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# Inter-oceanic comparison of planktonic copepod ecology (vertical distribution, abundance, community structure, population structure and body size) between the Okhotsk Sea and Oyashio region in autumn

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Several aspects of the ecology of planktonic copepods (vertical distribution, abundance, community structure, population structure and body size) were evaluated and compared between communities in the autumn, in the Okhotsk Sea and the adjacent Oyashio region in the western North Pacific. Vertically, copepods were concentrated primarily at depths of 250 to 500 m in the Okhotsk Sea but near the surface in the Oyashio region. The abundances of most of the copepods were greater in the Oyashio region with the exception of *Metridia okhotensis*, which showed significantly greater abundance in the Okhotsk Sea (30 times greater) and dominated the copepod community, accounting for approximately 70% of total copepod abundance. The population structure of the dominant copepods in the Okhotsk Sea was dominated by late copepod stages, suggesting that these copepods were in the resting phase. The prosome lengths of most of the copepods were larger in the Okhotsk Sea than in the Oyashio region and the larger body size is probably due to the lower habitat temperatures. The special ecological characteristics of planktonic copepods in the Okhotsk Sea are possibly related to the development of a strong pycnocline in the Okhotsk Sea. The consequences of differences in copepod communities between regions were discussed from the viewpoints of life cycle timing and the scale of active vertical flux.

**Keywords:** zooplankton; *Metridia okhotensis*; abundance; prosome length; vertical distribution



## Introduction

Planktonic copepods dominate the zooplankton community of the global ocean. They form a vital link between primary producers and higher trophic levels and can accelerate vertical flux of material (the biological pump) (cf. Mauchline 1998). Given their importance in marine ecosystems, an inter-oceanic comparison of their ecology is of special interest. Faunistic comparisons have revealed differences between the Arabian, Mediterranean and Red Seas (Halim 1984; Böttger-Schnack 1994); between the Japan Sea and North Pacific (Vinogradov 1973; Vinogradov and Sazhin 1978); and between the Sulu and Celebes Seas (Nishikawa et al. 2007; Matsuura et al. 2010). The life cycle stages of the dominant copepods also show inter-oceanic differences: *Calanus* and *Neocalanus* life stages dominate in the northern hemisphere (Conover 1988) and copepods are also dominant in the Southern Ocean (Atkinson 1998). The ecology of

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copepods has significant effects on higher trophic levels and the amount of vertical material flux, and the evaluation of detailed inter-oceanic differences is a key issue in biological oceanography.

The Okhotsk Sea is the southernmost limit of marginal sea ice coverage in the northern hemisphere (Zenkevitch 1963). The hydrographical conditions of the Okhotsk Sea are characterized by the presence of cold intermediate water below the thermocline (Kitani 1973). Although the plankton fauna of the Okhotsk Sea is similar to that of the Oyashio region (Pinchuk and Paul 2000), it has been reported that body sizes of several species from the former region were greater than those from the latter (Kobari and Ikeda 1999, 2001a, 2001b). Nevertheless, the zooplankton biomass, community structure and vertical distribution patterns in the Okhotsk Sea and adjacent western subarctic Pacific (Oyashio region) have not been thoroughly compared.

In the present study, ecological characteristics of the planktonic copepods (vertical distribution, abundance, community structure, population structure and body size of dominant species) were evaluated in the Okhotsk Sea and the adjacent Oyashio region in the autumn season from 1996 to 1998. The inter-oceanic differences in copepod ecology are analysed to determine the factors that govern their differences, and the consequences on life cycle timing and the scale of active vertical flux are discussed.



## Materials and methods

### *Field sampling*

In the autumn (September–December) of 1996–1998, vertically stratified samples were taken using 0.1 mm mesh closing nets fitted with flow-meters, to a depth of 2000 m (0–thermocline, thermocline–250 m, 250–500 m, 500–1000 m and 1000–2000 m). Vertically stratified sampling was performed at six stations in the Oyashio region and five stations in the Okhotsk Sea (Table 1, Figure 1). To evaluate diel

Table 1. Zooplankton sampling data at each station in the Oyashio region and Okhotsk Sea during September to December in 1996–1998. Two sampling gears were used for zooplankton sampling.

| Location/station | Position | Date (D/N) | Sampling gear | |
|---|---|---|---|---|
| | | | Closing net | IONESS |
| Oyashio region | | | | |
| St. 19 | 44°26′N, 149°40′E | 16 October 1996 (D) | • | • |
| HO96103 | 41°30′N, 145°47′E | 2 October 1996 (N) | • | |
| P18 | 41°00′N, 146°00′E | 8 December 1996 (D) | • | |
| P17 | 41°30′N, 146°00′E | 8 December 1996 (N) | • | |
| HO97165 | 41°30′N, 145°47′E | 5 October 1997 (D) | • | |
| HO97165 | 41°30′N, 145°47′E | 5 October 1997 (N) | • | |
| Okhotsk Sea | | | | |
| OK24 | 50°15′N, 151°15′E | 4 November 1996 (D) | • | • |
| OK30 | 46°00′N, 145°00′E | 9 November 1996 (D) | • | |
| HO97150 | 44°40′N, 145°20′E | 1 October 1996 (N) | • | |
| HO98093 | 44°40′N, 145°20′E | 20 September 1998 (D) | • | |
| HO98093 | 44°40′N, 145°20′E | 20 September 1998 (N) | • | |

Abbreviations: D, daytime; N, night time.

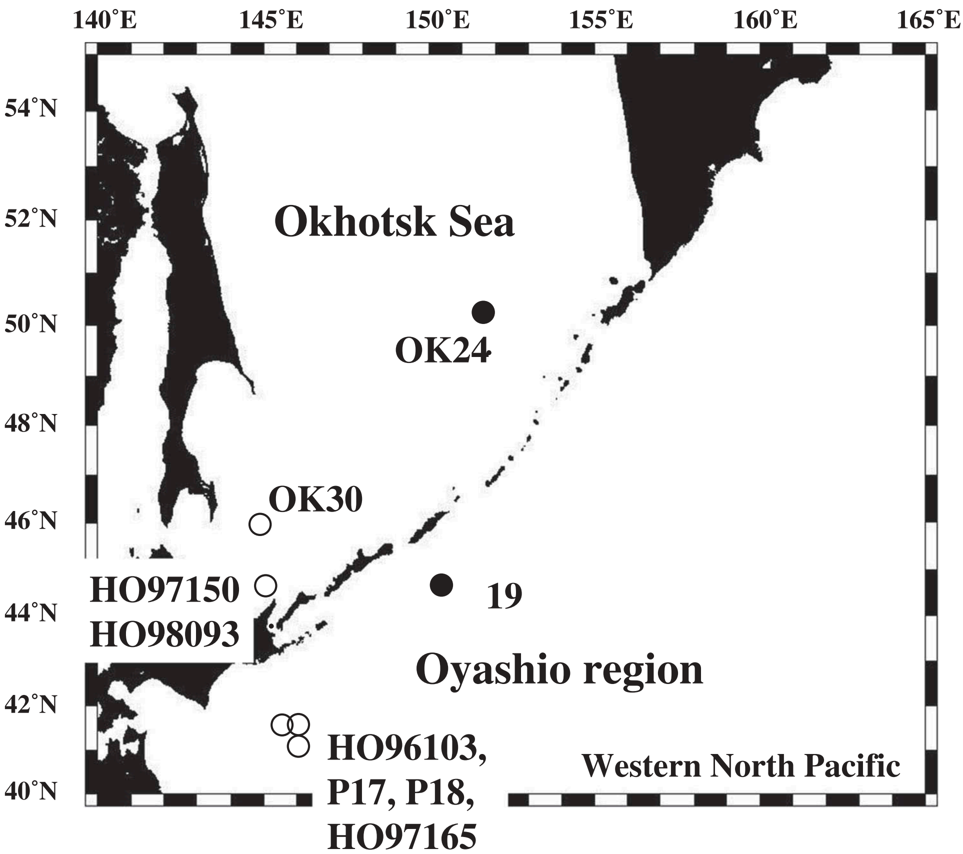


Figure 1. Location of the sampling stations in the Okhotsk Sea and Oyashio region from September to December in 1996–1998. ○: closing net sampling, ●: closing net and IONESS sampling.

vertical distribution, additional obliquely stratified samples to a depth of 500 m (0–25, 25–50, 50–250 and 250–500 m) with a 0.335 mm mesh IONESS (SEA Co. Ltd, Urayasu, Chiba, Japan, modified version of MOCNESS, Wiebe et al. 1985) were taken during the time periods 6:00–8:00, 10:00–12:00, 17:00–19:00 and 22:00–24:00 at one station each in the Oyashio region (St. 19, 16 October 1996) and in the Okhotsk Sea (St. OK24, 4 November 1996). After collection, all samples were preserved immediately in 5% borax-buffered formalin on board. At each station, water temperature was measured with a CTD (Neil Brown or Seabird Co. Ltd, Falmouth, MA, USA). For the IONESS stations, 1-L water samples collected using a Niskin rosette sampler were filtered with a GF/F filter, and chlorophyll *a* (chl. *a*) was measured using a fluorometer (Turner Design, Inc., Bellevue, WA, USA).

### *Sample analysis*

The zooplankton settling volumes of the samples collected by closing net were measured at a precision of 8.6 ml. For the IONESS samples, the zooplankton taxa and species/stages of the calanoid copepods were identified and counted. For species identification, we referred mainly to Brodsky (1967) and Frost (1989) for *Pseudocalanus* spp., and Miller (1988) for *Neocalanus flemingeri* Miller, 1988, as these species were not described by Brodsky. Prosome lengths (PL) of the dominant calanoid copepods collected by the IONESS (a total of 34 copepodid stages of 17 species) were measured by eye-piece micrometer at a precision of 0.02–0.10 mm. For inter-oceanic comparisons between the Oyashio region and Okhotsk Sea, a *U*-test was applied to zooplankton biovolume, taxon abundance, and PL of the dominant copepods.

## Results

### Hydrography

At all stations in the Okhotsk Sea, the vertical temperature profiles were characterized by a temperature sub-minimum (<2°C) between 50 and 400 m depths; this was not the case in the Oyashio region (Figure 2A). In the Okhotsk Sea, a strong thermocline occurred with a halocline, resulting in a strong pycnocline (Figure 2B). The development of the pycnocline, which prevents vertical admixture of water, and therefore chl. *a* in the Okhotsk Sea, was concentrated above the pycnocline (Figure 2B).

### Zooplankton biovolume

The vertical profiles of zooplankton biovolume in the Oyashio region and Okhotsk Sea were different; the profile peaked at the surface layer (0 m–thermocline) in the former and at a depth of 250–500 m in the latter (Figure 3). While the sampling period varied (from September to December), this vertical distribution pattern in zooplankton biovolume was common within the region. The zooplankton biovolume in the surface layer (0 m–thermocline) of the Okhotsk Sea was significantly less than that in the surface layer of the Oyashio region ($p < 0.01$ *U*-test, Table 2). Zooplankton biovolumes in the other layers showed no significant differences between regions. Consequently, the standing stock of zooplankton biovolume in the 0–2000 m water column showed no inter-oceanic differences (Table 2).

### Zooplankton community structure

A total of 14 zooplankton taxa and 34 calanoid copepod species were identified in the 0–500 m water column (Table 3). Calanoid copepods were the predominant taxon (>80% in abundance) in both the Okhotsk Sea and Oyashio region. Inter-oceanic differences in abundance were observed for six zooplankton taxa and seven species of calanoids. The overall abundance of the dominant zooplankton taxa was greater in the Oyashio region than in the Okhotsk Sea, with the exception of the calanoid copepod *Metridia okhotensis* (Brodsky, 1950), which showed the opposite pattern (Table 3): the abundance of *M. okhotensis* in the Okhotsk Sea (9369 ind. $m^{-2}$) was 30 times greater than in the Oyashio region (367 ind. $m^{-2}$) (Table 3).

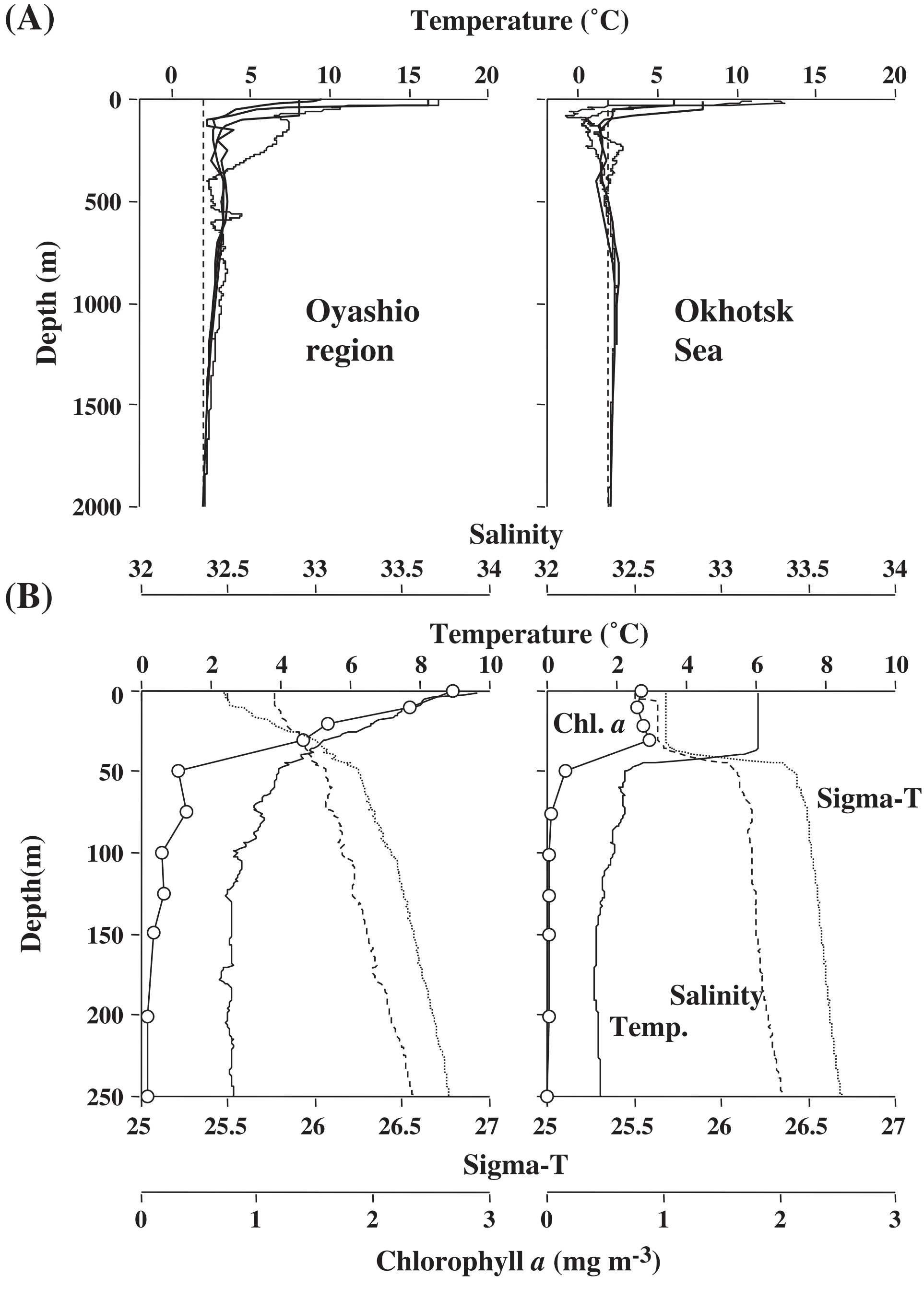


Figure 2. (A) Temperature profiles at all stations in the Oyashio region (left panel) and Okhotsk Sea (right panel); (B) temperature, salinity, sigma-T and chlorophyll *a* profiles at IONESS stations: St. 19 in the Oyashio region and St. OK24 in the Okhotsk Sea. Note that depth scales are different in A and B. For inter-oceanic comparison, positions of 2°C are indicated by dashed lines in A.

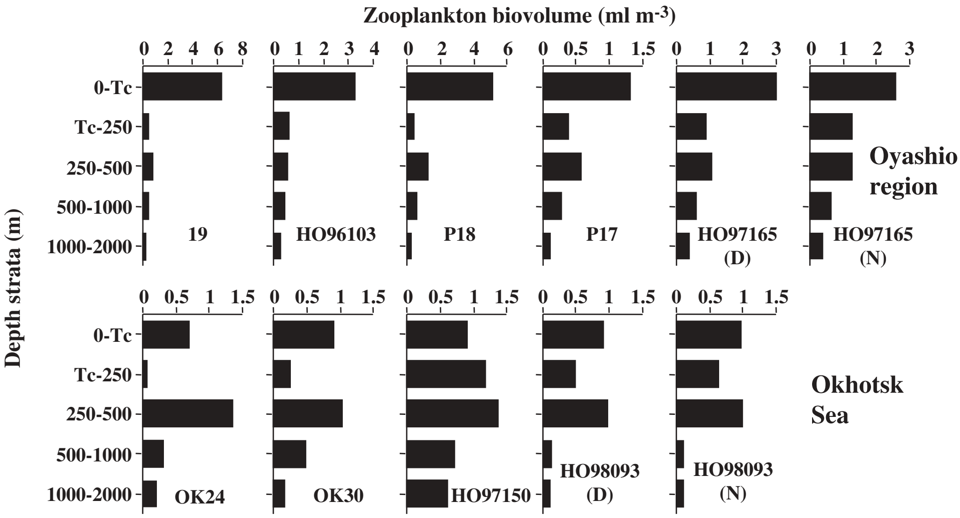


Figure 3. Vertical distribution of zooplankton biovolume in the Oyashio region (upper panels) and Okhotsk Sea (lower panels) from September to December in 1996–1998. Note that the biovolume axes are not the same between panels. Tc: thermocline.

Table 2. Inter-oceanic comparison of zooplankton biovolume (μl $l^{-1}$) collected by closing net during September–December 1996–1998. Differences between regions were tested with Mann–Whitney *U*-test.

| Depth strata (m) | Oyashio region (n = 6) | Okhotsk Sea (n = 5) | *U*-test |
|---|---|---|---|
| 0-Tc | 3593 ± 1809 | 876 ± 107 | ** |
| Tc-250 | 653 ± 356 | 528 ± 427 | ns |
| 250–500 | 903 ± 317 | 1141 ± 199 | ns |
| 500–1000 | 474 ± 122 | 365 ± 288 | ns |
| 1000–2000 | 246 ± 123 | 250 ± 236 | ns |
| 0–2000 | 527 ± 166 | 394 ± 233 | ns |

Notes: Tc, thermocline. Values are mean ± standard deviation. $^{**}p < 0.01$; ns: not significant.

### *Population structure of copepods*

Copepod communities in the Oyashio region were dominated by *Metridia pacifica*, followed by *Eucalanus bungii* (Figure 4), while in the Okhotsk Sea, copepod communities were dominated by *M. okhotensis*, followed by *M. pacifica*. These two *Metridia* species accounted for approximately 70% of copepod abundance in the Okhotsk Sea. The population structure of the dominant copepods also demonstrated inter-oceanic differences. The early copepodid stages were a significant component in the Oyashio region, whereas only late copepodid stages (C5 or C6) dominated in the Okhotsk Sea.

Table 3. Inter-oceanic comparison on abundance (ind. m$^{-2}$: 0–500 m) of zooplankton taxa/species collected by IONESS in the Oyashio region (St. 19) and Okhotsk Sea (OK24) during October to November 1996.

| Taxa/species | Oyashio region | | Okhotsk Sea | | *U*-test |
|---|---|---|---|---|---|
| | Mean | sd | Mean | sd | |
| Foraminiferans | 353 | 212 | 202 | 173 | |
| Hydrozoans | 69 | 50 | 68 | 16 | |
| Molluscs | **375** | 246 | 38 | 35 | * |
| Polychaetes | **48** | 22 | 2 | 3 | * |
| Ostracods | 1604 | 933 | 1053 | 198 | |
| Cyclopoid copepods | 83 | 43 | 0 | 0 | — |
| Poecilostomatoid copepods | **273** | 218 | 7 | 0 | * |
| Mysids | 18 | 6 | 14 | 7 | |
| Isopods | 8 | 6 | 14 | 3 | |
| Amphipods | **1000** | 732 | 82 | 23 | ** |
| Euphausiids | 276 | 254 | 80 | 69 | |
| Chaetognaths | **1447** | 749 | 713 | 56 | * |
| Appendicularians | **1400** | 1155 | 54 | 21 | *** |
| Larvae of fishes | 33 | 20 | 13 | 10 | |
| Calanoid copepods | | | | | |
| *Acartia longiremis* | 17 | 17 | 0 | 0 | — |
| *Aetideopsis pacificus* | 13 | 10 | 17 | 9 | |
| *Aetideopsis rostrata* | 19 | 14 | 0 | 0 | — |
| *Amallothrix inornata* | 34 | 32 | 0 | 0 | — |
| *Calanus pacificus* | 1654 | 1411 | 0 | 0 | — |
| *Candacia bipinnata* | 26 | 25 | 0 | 0 | — |
| *Centropages mcmurrichi* | 3 | 1 | 0 | 0 | — |
| *Chiridius pacificus* | 7 | 0 | 0 | 0 | — |
| *Eucalanus bungii* | **7719** | 4988 | 593 | 62 | *** |
| *Gaetanus simplex* | 267 | 179 | 129 | 39 | |
| *Gaidius variabilis* | 49 | 37 | 48 | 14 | |
| *Haloptilus pseudooxycephalus* | 9 | 6 | 0 | 0 | — |
| *Heterorhabdus tanneri* | 111 | 75 | 32 | 20 | |
| *Heterostylites major* | 14 | 0 | 9 | 0 | |
| *Mesocalanus tennuicornis* | 52 | 36 | 0 | 0 | — |
| *Metridia okhotensis* | 367 | 334 | **9369** | 3214 | ** |
| *Metridia pacifica* | **13,052** | 8290 | 1344 | 390 | ** |
| *Microcalanus pygmaeus* | 55 | 0 | 0 | 0 | — |
| *Neocalanus cristatus* | **445** | 130 | 114 | 10 | * |
| *Neocalanus flemingeri* | 172 | 102 | 271 | 178 | |
| *Neocalanus plumchrus* | 2390 | 328 | 1246 | 178 | |
| *Paracalanus parvus* | 718 | 0 | 0 | 0 | — |
| *Paraeuchaeta birostrata* | 51 | 37 | 14 | 7 | |
| *Paraeuchaeta elongata* | 288 | 198 | 241 | 13 | |
| *Pleuromamma scutullata* | **311** | 236 | 59 | 37 | * |
| *Pseudocalanus minutus* | **6674** | 3616 | 421 | 217 | ** |
| *Pseudocalanus newmani* | **6323** | 2804 | 10 | 2 | *** |
| *Racovitzanus antarcticus* | 142 | 80 | 51 | 22 | |

(*Continued*)

Table 3. (Continued).

| Taxa/species | Oyashio region | | Okhotsk Sea | | *U*-test |
|---|---|---|---|---|---|
| | Mean | sd | Mean | sd | |
| *Scaphocalanus affinis* | 1 | 0 | 0 | 0 | — |
| *Scaphocalanus magnus* | 29 | 20 | 0 | 0 | — |
| *Scolecithricella dentata* | 24 | 0 | 0 | 0 | — |
| *Scolecithricella minor* | 279 | 139 | 113 | 30 | |
| *Spinocalanus spinipes* | 33 | 16 | 0 | 0 | — |

Notes: Differences between regions were tested with Mann–Whitney *U*-test. sd, standard deviation. *$p$ < 0.05; **$p$ < 0.01; ***$p$ < 0.001. Bold numbers are significantly greater than the other region.

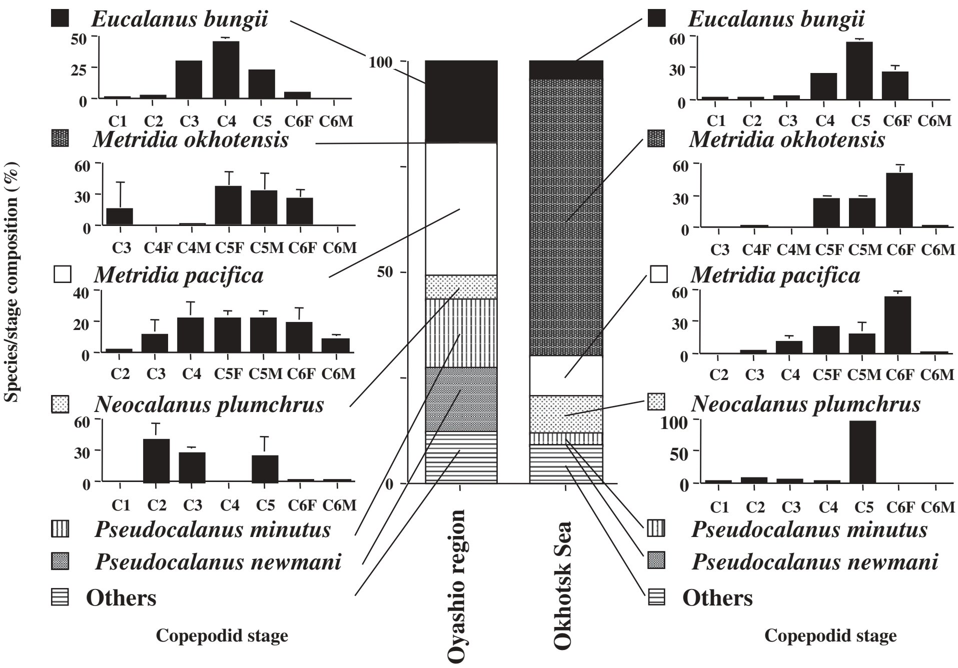


Figure 4. Copepod species composition (centre) and copepodid stage structures of the dominant species (left: Oyashio region, right: Okhotsk Sea). All data are integrated means of a 0–500 m water column based on the IONESS samples in the Oyashio region (St. 19) and Okhotsk Sea (St. OK24) from October to November 1996. Error bars for the copepodid stage indicate standard deviations of each daily duplicate.

### *Vertical distribution of copepods*

Throughout the day, four dominant copepods (*E. bungii, M. okhotensis, M. pacifica* and *Neocalanus plumchrus*) were distributed near the surface layer in the Oyashio region, but they were distributed at 250–500 m in the Okhotsk Sea (Figure 5). However, it should be noted that *M. pacifica* migrated upward at night. The

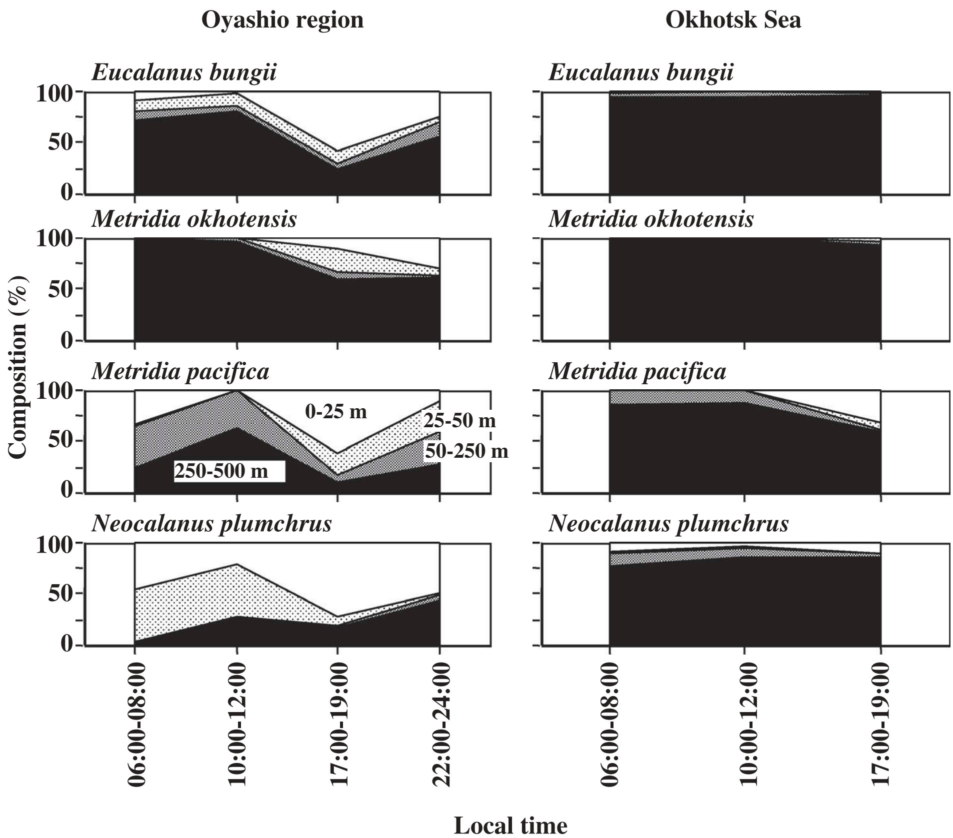


Figure 5. Diel changes in the vertical distribution of four dominant copepods (*Eucalanus bungii, Metridia okhotensis, M. pacifica* and *Neocalanus plumchrus*) at a 0–500 m water column evaluated by IONESS in the Oyashio region (St. 19, left) and the Okhotsk Sea (St. OK24, right) from October to November 1996.

dominant copepods in the Okhotsk Sea were distributed at 250–500 m throughout the day and corresponded to the vertical distribution of zooplankton biovolume (Figure 3). In view of the mesopelagic distribution throughout the day (Figure 5) and the dominance of late copepodid stages (Figure 4), it was assumed that most of the dominant copepods were in a resting state in the Okhotsk Sea.

### *Body size of copepods*

A total of 34 copepodid stages of 17 species were examined, and the PL of 14 copepodid stages of 10 species were significantly larger in the Okhotsk Sea than in the Oyashio region (Table 4). In contrast, the adult females of *Pseudocalanus newmani* (Frost 1989) from the Oyashio region exhibited a larger PL than in the Okhotsk Sea ($p < 0.001$, $U$-test).

Table 4. Inter-oceanic comparison on prosome length (mm) of calanoid copepods collected by IONESS in the Oyashio region (St. 19) and Okhotsk Sea (OK24) during October to November 1996.

| Species | Stage | Oyashio region | | | Okhotsk Sea | | | *U*-test |
|---|---|---|---|---|---|---|---|---|
| | | *n* | Mean | sd | *n* | Mean | sd | |
| *Aetideopsis rostrata* | C6F | 2 | 1.70 | 0.05 | 6 | 1.69 | 0.10 | |
| *Candacia bipinnata* | C6F | 3 | 3.43 | 0.06 | 1 | 3.45 | | |
| *Eucalanus bungii* | C4F | 121 | 3.69 | 0.21 | 2 | **3.98** | 0.04 | * |
| | C5F | 107 | 5.29 | 0.33 | 4 | **5.70** | 0.12 | * |
| | C5M | 91 | 4.85 | 0.27 | 13 | **5.14** | 0.13 | *** |
| | C6F | 91 | 7.04 | 0.43 | 22 | **7.20** | 0.39 | * |
| *Gaetanus simplex* | C6F | 17 | 2.73 | 0.08 | 8 | **2.80** | 0.07 | * |
| *Gaidius variabilis* | C6F | 23 | 2.75 | 0.09 | 9 | 2.81 | 0.11 | |
| *Heterorhabdus tanneri* | C5 | 57 | 1.86 | 0.07 | 7 | **2.01** | 0.13 | ** |
| | C6M | 5 | 2.55 | 0.04 | 1 | 2.67 | | |
| *Metridia okhotensis* | C5F | 23 | 2.10 | 0.08 | 16 | 2.08 | 0.08 | |
| | C5M | 30 | 1.88 | 0.05 | 16 | **1.92** | 0.05 | * |
| | C6F | 23 | 2.84 | 0.08 | 65 | 2.83 | 0.09 | |
| *Metridia pacifica* | C6F | 125 | 1.94 | 0.14 | 38 | **2.01** | 0.13 | * |
| *Neocalanus cristatus* | C5 | 16 | 6.84 | 0.28 | 41 | **7.04** | 0.21 | ** |
| *Neocalanus flemingeri* | C4 | 6 | 2.94 | 0.14 | 40 | 2.89 | 0.11 | |
| | C6F | 25 | 3.88 | 0.26 | 8 | 4.15 | 0.43 | |
| *Neocalanus plumchrus* | C5 | 104 | 3.70 | 0.15 | 172 | **3.79** | 0.13 | *** |
| *Paraeuchaeta elongata* | C5M | 6 | 3.79 | 0.17 | 1 | 4.35 | | |
| | C6F | 1 | 4.60 | | 12 | 5.13 | 0.14 | |
| *Pleuromamma scutullata* | C2 | 11 | 0.81 | 0.02 | 1 | 0.86 | | |
| | C3 | 11 | 1.06 | 0.03 | 3 | 1.05 | 0.01 | |
| | C5M | 3 | 1.74 | 0.06 | 1 | 1.77 | | |
| | C6F | 10 | 2.63 | 0.08 | 3 | 2.58 | 0.04 | |
| | C6M | 13 | 1.64 | 0.03 | 2 | **2.32** | 0.07 | * |
| *Pseudocalanus minutus* | C5F | 30 | 1.03 | 0.06 | 34 | 1.00 | 0.06 | |
| | C5M | 33 | 0.94 | 0.04 | 5 | 0.98 | 0.04 | |
| | C6F | 22 | 1.18 | 0.08 | 39 | 1.16 | 0.10 | |
| *Pseudocalanus newmani* | C6F | 110 | **0.84** | 0.04 | 25 | 0.79 | 0.05 | *** |
| *Racovitzanus antarcticus* | C5F | 12 | 1.44 | 0.03 | 6 | 1.45 | 0.03 | |
| | C5M | 16 | 1.47 | 0.05 | 5 | 1.47 | 0.04 | |
| | C6F | 45 | 1.72 | 0.04 | 13 | **1.75** | 0.05 | * |
| *Scolecithricella minor* | C6F | 85 | 1.19 | 0.03 | 52 | **1.20** | 0.03 | * |
| | C6M | 24 | 1.01 | 0.02 | 9 | **1.04** | 0.03 | ** |

Notes: Differences between regions were tested with Mann–Whitney *U*-test. *n*, number of measured specimens; sd, standard deviation; F, female; M, male. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Bold numbers are significantly greater than the other region.

## Discussion

This study described inter-oceanic differences in the ecology of zooplankton and calanoid copepods and showed: (1) smaller zooplankton biovolume near the surface layer in the Okhotsk Sea; (2) a predominance of *M. okhotensis* in the Okhotsk Sea; (3)

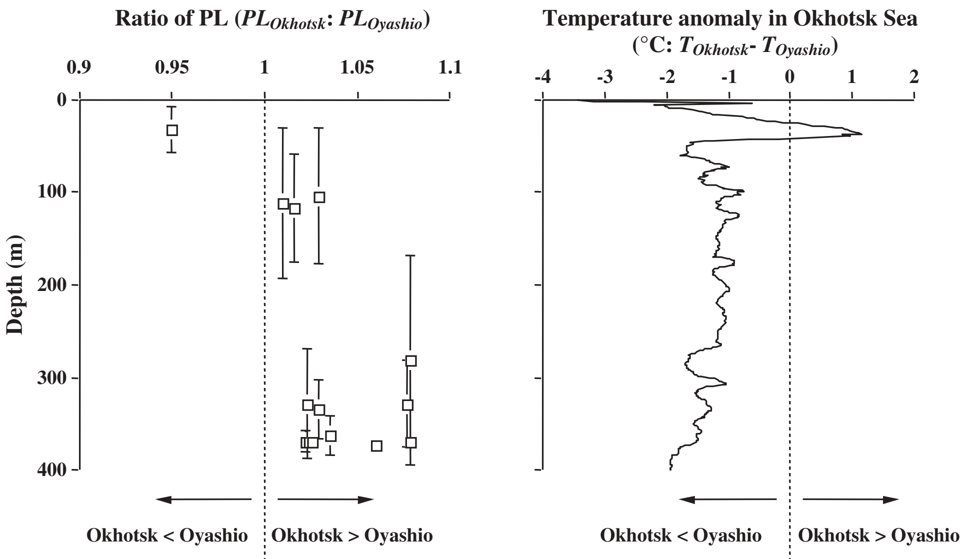


Figure 6. Vertical distribution of the prosome length ratios of the copepods ($PL_{Okhotsk}$: $PL_{Oyashio}$) (left) and temperature anomalies (°C: $T_{Okhotsk} - T_{Oyashio}$) (right) between the Okhotsk Sea (St. OK24) and Oyashio region (St. 19) evaluated by IONESS from October to November 1996. The vertical distribution of each copepod is calculated by daily duplicate samples in the Okhotsk Sea (symbols and bars indicate the means and standard deviations of $D_{50\%}$, respectively). For inter-oceanic comparison, the dashed lines in each panel indicate that the positions of values of both regions are equal.

most of the dominant copepods were in resting phase in the Okhotsk Sea but not in the Oyashio region; and (4) larger body size of calanoids in the Okhotsk Sea, with the exception of *P. newmani*. Interpretations of each of these aspects of zooplankton ecology are examined below.

Water temperature is one of the most important factors affecting the body size of copepods (cf. Corkett and McLaren, 1978). A comparison of relative temperatures and PL ratios of the copepods in the Okhotsk Sea and Oyashio region (Figure 6) showed that larger body size was associated with cooler temperatures below 50 m in the Okhotsk Sea, whereas the smaller size of *P. newmani* was associated with warmer temperatures at approximately 30–40 m in the Okhotsk Sea. This indicates that the large size of the zooplankton in the Okhotsk Sea reflects the cold temperature characteristic of the mesopelagic zone (Figure 2).

The zooplankton fauna of the Okhotsk Sea was similar to that of the Oyashio region (Zenkevitch 1963), but their biovolume, community structure and vertical distribution patterns were quite different between these regions. The zooplankton biovolume near the surface layer (0 m–thermocline) in the Okhotsk Sea was lower than in the Oyashio region (Figure 3, Table 2). Large copepods were distributed in the mesopelagic layer of the Okhotsk Sea but in the epipelagic of the Oyashio region (Figure 5). The vertical distribution of zooplankton biovolume, which peaked in the surface layer of the Oyashio region but at 250–500 m in the Okhotsk Sea, corresponds with the respective habitat depths of copepods in these regions. The resting phase of the dominant *Metridia* spp. in the Okhotsk Sea has been reported by Shebanova (1995, 2004).

The larger body size of zooplankton in the Okhotsk Sea suggests that their development occurred in the cooler mesopelagic zone (Table 3, Figure 6). The standing stock of most zooplankton taxa was smaller in the Okhotsk Sea, and only the copepod *Metridia okhotensis* was smaller in the Oyashio region (Table 2). The abundance of *M. okhotensis* in the Okhotsk Sea was 30 times greater than that in the Oyashio region, and it dominated in the Okhotsk Sea, comprising 60% of total copepod numbers, followed by the congener *M. pacifica* (Figure 4). Based on the samples collected from a large geographical range in the Okhotsk Sea, these two *Metridia* species are classified as indicator species of continental shelf/slope community (Itoh et al. 2014). The dominance of *Metridia* spp. in mesozooplankton biomass in the 0–300 m water column in the southern Okhotsk Sea throughout the year was also reported by Shimada et al. (2012). This suggests that the dominance of *M. okhotensis* is a common phenomenon of the Okhotsk Sea.

In terms of production, *M. okhotensis* is the most important species in the Okhotsk Sea (Shebanova 2007). Because it is known to perform strong diel vertical migration (Padmavati et al. 2004; Sato et al. 2011), its predominance in the Okhotsk Sea may be related to the development of a strong pycnocline. It should be noted that the other dominant copepods in the Okhotsk Sea (*E. bungii* and *N. plumchrus*) are known to exhibit little diel vertical migration or, at least, less diel vertical migration than *M. okhotensis* (Mackas et al. 1993; Sato et al. 2011). The development of a strong pycnocline in the Okhotsk Sea (Figure 2B) may be a key feature that affects the regional differences in zooplankton abundance, distribution and body size between the Okhotsk Sea and Oyashio region.

Life cycle timing of large dominant copepods (*E. bungii* and *Neocalanus* spp.) may also vary between these two regions. For these interzonal copepods, the late resting copepodid stages are commonly found in deeper waters (Miller et al. 1984). However, inter-regional differences in their dominant stage (Figure 4) and diel vertical migration (Figure 5) suggest that the resting phase may have started much earlier in the Okhotsk Sea than in the Oyashio region. Because the Okhotsk Sea is ice-covered for a period, the growth and development of large copepods in the epipelagic zone may be seasonally restricted. This is considered a possible cause of the earlier life cycle timing (entering resting phase faster) of large copepods in the Okhotsk Sea.

The effect of regional differences in copepod communities on vertical material flux is also of special interest. The active flux of copepods includes their diel vertical migration (Longhurst et al. 1990) and seasonal vertical migration (Bradford-Grieve et al. 2001). In the Oyashio region, both active fluxes of copepods were reported. The active flux by diel vertical migration of *Metridia* spp. was reported as 3.0 g C m$^{-2}$ year$^{-1}$, corresponding to 15% of the annual total POC flux at 150 m in the Oyashio region (Takahashi et al. 2009). The active flux of *Neocalanus* spp. by seasonal vertical migration was estimated as 4.3 g C m$^{-2}$ year$^{-1}$, corresponding to 91% of the annual total POC flux at 150 m in the Oyashio region (Kobari et al. 2003). Assuming individual mass flux and POC flux in the Okhotsk Sea are similar to those in the Oyashio region, we can estimate the active flux of *Metridia* spp. and *Neocalanus* spp. as 2.4 and 2.3 g C m$^{-2}$ year$^{-1}$, respectively, which corresponds to 12.0% and 49.4% of passive POC flux, respectively (Table 5). Because the copepod

Table 5. Estimation of active fluxes by diel vertical migration of *Metridia* spp. and seasonal vertical migration of *Neocalanus* spp. in the Okhotsk Sea. Abundance data are from Table 3. Assuming individual flux and POC flux were similar to those in the Oyashio region, active fluxes in the Okhotsk region were calculated with proportion of the abundance data.

| Active flux in the Oyashio region (g C $m^{-2}$ $year^{-1}$) | Abundance (ind. $m^{-2}$) | | Active flux in the Okhotsk Sea (g C $m^{-2}$ $year^{-1}$) | POC flux (g C $m^{-2}$ $year^{-1}$) | Active flux relative to POC flux (%) |
|---|---|---|---|---|---|
| | Oyashio region | Okhotsk Sea | | | |
| *Metridia* spp. | | | | | |
| 3.0* | 13,419 | 10,713 | 2.4 | 20.0* (at 150 m) | 12.0 |
| *Neocalanus* spp. | | | | | |
| 4.3** | 3,007 | 1,631 | 2.3 | 4.7** (at 1000 m) | 49.4 |

*Takahashi et al. 2009; **Kobari et al. 2003.

abundances in the Okhotsk Sea were relatively less than those in the Oyashio region, their active fluxes were estimated to be smaller in the Okhotsk Sea.

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