi and Ikeda, 2002a). The distribution depth of *P. elongata* in this study confirmed this depth. *P. birostrata* is reported to be distributed deeper than *P. elongata* at about 800 m (Yamaguchi and Ikeda, 2002a). *P. birostrata* was distributed between 500 and 1000 m in this

study, thus the vertical separation within *Paraeuchaeta* species was also observed in this study. The vertical separation within the congener species is considered to have the function of reducing food competition in the food-limited mesopelagic zone (Yamaguchi and Ikeda, 2002a).

The nocturnal ascent DVM was observed for *P. elongata* throughout the study period (Fig. 11B). For epipelagic species (*M. pacifica* and *M. okhotensis*) and mesopelagic suspension feeders (*P. scutullata* and *G. simplex*), cessation of DVM was observed after 11 or 23 April in the study period (Yamaguchi et al., 2010b; Figs. 6A, 11A). However, the cessation of DVM was not observed for *P. elongata*. The cessation of DVM of epipelagic and mesopelagic suspension feeders is considered to be caused by the fact that they can obtain enough food by increasing POC flux after mid-April. Continuous DVM of *P. elongata* during the same period suggests that the increase of POC flux may have little effect on carnivorous species. Concerning food for carnivorous copepods, total zooplankton biomass increased twice during the studied period (Yamaguchi et al., 2010a). However, they seem to have little effect on DVM behavior of *P. elongata*.

C6F of *H. tanneri* and *H. major* were distributed between 216–525 m (Daytime $D_{50\%}$) and 625–875 m, respectively (Fig. 10). Thus, the vertical separation within the family Heterorhabdidae is similar to that of Euchaetidae. For carnivores, the vertical separation within the family is considered to be a special feature of this feeding mode. The vertical separation within the family is considered to have the function of reducing feeding competition in the food-limited mesopelagic zone. While the twice increment was observed for total zooplankton biomass in the study period (Yamaguchi et al., 2010a), this may have little effect on vertical segregation of Heterorhabdidae species.

With reduced mouthpart appendages, C6M of *P. elongata* are known to cease feeding and stay in the mesopelagic layer without DVM (Yamaguchi and Ikeda, 2002a). However, in the present study, nocturnal ascent DVM with magnitude of 200 m was detected for C6M (Fig. 11B). This may have been caused by C5M molting to C6M in the surface layer at night. Twice increment in total zooplankton biomass during the study period (Yamaguchi et al., 2010a) may accelerate development of C5M to C6M. OVM of *P. elongata* was characterized with developmental ascent (Fig. 11B). This pattern corresponded well with previous studies (Morioka, 1975; Yamaguchi and Ikeda, 2002a).

For the congener *P. birostrata*, the OVM pattern greatly varied from that of *P. elongata*. The OVM pattern of *P. birostrata* was characterized by a mixture of developmental ascent in the early copepodid stages and developmental descent in late copepodid stages (Fig. 11C). Throughout the year, C4 is reported to be the shallowest living stage of *P. birostrata*, and C1 and C6 are known to be distributed at the deepest depths of this species (Yamaguchi and Ikeda, 2002a). The mixture of OVM pattern recorded in this study corresponds well with this pattern. The OVM pattern of *Paraeuchaeta* spp. is known to be related to the inter-molt growth of each developmental stage, and the shallowest stage is known to achieve the greatest inter-molt growth within the species (Yamaguchi and Ikeda, 2002b).

In conclusion, responses of mesopelagic copepods to the spring bloom in the Oyashio region is summarized following. Copepodid stage structure was not showed clear responses because of the newly born individuals were eggs or nauplii. DVM behavior of suspension feeders was cease, while carnivores continued DVM throughout the bloom. The gut content analysis and estimated ingestion rate suggest that the suspension feeding mesopelagic copepods could meet sufficient amount of food by sinking POC flux from overlaying layer without DVM during the bloom period. This is why the DVM behavior ceased only for suspension feeders during the bloom.

Acknowledgments

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