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Vertical Distribution Patterns of Pelagic Copepods as Viewed from the Predation Pressure Hypothesis

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Atsushi Yamaguchi, Tsutomu Ikeda, Yuji Watanabe and Joji Ishizaka (2004) Vertical distribution patterns of pelagic copepods as viewed from the predation pressure hypothesis. *Zoological Studies* **43**(2): 475-485. As habitats of pelagic copepods, epipelagic oceanic environments are characterized by greater food availability but higher risks of predation. Both food supply and predation risk rapidly drop with increasing depth. We studied day/night vertical distribution patterns of copepodid stages of 6 epipelagic (*Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, *Eucalanus bungii*, *Metridia pacifica*, and *M. okhotensis*), 2 mesopelagic (*Gaetanus simplex* and *Pleuromamma scutullata*), and 6 bathypelagic copepods (*Gaidius variabilis*, *Paraeuchaeta elongata*, *P. birostrata*, *P. rubra*, *M. asymmetrica*, and *M. curticauda*) based on zooplankton samples collected from depths of 0~4000 m at stn. Knot (44°N, 155°E) in the western subarctic Pacific. All epipelagic species exhibited ontogenetic vertical migration (OVM) characterized by descent with progression of copepodid stages, although species-specific variations in the degree of its magnitude were seen. One of the 6 epipelagic species (*M. pacifica*) showed diel vertical migration (DVM) behavior by its ascent to upper layers at night. Mesopelagic species were characterized by a lack of OVM, although their older copepodid stages undertook DVM. Bathypelagic species underwent OVM in a pattern that was the opposite (ascent with progression of development) of that of epipelagic species. No DVM behavior was recognized for bathypelagic species. From the viewpoint of the predation pressure hypothesis, these differential vertical distribution modes of copepods living in dissimilar bathymetric strata can be interpreted as results of life history traits toward reducing predation mortality of early (bathypelagic copepods) or late copepodid stages (epipelagic copepods). The absence of OVM in mesopelagic copepods is a life history trait that falls somewhere between these 2 extremes (the DVM behavior of their late copepodid stages apparently imparts an advantage for better feeding). This explanation appears to be consistent with the observation that the fecundity of these copepods decrease with increasing depth.
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Key words: Diel vertical migration, Ontogenetic vertical migration, Oceanic, Mesopelagic, Bathypelagic.

Among various animal taxa occurring as metazooplankton in the world's oceans, copepods are the most numerous taxa (55%~95%) in most sea areas (Longhurst 1985). Copepods play integral roles in energy flow and material cycling in the entire water column (Mauchline 1998). In the subarctic Pacific, some large interzonal copepods (e.g., *Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, and *Eucalanus bungii*) are known to perform seasonal vertical migration (Vinogradov and Arashkevich 1969, Vinogradov 1970). Because of their large biomass (around 80%~90% of the zooplankton, Vinogradov 1970) and trophic importance (prey organisms of salmon and other animals at higher trophic levels, Mackas and Tsuda 1999), available information about the vertical distribution of oceanic copepods in this region is largely limited to those species. Fulton (1973) and

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Krause and Lewis (1979) observed ontogenetic vertical migration (OVM) of *N. plumchrus* and *E. bungii*, but both studies were of endemic populations in fjords of western Canada. In oceanic regions, Marlowe and Miller (1975) observed diel vertical migration (DVM) of epipelagic copepods at stn. P (50°N, 145°W) in summer, and categorized various migration patterns. In the 1980s, a program of time-series sampling was performed at stn. P, and detailed information about DVM and OVM became available for the first time for *Neocalanus* spp., *E. bungii* (Miller et al. 1984, Miller and Clemons 1988), and *Metridia pacifica* (Batchelder 1985). Recent JGOFS studies have also provided valuable information on the vertical distribution of oceanic copepods in this region (see Goldblatt et al. 1999).

Compared to the eastern subarctic Pacific, few studies on the vertical distribution of oceanic copepods have been made in the western subarctic Pacific until recently. As incidental studies, Hattori (1989) noted the bimodal vertical distribution of metridinid copepods, and Tsuda and Sugisaki (1994) estimated feeding pressure of copepod assemblages in summer. In 1996~1997, a time-series zooplankton sampling program (down to ≤ 2000 m) was carried out at “site H” (encompassing 41°30’ to 42°30’N latitude and 145°00’ to 146°00’E longitude) in the Oyashio region, and information about DVM and OVM of *N. cristatus*, *N. flemingeri* and *N. plumchrus* has been rapidly accumulating (Kobari and Ikeda 1999 2001a b).

Those previous studies in the eastern and western subarctic Pacific were largely on epipelagic copepods, and little attention has been paid to meso-, bathy-, or abyssopelagic copepods. Notable exceptions include Vinogradov (1970) who described vertical changes in zooplankton biomass, separating them by taxa and feeding habits (filter feeders, predators, and euryphages), and Markhaseva and Razzhivin (1992) who described the vertical partitioning of aetideid copepods in the Kurile-Kamchatka Trench. Recently, detailed data on vertical distribution, population structure, and life cycles of mesopelagic copepods (*Pleuromamma scutullata*, *Heterorhabdus tanneri*, *Gaidius variabilis*, *Paraeuchaeta elongata*, *P. birostrata*, and *P. rubra*) have been reported (Yamaguchi and Ikeda 2000a b 2001). Nevertheless, there are still many gaps in our knowledge of bathy- and abyssopelagic copepods in the subarctic Pacific.

As a possible major mechanism for maintenance of the vertical structure of copepod communities, biological interactions rather than physical gradients have been considered important (McGowan and Walker 1979). In fact, DVM of epipelagic species has been interpreted as a behavioral response for escaping visual predators (Gliwicz 1986, Bollens and Frost 1989). Predator avoidance is also considered to be a major mechanism of why copepods enter into diapause at depth (Richter 1995, Kaatvedt 1996, Dale et al. 1999). Compared with epipelagic copepods, studies on OVM of deep-sea copepods have been very scarce (Morioka 1975, Weikert and Koppelmann 1993, Richter 1994, Falkenhaug et al. 1997). However, it is interesting to note that OVM patterns of deep-sea copepods are all characterized by developmental ascent, an opposite pattern (developmental descent) of epipelagic copepods (see Falkenhaug et al. 1997).

In the present study, we observed day and night vertical distribution patterns of 14 copepods of 7 genera down to 4000 m in depth at stn. Knot (44°N, 155°E; at around 5340 m in depth) in the western subarctic Pacific. We analyzed the same samples we previously used to evaluate the feeding impact of the copepod community on carbon flux, where we showed that an average of 32% of the particulate carbon flux is consumed by copepods in the 0~4000 m water column (Yamaguchi et al. 2002). In the present study, each copepodid stage was identified and enumerated whenever possible to analyze species-specific DVM and OVM patterns of each copepod. The DVM and OVM patterns were elucidated in accordance with the bathymetric distribution of each copepod to test the predation pressure hypothesis.

MATERIALS AND METHODS

Field sampling and enumeration

As part of the research program “WEST-COSMIC” (“Western Pacific Environment Assessment Study on CO_2 Ocean Sequestration for Mitigation of Climate Change”, see Ishizaka 1999), a set of day and night deep samplings was made at stn. Knot (44°N, 155°E; with a depth of around 5340 m) located in the western subarctic Pacific during 19~21 Aug. 1998 (Fig. 1). Zooplankton were collected from discrete depth intervals using closing-NORPAC nets (with a mesh size of 90 μm and a mouth opening of 0.16 m^2, see Motoda 1957) from 0~100 and 100~200 m, and using VMPS (Vertical Multiple Plankton

Sampler, with a mesh size of 90 µm and a mouth opening of 1.0 m^2, Tsurumi Seiki, Kanagawa, Japan; Terazaki and Tomatsu 1997) from 200~500, 500~1000, 1000~1500, 1500~2000, 2000~3000, and 3000~4000 m (Table 1). A flow meter (Rigosha, Saitama, Japan) was mounted in the mouth of the net to register the volume of water passing through the net. Daytime samplings were made during 10:59~14:25 (local time) and night samplings during 00:19~03:55. Zooplankton samples were split on board, and 1/2 aliquots were immediately preserved with 5% borax-buffered formalin-seawater, and the other 1/2 aliquots were filtered through 50-µm-mesh netting and stored at -80°C for later determination of total zooplankton biomass and chemical composition.

Vertical profiles of water temperature and salinity were determined using a CTD system (Seabird SBE-9, Washington, USA). Dissolved oxygen was measured using the Winkler titration method on water samples from 12-L Niskin bottles (General Oceanics, Miami, USA) rosette-mounted onto the CTD system.

At the land-based laboratory, copepods in the zooplankton samples were identified and counted under a dissecting microscope. The copepodid stages of most of the copepod species studied in the present investigation have not been described. Therefore, we created a brief identification key for each congener species. For *Neocalanus* copepods, their prosome lengths (PLs) at given copepodid (C) stages were found to be bimodal. We assigned the large form (mean PL ± 1 SD all in mm: 0.90 ± 0.05 for C1, 1.71 ± 0.07 for C2, 2.79 ± 0.18 for C3, 4.45 ± 0.15 for C4, and 7.81 ± 0.44 for C5) to be *N. cristatus* and the small form (0.78 ± 0.02 for C1, 1.21 ± 0.04 for C2, 1.85 ± 0.04 for C3, 2.53 ± 0.07 for C4, and 3.86 ± 0.11 for C5) to be *N. plumchrus*. While *N. flemingeri* is reported to be distinguishable from *N. plumchrus* from C2 onward (Kobari and Ikeda 2001a), we did not attempt to separate these 2 species. This was largely because *N. plumchrus* is known to be dominant in the present study site during Aug. (Kobari and Ikeda 2001b). Therefore, C1~C4 *N. plumchrus* of this study may have included some C1~C4 *N. flemingeri*. After C5, we identified *N. flemingeri* (small maxilla) from *N. plumchrus* (large maxilla) based on the proportion of the maxilla to the prosome (see Miller 1988). Based on the degree of lipid deposition, C5 *N. cristatus* and *N. plumchrus* were classified into 3 stages: 1, no lipid; 2, some lipids; and 3, nearly full of lipids. Adult females of *N. cristatus* and *N. flemingeri* were classified into 3 and 4 maturing stages, respectively, depending on the developmental condition of the ovaries (Kobari and Ikeda 1999 2001a).

For aetideid copepods, *Gaetanus simplex* and *Gaidius variabilis* could be identified from the C1 stage. The length of the frontal dorsal spine of *Gae. simplex* is longer than that of *Gai. variabilis*

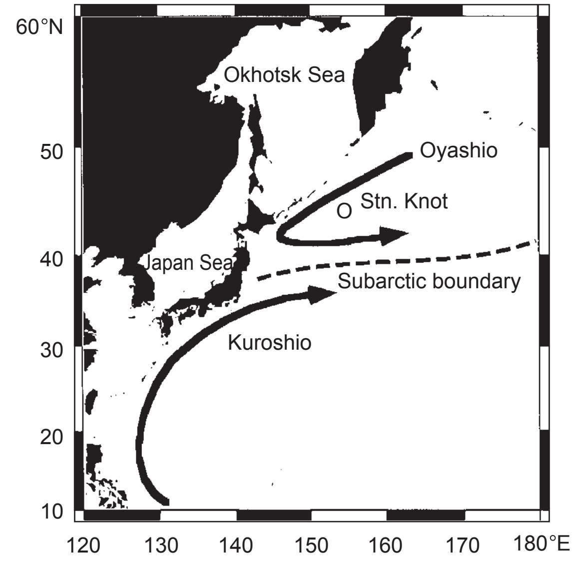

Fig. 1. Location of stn. Knot (44°N, 155°E) in the western subarctic Pacific Ocean. The water current system and approximate position of the subarctic boundary are shown.

Table 1. Plankton sampling data at stn. KNOT in the western subarctic Pacific. VMPS: Vertical Multiple Plankton Sampler, C-NORPAC: closing NORPAC net

Date	Local time	Type of net	Depth strata (m)	Water volume filtered (m^3)
19 Aug. 1998	10:59-11:27	VMPS	3000-4000	950
(Day)	11:27-11:56	VMPS	2000-3000	950
	11:56-12:10	VMPS	1500-2000	475
	12:10-12:24	VMPS	1000-1500	476
	12:24-12:38	VMPS	500-1000	474
	12:38-12:46	VMPS	200-500	285
	14:10-14:17	C-NORPAC	100-200	45
	14:22-14:25	C-NORPAC	0-100	46
21 Aug. 1998	0:19-0:52	VMPS	3000-4000	951
(Night)	0:52-1:25	VMPS	2000-3000	951
	1:25-1:41	VMPS	1500-2000	475
	1:41-1:57	VMPS	1000-1500	476
	1:57-2:14	VMPS	500-1000	474
	2:14-2:24	VMPS	200-500	285
	3:41-3:48	C-NORPAC	100-200	44
	3:52-3:55	C-NORPAC	0-100	45

(with a frontal spine length/PL of ≥ 0.10 for the former and ≤ 0.07 for the latter). C1 of both species lacks the frontal spine, but they differ in body width (0.24 ± 0.01 mm for *Gae*. *simplex* and 0.30 ± 0.01 mm for *Gai*. *variabilis*). *Paraeuchaeta* species are also distinguishable by body width (Yamaguchi and Ikeda 2001).

Five metridinid copepods (*Metridia pacifica*, *M*. *okhotensis*, *M*. *asymmetrica*, *M*. *curticauda*, and *Pleuromamma scutullata*) are dominant in the study region. Epi- and mesopelagic species (*M*. *pacifica* and *M*. *okhotensis*) are characterized by dissimilar body sizes (with a total length in adult females of 2.6~3.1 and 4.5 mm, respectively; see Brodsky 1967), and the features are persistent down to C1. The mesopelagic *Ple*. *scutullata* has large outer denticles in the proximal part of the antennules from C2. The body size of C1 of *Ple*. *scutullata* is somewhere between those of *M*. *pacifica* and *M*. *okhotensis*. There is limited information about the bathy- and abyssopelagic *M*. *asymmetrica* and *M*. *curticauda*, but these 2 species can be identified as a large form (mean PL ± 1 SD all in mm: 0.75 ± 0.03 for C1, 0.93 ± 0.05 for C2, 1.31 ± 0.05 for C3, 1.73 ± 0.03 for C4F/M, and 2.38 ± 0.08 for C5F/M) for *M*. *asymmetrica* (adult female: 2.62 ± 0.07 mm) and a small form (0.55 ± 0.03 for C1, 0.78 ± 0.03 for C2, 1.09 ± 0.05 for C3, 1.39 ± 0.05 for C4, and 1.69 ± 0.10 for C5) for *M*. *curticauda* (adult female: 1.81 ± 0.08 mm). More details of the identification keys used for the copepodids of individual copepod species will be published elsewhere.

Depth where populations resided

To make quantitative comparisons possible, the depth above and below that at which 50% of the population resided ($D_{50\%}$) was calculated for each copepod species (see Pennak 1943). Additional calculations were made of depths above which 10% ($D_{10\%}$), 25% ($D_{25\%}$), 75% ($D_{75\%}$), and 90% ($D_{90\%}$) of the population occurred. Because of the large intervals between sampled strata in the present study (minimum of 100 m), the absence/presence of DVM was tested by overlapping/non-overlapping depth ranges of $D_{25\%}$ and $D_{75\%}$ for daytime and nighttime, respectively. DVM was tested with day-night comparisons using the Wilcoxon test, and OVM was tested using the $D_{50\%}$ value by one-way ANOVA. To avoid errors due to the small sample size in the DVM analysis, comparisons were made only for stages at which the abundance was > 20 individuals/m^2.

RESULTS

Hydrography

At stn. Knot, the surface temperature (13.5 °C) decreased with increasing depth, showing a sub-minimum of 1.9°C at 150 m and a sub-maximum of 3.3°C at 500 m (Fig. 2). The decrease in temperature with depth lessened below 500 m and reached 1.5°C at a depth of 4000 m. Integrated mean temperatures for each zooplankton sampling layer were 5.1°C for 0~100 m, 2.3°C for 100~200 m, 3.2°C for 200~500 m, 2.9°C for 500~1000 m, 2.3°C for 1000~1500 m, 2.0°C for 1500~2000 m, 1.7°C for 2000~3000 m, and 1.5°C for 3000~4000 m.

Salinities ranged from 32.7 to 34.7 psu and increased with depth, which is a common feature throughout the subarctic Pacific (Dodimead et al. 1963). General hydrographical features seen at stn. Knot of this study were similar to those of the Oyashio region during the same season (Kono

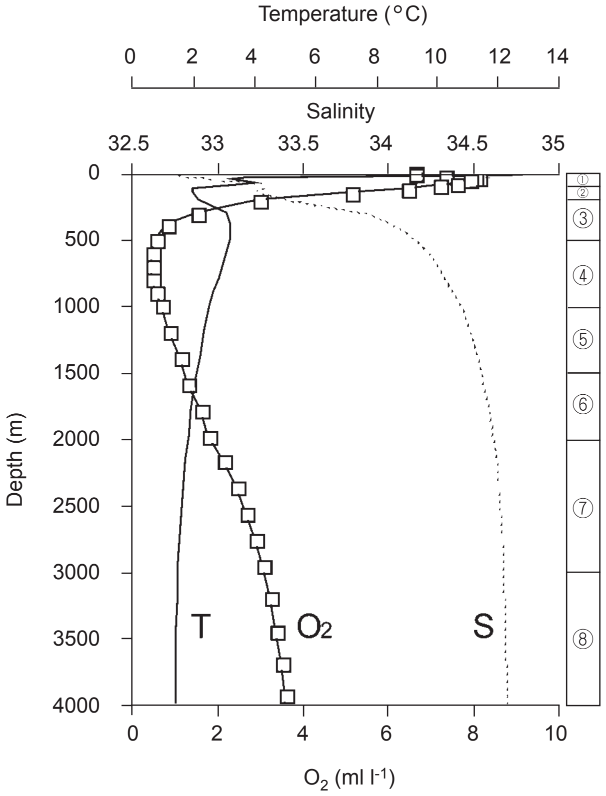

Fig. 2. Vertical profiles of temperature (°C), salinity psu, and dissolved oxygen (ml/l) at stn. Knot in the western subarctic Pacific Ocean, 19~21 August 1998. Circled numbers in the right column indicate the depth strata of the zooplankton sampling.

1997), i.e., the presence of a subsurface minimum temperature at 100 m, a maximum temperature at 300 m, and the halocline at 200~300 m.

Dissolved oxygen content was highest in the subsurface layer (with a maximum of 8.2 ml/l at 30 m), decreasing rapidly with increasing depth and reaching a minimum (0.46 ml/l) at 600~800 m. Dissolved oxygen lower than 2 ml/l extended to 300~2000 m depth. The integrated mean dissolved oxygen concentrations for each zooplankton sampling layer were 7.47 (0~100 m), 5.22 (100~200 m), 1.36 (200~500 m), 0.51 (500~1000 m), 1.18 (1000~1500 m), 1.25 (1500~2000 m), 2.47 (2000~3000 m), and 3.29 ml/l (3000~4000 m).

VERTICAL DISTRIBUTION OF COPEPODS

Epipelagic copepods

C5 or adult females of large grazing copepods (*Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, and *Eucalanus bungii*) were found in the mesopelagic layer (Fig. 3). On the other hand, their early copepodid stages (C1~C4 of *N. cristatus*, C1~C4 and C5 (1) of *N. plumchrus*, and C1 and C2 of *E. bungii*) were distributed near the surface layer both day and night. Thus, OVM behavior was evident for these 4 species ($p < 0.01$, one-way ANOVA). Across all copepodid stages, diel changes in $D_{50\%}$ were observed to a small extent, and their vertical distribution ranges significantly overlapped between day and night. As one exception, adult female (stage 3) *N. cristatus* occurred from a wide depth stratum in low numbers (< 20 individuals/m^2 throughout the water column). Within the same copepodid stage, vertical distribution patterns varied with gonad developmental condition (Fig. 3). C5 and adult female *N. cristatus* and C5 *N. plumchrus* showed developmental descent. Adult female specimens in diapause (adult female stage 1) of *N. flemingeri* occurred from deeper layers than those of reproducing adult female stage 2~4 specimens. The depths at where they were in diapause and reproducing varied with species: those of C5 stage 3 *N. cristatus* occurred at 500~1500 m, of adult female stage 1 *N. flemingeri* occurred at 500~1000 m, of C5 stage 2 or 3 *N. plumchrus* occurred at 200~800 m, and of C5F/M *E. bungii* occurred at 300~800 m.

Meso- and bathypelagic copepods

Two mesopelagic copepods (*Gae. simplex* and *Ple. scutullata*) showed similar vertical distribution patterns: early copepodid stages (C1~C3 for *Gae. simplex* and C1~C5 for *Ple. scutullata*) were found at 300~400 m both day and night, while late copepodid stages (C5M and adult female *Gae. simplex*, and adult female *Ple. scutullata*) migrated upwards at night ($p < 0.05$, Wilcoxon test, Fig. 4). Adult female *Ple. scutullata* underwent a nocturnal ascent, but this was not the case for adult males of this species.

In the lower mesopelagic or upper bathypelagic realm, *Gai. variabilis* showed an ontogenetic migration toward shallower layers with progression of development; the deepest (800~1200 m) stage was C1, and the shallowest stage (300~500 m) was adult females/males (Fig. 4). Thus, the OVM pattern was confirmed for *Gai.*

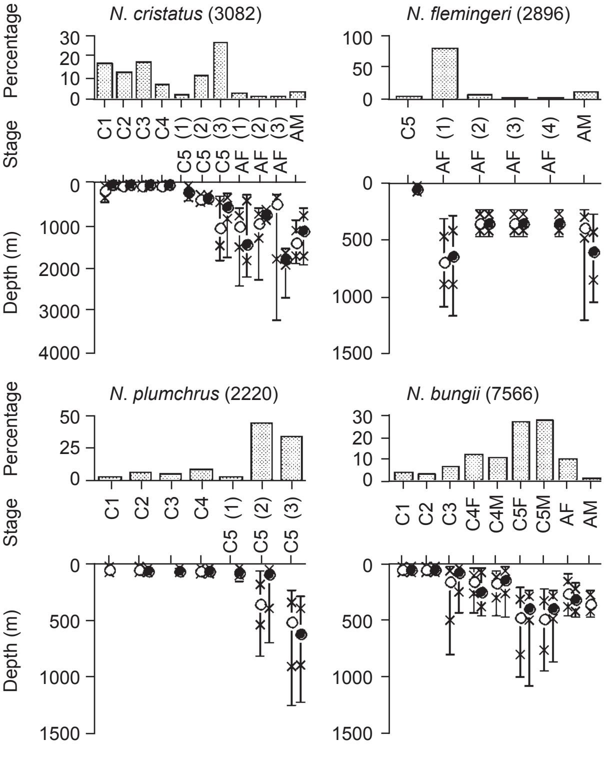

Fig. 3. Epipelagic copepods (*Neocalanus cristatus*, *N. flemingeri*, *N. plumchrus*, and *Eucalanus bungii*). Copepodid stage 5 and adult females of *Neocalanus* sp. were distinguished by lipid storage and gonad developmental stages (shown in parentheses). The total abundance (individuals/m^2: 0~4000 m) of all copepodids of each species is shown in parentheses, while the percentage composition of each copepodid stage to the total is presented in the histogram. Open and solid symbols indicate depths of the 50% population distribution ($D_{50\%}$) for day and night samples, respectively. Crosses indicate the depths of $D_{25\%}$ and $D_{75\%}$, and bars indicate the depth ranges of $D_{10\%}$ and $D_{90\%}$. AF, adult female; AM, adult male.

variabilis ($p < 0.01$, one-way ANOVA), although the species did not show a DVM pattern.

Paraeuchaeta species

Among 3 *Paraeuchaeta* species (*P. elongata*, *P. birostrata*, and *P. rubra*) which are dominant in this region, vertical partitioning of each species was evident (Fig. 5). *Paraeuchaeta elongata* is largely distributed in the shallowest layer (< 500 m for adult females) and *P. rubra* in the deepest layer (1000~2000 m), with *P. birostrata* found at an intermediate layer (500~1000 m). All these *Paraeuchaeta* species exhibited OVMs characterized by developmental ascent; C1 occurred from the deepest layer, while the rest of the stages (C2 to adult for *P. elongata* and *P. birostrata*, and C4 to adult for *P. rubra*) were distributed in shallower layers than the C1s ($p < 0.05$, one-way ANOVA). C5M and adult female *P. elongata* exhibited shallower distributions at night ($p < 0.05$, Wilcoxon test). It was noted that C1 and C5F of *P. birostrata*, and C1, C2, and C5M of *P. rubra* showed day-night vertical distributions which did not overlap, but these may have been in error due to the small sample size.

Metridia species

Four *Metridia* species (*M. pacifica*, *M. okhotensis*, *M. asymmetrica*, and *M. curticauda*) are dominant in this region. As observed for the *Paraeuchaeta* species above, vertical habitat partitioning was also seen in *Metridia* species: from shallow to deep, *M. pacifica* (0~300 m for adult females), *M. okhotensis* (400~800 m), *M. asymmetrica* (1500~2500 m), and *M. curticauda* (2500~3500 m) (Fig. 6). Abundance of each species decreased with increasing depth. *Metrida pacifica* was distributed more deeply with progression of its development, and adult females showed a clear nocturnal DVM ($p < 0.05$, Wilcoxon test). C1~C4 of *M. okhotensis* were very scarce, and its C5 and adults were distributed to the mesopelagic zone (300~600 m for C5F/M and 400~800 m for adult females) throughout both day and night. *Metrida asymmetrica* underwent OVM which was characterized by developmental ascent ($p < 0.05$, one-way ANOVA), but no DVM was detected. The deepest occurring *M. curticauda* also underwent OVM which was characterized by developmental ascent ($p < 0.05$, one-way ANOVA), but no DVM.

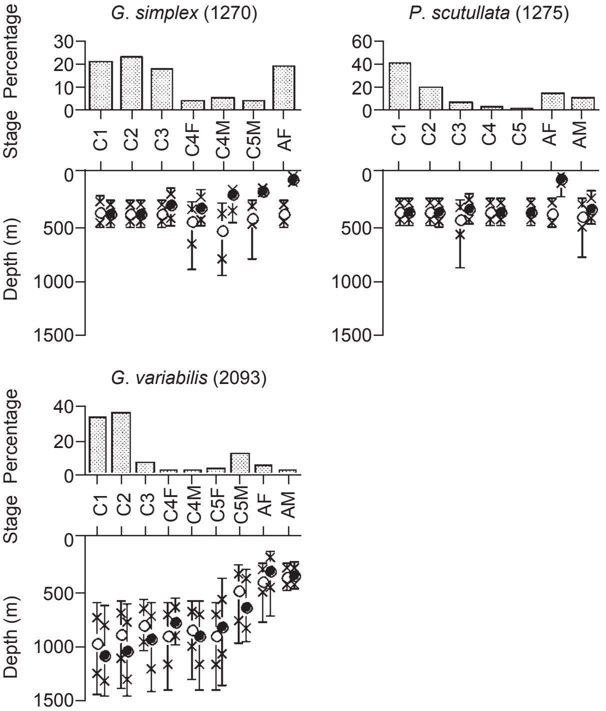

Fig. 4. As in Fig. 3, but for 2 mesopelagic (*Gaetanus simplex* and *Pleuromamma scutullata*) and 1 bathypelagic (*Gaidius variabilis*) copepods.

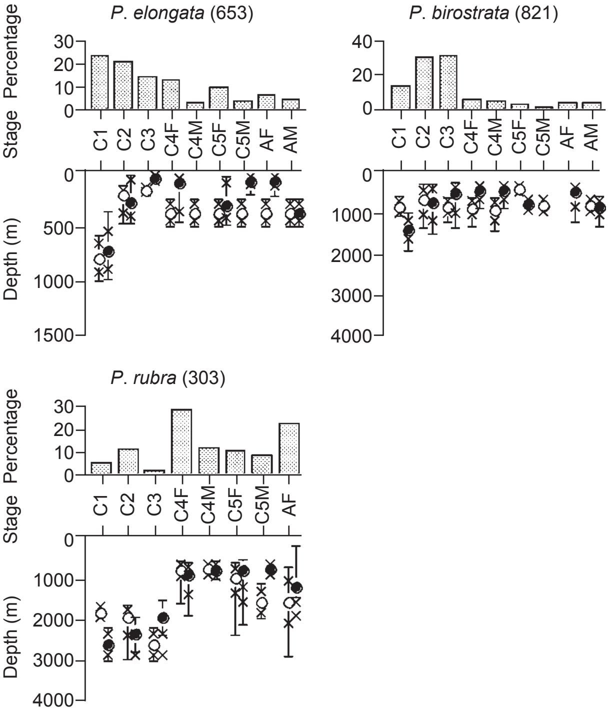

Fig. 5. As in Fig. 3, but for 3 Euchaetid copepods (*Paraeuchaeta elongata*, *P. birostrata*, and *P. rubra*).

DISCUSSION

Vertical habitat partitioning

In oceanic habitats, congeners usually have similar food habits and migratory behaviors, thereby competition may be a major mechanism separating their vertical distributions. In fact, “sibling copepod species” have been known to exhibit their maximum abundances at different depths during day through night (Ambler and Miller 1987). The strongest gradients in all biotic and abiotic factors parallel the depth gradient, suggesting that vertical partitioning of habitats among species is a main mechanism creating niche separation. McGowan and Walker (1979) examined the depth dimension of niche diversification for adult copepods in the central gyre of the North Pacific Ocean. They concluded that the vertical dispersion of these copepods provides a major contribution to niche diversification.

The vertical partitionings of 5 meso- and bathypelagic aetideid copepods were reported from the Greenland Sea Gyre (Richter 1995). Several other studies have indicated that vertical partitioning among deep-sea copepods is a common feature in oceanic regions (Richter 1994 1995, Auel 1999). Fourteen Euchaeta copepods inhabiting the Rockall Trough were partitioned vertically in the 2500 m water column (Mauchline 1992 1994 1995). Spatial separation of copepods in the water column appears to be a widespread strategy for minimizing competition among congeneric species. Further, Mackas et al. (1993) observed small-scale vertical partitioning among epipelagic copepods during their annual growing season in the surface layer, i.e. *Neocalanus cristatus* resides below *N. flemingeri* and *N. plumchrus*. The results of the present study are consistent with those previous findings.

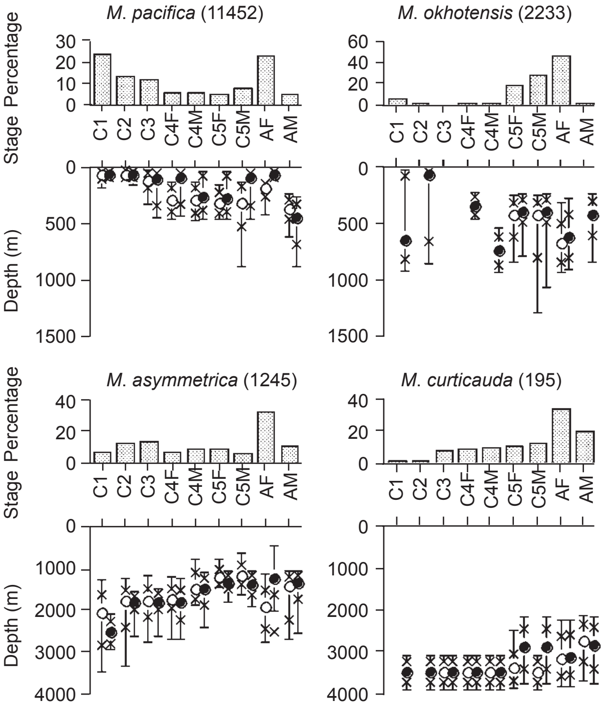

Fig. 6. As in Fig. 3, but for 4 Metridinid copepods (*Metridia pacifica*, *M. okhotensis*, *M. asymmetrica*, and *M. curticauda*).

The OVM pattern was similar within *Neocalanus* (developmental descent) and *Paraeuchaeta* species (C1 distributed in the deepest layer), while it varied within *Metridia* species: epipelagic species (*M. pacifica* and *M. okhotensis*) showed developmental descent, while bathypelagic species (*M. asymmetrica* and *M. curticauda*) showed an opposite OVM pattern (developmental ascent) (Fig. 6). As discussed below, OVM characterized by developmental ascent seems to be a common phenomenon for bathypelagic copepods.

Diel/ontogenetic vertical migration

Table 2 summarizes the DVM and OVM patterns of 13 copepod species (7 genera) examined in the present study. DVM was observed for late copepodid stages of 4 species of which adult females were distributed above 360 m. Dormant *Eucalanus bungii* (see Miller et al. 1984) was an exception to this. These results indicate that the role of copepod DVM as a “biological pump” (see Dam et al. 1995, Morales 1999) is limited to < 500 m depth in this region. Adopting the “ladder of migration” hypothesis (Vinogradov 1962), active agents which transport materials below 500 m depth, are not copepods, but other macrozooplankton taxa (such as euphausiids or mysids) or micronektonic fish or shrimp in this region. Moku et al. (2000) discussed some quantitative aspects of the role of DVM of mesopelagic fishes in the vertical transport of materials in this region.

The seasonal OVM behavior has been well documented for large grazing copepods in high-latitude seas (see Miller et al. 1984, Atkinson and Sinclair 2000). In the western subarctic Pacific, seasonal OVM has been reported for *N. cristatus*, *N. flemingeri*, *N. plumchrus*, and *Eucalanus bungii* (Miller et al. 1984, Kobari and Ikeda 1999 2001a b). It was noted that *M. okhotensis* populations were dominated by C5M and adult females in our samples (Fig. 6). These stages occurred from the mesopelagic layer (300~800 m) without DVM behavior. The population structure and vertical distribution of *M. okhotensis* may be indicative of a dormant state in the present study season (August). *Metrida okhotensis* is the subarctic Pacific counterpart of the North Atlantic *M. longa* or the Southern Ocean *M. gerlachei*. However, ecological information about *M. okhotensis* was long limited until the study of Padmavati et al. (2004) and Ikeda (pers. comm.). According to Padmavati et al. (2004) and Ikeda (pers. comm.), *M. okhotensis* in the western subarctic Pacific has a life cycle characterized by overwintering at C1 and adult females, but since these overwintering stages continue feeding, they are not dormant.

The dormant stages of large grazing copepods (C5 of *E. bungii*, *N. plumchrus*, and *N. cristatus*, and adult females of *N. flemingeri*) and their resident depths (300~800 m for *E. bungii* and *N. plumchrus*, 500~1000 m for *N. flemingeri*, and 500~1500 m for *N. cristatus*) obtained in this study are in good agreement with previous findings (Sekiguchi 1975, Tsuda et al. 1999, Kobari and Ikeda 1999). As possible parameters which decide the depth at where copepods enter dormancy, the oxygen minimum layer (Weikert 1980), presence of predators (Richter 1995, Kaartvedt 1996, Dale et al. 1999), and water masses (Weikert et al. 2001) have been considered. In the present study, the oxygen minimum layer (< 2 ml/l: 300~2000 m, Fig. 2) was found to be within the range of the depth distribution of these copepods. It is interesting to note that the depths (> 300 m) where dormant specimens occurred corresponded to the depth beyond which no DVM behavior was observed (see above). Considering their large body size, vivid coloration, and oil droplets in the prosome, the dormant copepods are thought to be under high risk of predation by epipelagic (Taka et al. 1982) and mesopelagic fishes (Beamish et al. 1999, Moku et al. 2000). From this view, twilight depths at which the dormant copepods occur are advantageous for reducing predation mortality caused by visual predators (fishes).

Table 2. Summary of vertical distribution pattern of calanoid copepods at stn. Knot in the western subarctic Pacific during 19-21 Aug. 1998. DVM was detected by Wilcoxon test and defined its magnitudes by the distances from (day $D_{50\%}$-night $D_{50\%}$). Note that DVM for copepodid stages which occurred a few number (<20 individuals m^{-2}) was not analyzed. Magnitude of OVM was calculated from the difference in depth distribution of day $D_{50\%}$ value of C1 and adult female ($D_{50\%}$ [adult female]-D [C1]). ● : dormant copepods

Species	Day $D_{50\%}$ of adult female(m)	DVM (magnitude: m)	Magnitude of OVM(m)
Metridia pacifica	179	adult female (125)	111
Eucalanus bungii ●	266	no	239
Gaetanus simplex	350	C5M (238), adult female (300)	10
Paraeuchaeta elongata	350	C5M (275), adult female (271)	-400
Pleuromamma scutullata	361	adult female (297)	11
Gaidius variabilis	388	no	-543
Neocalanus flemingeri ●	669	no	300
Metridia okhotensis	680	no	-26
Paraeuchaeta birostrata	750	no	-585
Neocalanus cristatus ●	939	no	779
Paraeuchaeta rubra	1500	no	-536
Metridia asymmetrica	1939	no	-306
Metridia curticauda	3167	no	-348

Predation pressure hypothesis

In contrast to the fact that the OVM pattern of all epipelagic copepods (including interzonal species) is characterized by developmental descent, those residing at lower mesopelagic zones (*Gai. variabilis*, *P. elongata*, and *P. birostrata*) and in bathypelagic zones (*P. rubra*, *M. asymmetrica*, and *M. curticauda*) are characterized by developmental ascent. This shift of OVM patterns of copepods occurs at around 360 m (see Table 2). Interestingly, this depth corresponds to the bound-

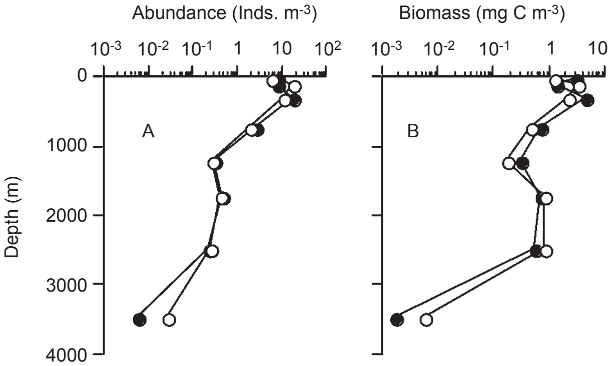

Fig. 7. Vertical distribution of abundance (A) and biomass (B) of chaetognaths at stn. Knot in the western subarctic Pacific Ocean, 19~21 Aug. 1998. Note that the abundance and biomass scales are log-scales.

ary between the presence (copepods living above the depth) and absence (those living below the depth) of DVM behavior as mentioned above.

As an OVM pattern, developmental ascent behavior has been reported for some meso- and bathypelagic zooplankton: *P. elongata* in the Japan Sea (Morioka 1975), *Lucicutia longicauda* in the Red Sea (Weikert and Koppelmann 1993), *Chiridius obtusifrons* in the Greenland Sea (Richter 1994), and *Chiridius armatus* in a Nordic fjord (Falkenhaug et al. 1997). In the present study region, copepods including *Gai. variabilis*, *P. elongata*, and *P. birostrata* (Yamaguchi and Ikeda 2000b 2002a), and ostracods including *Discoconchoecia pseudodiscophora*, *Orthoconchoecia haddoni*, and *Metaconchoecia skogsbergi* (Kaeriyama and Ikeda 2002) are reported to exhibit this OVM pattern. The OVM pattern of developmental ascent of ostracods has also been reported in the Greenland Sea (Richter 1994).

In an attempt to postulate a decrease in predation pressures on copepods with increasing depth at stn. Knot, the number and biomass of typical predatory zooplankters, i.e., chaetognaths, were enumerated or estimated for the present samples. Biomass was calculated based on biovolume data by multiplying by 0.06 pg C/μm^3 (Parsons et al. 1984). As a result, it was shown that the abundance and biomass of chaetognaths decreased rapidly with increasing depth (Fig. 7). The presence of abundant predators is known to induce DVM behavior in epipelagic copepods (Ohman et al. 1983, Bollens and Frost 1989), which was also postulated in the present results (Table 2). The lack of DVM in meso- and bathypelagic copepods in the present results is indicative of their relaxation from predation pressure. A pattern of progressive decrease in predation toward greater depths is consistent with an observation of a gradual reduction in lifetime fecundities in deeper-living species including *Euchaeta* copepods in the North Atlantic (Auel 1999), *Paraeuchaeta* copepods in this study (Table 3), and pelagic animals in general (Mauchline 1991). In other words, deeper-living species can maintain their population by releasing fewer eggs.

Table 3. Day D$_{50\%}$ and lifetime fecundity of *Paraeuchaeta* spp. (Yamaguchi and Ikeda 2002b). Note that fecundity of *Paraeuchaeta* spp. were estimated assuming the number of broods as three for this genus (Ozaki 1998)

Species	Day D$_{50\%}$ of adult female (m)	Lifetime fecundity (eggs female)
P. elongata	350	79
P. birostrata	750	26
P. rubra	1500	22

From the viewpoint of a pronounced vertical gradient in predation pressure in the ocean, a developmental descending pattern of OVM seen in epipelagic species in this study implies that they are spending their juvenile lives in shallow layers which are characterized by rich food/high predation risks, then shifting to deep layers characterized by a reduced food supply/lower predation. Recently, De Robertis (2002) proposed that planktonic animals select their habitats to minimize the ratio of mortality risk/energy gain incorporating light- and size-dependent vulnerability to visual predators. Dale et al. (1999) considered that the OVM of *Calanus* spp. is a result of predator avoidance. On the other hand, a developmental ascending pattern of OVM observed in bathypelagic species suggests that they spend juvenile stages in lower-predation environments (deep layer) and ascend to higher-food environments with development, thereby running increased risks of predation by other animals. Since their lifetime fecundity is low, reducing predation mortality at the juvenile stage is the prime importance of the OVM strategy for bathypelagic species. In addition to these 2 extreme life history traits shown by epipelagic and bathypelagic species, the absence of an OVM in mesopelagic species (Table 2) is the 3rd life history trait. DVM behavior of late copepodid stages of mesopelagic species may be interpreted as being advantageous to secure nutrition for their reproduction.

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