

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

Atsushi Yamaguchi*

Laboratory of Marine Biology, Graduate School of Fisheries Science, Hokkaido University, Hakodate, Hokkaido, Japan

(Received 23 September 2014; accepted 5 February 2015)

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

*Email: a-yama@fish.hokudai.ac.jp

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 sub-arctic 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.

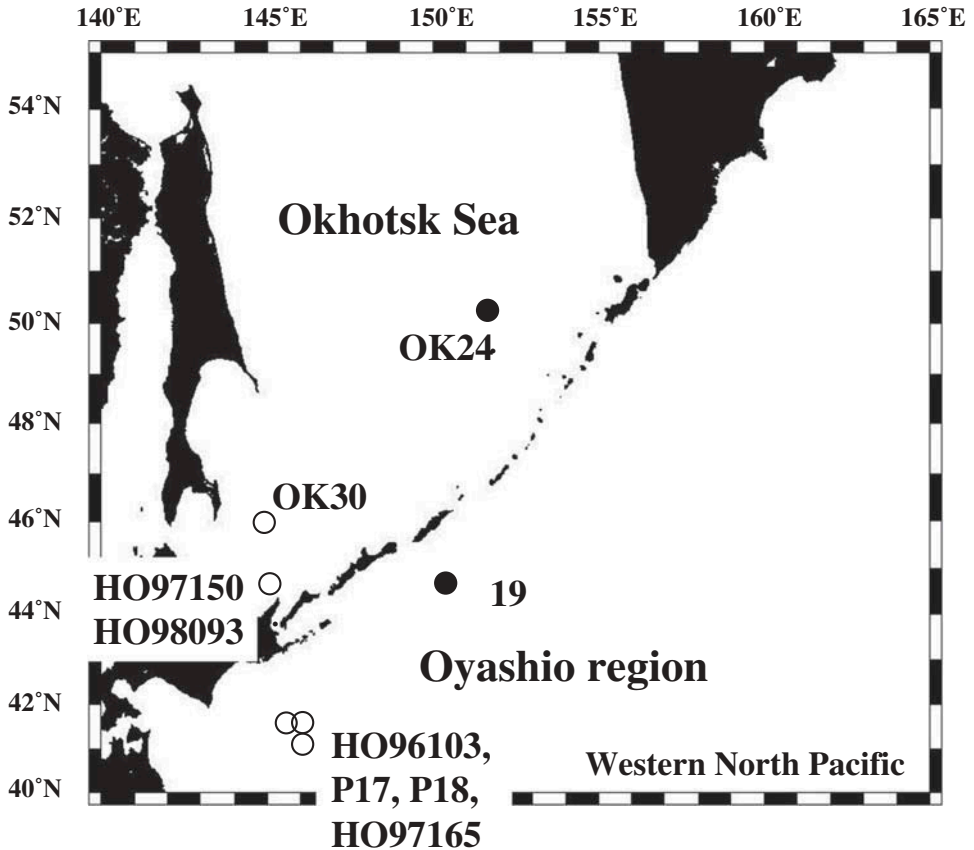


Figure 1. Location of the sampling stations in the Okhotsk Sea and Oyashio region from September to December in 1996–1998. ○: closing net sampling, ●: closing net and IONESS sampling.

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).

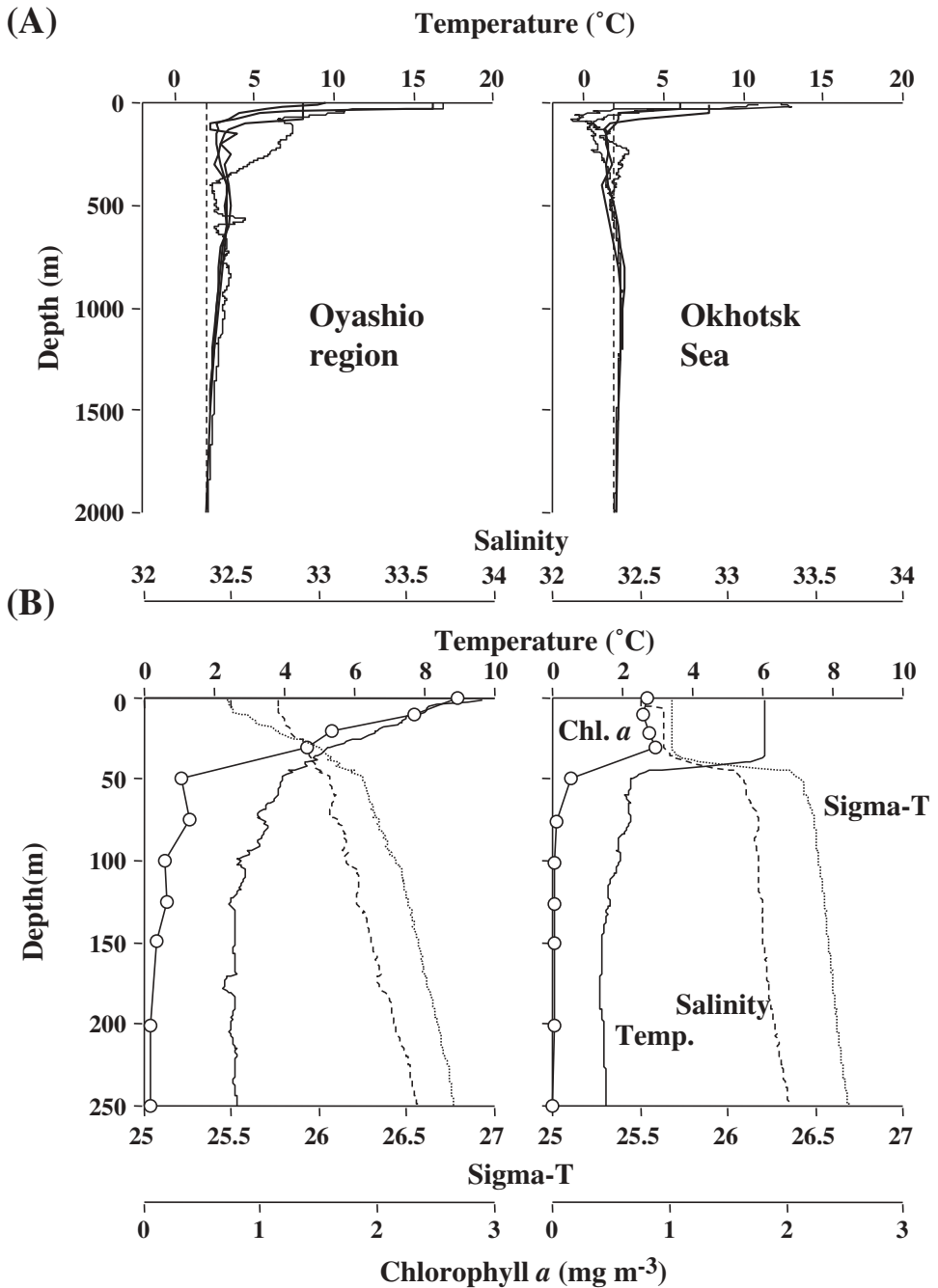


Figure 2. (A) Temperature profiles at all stations in the Oyashio region (left panel) and Okhotsk Sea (right panel); (B) temperature, salinity, sigma-T and chlorophyll *a* profiles at IONESS stations: St. 19 in the Oyashio region and St. OK24 in the Okhotsk Sea. Note that depth scales are different in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

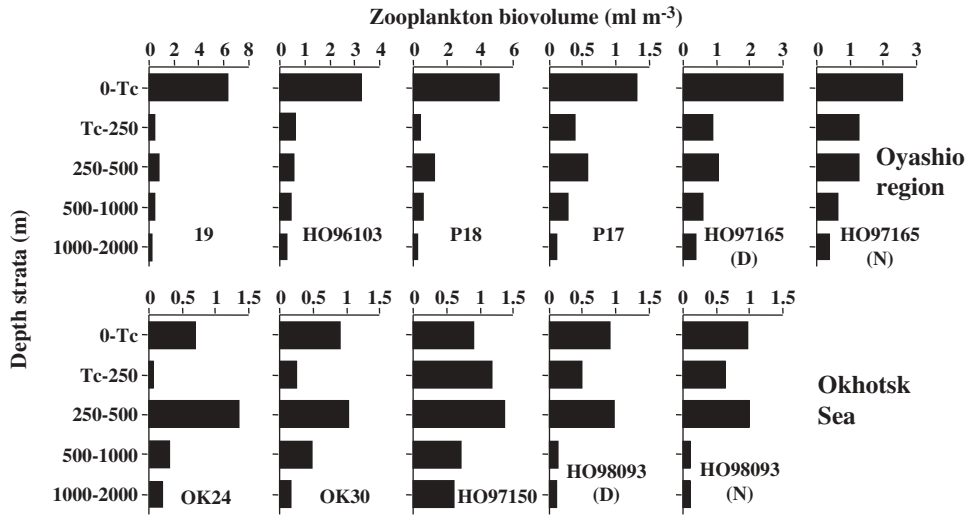


Figure 3. Vertical distribution of zooplankton biovolume in the Oyashio region (upper panels) and Okhotsk Sea (lower panels) from September to December in 1996–1998. Note that the biovolume axes are not the same between panels. Tc: thermocline.

Table 2. Inter-oceanic comparison of zooplankton biovolume ($\mu\text{l l}^{-1}$) 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 \pm 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					
<i>Acartia longiremis</i>	17	17	0	0	—
<i>Aetideopsis pacificus</i>	13	10	17	9	
<i>Aetideopsis rostrata</i>	19	14	0	0	—
<i>Amallothrix inornata</i>	34	32	0	0	—
<i>Calanus pacificus</i>	1654	1411	0	0	—
<i>Candacia bipinnata</i>	26	25	0	0	—
<i>Centropages mcmurrici</i>	3	1	0	0	—
<i>Chiridius pacificus</i>	7	0	0	0	—
<i>Eucalanus bungii</i>	7719	4988	593	62	***
<i>Gaetanus simplex</i>	267	179	129	39	
<i>Gaidius variabilis</i>	49	37	48	14	
<i>Haloptilus pseudooxycephalus</i>	9	6	0	0	—
<i>Heterorhabdus tanneri</i>	111	75	32	20	
<i>Heterostylites major</i>	14	0	9	0	
<i>Mesocalanus tenuicornis</i>	52	36	0	0	—
<i>Metridia okhotensis</i>	367	334	9369	3214	**
<i>Metridia pacifica</i>	13,052	8290	1344	390	**
<i>Microcalanus pygmaeus</i>	55	0	0	0	—
<i>Neocalanus cristatus</i>	445	130	114	10	*
<i>Neocalanus flemingeri</i>	172	102	271	178	
<i>Neocalanus plumchrus</i>	2390	328	1246	178	
<i>Paracalanus parvus</i>	718	0	0	0	—
<i>Paraeuchaeta birostrata</i>	51	37	14	7	
<i>Paraeuchaeta elongata</i>	288	198	241	13	
<i>Pleuromamma scutullata</i>	311	236	59	37	*
<i>Pseudocalanus minutus</i>	6674	3616	421	217	**
<i>Pseudocalanus newmani</i>	6323	2804	10	2	***
<i>Racovitzanus antarcticus</i>	142	80	51	22	

(Continued)

Table 3. (Continued).

Taxa/species	Oyashio region		Okhotsk Sea		U-test
	Mean	sd	Mean	sd	
<i>Scaphocalanus affinis</i>	1	0	0	0	—
<i>Scaphocalanus magnus</i>	29	20	0	0	—
<i>Scolecithricella dentata</i>	24	0	0	0	—
<i>Scolecithricella minor</i>	279	139	113	30	—
<i>Spinocalanus spinipes</i>	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.

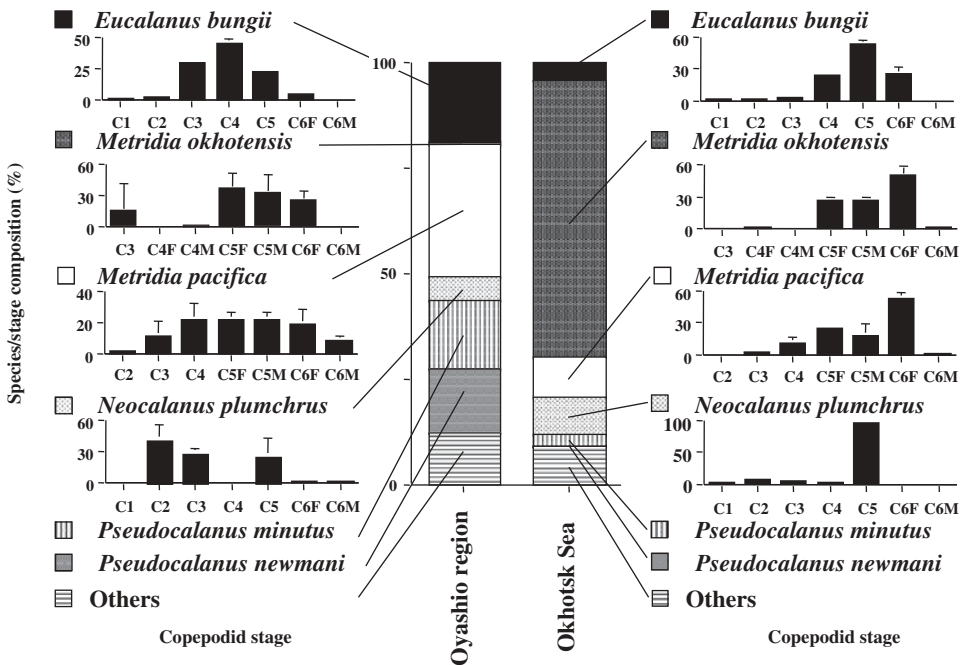


Figure 4. Copepod species composition (centre) and copepodid stage structures of the dominant species (left: Oyashio region, right: Okhotsk Sea). All data are integrated means of a 0–500 m water column based on the IONESS samples in the Oyashio region (St. 19) and Okhotsk Sea (St. OK24) from October 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

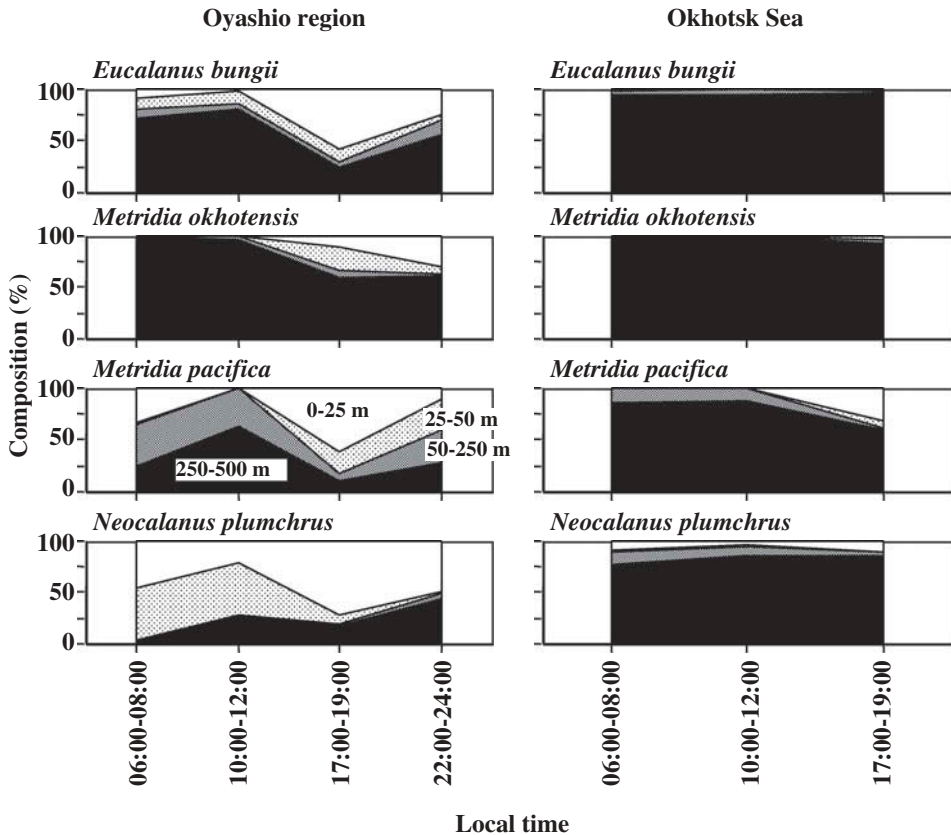


Figure 5. Diel changes in the vertical distribution of four dominant copepods (*Eucalanus bungii*, *Metridia okhotensis*, *M. pacifica* and *Neocalanus plumchrus*) at a 0–500 m water column evaluated by IONESS in the Oyashio region (St. 19, left) and the Okhotsk Sea (St. OK24, right) from October to 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	
<i>Aetideopsis rostrata</i>	C6F	2	1.70	0.05	6	1.69	0.10	
<i>Candacia bipinnata</i>	C6F	3	3.43	0.06	1	3.45		
<i>Eucalanus bungii</i>	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	*
<i>Gaetanus simplex</i>	C6F	17	2.73	0.08	8	2.80	0.07	*
<i>Gaidius variabilis</i>	C6F	23	2.75	0.09	9	2.81	0.11	
<i>Heterorhabdus tanneri</i>	C5	57	1.86	0.07	7	2.01	0.13	**
	C6M	5	2.55	0.04	1	2.67		
<i>Metridia okhotensis</i>	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	
<i>Metridia pacifica</i>	C6F	125	1.94	0.14	38	2.01	0.13	*
<i>Neocalanus cristatus</i>	C5	16	6.84	0.28	41	7.04	0.21	**
<i>Neocalanus flemingeri</i>	C4	6	2.94	0.14	40	2.89	0.11	
	C6F	25	3.88	0.26	8	4.15	0.43	
<i>Neocalanus plumchrus</i>	C5	104	3.70	0.15	172	3.79	0.13	***
<i>Paraeuchaeta elongata</i>	C5M	6	3.79	0.17	1	4.35		
	C6F	1	4.60		12	5.13	0.14	
<i>Pleuromamma scutullata</i>	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	*
<i>Pseudocalanus minutus</i>	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	
<i>Pseudocalanus newmani</i>	C6F	110	0.84	0.04	25	0.79	0.05	***
<i>Racovitzanus antarcticus</i>	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	*
<i>Scolecithricella minor</i>	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)

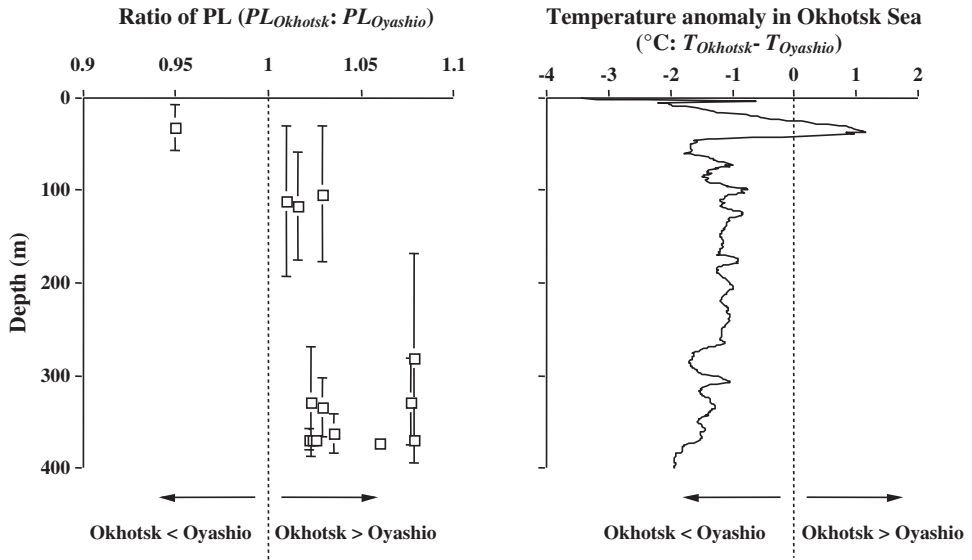


Figure 6. Vertical distribution of the prosome length ratios of the copepods ($PL_{Okhotsk}: PL_{Oyashio}$) (left) and temperature anomalies ($^{\circ}\text{C}: T_{Okhotsk} - T_{Oyashio}$) (right) between the Okhotsk Sea (St. OK24) and Oyashio region (St. 19) evaluated by IONESS from October to November 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 $3.0 \text{ g C m}^{-2} \text{ year}^{-1}$, 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 $4.3 \text{ g C m}^{-2} \text{ year}^{-1}$, 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 $2.3 \text{ g C m}^{-2} \text{ year}^{-1}$, 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			
<i>Metridia</i> spp. 3.0*	13,419	10,713	2.4	20.0* (at 150 m)	12.0
<i>Neocalanus</i> 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.

Acknowledgements

I am very thankful to Prof. Wonchoel Lee for providing the opportunity to present this study to the proceedings of the 12th International Conference on Copepoda. I am grateful to the captain and crew of the R/V Kaiyo-Marui for their help in field sampling. I thank Dr Yasuhiro Ueno, chief scientist of the cruise, for organizing and arranging the samplings used for this study.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This study was supported by a Grant-in-Aid for Scientific Research [(A) 24248032]; and a Grant-in-Aid for Scientific Research on Innovative Areas [24110005] from the Japan Society for the Promotion of Science (JSPS).

References

- Atkinson A. 1998. Life cycle strategies of epipelagic copepods in the Southern Ocean. *J Mar Syst.* 15:289–311.
- Böttger-Schnack R. 1994. The microcopepod fauna in the eastern Mediterranean and Arabian Seas: a comparison with the Red Sea fauna. *Hydrobiologia.* 292–293:271–282.
- Bradford-Grieve JM, Nodder SD, Jillett JB, Currie K, Lassey KR. 2001. Potential contribution that the copepod *Neocalanus tonsus* makes to downward carbon flux in the Southern Ocean. *J Plankton Res.* 23:963–975.
- Brodsky KA. 1967. Calanoida of the far eastern seas and polar basin of the USSR. Jerusalem: Israel Program for Scientific Translations.

- Conover RJ. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*. 167–168:127–142.
- Corkett CJ, McLaren IA. 1978. The biology of *Pseudocalanus*. *Adv Mar Biol*. 15:1–231.
- Frost BW. 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can J Zool*. 67:525–551.
- Halim Y. 1984. Plankton of the Red Sea and the Arabian Gulf. *Deep-Sea Res A*. 31:969–982.
- Itoh H, Nishioka J, Tsuda A. 2014. Community structure of mesozooplankton in the western part of the Sea of Okhotsk in summer. *Prog Oceanogr*. 126:224–232.
- Kitani K. 1973. An oceanographic study of the Okhotsk Sea –Particularly in regard to cold waters. *Bull Far Seas Fish Res Lab*. 9:45–77.
- Kobari T, Ikeda T. 1999. Vertical distribution, population structure and life cycle of *Neocalanus cristatus* (Crustacea: Copepoda) in the Oyashio region, with notes on its regional variations. *Mar Biol*. 134:683–696.
- Kobari T, Ikeda T. 2001a. Ontogenetic vertical migration and life cycle of *Neocalanus plumchrus* (Crustacea: Copepoda) in the Oyashio Region, with notes on regional variations in body sizes. *J Plankton Res*. 23:287–302.
- Kobari T, Ikeda T. 2001b. Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations. *Mar Ecol Prog Ser*. 209:243–255.
- Kobari T, Shinada A, Tsuda A. 2003. Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Prog Oceanogr*. 57:279–298.
- Longhurst AR, Bedo AW, Harrison WG, Head EJH, Sameoto DD. 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. *Deep-Sea Res A*. 37:685–694.
- Mackas DL, Sefton H, Miller CB, Raich A. 1993. Vertical habitat partitioning by large calanoid copepods in the oceanic subarctic Pacific during spring. *Prog Oceanogr*. 32:259–294.
- Matsuura H, Nishida S, Nishikawa J. 2010. Species diversity and vertical distribution of the deep-sea copepods of the genus *Euaugaptilus* in the Sulu and Celebes Seas. *Deep-Sea Res II*. 57:2098–2109.
- Mauchline J. 1998. The biology of calanoid copepods. *Adv Mar Biol*. 33:1–710.
- Miller CB. 1988. *Neocalanus flemingeri*, a new species of Calanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. *Prog Oceanogr*. 20:223–273.
- Miller CB, Frost BW, Batchelder HP, Clemons MJ, Conway RE. 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus* and *Eucalanus bungii* in the northeast Pacific. *Prog Oceanogr*. 13:201–243.
- Nishikawa J, Matsuura H, Castillo LV, Campos WL, Nishida S. 2007. Biomass, vertical distribution and community structure of mesozooplankton in the Sulu Sea and its adjacent waters. *Deep-Sea Res II*. 54:114–130.
- Padmavati G, Ikeda T, Yamaguchi A. 2004. Life cycle, population structure and vertical distribution of *Metridia* spp. (Copepoda: Calanoida) in the Oyashio region (NW Pacific Ocean). *Mar Ecol Prog Ser*. 270:181–198.
- Pinchuk AI, Paul AJ. 2000. Zooplankton of the Okhotsk Sea: a review of Russian studies. Fairbanks: University of Alaska Sea Grant.
- Sato K-I, Yamaguchi A, Ueno H, Ikeda T. 2011. Vertical segregation within four grazing copepods in the Oyashio region during early spring. *J Plankton Res*. 33:1230–1238.
- Shebanova MA. 1995. Distribution of *Metridia pacifica* copepods in winter in the epipelagic layer of the Okhotsk Sea. *Russ J Mar Biol*. 6:426–429.
- Shebanova MA. 2004. Distribution and age structure of *Metridia okhotensis* in the Okhotsk Sea during the year. *PICES Sci Rep*. 26:195.
- Shebanova MA. 2007. Production of some mass copepod species in the Sea of Okhotsk in summer and fall. *Izv TINRO*. 148:221–237.

- Shimada H, Sakaguchi K, Mori Y, Watanobe M, Itaya K, Asami H. 2012. Seasonal and annual changes in zooplankton biomass and species structure in four areas around Hokkaido (Doto and Donan areas of the North Pacific, the northern Japan Sea and the southern Okhotsk Sea). *Bull Plankton Soc Jpn.* 59:63–81.
- Takahashi K, Kuwata A, Sugisaki H, Uchikawa K, Saito H. 2009. Downward carbon transport by diel vertical migration of the copepods *Metridia pacifica* and *Metridia okhotensis* in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res I.* 56:1777–1791.
- Vinogradov ME. 1973. New data on the quantitative distribution of plankton in the deep layers of the Sea of Japan. *Oceanology.* 13:904–907.
- Vinogradov ME, Sazhin AF. 1978. Vertical distribution of the major groups of zooplankton in the northern part of the Sea of Japan. *Oceanology.* 18:205–209.
- Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR. 1985. New development in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar Biol.* 87:313–323.
- Zenkevitch L. 1963. *Biology of the seas of the U.S.S.R.* London: George Allen and Unwin.