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Vertical changes in abundance, biomass, and community structure of copepods in the northern North Pacific and Bering Sea at 0–3,000 m depth, and their role on the vertical flux of surface-produced organic material

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Abstract

To evaluate vertical changes in the abundance, biomass, and community structure of copepods and their effect on material flux, stratified samples were collected at 15 discrete depths between 0 and 3,000 m with a fine mesh size (60 μm) Vertical Multiple Plankton Sampler in the southern Bering Sea and northern North Pacific on 14 and 16 June 2006. Both copepod abundance and biomass decreased with increasing depth, and both decreases were described well with a power model. A total of 72 calanoid copepod species belonging to 34 genera and 15 families were identified in the Bering Sea and 63 species belonging to 32 genera and 13 families were identified in the northern North Pacific. At both stations, the copepod communities comprised five groups that had distinct vertical distribution patterns. The groups at 500–1,500 m were adapted to the oxygen minimum zone, and copepod carcasses outnumbered living specimens at 500–750 m in the northern North Pacific and at 750–1,000 m in the Bering Sea. Oxygen levels were very low in the minimum zone in both regions, so the occurrence of a specialized community and the abundance of carcasses are considered to be a special characteristics at these depth. Based on metabolic rates estimated from an empirical equation, copepods were estimated to consume 20±13% (mean±sd) of the particle organic carbon flux throughout the water column in the Bering Sea and 32±19% of the flux in the northern North Pacific. The feeding impact of copepods was estimated to be greatest at 0–100 m. As the fate of POC flux, heterotrophic bacteria was estimated to be important at 100–1,000 m, while most of them were considered to be directly sinking at 1,000–3,000 m.

Key words : bathypelagic, mesopelagic, oxygen minimum zone, species diversity, vertical flux

Introduction

The oceanic ecosystem can be vertically separated into epipelagic (0–200 m), mesopelagic (200–1,000 m), bathypelagic (1,000–3,000 m), abyssopelagic (3,000–7,000 m) and hadopelagic (below 7,000 m) zones (Lalli and Parsons, 1993). The average depth of the oceans is 3,800 m, and 95% of the total volume of all oceans occurs below 200 m depth (aphotic zone). Assuming the average thickness of the terrestrial biosphere (depth of live soil and the zone of plant and animal life on and above the surface) is 38 m (30 m above ground and 8 m below the surface) and a ratio between land and ocean of 70.8 : 29.2, results in an ocean : terrestrial volume ratio of 242 : 1. Thus, most of Earth's biosphere is in the deep sea. The major food source for deep-sea ecosystems is the surface layer through various biological processes, such as the "biological pump", and an important contributor to these processes are copepods (Angel, 1989 ; Longhurst, 1991).

Particulate material fluxes in the southern Bering Sea (St. AB) and northern North Pacific (St. SA) have been monitored since 1990 using sediment traps, and seasonal and annual variation in the flux of particulate organic carbon at 3,200 m (St. AB) and 4,830 m (St. SA) have been reported (Takahashi et al., 2000, 2002). Plankton community structure at these stations has been studied mainly in the microplankton, including diatoms (Onodera and Takahashi, 2009), radiolarians (Katsuki and Takahashi, 2005 ; Tanaka and Takahashi, 2008) and foraminiferans (Asahi and Takahashi, 2007). For metazoans, major transporters in the biological pump, the community structure has been reported at St. AB (Homma and Yamaguchi, 2010), but no information is available from St. SA.

Copepods are the major component of zooplankton biomass in the southern Bering Sea and subarctic Pacific, and their ingestion and egestion affect carbon transport to the deep sea (Nagasawa et al., 1999). While there have been several

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studies on the copepod community structure in this region (Vinogradov, 1968 ; Minoda, 1971, 1972), most concern distribution, and little information is available on their role in vertical flux of organic material.

Most studies of copepod community structure down to great depths have been conducted using ca. 300 μm mesh size plankton nets. However, recent studies have shown the importance of using fine mesh nets (<100 μm) to collect small-sized copepods (e.g. Cyclopoida and Poecilostomatoida), which dominate in abundance (Böttger-Schnack, 1996 ; Homma and Yamaguchi, 2010). All studies on copepod communities in the Bering Sea and subarctic Pacific mentioned above used large (ca. 300 μm) mesh size plankton nets (Vinogradov, 1968 ; Minoda, 1971, 1972).

The role of copepod communities in the vertical flux of organic material (i.e., ingestion and egestion) is commonly estimated from metabolic rates (Sasaki et al., 1988 ; Yamaguchi et al., 2002) based on empirical equations for epipelagic zooplankton/copepods (Ikeda, 1985 ; Ikeda et al., 2001). However, the metabolic rates of copepods are known to decrease with increasing depth (Thuesen et al., 1998), so past estimates of ingestion and egestion of copepods (e.g., in Sasaki et al., 1988 and Yamaguchi et al., 2002) probably overestimated the true values, especially in the meso- and bathypelagic zones. Ikeda et al. (2007) presented an empirical equation that describes the metabolism of copepods based on four independent variables (body mass, habitat temperature, oxygen saturation and depth) that can be used from the epipelagic to bathypelagic zones. Ingestion and egestion of copepods can be more accurately estimated using their new equation, which considers the effect of depth, and data with fine depth resolution (Ikeda et al., 2007).

In the present study, zooplankton samplings were conducted with 60-μm fine mesh nets at 15 discrete depth intervals between 0 and 3,000 m depth at St. AB and St. SA in June 2006, and the copepod community structure in the two adjacent regions were compared. The ingestion and egestion by copepods were estimated throughout the water column using Ikeda et al.'s equation and a carbon budget model (Ikeda and Motoda, 1978). The estimated passive flux of carbon due to copepods was compared with the particle organic carbon (POC) flux in deep water (Takahashi et al., 2000, 2002) to evaluate the quantitative role of copepods in the vertical carbon flux in the two regions.

Materials and Methods

Field sampling

Zooplankton were sampled in the southern Bering Sea at St. AB (Aleutian Basin : 53°28′N, 177°00′W, depth 3,779 m) and in the subarctic Pacific St. SA (Subarctic Pacific : 49°00′N, 174°00′W, depth 5,405 m) on 14 and 16 June 2006, respectively (Fig. 1) aboard the T/S *Oshoro-Maru*. Samples

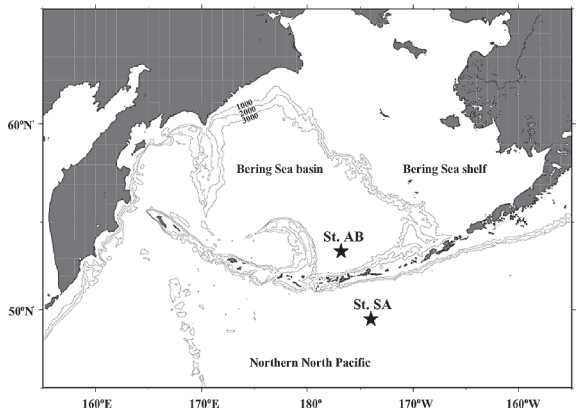

Fig. 1. Location of St. AB in the Aleutian Basin of the southern Bering Sea and St. SA in the subarctic Pacific. Depth contours (1,000, 2,000 and 3,000 m) are superimposed.

were collected at fifteen discrete depth intervals between 0 and 3,000 m (0-25, 25-50, 50-75, 75-100, 100-150, 150-250, 250-350, 350-500, 500-750, 750-1,000, 1,000-1,250, 1,250-1,500, 1,500-2,000, 2,000-2,500 and 2,500-3,000 m) using a Vertical Multiple Plankton Sampler (VMPS, mouth opening 0.25 m^2, mesh size 60 μm, cf. Terazaki and Tomatsu, 1997) (Table 1). Samples were collected during 06 :18-09 :39 (St. AB) and 13 :59-17 :25 (St. SA) local time. The volume of water filtered was estimated using a flowmeter mounted in the mouth of the net, and ranged from 2.9 to 135.9 m^3 (Table 1). Zooplankton samples were split with a Motoda splitting device (Motoda, 1959) on board, and a 1/2 aliquot was preserved immediately in 5% borax-buffered formalin-seawater after collection.

Water temperature, salinity and dissolved oxygen were measured with a Sea-Bird SBE911 Plus CTD system. At St. AB, zooplankton were collected from the surface to 3,000 m, but hydrographic data were collected to only 2,000 m. Temperature, salinity and dissolved oxygen data are needed to estimate metabolism in Ikeda et al.'s equation, so hydrographic data collected at 2,000-3,000 m at St. AB on 14 July 2005 were used (Hokkaido University, 2006).

Identification and enumeration

In the land laboratory, copepods were identified and enumerated under a dissecting microscope. Calanoid copepods were identified to species level and assigned to developmental-stage levels. For species identification, we referred mainly to Brodskii (1967). For species described after this paper, we cited Frost (1974) for *Calanus marshallae*, Frost (1989) for *Pseudocalanus mimus, P. minutus, P. moultoni* and *P. newmani*, and Miller (1988) for *Neocalanus flemingeri*. For juvenile copepodid stages, the total length (TL) was calculated by multiplying the TL of the adult stage by the following ratios : (C1, 0.34 ; C2, 0.40 ; C3, 0.49 ; C4, 0.60 ; C5, 0.75 ; cf. Yamaguchi 1999). Small copepods (Cyclopoida, Harpacticoida and Poecilostomatoida) were

Table 1. Sampling data collected using a Vertical Multiple Plankton Sampler (VMPS) (depth layer, local time and volume of water filtered) and environmental parameters (integrated mean temperature, salinity and dissolved oxygen) at each depth layer used for flux estimation (cf. Fig. 10) at Sts. AB and SA.

Station/ Depth layer (m)	Local time	Water filtered (m^3)	Integrated mean temperature (°C)	Integrated mean salinity	Dissolved oxygen (ml L^{-1})
St. AB	14 June 2006				
0-25	09 : 38-09 : 39	5.593	5.23	33.04	7.13
25-50	09 : 38-09 : 38	5.966	4.47	33.14	6.70
50-75	09 : 37-09 : 38	5.779	4.08	33.22	6.38
75-100	09 : 26-09 : 27	5.593	3.70	33.25	6.88
100-150	09 : 25-09 : 26	12.49	3.28	33.25	6.94
150-250	09 : 23-09 : 25	24.61	3.48	33.36	5.87
250-350	09 : 05-09 : 07	20.88	3.88	33.58	3.81
350-500	09 : 03-09 : 05	35.98	3.89	33.86	1.65
500-750	08 : 58-09 : 03	57.61	3.58	34.10	0.77
750-1,000	07 : 43-07 : 47	60.34	3.17	34.26	0.49
1,000-1,250	07 : 39-07 : 43	64.85	2.68	34.38	0.51
1,250-1,500	07 : 35-07 : 39	63.72	2.34	34.46	0.62
1,500-2,000	06 : 34-06 : 42	116.6	1.96	34.55	0.93
2,000-2,500	06 : 26-06 : 34	135.9	1.65	34.60	1.27
2,500-3,000	06 : 18-06 : 26	120.5	1.46	34.64	1.65
St. SA	16 June 2006				
0-25	17 : 24-17 : 25	2.874	7.20	32.78	7.33
25-50	17 : 24-17 : 24	7.902	5.61	32.80	7.54
50-75	17 : 23-17 : 24	4.885	4.68	32.83	7.36
75-100	17 : 12-17 : 12	3.161	4.12	32.85	7.29
100-150	17 : 11-17 : 12	13.51	3.72	33.19	5.62
150-250	17 : 09-17 : 11	20.98	3.88	33.77	1.95
250-350	16 : 50-16 : 51	17.24	3.69	33.94	0.91
350-500	16 : 47-16 : 50	38.79	3.61	34.09	0.64
500-750	16 : 42-16 : 47	53.45	3.36	34.23	0.45
750-1,000	15 : 27-15 : 31	56.13	2.92	34.35	0.50
1,000-1,250	15 : 23-15 : 27	50.88	2.54	34.43	0.63
1,250-1,500	15 : 19-15 : 23	52.19	2.26	34.49	0.81
1,500-2,000	14 : 14-14 : 22	113.8	1.93	34.56	1.21
2,000-2,500	14 : 07-14 : 14	104.0	1.62	34.62	1.86
2,500-3,000	13 : 59-14 : 07	102.5	1.42	34.65	2.48

identified to order level, and the TLs of subsamples (1/2-1/1,546 of total volume, collected with a wide-bore pipette) were measured. Copepod carcasses (exoskeletons with some body tissue inside, cf. Wheeler, 1967 ; Terazaki and Wada, 1988) were also identified and counted separately.

Data analysis

Biomass

The dry mass of each copepod was estimated from its TL using allometric equations. For the Calanoida, we used the allometric equation

$$\mathrm{Log}_{10}\, DM = 2.546 \log_{10} TL - 6.697 \qquad (1)$$

where *DM* is individual dry mass (mg *DM* ind.$^{-1}$), and *TL* is total length (mm) (Mizdalski, 1988). *DM* was converted to carbon mass, assuming the carbon content of copepods is 44.7% of the *DM* (Båmstedt, 1986).

For the Harpacticoida, we used the allometric equation

$$CM = 2.65\times10^{-6}\times BL^{1.95} \qquad (2)$$

where *CM* is the individual carbon mass (mg C ind.$^{-1}$) and *BL* is the body length (assumed to be half of the total length [mm]) (Uye et al., 2002).

For the Cyclopoida, we used the allometric equation

$$\mathrm{Log}_{10}\, DM = 2.163 \log_{10} TL - 6.207 \qquad (3)$$

where *DM* is the individual dry mass (mg *DM* ind.$^{-1}$) and *TL*

is the total length (mm) (Kaneko, 2005). The carbon content of Cyclopoida was assumed to be 42.5% of the *DM* (James and Wilkinson, 1988).

For the Poecilostomatoida, we used the allometric equation

$$\mathrm{Log}_{10}\, DM = 2.895 \log_{10} TL - 7.993 \qquad (4)$$

where *DM* is individual dry mass (mg *DM* ind.$^{-1}$) and *TL* is the total length (mm) (Nishibe, 2005). Nishibe and Ikeda (2008) reported the carbon content of the Poecilostomatoida was 49–57% of the *DM*. In the present study we assumed the carbon content of the Poecilostomatoida to be 53% of the *DM*, which is the median of 49–57%.

Population depth

To make quantitative comparisons between the two sampling stations, the depth at which the 50th percentile of the population resided ($D_{50\%}$) was calculated for each species (cf. Pennak, 1943). Additional calculations were made to determine the depths at which the 25th ($D_{25\%}$) and 75th ($D_{75\%}$) percentiles occurred. Note that these calculations dealt with the entire population of the species, including all developmental stages.

Community structure

For calanoid copepod populations, a species diversity index (H') (Shannon and Weaver, 1949) was calculated as

$$H' = -\sum n/Ni \ln n/Ni \qquad (5)$$

where n is the abundance (inds. m^{-2}) of each species in the ith layer, and Ni is the total abundance in the ith layer. H' was calculated based on both abundance (inds. m^{-2}) and biomass (mg C m^{-2}).

Q-mode analysis (layer similarity) (cf. Chiba et al., 2001 ; Chiba and Saino, 2003) was conducted based on calanoid copepod abundance. In the Q-mode analysis, abundances (X : inds. m^{-3}) were log transformed ($\mathrm{Log}_{10}[X+1]$) prior to analysis. A dissimilarity matrix between each layer was constructed based on differences in species composition using the Bray-Curtis index (Bray and Curtis, 1957). The matrix was analyzed by cluster analysis coupled with the unweighted pair-group method using arithmetic means to indentify groups with similar community composition. BIOSTAT II software was used for these analyses. To clarify the indicator species for each group, one-way ANOVA was used for copepod abundance data.

Carbon flux and copepod ingestion/egestion

Oxygen consumption rates of copepods were calculated based on Ikeda et al.'s (2007) formula :

$$\ln R = -0.815 + 0.750 \ln B + 0.064T + 0.539OS - 0.091 \ln Z \qquad (6)$$

where R is the respiration rate (μl O_2 ind.$^{-1}$ h^{-1}), B is the biomass of a copepod (mg C ind.$^{-1}$), T is temperature (°C) represented by the integrated mean temperature of each sampling stratum (Table 1), OS is the oxygen saturation (ratio to saturated oxygen) and Z is the mean depth of the sampling stratum. In this equation, respiration decreases with increasing depth and decreasing dissolved oxygen, and the equation is applicable from the surface to the deep sea.

The carbon budgets of living copepods can be expressed as : Ingestion (I) = Metabolism (M) + Growth (G) + Egestion (E). Metabolism (M) is assumed to equal respiration (R). The assimilation efficiency ($[G + R]/I$) and gross growth efficiency (G/I) were assumed to be 70% and 30%, respectively (Ikeda and Motoda, 1978). The ingestion rate was estimated from following equation :

$$I = R \times \frac{12}{22.4} \times 0.97 \times \frac{1}{0.4} \times \frac{1}{1000} \times 24 \qquad (7)$$

where I is the ingestion rate (mg C ind.$^{-1}$ h^{-1}), R is the respiration rate (μl O_2 ind.$^{-1}$ h^{-1}), 12/22.4 is the carbon weight (12 g C) of one-mole of carbon dioxide (22.4 L), 0.97 is a respiratory quotient ($[CO_2]/[O_2]$) (Gnaiger, 1983), 1/0.4 is I/R, 1/1,000 is the conversion from μg to mg, and 24 is the number of hours in one day (24 h). From the ingestion rates, egestion rates (E : mg C ind.$^{-1}$ day^{-1}) were calculated as :

$$E = 0.3 \times I. \qquad (8)$$

The feeding patterns of copepods were classified into four types based on their gut contents and mouthpart morphology (Arashkevich, 1972 ; Ohtsuka and Nishida, 1997) : suspension feeders, suspension feeders in diapause, detritivores and carnivores. Suspension feeders in diapause include C5 and C6 of three *Neocalanus* spp. (*N. cristatus, N. plumchrus, N. flemingeri*), C3-C6 of *E. bungii* (Miller et al., 1984), and C5 and C6 of *Calanus pacificus, C. glacialis, C. marshallae* and *P. minutus* (Conover, 1988 ; Osgood and Frost, 1994 ; Yamaguchi et al., 1998).

POC has been measured at St. AB and St. SA using sediment traps since 1990 (Takahashi et al., 2000, 2002). The mean POC flux in summer was reported to be 9.45 mg C m^{-2} day^{-1} (3,200 m) at St. AB and 5.89 mg C m^{-2} day^{-1} (4,830 m) at St. SA (Takahashi et al., 2000). Applying the equation from Suess (1980) :

$$C_{flux} = C_{prod}/(0.0238Z + 0.212) \qquad (9)$$

where C_{prod} is primary production (mg C m^{-2} day^{-1}), and C_{flux} is the passive carbon flux (mg C m^{-2} day^{-1}) at a given depth (Z : m), primary production was estimated to be 722 mg C m^{-2} day^{-1} at St. AB and 678 mg C m^{-2} day^{-1} at St. SA. These values correspond well to the mean values of June in this region (440-880 mg C m^{-2} day^{-1} in the southern Bering Sea and 380-1,480 mg C m^{-2} day^{-1} in the northern North Pacific, Sorokin, 1999). The POC flux to each sampling layer was calculated from these primary production values and Suess's (1980) equation. To quantify the role of ingestion and eges-

tion of copepods in the vertical flux, the passive POC flux at each sampling layer was compared with the ingestion rate of suspension feeders and detritivores, and the egestion rates of all feeding groups except the suspension feeders in diapause.

Results

Hydrography

Sea surface temperature ranged from 6.0 to 7.9ºC and was higher at St. SA than St. AB (Fig. 2). A subsurface temperature maximum was observed at 380 m (St. AB) and 170 m (St. SA), and below these depths, the temperature decreased gradually to 1.3–1.4ºC at 3,000 m. Salinity was 33.0–34.6 at St. AB and 32.8–34.7 at St. SA, and increased with increasing depth. Dissolved oxygen (DO) levels were greatest at the surface (maximum : 7.2–7.6 ml L^{-1}) and decreased rapidly with increasing depth. DO (0.43–0.48 ml L^{-1}) was lowest at 900 m at St. AB and 700 m at St. SA. The oxygen minimum zone (OMZ) was defined as the depth range at which DO < 1.4 ml L^{-1}. This zone occurred at 450–2,400 m at St. AB and at 240–1,900 m at St. SA. DO levels were below <0.7 ml L^{-1} at 640–1,500 m at St. AB and 340–1,230 m at St. SA. Thus the OMZ was shallower at St. SA than at St. AB (Fig. 2).

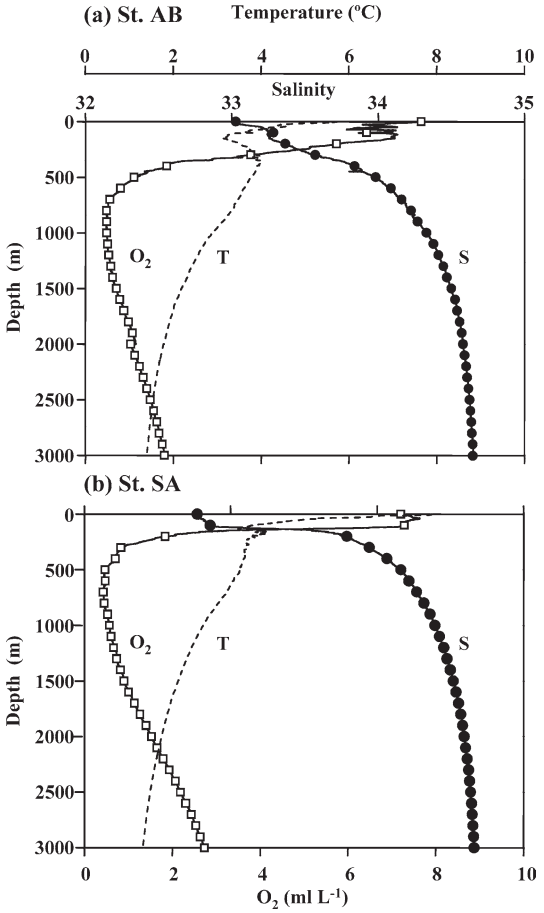

Fig. 2. Vertical distribution patterns of temperature (T : ºC), salinity (S) and dissolved oxygen (O_2 : ml L^{-1}) at St. AB (a) and St. SA (b) on 14 and 16 June 2006, respectively. In (a), data below 2,000 m were collected on 14 July 2005.

Copepod community

Abundance and biomass

Copepod abundance ranged from 12 to 23,400 inds. m^{-3} at St. AB and from 7 to 39,000 inds. m^{-3} at St. SA. It was highest at 0–25 m, decreased with increasing depth, and was lowest at 2,500–3,000 m (Fig. 3a, c). Copepod carcasses occurred throughout the water column, and ranged in abundance between 4 inds. m^{-3} (0–25 m) and 402 inds. m^{-3} (25–50 m) at St. AB and between 0 inds. m^{-3} (0–25 m) and 961 inds. m^{-3} (50–75 m) at St. SA. The ratio of carcasses to living specimens was lowest at the surface and highest at 750–1,000 m (St. AB) and 500–750 m (St. SA), and the carcass/living specimen ratios in abundance at these layers were 2.3 St. AB and 1.9 at St. SA (Fig. 3a, c).

Copepod biomass ranged from 0.06 to 100 mg C m^{-3} at St. AB and from 0.07 to 79 mg C m^{-3} at St. SA, and was highest at the surface and decreased with increasing depth at both stations (Fig. 3b, d). Copepod carcass biomass varied from 0 to 0.01 mg C m^{-3} at St. AB and from 0 to 1.5 mg C m^{-3} at St. SA. The biomass ratio of carcasses to living specimens was less than 0.23.

The contribution of Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida to total copepod abundance was 17–100%, 0–73%, 0–8% and 0–70%, respectively, and varied greatly with depth (Fig. 4a, c). Calanoida and Cyclopoida were the dominant taxa at most depths, and Cyclopoida was abundant at 0–750 m at St. AB (Fig. 4a, c). In terms of biomass, Calanoida dominated throughout the water column (42–100% at St. AB and 52–93% at St. SA), and Poecilostomatoida accounted for the residual composition (Fig. 4b, d). Cyclopoida composed 0.1–11% of the total biomass, and Poecilostomatoida composed 2–38%. Calanoid copepods composed most of the total copepod biomass (90% at St. AB and 81% at St. SA) at 0–3,000 m.

A total of 72 calanoid copepod species belonging to 34 genera and 15 families were collected at St. AB, and 63 calanoid copepods belonging to 32 genera and 13 families were collected at St. SA. Cyclopoida, Harpacticoida and Poecilostomatoida occurred at 0–3,000 m at both stations (Tables 2, 3). For the suspension feeders, the most numerous calanoid copepods were *Microcalanus pygmaeus*, *Metridia pacifica* and *Pseudocalanus* spp. In terms of biomass, the most dominant species of suspension feeders was *Eucalanus bungii*, followed by *N. cristatus, N. flemingeri* and *N. plumchrus*, all of which have a diapause phase. Among the detritivorous species, *Scolecithricella minor* and *S. ovata* dominated in abundance, but the large calanoid copepods, *Scaphocalanus magnus* and *Racovitzanus antarcticus* dominated in biomass. Among the carnivores, *Paraeuchaeta* spp., the family

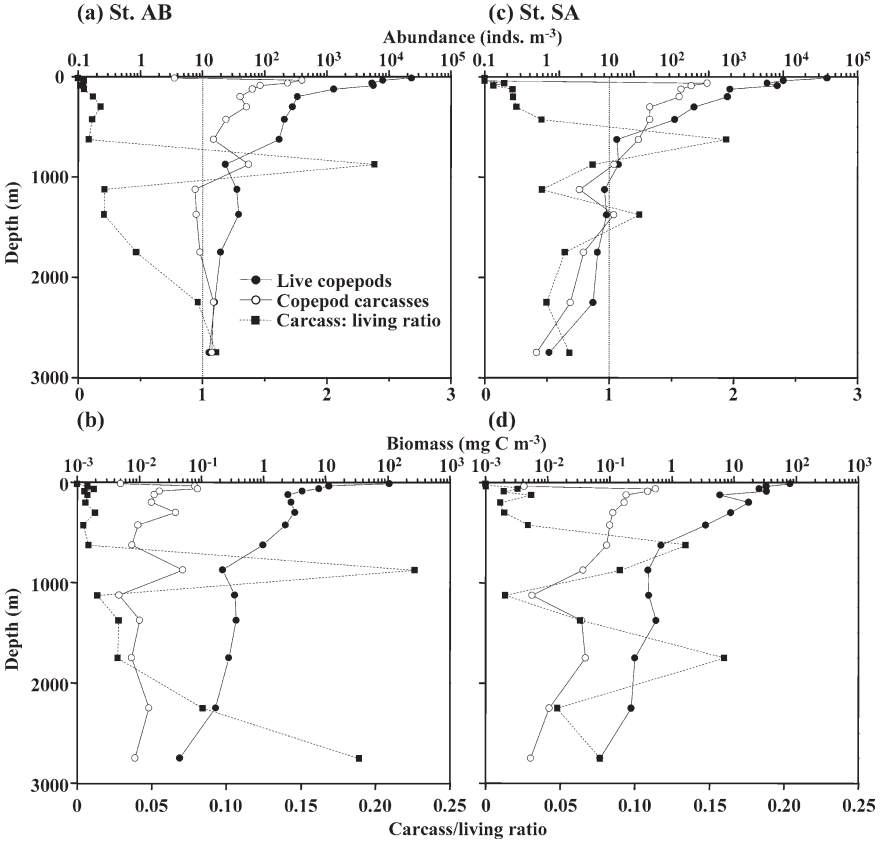

Fig. 3. Vertical distribution of abundance and biomass of copepods at St. AB (a, b) in the southern Bering Sea and at St. SA (c, d) in the subarctic Pacific on 14 and 16 June 2006, respectively. Copepods were classified as live or carcasses, and the ratio of carcass to live copepods was also calculated. Abundance and biomass scales are in log scales. Vertical dashed lines in (a, c) indicate a carcass to live ratio of 1 : 1.

Heterorhabdidae and *Haloptilus pseudooxycephalus* dominated both in abundance and biomass.

Interestingly, all of the suspension feeders that showed large regional differences in vertical distribution are species that have a diapause phase in deep water (Fig. 5). For instance, species that occurred deep at St. AB were *N. flemingeri* (Species no. 11), *N. cristatus* (no. 13) and *Calanus marshallae* (no. 16), while the reverse depth distribution (St. AB< St. SA) were observed for *E. bungii* (no. 5), *P. minutus* (no. 7) and *C. pacificus* (no. 24) (Fig. 5). For detritivores, large regional distribution differences in vertical distribution were seen for *Scaphocalanus affinis* (no. 68) and *Amallothrix valida* (no. 65) (Fig. 6a). For carnivores, the depth distribution depth showed little difference between St. AB and St. SA for all species except *Pachyptilus pacificus* (no. 79) (Fig. 6b).

Fig. 7 shows the contribution of each calanoid copepod family to the total calanoid copepod abundance and biomass. In terms of abundance, Clausocalanidae, which comprised mainly *M. pygmaeus*, dominated (33–98% at St. AB, 29–94% at St. SA) (Fig. 7a, c). In terms of biomass, Calanidae dominated, followed by Euchaetidae and Metridiidae (Fig. 7b, d). Families that occurred only below 1,000 m were Heterorhabdidae, Lucicutiidae, Phaennidae and Spinocalanidae.

Community structure

The number of calanoid copepod species was low at the surface, higher at 500–1,500 m (25 species), peaked at 1,500–2,000 m (33 species), then decreased rapidly below 2,000 m (Fig. 8a) at St. AB. Similar vertical distribution patterns were also observed at St. SA ; species number was low at the surface, fluctuated between 15 and 25 species below 500 m, and peaked at 500–750 m and 1,500–2,000 m (Fig. 8d). The species diversity index (H') and number of species showed similar vertical patterns, but H' based on biomass showed larger variability than abundance at St. SA (Fig. 8b, e).

Based on the Q-mode analysis, the copepod community was classified into five groups at a 43% (St. AB) and 51% (St. SA) dissimilarity level (Fig. 8c, f). The vertical distributions of each group were distinct : group A, 0–75 m ; group B, 75–500 m ; group C, 500–750 m ; group D, 750–1,500 m ; group E, 1,500–3,000 m at St. AB, and group A, 0–75 m ; group B, 75–500 m ; group C, 500–1,000 m and 1,250–1,500 m ; group D, 1,000–1,250 m ; group E, 1,500–3,000 m at St. SA.

The indicator species of each group were identified by one-

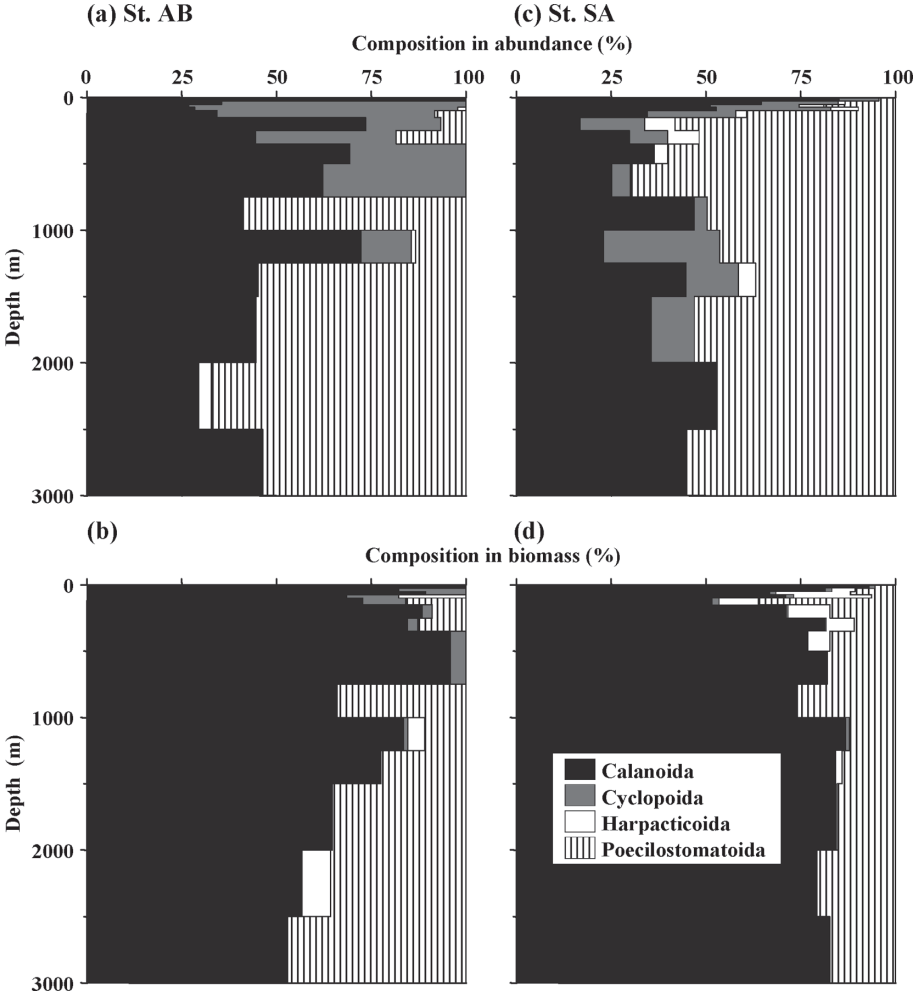

Fig. 4. Vertical changes in the composition of four orders (Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida) to total copepods in terms of abundance (a) and biomass (b) at St. AB in the southern Bering Sea on 14 June 2006 and at St. SA (c, d) in the subarctic Pacific on 16 June 2006.

way ANOVA and Fisher's PLSD. At St. AB, they were Cyclopoida, *E. bungii, M. pacifica* and *Pseudocalanus* spp. for group A, *M. pygmaeus* and Poecilostomatoida for group B, *Lucicutia ovaliformis* for group C and *S. ovata* for group D (Table 4). Because of the low abundances below 1,500 m, no indicator species was detected for group E. At St. SA, the indicator species were *M. pacifica, N. cristatus, N. flemingeri, N. plumchrus, P. mimus, P. minutus, Pseudocalanus* spp., *S. minor,* Cyclopoida, Harpacticoida, Poecilostomatoida and nauplii for group A, *Gaetanus simplex* and *Paraeuchaeta elongata* for group B, *Heterostylites major, L. ovaliformis* and *P. rubra* for group C, *Amallothrix profunda, M. curticauda* and *S. ovata* for group D and *A. paravalida* for group E (Table 5).

Effect on vertical flux of material

Suspension feeders and detritivores were the two dominant feeding patterns, composing 99% of the total copepod abundance throughout the water column at both stations (Fig. 9a, c). In terms of biomass, the contribution of the four feeding patterns differed from those expressed by abundance ; carnivores and suspension feeders in diapause dominated below 250 m depth (Fig. 9b, d).

The mass balance between ingestion (suspension feeder and detritivores) and egestion (all feeding patterns except diapause) of copepods and POC flux in the entire 0–3,000 m water column is summarized in Fig. 10. Copepods consumed 14–60% (St. AB) and 14–71% (St. SA) of the POC flux in each depth layer (Fig. 10a, c). The effect of copepod feeding on the POC flux was greatest in the upper 100 m of both stations. Throughout the water column, copepods consumed 20±13% (mean±sd) and 32±19% of the POC flux at St. AB and SA, respectively (Fig. 10b, d).

Discussion

Abundance and biomass

Table 6 compares the abundance of copepods from various regions. The abundance of copepods at 0–250 m in the present study was 16–28 times greater than that of Minoda (1972)

Table 2. List of species of calanoid copepods at St. AB in the southern Bering Sea. Abundance (inds. m^{-2} : 0–3,000 m) and biomass (mg C m^{-2} : 0–3,000 m) of each species and those of Cyclopoida, Harpacticoida and Poecilostomatoida are also shown. Based on the feeding pattern, species were divided into four types : suspension feeders, suspension feeders in diapause, detritivores and carnivores. Species marked with asterisks indicate that their late copepodid stages below 250 m were treated as suspension feeders in diapause.

No.	Species	inds. m^{-2}	mg C m^{-2}	No.	Species	inds. m^{-2}	mg C m^{-2}	No.	Species	inds. m^{-2}	mg C m^{-2}
Suspention feeders				27	*Spinocalanus spinipes*	105	0.8	Detritivores			
1	Cyclopoida	412,862	107.0	28	*Metridia brevicauda*	100	0.9	57	Poecilostomatoida	208,143	495.8
2	*Microcalanus pygmaeus*	87,842	201.1	29	*Metridia okhotensis*	99	4.8	58	*Scolecithricella minor*	1,645	8.9
3	*Metridia pacifica*	35,539	295.3	30	*Acartia longiremis*	97	0.1	59	*Scolecithricella ovata*	997	11.8
4	*Pseudocalanus* spp. (C1–C3)	25,058	62.3	31	*Pseudochirella polyspina*	57	8.3	60	*Racovitzanus antarcticus*	352	7.5
5	*Eucalanus bungii**	14,358	1,519.7	32	*Calanus glacialis**	43	6.2	61	*Scaphocalanus magnus*	95	13.0
6	*Pseudocalanus newmani*	12,663	84.9	33	*Spinocalanus similis*	41	0.1	62	*Amallothrix inornata*	56	4.7
7	*Pseudocalanus minutus**	11,153	198.6	34	*Aetideus pacificus*	41	1.5	63	*Scaphocalanus medius*	25	0.5
8	Harpacticoida	5,399	5.8	35	*Spinocalanus pseudospinipes*	33	0.2	64	*Scaphocalanus subelongatus*	25	0.6
9	*Pseudocalanus mimus*	5,388	38.3	36	*Euchirella mensinensis*	33	1.4	65	*Amallothrix valida*	23	2.0
10	*Neocalanus plumchrus**	3,917	249.4	37	*Lucicutia ellipsoidalis*	24	0.5	66	*Xanthocalanus kurilensis*	16	0.6
11	*Neocalanus flemingeri**	2,997	442.6	38	*Cornucalanus indicus*	17	2.0	67	*Amallothrix paravalida*	9	0.2
12	*Gaetanus simplex*	1,619	37.0	39	*Pseudochirella pacifica*	17	6.7	68	*Scaphocalanus affinis*	7	0.3
13	*Neocalanus cristatus**	1,395	584.3	40	*Metridia ornata*	16	1.2	Carnivores			
14	*Lucicutia ovaliformis*	958	10.3	41	*Pseudochirella spinifera*	16	2.2	72	*Paraeuchaeta elongata*	699	64.5
15	*Metridia asymmetrica*	747	67.3	42	*Chiridiella abyssalis*	9	0.2	73	*Heterorhabdus tanneri*	516	24.7
16	*Calanus marshallae**	678	73.8	43	*Lucicutia pacifica*	9	0.3	74	*Heterostylites major*	334	44.2
17	*Pleuromamma scutullata*	559	54.6	44	*Aetideopsis rostrata*	9	0.7	75	*Paraeuchaeta birostrata*	294	56.8
18	*Spinocalanus stellatus*	546	15.3	45	*Lucicutia grandis*	9	7.1	76	*Paraeuchaeta rubra*	123	23.6
19	*Pseudocalanus moultoni*	360	7.3	46	*Spinocalanus magnus*	9	0.5	77	*Haloptilus pseudooxycephalus*	58	8.3
20	*Gaidius variabilis*	290	16.0	47	*Temorites brevis*	9	0.2	78	*Haloptilus longicirrus*	17	0.9
21	*Gaidius brevispinus*	287	22.1	48	*Gaetanus brevicornis*	8	1.3	79	*Pachyptilus pacificus*	9	1.0
22	*Metridia similis*	251	5.0	49	*Mimocalanus distinctocephalus*	8	0.4	80	*Heterorhabdus compactus*	8	0.7
23	*Metridia curticauda*	221	10.5	50	*Onchocalanus magnus*	8	0.9	81	*Candacia columbiae*	8	0.2
24	*Calanus pacificus**	179	3.6	51	*Spinocalanus polaris*	8	0.1	82	*Candacia parafalcifera*	7	0.2
25	*Gaidius tenuispinus*	166	2.4	52	*Cephalophanes frigidus*	7	0.3				
26	*Pseudogaetanus robustus*	140	12.7	53	*Lucicutia longifurca*	7	2.6				

Table 3. As in Table 2, but for St. SA in the subarctic Pacific. Note that the species no. are applied same to those of St. AB (cf. Table 2).

No.	Species	inds. m^{-2}	mg C m^{-2}	No.	Species	inds. m^{-2}	mg C m^{-2}	No.	Species	inds. m^{-2}	mg C m^{-2}
Suspention feeders				19	*Pseudocalanus moultoni*	51	0.3	65	*Amallothrix valida*	18	0.9
1	Cyclopoida	351,052	85.7	20	*Gaidius variabilis*	50	0.7	68	*Scaphocalanus affinis*	18	0.3
2	*Microcalanus pygmaeus*	224,113	492.0	38	*Cornucalanus indicus*	46	10.8	71	*Scaphocalanus subbrevicornis*	18	0.4
8	Harpacticoida	64,450	673.8	54	*Lucicutia orientalis*	20	2.1	Carnivores			
3	*Metridia pacifica*	12,335	185.8	40	*Metridia ornata*	19	10.0	72	*Paraeuchaeta elongata*	850	147.9
5	*Eucalanus bungii**	6,969	2,155.4	37	*Lucicutia ellipsoidalis*	19	0.6	74	*Heterostylites major*	629	72.4
4	*Pseudocalanus* spp. (C1-C3)	6,870	22.9	18	*Spinocalanus stellatus*	18	0.7	76	*Paraeuchaeta rubra*	199	37.2
11	*Neocalanus flemingeri**	5,112	626.9	21	*Gaidius brevispinus*	12	0.7	75	*Paraeuchaeta birostrata*	158	29.0
10	*Neocalanus plumchrus**	4,825	324.6	42	*Chiridiella abbysalis*	10	0.6	77	*Haloptilus pseudooxycephalus*	115	17.2
13	*Neocalanus cristatus**	3,776	1,933.7	55	*Chiridiella pacifica*	10	0.7	73	*Heterorhabdus tanneri*	90	4.9
7	*Pseudocalanus minutus**	2,913	46.9	52	*Cephalophanes frigidus*	10	2.3	81	*Candacia columbiae*	88	7.0
6	*Pseudocalanus newmani*	2,751	23.8	45	*Lucicutia grandis*	10	2.9	80	*Heterorhabdus compactus*	38	1.6
24	*Calanus pacificus**	2,559	56.9	44	*Aetideopsis rostrata*	10	0.8	83	*Euaugaptilus graciloides*	27	5.4
14	*Lucicutia ovaliformis*	1,181	10.7	34	*Aetideus pacificus*	10	0.6	84	*Neoaugaptilus distinctus*	19	15.1
17	*Pleuromamma scutullata*	1,124	85.3	50	*Onchocalanus magnus*	9	0.6	79	*Pachyptilus pacificus*	9	1.9
9	*Pseudocalanus mimus*	1,071	9.7	56	*Euchirella galeata*	9	4.1	85	*Heterorhabdus robustoides*	9	2.0
33	*Spinocalanus similis*	1,065	4.7	Detritivores							
23	*Metridia curticauda*	533	28.1	57	Poecilostomatoida	482,704	1,079.9				
12	*Gaetanus simplex*	462	12.6	58	*Scolecithricella minor*	910	3.0				
15	*Metridia asymmetrica*	344	36.5	59	*Scolecithricella ovata*	899	10.6				
27	*Spinocalanus spinipes*	275	4.8	60	*Racovitzanus antarcticus*	671	13.1				
26	*Pseudogaetanus robustus*	221	50.4	69	*Scaphocalanus brevicornis*	190	4.1				
25	*Gaidius tenuispinus*	207	4.6	67	*Amallothrix paravalida*	111	3.2				
22	*Metridia similis*	114	3.9	61	*Scaphocalanus magnus*	83	9.9				
50	*Onchocalanus magnus*	82	9.5	63	*Scaphocalanus medius*	72	2.5				
31	*Pseudochirella polyspina*	55	10.7	62	*Amallothrix inornata*	63	3.7				
16	*Calanus marshallae**	52	2.3	70	*Amallothrix profunda*	57	2.2				

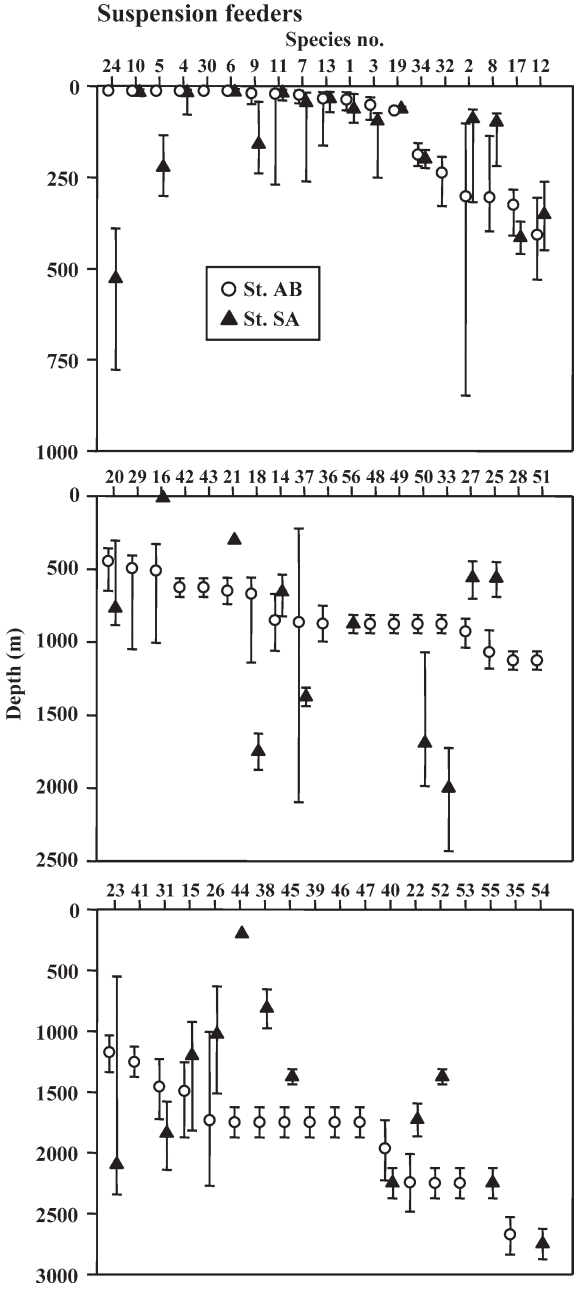

Fig. 5. Vertical distribution of suspension feeding copepods at St. AB in the southern Bering Sea and St. SA in the subarctic Pacific. Of each species, symbols indicate 50% distribution depth ($D_{50\%}$). Vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number, see Tables 2 and 3. Note that the vertical depth scales are not the same among panels.

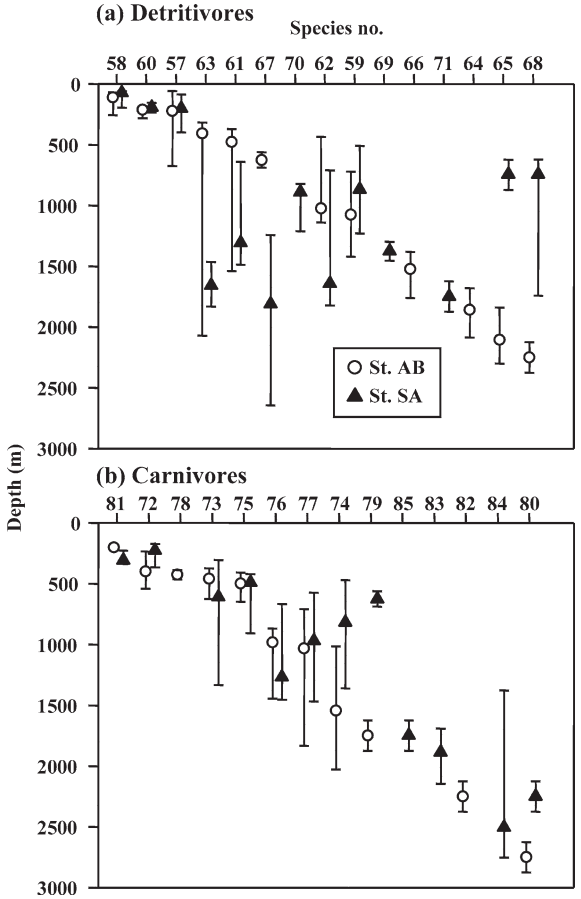

Fig. 6. Vertical distribution of detritivorous (a) and carnivorous (b) copepods at St. AB in the southern Bering Sea and St. SA in the subarctic Pacific. Symbols indicate 50% distribution depth ($D_{50\%}$), and vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number, see Tables 2 and 3.

in the southern Bering Sea. Since the mesh size of the present study (60 μm) was much smaller than that used by Minoda (330 μm), smaller copepods were presumably caught more efficiently in this study. Böttger-Schnack (1996) used 55 μm mesh nets in the epi- to mesopelagic zone of the Arabian Sea and noted that Poecilostomatoida contributed 60-80% of the total copepod abundance. In the present study, small Poecilostomatoida composed 0-70% of the total copepod abundance. A high composition of Poecilostomatoida to total copepod abundance (47-93%) was also reported by Yamaguchi et al. (2002) who used 90 μm mesh net in the western subarctic Pacific. These results suggest that for accurate evaluation of small copepods (Cyclopoida and Poecilostomatoida), fine-mesh size nets (<100 μm) are needed.

Table 6 compares the proportion of abundance of copepods at epipelagic (0-250 m), mesopelagic (250-1,000 m) and bathypelagic (1,000-3,000 m) zones collected with <100 μm mesh nets. In the southern Bering Sea, 74-86% occurred in the epipelagic, 10-16% occurred in the mesopelagic, and 4-9% occurred in the bathypelagic. This result may reflect that the food of deep-sea copepods comes from the surface. Similar proportions were reported by Vinogradov (1968) for zooplankton biomass at 0-4,000 m depth in the North Pacific ; 65% occurred at 0-500 m, and 35% occurred at 500-4,000 m. In the present study, 74-86% occurred at 0-250 m, which is much higher than reported by Vinogradov

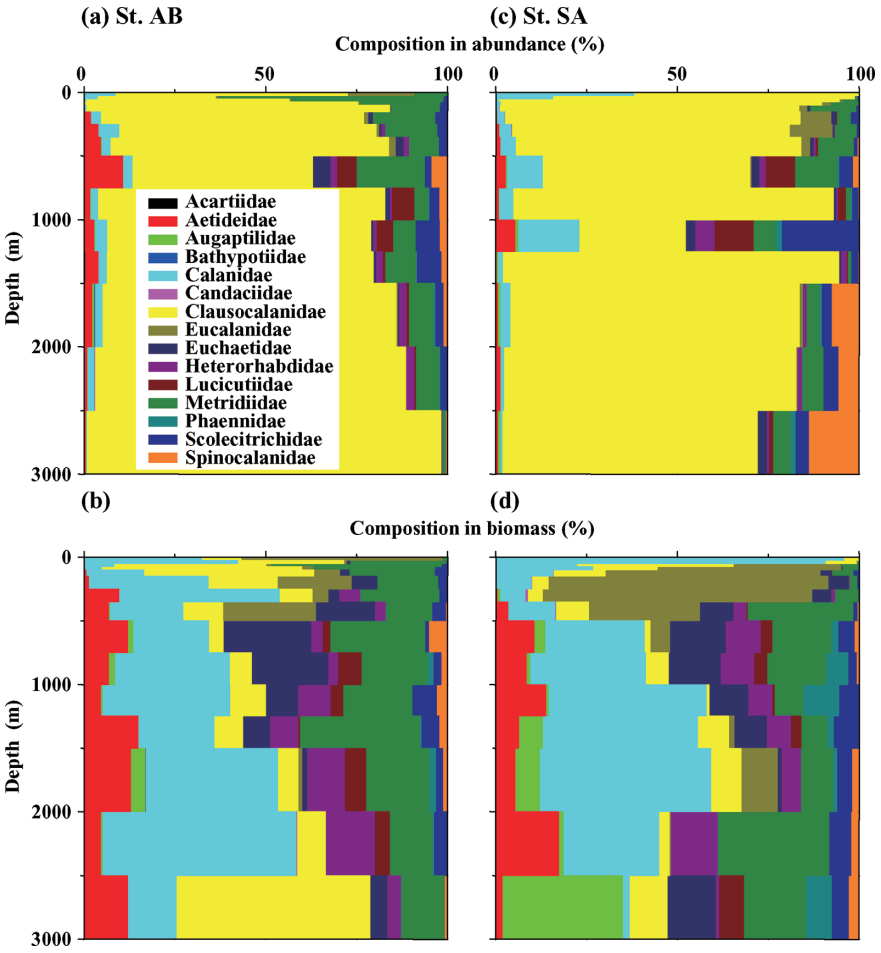

Fig. 7. Vertical changes in the composition of families of calanoid copepods in terms of abundance (a) and biomass (b) at St. AB in the southern Bering Sea and those at St. SA (c, d) in the subarctic Pacific during 14 and 16 June 2006, respectively.

(1968). This difference was probably due to the fact that the present study measured abundance, while Vinogradov (1968) measured biomass. Generally, small copepods dominated in the surface layer. It has been clearly shown that abundance decreases more rapidly with increasing depth than biomass does within the same region (Yamaguchi et al., 2002 ; Homma and Yamaguchi, 2010, Table 7). The effect of small-sized copepods may have been magnified in this study, which used small mesh size plankton nets.

Both abundance and biomass of copepods decreased with increasing depth, but the rates of decrease varied (Fig. 3). To express depth (X) decreasing pattern of abundance and biomass of zooplankton (Y), two models have been proposed. One is an exponential model ($\mathrm{Log}_{10}Y=a+bX$; where a and b are fitted constants) by Vinogradov (1968), and the other is a power model ($\mathrm{Log}_{10}Y=a'+b'\,\mathrm{Log}_{10}X$; where a' and b' are fitted constants) by Koppelmann and Weikert (1992) (Table 7). Abundance and biomass data in the present study showed a better fit to the power model ($r^2=0.91$–0.97) than to the exponential model ($r^2=0.67$–0.81). The slope (b') in the power model shows the depth-decreasing rate (Koppelmann and Weikert, 1992), which was higher for abundance ($b'=-1.48\sim-1.40$) than for biomass ($b'=-1.30\sim-1.15$), probably due to copepod body size. As discussed above, small-sized copepods were abundant near the surface layer.

Copepod carcasses are abundant in deep water in the North Atlantic Ocean (Roe, 1988) and Sargasso Sea (Wheeler, 1967). In the present study, carcasses outnumbered living copepods at 750–1,000 m at St. AB and 500–750 m at St. SA (Fig. 3a, c). These layers corresponded closely to the OMZ of both stations (Fig. 2). Micronektonic fishes are known to avoid the OMZ (Sameoto, 1986 ; Herring et al., 1998), so the pronounced increased abundance of carcasses in the OMZ may have caused by low predation pressure by micronectonic fishes. Another possibility is decomposition of copepod carcasses by bacteria may be slow in the OMZ due to the low DO. In the present study, the depth where carcasses outnumbered living specimen at St. SA (500–750 m) was shallower than that at St. AB (750–1,000 m). This may have been related to the depth of the OMZ, which was shallower at St. SA (340–1,230 m) than at St. AB (640–1,500 m) (Fig. 2).

Species diversity and community structure

A total of 72 and 63 calanoid copepod species occurred in

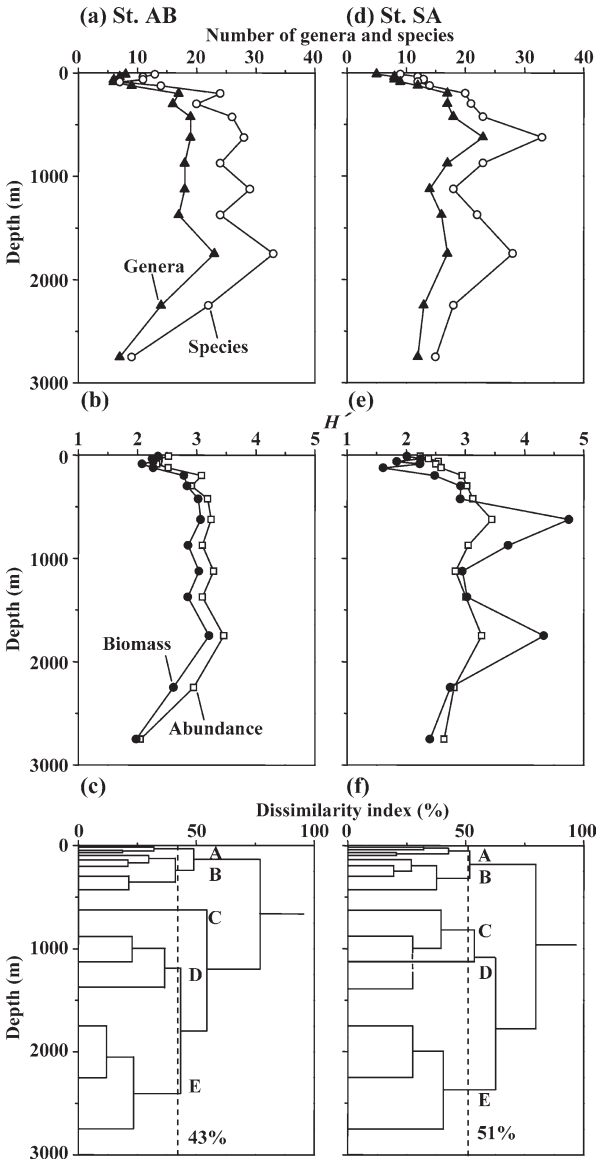

Fig. 8. Vertical distribution of the number of genera and species of calanoid copepods (a), species diversity indices (H') based on abundance and biomass data (b) and results of cluster analysis based on Bray-Curtis dissimilarity index (%) (c) at St. AB in the southern Bering Sea and at St. SA in the subarctic Pacific (d, e, f). Five groups (A-E) were recognized at 43% (c) and 51% (f) dissimilarity indices by cluster analysis.

the 0-3,000 m water column at St. AB and SA, respectively (Tables 2, 3). The number of calanoid copepod species from the surface to great depths has been reported to be 52 in the Arctic Ocean (0-3,500 m) (Kosovokova and Hirche, 2000), 37 in the Greenland Sea (0-3,000 m) (Richter, 1994), 101 in the western subarctic Pacific (0-3,000 m) (Yamaguchi et al., 2002), 48 in the eastern Mediterranean Sea (0-3,250 m) (Koppelmann and Weikert, 2007) and 66 in the Weddell Sea (0-1,000 m) (Schnack-Schiel et al., 2008). Thus the numbers of species in the present study (72 and 63 species) are similar to those in other regions.

Calanoid copepods were the most abundant order collected throughout the water column. Cyclopoida dominated in the surface layer, while Poecilostomatoida dominated below 750 m at St. AB and below 350 m at St. SA (Fig. 4a, b). Cyclopoida and Poecilostomatoida copepods are both small (TL ca. 1 mm), but their feeding patterns vary. Cyclopoida feed on small sinking particles, especially faecal pellets (Svensen and Nejstgaard, 2003 ; Poulsen and Kiørboe, 2006), while Poecilostomatoida attach to and feed on large detritus such as marine snow and giant larvacean houses (Steinberg et al., 1994, 1998). Also, in the western subarctic Pacific, Yamaguchi et al. (2002) reported that Cyclopoida occurs at the surface and Poecilostomatoida occurs in deep water. This vertical segregation between Cyclopoida and Poecilostomatoida was presumably the reason why the food habits differed.

In terms of copepod biomass, Calanidae dominated throughout the water column followed by Eucalanidae and Metridiidae, and the biomass of Euchaetidae, Heterorhabdidae, Lucicutiidae, Phaennidae and Spinocalanidae increased below 1,000 m (Fig. 7). Vinogradov (1968) listed Euchaetidae, Heterorhabdidae and Lucicutiidae as deep sea families. The genus *Heterorhabdus* (family Heterorhabdidae) injects venom from a mandible tooth into prey, which is considered to be an adaptation for capturing prey in the food-limited deep sea (Nishida and Ohtsuka, 1996). Like *Heterorhabdus*, various deep-sea copepods have specialized feeding patterns that allow them to adapt to the food-limited deep-sea (Nishida and Ohtsuka, 1997 ; Matsuura and Nishida, 2000).

The species diversity (H') of calanoid copepods was 1.5-2.6 at the surface, 2.8-4.7 at 250-2,000 m, and decreased with increasing depth below 2,000 m (Fig. 8b, e). In the Greenland Sea, Richter (1994) reported that the H' of calanoid copepods was low (0.8) at the surface, increased gradually with depth to 1.8 at 1,500 m, and decreased below 1,500 m. In Sagami Bay, Shimode et al. (2006) reported that H' was low (0.2) at the surface, and increased below 300 m, and varied between 2.0 and 2.5 at 300-1,500 m. In the western subarctic Pacific, H' is around 1.6 at the surface, then increases to 2.5 at 500-1,500 m, and decreases below 1,500 m (Yamaguchi et al., 2002). The general pattern is the species diversity of copepods tends to be low at the surface, high at mesopelagic depths, and decrease below 1,000-2,000 m.

The most important factor in the speciation of calanoid copepods is considered to be the differences in feeding patterns (Ohtsuka and Nishida, 1997). High variability in food habits in the deep-sea (e.g., phytoplankton aggregates, faecal pellets, marine snow, giant larvacean houses, dead and living copepods) has lead to specialized feeding modes in deep-sea copepods. For example, *Heterorabdus* spp. use venom or anesthetic injection (Nishida and Ohtsuka, 1996), *Cephalophanes* spp. have an optic system to detect bacterial luminescence (Nishida et al., 2002), *Augaptilus* spp. have button setae

Table 4. Mean abundance of dominant calanoid copepod species in each group (A–E), derived from cluster analysis at St. AB in the southern Bering Sea (cf. Fig. 8c). Differences between communities were tested by one-way ANOVA. For each species, the group with the greatest abundance is underlined. * : $p< 0.05$, ** : $p<0.01$, *** : $p<0.001$, ns : not significant

Species	Group and abundance (log_{10}[inds. m^{-3}+1])					F	Results of one-way ANOVA
	A	B	C	D	E		
Calanus marshallae	0.00	0.12	0.18	0.13	0.01	0.74	ns
Cyclopoida	3.63	2.07	0.83	0.47	0.31	19.57	***
Eucalanus bungii	1.39	0.32	0.00	0.00	0.01	3.68	*
Gaetanus simplex	0.00	0.36	0.45	0.00	0.002	2.64	ns
Harpacticoida	0.78	0.83	0.00	0.05	0.12	2.44	ns
Lucicutia ovaliformis	0.00	0.00	0.38	0.23	0.01	10.23	**
Metridia asymmetrica	0.00	0.00	0.07	0.15	0.09	3.20	ns
Metridia pacifica	2.57	1.43	0.76	0.06	0.16	33.35	***
Microcalanus pygmaeus	2.07	2.14	1.17	1.17	0.98	11.75	***
Nauplii	3.46	2.20	1.01	1.09	0.32	10.57	**
Neocalanus flemingeri	1.06	0.33	0.02	0.03	0.02	4.03	*
Pleuromamma scutullata	0.00	0.21	0.03	0.02	0.00	1.13	ns
Poecilostomatoida	1.79	2.20	0.43	0.78	0.74	3.12	*
Pseudocalanus mimus	1.65	0.41	0.00	0.00	0.00	15.00	***
Pseudocalanus minutus	1.93	0.62	0.07	0.05	0.03	24.5	***
Pseudocalanus newmani	1.67	0.23	0.00	0.00	0.02	8.37	**
Pseudocalanus spp.	1.93	0.20	0.00	0.00	0.00	10.97	**
Scolecithricella ovata	0.00	0.08	0.16	0.27	0.02	6.23	**

Table 5. Mean abundance of dominant calanoid copepod species in each group (A–E), derived from cluster analysis at St. SA in the subarctic Pacific (cf. Fig. 8f). Differences between communities were tested by one-way ANOVA. For each species, the group with the greatest abundance is underlined. * : $p<0.05$, ** : $p<0.01$, *** : $p<0.001$, ns : not significant

Species	Group and abundance (log_{10}[inds. m^{-3}+1])					F	Results of one-way ANOVA
	A	B	C	D	E		
Amallothrix paravalida	0.00	0.00	0.02	0.00	0.23	2.74	ns
Amallothrix profunda	0.00	0.00	0.02	0.48	0.00	9.44	***
Cyclopoida	3.40	1.81	0.95	1.28	0.28	8.97	**
Gaetanus simplex	0.00	0.27	0.03	0.00	0.00	11.96	***
Harpacticoida	1.94	1.8	0.24	0.00	0.00	4.88	*
Heterostylites major	0.00	0.11	0.14	0.09	0.02	1.96	ns
Lucicutia ovaliformis	0.09	0.12	0.28	0.17	0.00	1.49	ns
Metridia curticauda	0	0.07	0.03	0.70	0.09	14.9	***
Metridia pacifica	1.23	1.13	0.26	0.02	0.02	2.8	ns
Nauplii	3.64	2.02	0.76	1.01	0.82	15.3	***
Neocalanus cristatus	1.45	0.27	0.05	0.05	0.03	40.6	***
Neocalanus flemingeri	1.14	0.38	0.02	0.00	0.03	3.34	ns
Neocalanus plumchrus	1.3	0.02	0.01	0.00	0.00	7.58	**
Paraeuchaeta elongata	0.15	0.41	0.06	0.02	0.00	4.87	*
Paraeuchaeta rubra	0.00	0.00	0.07	0.03	0.01	3.66	*
Poecilostomatoida	3.11	2.8	1.81	1.45	1.23	34.66	***
Pseudocalanus mimus	0.42	0.37	0.00	0.00	0.01	1.23	ns
Pseudocalanus minutus	1.08	0.48	0.01	0.00	0.01	6.78	**
Pseudocalanus spp.	1.25	0.49	0.01	0.00	0.01	3.6	*
Scolecithricella minor	0.66	0.2	0.02	0.03	0.01	3.26	ns
Scolecithricella ovata	0.00	0.12	0.14	0.22	0.05	1.38	ns

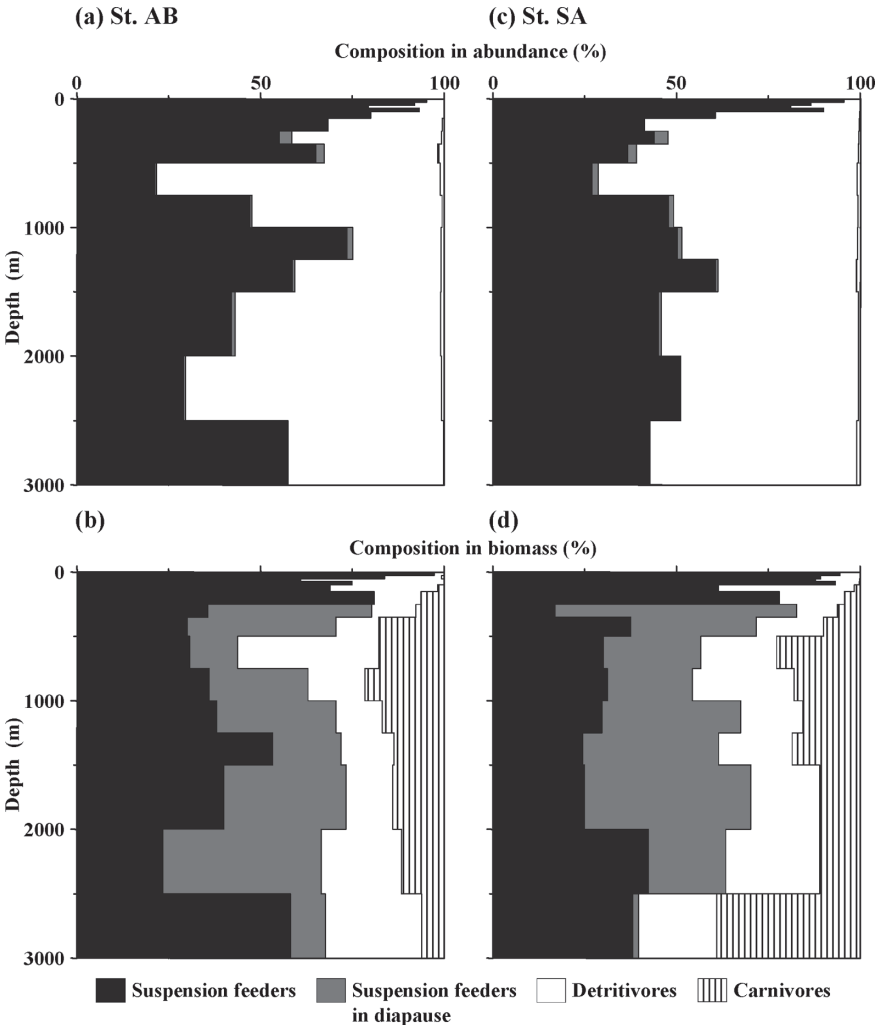

Fig. 9. Percentage composition of four feeding types of copepods in terms of abundance (a) and biomass (b) at St. AB in the southern Bering Sea and at St. SA in the subarctic Pacific (c, d) on 14 and 16 June 2006, respectively.

on their mouthparts (Matsuura and Nishida, 2000), and *Scolecithricella* spp. have specialized setae to detect chemicals (Nishida and Ohtsuka, 1997). The decrease in species diversity below 1,000–2,000 m was probably caused by limited food in the deep sea. Under such conditions it could be difficult to maintain or sustain specialized feeding modes, which could cause reduced species diversity.

Yamaguchi et al. (2002) classified the copepod community into three groups (0–200 m, 200–1,000 m and 1,000–4,000 m) in the western subarctic Pacific. In the Greenland Sea, Richter (1994) classified the copepod community into three groups (0–300 m, 300–1,000 m and 1,000–3,000 m). In the Arctic Ocean, Auel and Hagen (2002) also identified three groups (0–300 m, 300–1,000 m and 1,000–3,000 m). Generally, zooplankton are classified vertically into epipelagic (0–200 m), mesopelagic (200–1,000 m), bathypelagic (1000–3,000 m) and abyssopelagic (>3,000 m) communities (Vinogradov, 1968). The classifications of the copepod community in the present study showed additional boundaries at the thermocline (75 m) and at the top of the OMZ (500 m) (Fig. 8c, f). The vertical separation of the copepod community at the OMZ is considered to be a special feature of the Bering Sea and subarctic Pacific. These two areas are located near the area where deep water mixes upward due to thermohaline circulation, which intensify the OMZ (Broecker, 1991).

Comparison between Bering Sea and subarctic Pacific

The vertical distribution of suspension feeders in diapause greatly varied between St. AB in the Bering Sea and St. SA in the subarctic Pacific. At St. AB, *N. flemingeri*, *N. cristatus* and *C. marshallae* occurred deep, while at St. SA, the deep species were *E. bungii*, *P. minutus* and *C. pacificus* (Fig. 5). In the subarctic Pacific, descent occur during May to July for *N. flemingeri* (Miller, 1988 ; Tsuda et al., 1999), between July and August for *N. cristatus* (Miller et al., 1984 ; Kobari and Ikeda, 1999), in June for *C. marshallae* (Osgood and Frost, 1994), between July and September for *E. bungii* (Miller et al., 1984 ; Shoden et al., 2005), and after

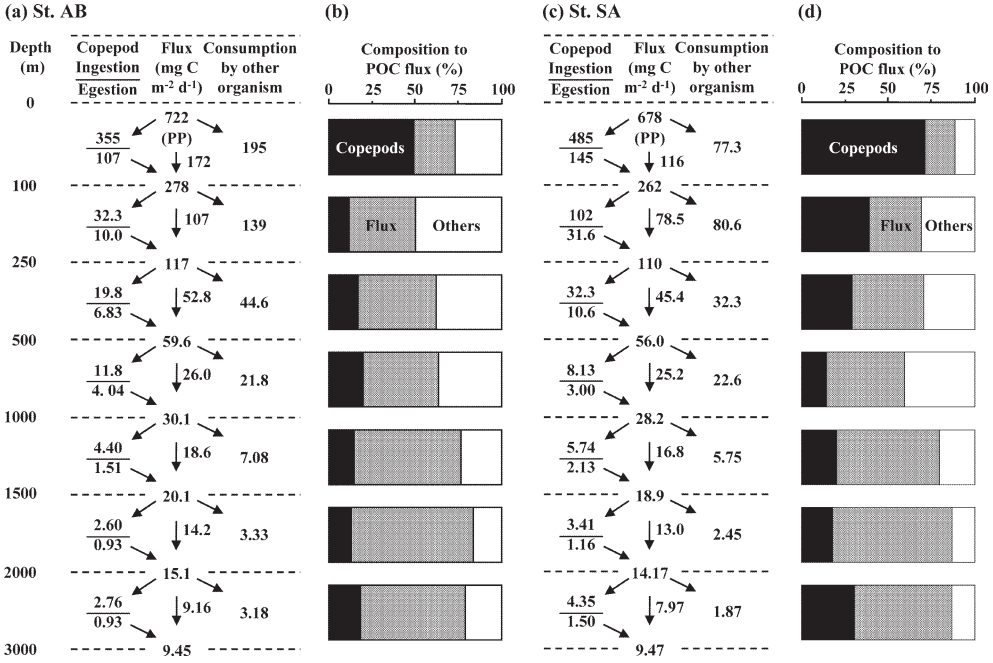

Fig. 10. Schematic diagram showing particle organic carbon (POC) flux (mg C m^{-2} day^{-1}) in the 0–3,000 m water column via seven depth strata at St. AB in the Bering Sea (a) and St. SA in the subarctic Pacific (c). PP : Primary production. As the POC flux fate, copepod consumption, direct sedimentation and consumption by other organisms are assumed, and their percentage compositions are shown in (b) and (d).

Table 6. Comparison in copepod abundance (inds. m^{-2}) in the Bering Sea (A, D), subarctic Pacific (B, C), and Arabian Sea (E). Values in the parentheses indicate composition (%) within the water column. For regional comparison, ratios between region were calculated.

Region	(A) Southern Bering Sea (St. AB)	(B) Northern subarctic Pacific (St. SA)	(C) Western Subarctic Pacific	(D) Southern Bering Sea	(E) Arabian Sea	
Mesh size (μm)	60	60	90	330	55	
References	This study	This study	Yamaguchi et al. (2002)	Minoda (1972)	Bottger-Schnack (1996)	
Depth (m)						Ratio A : B : C : D : E
0–250	1,165,990 (84)	1,970,242 (86)	710,725 (74)	99,825 (87)	474,000 (86)	1.6 : 2.8 : 1.0 : 0.1 : 0.7
250–1,000	154,106 (11)	230,705 (10)	155,163 (16)	14,953 (13)	75,790 (14)	1.0 : 1.4 : 1.0 : 0.1 : 0.5
1,000–3,000	65,920 (5)	93,160 (4)	89,672 (9)			0.7 : 1.0 : 1.0 : – : –

summer for *P. minutus* (Yamaguchi et al., 1998). The present study was conducted in June at the onset of diapause. The observed species-specific regional differences in vertical distribution may have been due to differences in the timing of the life cycle events of copepods, to differences in the magnitude and timing of primary production at the surface layer between St. AB and St. SA, or to both.

The inter-regional differences in vertical distribution of copepods varied with feeding modes. Regional differences in vertical distribution were greater in detritivores than in carnivores (Fig. 6). Detritivores tend to attach to large detritus, marine snow and larvacean houses (Steinberg et al., 1994, 1998), which are characterized by uneven heterogeneous distributions, while carnivores have no such habitat-associated distribution. Thus, the uneven and heterogeneous distribution of large detritus may have induced the large regional differences in vertical distribution of detritivores.

A remarkable feature of the copepod communities in the Bering Sea and subarctic Pacific is that they include specialized communities in the OMZ. The indicator species in the OMZ (500–1,500 m, group C and D) were *L. ovaliformis* and *S. ovata* at St. AB, and *H. major, L. ovaliformis, P. rubra, A. profunda, M. curticauda* and *S. ovata* at St. SA (Tables 4, 5). *Lucicutia ovaliformis* and *S. ovata* were common indicator species of the OMZ at both stations. *Lucicutia* species in the Arabian Sea are known to inhabit the OMZ (Gowing and Wishner, 1998 ; Wishner et al., 2000 ; Koppelmann and Weikert, 2005), and *Lucicutia* species can adapt to the OMZ

Table 7. Regression statistics for abundance/biomass of copepods on depth at St. AB in the southern Bering Sea and St. SA in the subarctic Pacific on 14 and 16 June 2006, respectively. Regression models are exponential (Log_{10} $Y=a+bX$) and power (Log_{10} $Y=a'+b'Log_{10}$ X) ones, where Y is abundance (inds. 1,000 m^{-3}) or biomass (μg C m^{-3}), X is depth in m, and a, b, a' and b' are fitted constants.

Exponential model Unit	Station	a	b	r^2	p
Abundance	AB	6.30	-9.42×10^{-4}	0.67	<0.001
	SA	6.60	-1.07×10^{-3}	0.78	<0.0001
Biomass	AB	3.82	-8.31×10^{-4}	0.75	<0.0001
	SA	4.23	-9.90×10^{-4}	0.81	<0.0001
Power model Unit	Station	a'	b'	r^2	p
Abundance	AB	9.09	−1.40	0.97	<0.0001
	SA	9.48	−1.48	0.97	<0.0001
Biomass	AB	6.07	−1.15	0.94	<0.0001
	SA	6.73	−1.30	0.91	<0.0001

due to high lactate dehydrogenase activities in the tricarboxylic acid cycle (Thuesen et al., 1998). Thus, the indicator species in the OMZ may have specialized mechanisms to adapt to the low DO condition.

Effect on vertical flux of material

The suspension feeders and detritivores were the two dominant feeding modes in terms of abundance throughout the water column at both stations (99% of the total copepod abundance) (Fig. 9a, c). In terms of biomass, the contribution of the four feeding modes differed from that expressed by abundance ; carnivores and suspension feeders in diapause dominated below 250 m depth (Fig. 9b, d). This difference in the contribution of each feeding mode between abundance and biomass was caused by the differences in body size of the numerically dominant copepods. Most suspension feeders and detritivores are small (e.g., Cyclopoida, Poecilostomatoida and *M. pygmaeus* [Tables 2, 3]). On the other hand, carnivores (*Paraeuchaeta* spp. and Heterorhabdidae) and suspension feeders in diapause (*Neocalanus* spp. and *E. bungii*) are large, so their contribution in terms of biomass increased.

Copepods were estimated to consume 20±13% or 32±19% (mean±1sd) of the POC flux at St. AB and SA, respectively. The effect of copepod feeding on the POC flux was greatest in the upper 100 m (Fig. 10a, c). Based on similar methods, copepods have been reported to consume 38% (Sasaki et al. 1988) or 32% (Yamaguchi et al., 2002) of POC flux in the western North Pacific. However both of these studies estimated the metabolic rate of copepods by applying an empirical equation from the epipelagic zone (Ikeda, 1985 ; Ikeda et al., 2001). Since the metabolic rate of copepods decreases with increasing depth (Thuesen et al., 1998 ; Ikeda et al., 2007), ingestion rate estimated by Sasaki et al. (1988) and Yamaguchi et al. (2002) presumably overestimated the true values.

In the present study, a new equation was used to estimate metabolic rates of copepods based on four independent variables (body mass, habitat temperature, oxygen saturation and depth, see Ikeda et al., 2007) from epi- to bathypelagic depths. We also re-calculated respiration rates using the formula for epipelagic copepods reported by Ikeda et al. (2001), and showed that copepods consume an average of 38±12% (St. AB) and 58.3±17% (St. SA) of the POC flux, which are substantially greater than the values (20-32%) calculated using the newer formula in this study.

The present study examined the effect of ingestion by copepods on passive POC flux, but did not examine their active carbon flux (diel and seasonal vertical migration). Kobari et al. (2008) reported that the active carbon flux caused by diel vertical migration of *M. pacifica* (i.e., respiration and mortality at depth) was 4-17 mg C m^{-2} day^{-1}, and the active carbon flux by *N. cristatus* and *N. flemingeri* ontogenetic vertical migration was 1,719 mg C m^{-2} $year^{-1}$. If we consider these to be the active carbon fluxes caused by diel and seasonal vertical migration, the estimated total vertical carbon flux due to the copepod community is larger than the values obtained in this study.

As consumers of the POC flux, copepods and heterotrophic bacteria are important taxa throughout the water column (Nagata et al., 2000, 2001 ; Koppelmann et al., 2004). In the present study, the mean fraction of the POC flux consumed by heterotrophic bacteria was 33±12% (mean±sd) at St. AB and 22±11% at St. SA (Fig. 10b, d). In the subarctic-subtropical North Pacific, heterotrophic bacteria consume 23-51% of the POC flux throughout the water column (Nagata et al., 2000, 2001). In the Mediterranean Sea, 19-39% of the POC flux is consumed by heterotrophic bacteria (Tanaka and Rassoulzadegan, 2004). In the present study, the fraction of bacterial consumption (22-33%) is close to the values reported in other studies (Fig. 10). Consumption of POC flux by heterotrophic bacteria is supposed by consumption on labile DOC of solute plume by sinking POC

(Kiørboe and Jackson, 2001).

In the present study, the POC flux in each layer was assumed to have one of three fates : consumption by copepods, consumption by other organisms (mainly heterotrophic bacteria), and direct sinking. In the 0–100 m layer at both stations, copepods were estimated to be the main consumer of POC, while bacteria were the main consumer of POC at 100–1,000 m, and the fraction of direct sinking POC increased at 1,000–3,000 m (Fig. 10b, d). These vertical changes in the main consumers and the fate of POC (copepods at 0–100 m, heterotrophic bacteria at 100–1,000 m and directly sinking at 1,000–3,000 m) are reasonable from the viewpoint of particle "repacking". The increased proportion of direct sinking of the POC at 1,000–3,000 m suggests that the repeated repacking on POC in shallower water may reduce the nutritional value of the POC. The rapid decrease of nitrogen (contained in amino acids) from passive sinking materials is a common phenomenon in the open ocean (Smith et al., 1992 ; Karl et al., 1996).

Miller et al. (1984) reported that copepods in diapause were observed below 250 m in the North Pacific. Conover (1988) have also reported that the abundance of diapausing *N. cristatus* adult females showed a peak at the depth of 500–1,000 m. In the Bering Sea and the subarctic Pacific, the OMZ was well developed in deep waters (640–1,500 m at St. AB and 340–1,230 m at St. SA), and a major part of copepod populations diapaused in the OMZ. Thus, diapausing copepod populations in OMZ could avoid predation by micronectonic fishes (lanternfish, etc) and maintain their abundance. However, diapausing copepods above the OMZ may suffer predation pressure by micronektonic fish, and consequently those micronectonic fishes will play an important role as food of commercial fish species such as salmon (Pearcy et al., 1988). Therefore, copepods above the OMZ presumably support marine ecosystems especially during autumn and winter when there are no phytoplankton blooms.

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