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Vertical changes in abundance, biomass and community structure of copepods down to 3000 m in the southern Bering Sea

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ABSTRACT

Vertical changes in abundance, biomass and community structure of copepods down to 3000 m depth were studied at a single station of the Aleutian Basin of the Bering Sea (53°28'N, 177°00'W, depth 3779 m) on the 14th June 2006. Both abundance and biomass of copepods were greatest near the surface layer and decreased with increase in depth. Abundance and biomass of copepods integrated over 0–3000 m were 1,390,000 inds. m⁻² and 5056 mg C m⁻², respectively. Copepod carcasses occurred throughout the layer, and the carcass:living specimen ratio was the greatest in the oxygen minimum layer (750–100 m, the ratio was 2.3). A total of 72 calanoid copepod species belonging to 34 genera and 15 families occurred in the 0–3000 m water column (Cyclopoida, Harpacticoida and Poecilostomatoida were not identified to species level). Cluster analysis separated calanoid copepod communities into 5 groups (A–E). Each group was separated by depth, and the depth range of each group was at 0–75 m (A), 75–500 m (B), 500–750 m (C), 750–1500 m (D) and 1500–3000 m (E). Copepods were divided into four types based on the feeding pattern: suspension feeders, suspension feeders in diapause, detritivores and carnivores. In terms of abundance the most dominant group was suspension feeders (mainly Cyclopoida) in the epipelagic zone, and detritivores (mainly Poecilostomatoida) were dominant in the meso- and bathypelagic zones. In terms of biomass, suspension feeders in diapause (calanoid copepods *Neocalanus* spp. and *Eucalanus bungii*) were the major component (ca. 10–45%), especially in the 250–3000 m depth. These results are compared with the previous studies in the same region and that down to greater depths in the worldwide oceans.

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1. Introduction

Copepods are known to be the most important taxa of the mesozooplankton in the worldwide oceans (cf. Mauchline, 1998). Vertical distribution of copepod community structure down to greater depths has been studied in the Arctic Ocean (Auel and Hagen, 2002; Darnis et al., 2008), Arabian Sea (Koppelman and Weikert, 2005), Greenland Sea (Richter, 1994), western subarctic Pacific (Yamaguchi et al., 2002), Red Sea (Weikert, 1982) and Mediterranean Sea (Weikert and Trinka, 1990). To evaluate accurate copepod community structure the mesh sizes of the nets are important. Böttger-Schnack (1996) reported that the use of fine mesh nets (< 100 μm) is needed to collect small copepods (Cyclopoida and Poecilostomatoida), which dominate in abundance. While numerous studies have been made on community structure of copepods down to greater depth, most of these studies applied large mesh size (200–500 μm) plankton nets. This indicates that the present information on community structure,

especially of smaller sizes, is an underestimate and has not been well evaluated.

The Bering Sea is known to be a sink region for CO₂ (Takahashi et al., 2000, 2002). In the southeastern Bering Sea shelf, numerous studies on the zooplankton community have been made, but comparable knowledge in the southern Bering Sea basin is limited in extent (Vinogradov, 1968; Minoda, 1971, 1972; Motoda and Minoda, 1974). Most of the studies in the Bering Sea basin are mainly concerning the distribution of zooplankton, especially copepods, and little information is available on their community structure. Copepods are the major component of zooplankton biomass in the southern Bering Sea basin (Nagasawa et al., 1999). As the basis of understanding marine ecosystem, information on community structure of copepods through the entire water column is necessary. While a long-term particle flux study using sediment traps has been conducted at a single station in the southern Bering Sea from 1990 to present (Takahashi et al., 2000, 2002), information on zooplankton community in the overlying pelagic zone is currently lacking.

In the present study, stratified zooplankton samples were collected with fine (60 μm) mesh nets from fifteen discrete depth intervals through 0–3000 m at a single station in the southern

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Bering Sea basin in summer 2006. Based on these samples, vertical changes in abundance, biomass and community structure of copepods were evaluated, and compared with the previous studies within the Bering Sea and those in the other oceans.

2. Material and methods

2.1. Zooplankton sampling

Zooplankton samplings were conducted at St. AB (Aleutian Basin: 53°28'N, 177°00'W, depth 3779 m) in the southern Bering Sea during the cruise of T/S *Oshoro-Maru* on 14 June 2006 (Fig. 1). Samples were collected from fifteen discrete depth intervals between 0 and 3000 m (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–350, 350–500, 500–750, 750–1000, 1000–1250, 1250–1500, 1500–2000, 2000–2500, 2500–3000 m) by Vertical Multiple Plankton Sampler (VMPS, mouth opening 0.25 m², mesh size 60 μm, cf. Terazaki and Tomatsu, 1997). Zooplankton samplings were made between 06:18 and 09:39 (local time). The volume of water filtered was estimated by reading a flow meter mounted in the mouth of the net, and ranged from 5.59 to 135.9 m³ (Table 1). Zooplankton samples were split with a Motoda splitting device (Motoda, 1959) on board and 1/2 aliquot preserved immediately in 5% borax-buffered formalin-seawater after collection (the remaining 1/2 aliquot was used for other studies).

Profiles of water temperature, salinity and dissolved oxygen were obtained with a Sea-Bird SBE911Plus CTD system. Hydrographic data was measured only between 0 and 2000 m on 14 June 2006. For the hydrographic data at 2000–3000 m in the St. AB, we refer the data at same station measured on 14 July 2005.

2.2. Enumeration and body length

In the laboratory ashore, copepods in the samples were identified and counted under a dissecting microscope. For Calanoida, identification was done at the species and developmental stage levels. For the species identification, we referred mainly to Brodskii (1967). For species reported later than Brodskii (1967), we referred to Frost (1974) for *Calanus marshallae*, Frost (1989) for *Pseudocalanus mimus*, *P. minutus*, *P. moultoni*,

P. newmani and Miller (1988) for *Neocalanus flemingeri*. Calanoid family systematic was followed using Mauchline (1998). For *Pseudocalanus* spp., species identification was made only for C4–C6, and C1–C3 treated as *Pseudocalanus* spp.

The total length (TL) of adults (C6) of each copepod species was referred to Brodskii (1967), Frost (1974, 1989) and Miller (1988). For juvenile copepodid stages, TL was calculated by multiplying TL of C6 with the ratio of C1–C5 to C6 (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 identified at the order level.

The feeding patterns of copepods were classified into four types based on their gut contents and mouthpart morphology (Arashkevich, 1969; Ohtsuka and Nishida, 1997): i.e., suspension feeders (Cyclopoida, Harpacticoida and most of the calanoid families except listed below), suspension feeders in diapause, detritivores (Poecilostomatoida and calanoid families: Diaixidae, Parkiidae, Phaennidae, Scolecitrichidae, Tharybidae) and carnivores (calanoid families: part of Aetideidae, Arietellidae, Augaptilidae, Bathypontiidae, Candaciidae, Euchaetidae, part of Heterorhabdidae, Hyperbionychidae, part of Phaennidae, Phyllopodidae, part of Pontellidae) (cf. Ohtsuka and Nishida, 1997).

Table 1
Sampling data of VMPS at St. AB in the southern Bering Sea during 14 June 2006.

Depth layer (m)	Local time	Water filtered (m ³)
0–25	09:38–09:39	5.593
25–50	09:38–09:38	5.966
50–75	09:37–09:38	5.779
75–100	09:26–09:27	5.593
100–150	09:25–09:26	12.49
150–250	09:23–09:25	24.61
250–350	09:05–09:07	20.88
350–500	09:03–09:05	35.98
500–750	08:58–09:03	57.61
750–1000	07:43–07:47	60.34
1000–1250	07:39–07:43	64.85
1250–1500	07:35–07:39	63.72
1500–2000	06:34–06:42	116.6
2000–2500	06:26–06:34	135.9
2500–3000	06:18–06:26	120.5

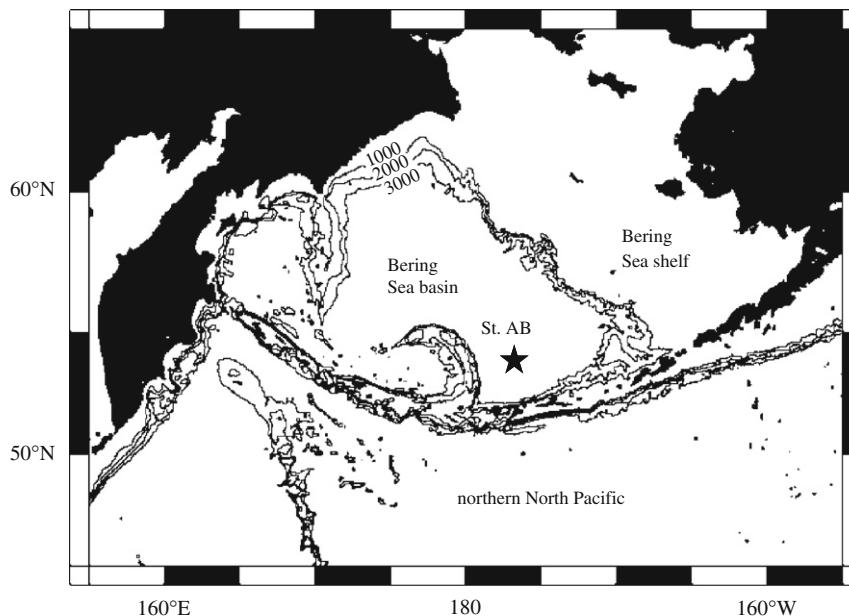


Fig. 1. Location of the St. AB (53°28'N, 177°00'W) in the southern Bering Sea basin. Depth contours (1000, 2000 and 3000 m) are superimposed.

Suspension feeders in diapause include C5 and C6 of three *Neocalanus* spp. (*N. cristatus*, *N. flemingeri*, *N. plumchrus*), C3–C6 of *E. bungii* (Miller et al., 1984), C5 and C6 of *C. pacificus*, *C. glacialis*, *C. marshallae* and *P. minutus* (Conover, 1988; Osgood and Frost, 1994; Yamaguchi et al., 1998) occurred below 250 m depth. Copepod carcasses (exoskeletons with some body tissue inside, cf. Wheeler, 1967; Terazaki and Wada, 1988) were also identified and counted separately with living specimen.

2.3. Data analysis

2.3.1. Biomass

Dry mass of each copepod was estimated from its TL using allometric equations. For Calanoida, the allometric equation

$$\text{Log}_{10}DM = 2.546\text{Log}_{10}TL - 6.697$$

where DM is individual dry mass (mg DM ind.⁻¹) and TL is total length (μm) was applied (Mizdalski, 1988). Then, DM was converted to carbon mass, assuming the carbon content of copepods to be 44.7% of DM (Båmstedt, 1986). For Harpacticoida, the allometric equation

$$CM = 2.65 \times 10^{-6} \times TL^{1.95}$$

where CM is the individual carbon mass (μg C ind.⁻¹) and TL is the total length (μm) applied (Uye et al. 2002). For Cyclopoida, the allometric equation

$$\text{Log}_{10}DM = 2.163\text{Log}_{10}TL - 6.207$$

where DM is the individual dry mass (mg DM ind.⁻¹) and TL is the total length (μm) applied (Kaneko, 2005). The carbon content of Cyclopoida was assumed to be 42.5% of DM (James and Wilkinson, 1988). For Poecilostomatoida, the allometric equation is

$$\text{Log}_{10}DM = 2.895\text{Log}_{10}TL - 7.993,$$

where DM is individual dry mass (mg DM ind.⁻¹) and TL is the total length (μm) applied (Nishibe, 2005). Nishibe and Ikeda (2008) reported that carbon content of Poecilostomatoida was 49–57% of DM. In the present study we assumed carbon content of Poecilostomatoida to be 53% of DM, which is the median of 49–57%.

2.3.2. Depth where population resided

To make a quantitative comparison possible the depth where the 50th percentile of the population resided ($D_{50\%}$) was calculated for each copepod species (cf. Pennak, 1943). Additional calculations were made to give depths where the 25th ($D_{25\%}$) and 75th ($D_{75\%}$) percentiles of the population occurred. Note that these calculations dealt with the whole population of a given copepod species, including all developmental stages.

2.4. Community structure

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

$$H' = - \sum n/Ni \ln n/Ni$$

where n is abundance (inds. m⁻²) of each species at the i th layer and Ni is total abundance of calanoid copepods in the i th layer. We calculated H' based on both abundance (inds. m⁻²) and biomass (mg C m⁻²).

We conducted both Q-mode (layer similarity) and R-mode (species association) analyses (cf. Chiba et al., 2001; Chiba and Saino, 2003) based on calanoid copepod abundance. In Q-mode analysis, abundances (X : inds. m⁻³) were transformed by $\text{Log}_{10}(X+1)$ 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 classify the layer into several groups with similar community composition. Computer software, BIOSTAT II was employed for these analyses. To clarify indicator species for each group, one-way ANOVA and Fisher's PLSD test were applied for copepod abundance data. In R-mode analysis, only dominant species (> 2% in total abundance of any one sampling layer) were examined (thus, 22 species). Species abundance data were standardized prior to analysis as follows: the contribution of each species to the total abundance of calanoid copepods (%: ten times of %) in each sampling layer. For R-mode analysis, we also conducted cluster analysis similar to Q-mode analysis.

3. Result

3.1. Hydrography

The surface temperature at St. AB was 5.9 °C (Fig. 2). Water temperature decreased rapidly at 150 m (3.1 °C) and increased at 380 m, forming a sub-maximum (4.0 °C) at 370 m, and again decreased with increase in depth and was 1.4 °C at 3000 m. Salinities ranged from 33.0 to 34.6 and increased with increase in depth. Dissolved oxygen was highest in the surface layer (maximum: 7.6 ml l⁻¹), then decreased with increase in depth. An oxygen minimum layer was observed around 750–1250 m (minimum: 0.48 ml l⁻¹ at 800 m), and dissolved oxygen again increased at 3000 m (1.8 ml l⁻¹).

3.2. Abundance and biomass

Copepods were most numerous at 0–25 m (23,429 inds. m⁻³) and declined consistently downward to 2500–3000 m depth (12 inds. m⁻³). The abundance of living copepods decreased drastically 0–1000 m and moderately below 1000 m (Fig. 3a). Copepod carcasses occurred throughout the water column varying between 3.5 inds. m⁻³ (0–25 m) and 402 inds. m⁻³ (25–50 m). The ratio of carcasses to living specimens was lowest in the surface layer (0–25 m) and had a maximum at 750–1000 m (carcass:living specimen abundance was 2.3) (Fig. 3a). Below 1000 m, carcass:living specimen ratio increased with increase in depth, carcasses were slightly more numerous than living specimens at 2500–3000 m. Copepod biomass varied between 0.06 mg C m⁻³ (2500–3000 m) and 106 mg C m⁻³ (0–25 m) (Fig. 3b).

The contribution of Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida to total copepod abundance was 29–74%, 3–56%, 0.2–7% and 5–77%, respectively, and varied greatly with depth (Fig. 4a). In the upper 100 m, Cyclopoida dominated, while Calanoida and Poecilostomatoida dominated below 500 m. Below 500 m, the average ratio of Calanoida:Poecilostomatoida was nearly 1:1 (Fig. 4a). Throughout the water column, Calanoida (55%) and Cyclopoida (30%) were the dominant taxa (Fig. 4a). In terms of biomass, however, the order of the relative contribution by the four groups differed from that expressed by abundance; Calanoida dominated throughout the water column (50–96% of the total, Fig. 4b). The composition of Cyclopoida was 0.1–11% and Poecilostomatoida was 2–38%. Throughout the water column, Calanoida (87%) and Poecilostomatoida (10%) were the two dominant copepod taxa contributing biomass.

A total of 72 calanoid copepods belonging to 34 genera and 15 families, Cyclopoida, Harpacticoida and Poecilostomatoida occurred in the 0–3000 m water column (Table 2). Suspension

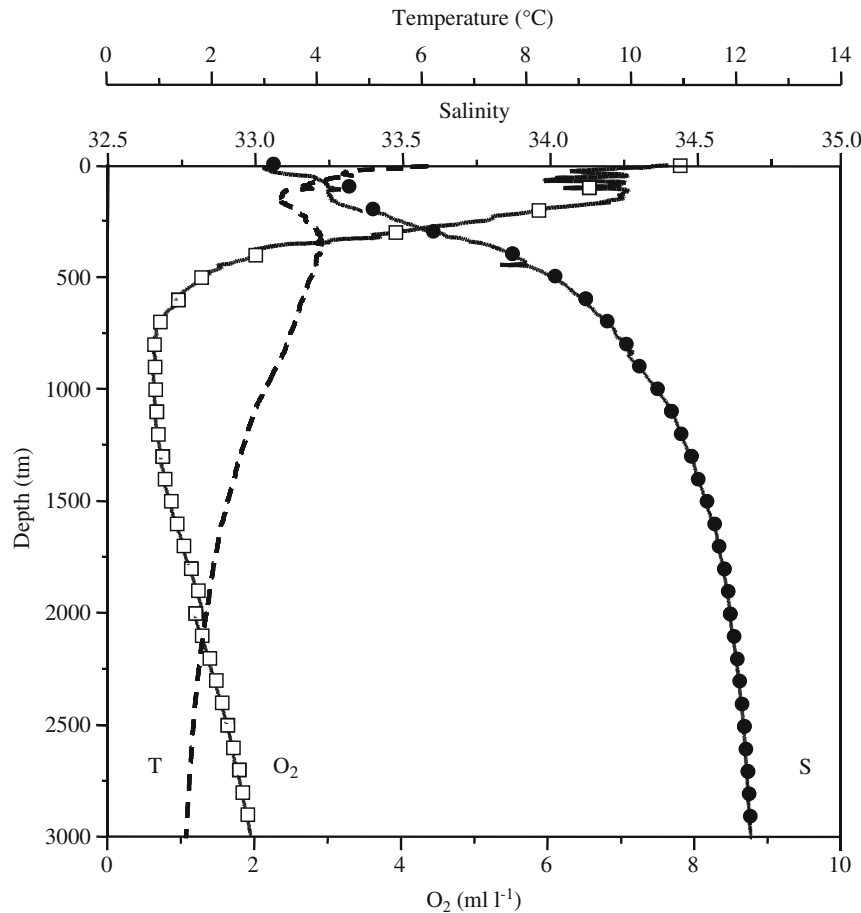


Fig. 2. Vertical distribution patterns of temperature (dashed line), salinity (solid circle symbols) and dissolved oxygen (open square symbols) at St. AB in the southern Bering Sea, 14 June 2006. Note that the data below 2000 m are those in 14 July 2005.

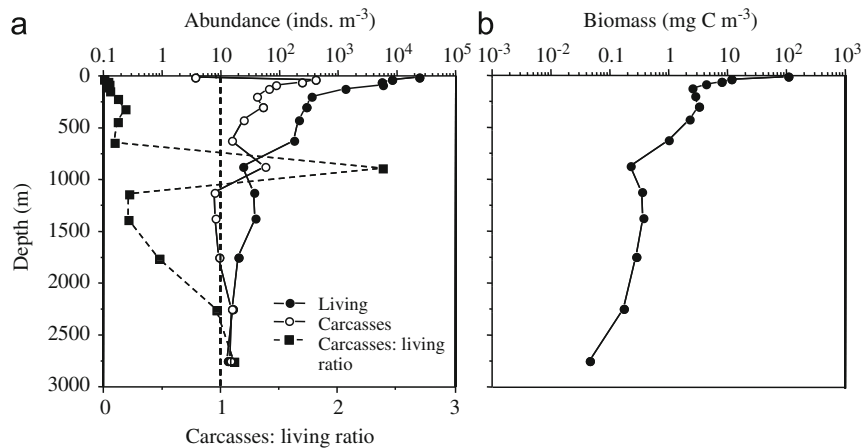


Fig. 3. Vertical distribution of abundance (a) and biomass (b) of copepods at St. AB in the southern Bering Sea, 14 June 2006. Data were separated with living and carcasses, and their ratio (carcasses: living) was also calculated. Note that the scales of abundance and biomass are in log scales, vertical line in (a) indicates carcasses: living ratio=1:1.

feeders included 44 calanoid species, Cyclopoida and Harpacticoida, detritivores included 11 calanoid copepods and Poecilostomatoida and carnivores included 11 calanoid copepods.

For suspension feeders, the most numerous calanoid copepods were *Microcalanus pygmaeus*, *Metridia pacifica* and *Pseudocalanus* spp. (Table 2). In terms of biomass, the most dominant species in suspension feeders was *Eucalanus bungii* followed by *N. cristatus* and *N. flemingeri*, all of which have a diapause phase in deep layers (Table 2). In the detritivore group, *Scolecithricella minor* and

S. ovata dominated in abundance, but large calanoid copepods, *Scaphocalanus magnus* dominated in biomass. For carnivores, *Paraeuchaeta* spp. and Heterorhabdidae dominated both in abundance and biomass.

Vertical changes in contribution of the four feeding patterns of copepods to abundance and biomass are shown in Fig. 4c, d. In terms of abundance, suspension feeders dominated with 79–93% at 0–150 m and 55–68% at 150–500 m of the total copepods (Fig. 4c). Detritivores dominated with 77% at 500–750 m.

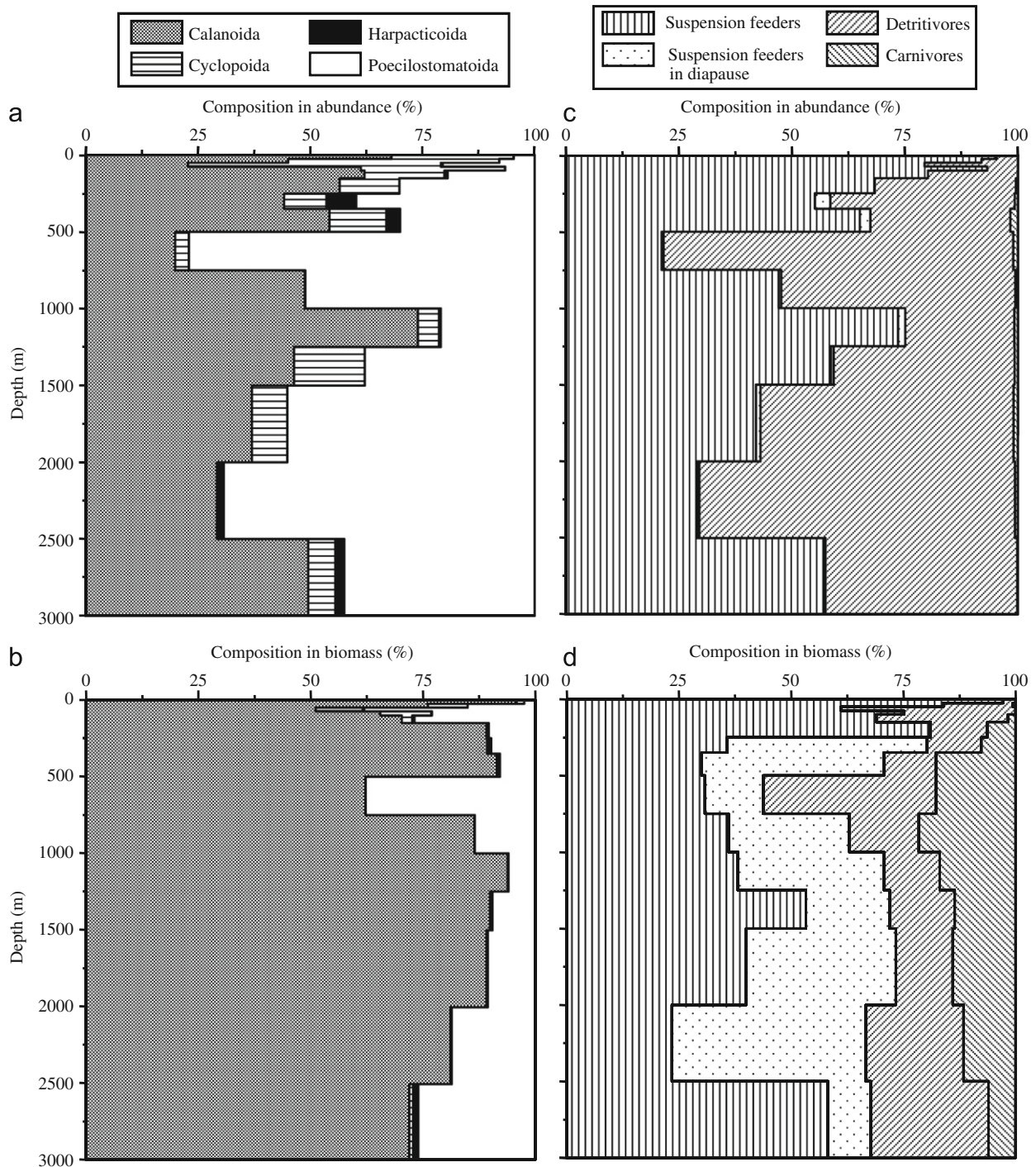


Fig. 4. Vertical changes in the composition of four orders (Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida) of copepods in terms of abundance (a) and biomass (b) at St. AB in the southern Bering Sea, 14 June 2006. Percentage composition of four feeding types of copepods (suspension feeders, suspension feeders in diapause, detritivores and carnivores) at same occasion are also shown in terms of abundance (c) and biomass (d).

Suspension feeders and detritivores were the two dominant copepod taxa contributing to abundance throughout the water column (99% of the total copepod abundance). In terms of biomass, the contribution of the four feeding groups differed from that expressed by abundance, suspension feeders dominated with 62–97% in the upper 250 m, while carnivores and suspension feeders in diapause dominated below 250 m depth (Fig. 4d).

For suspension feeders, most of the species showed restricted particular depth ranges. In terms of $D_{50\%}$, 13 species resided in the upper 100 m, 8 species resided in 100–500 m, 13 species were in

the 500–1000 m layer and the remaining 19 species resided below 1000 m (Fig. 5). Both detritivores and carnivores also had species-specific depth distribution (Fig. 6). It was notable that the $D_{50\%}$ values of carnivores resided below 200 m depths.

The contribution of calanoid copepod family to total calanoid copepod abundance and biomass is shown in Fig. 7. In terms of abundance, Clausocalanidae, which mainly consisted of *M. pygmaeus* dominated (33–98%) throughout the water column (Fig. 7a). In terms of biomass, the compositions of the family Aetideidae, Calanidae, Euchaetidae, Metridiidae, Heterorhabdidae

Table 2
List of species of calanoid copepods at St. AB in the southern Bering Sea. Abundance (inds. m^{-2} : 0–3000 m) and biomass (mg C m^{-2} : 0–3000 m) of each species and that of Cyclopoida, Harpacticoida and Poecilostomatoida are also shown. Based on the feeding pattern, each copepod divided into four types: suspension feeders, suspension feeders in diapause, detritivores and carnivores.

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}
Suspension feeders				27	<i>Spinocalanus spinipes</i>	105	0.8		Detritivores		
1	Cyclopoida	412,862	107	28	<i>Metridia brevicauda</i>	100	0.9	54	Poecilostomatoida	208143	495.8
2	<i>Microcalanus pygmaeus</i>	87,842	201.1	29	<i>Metridia okhotensis</i>	99	4.8	55	<i>Scolecithricella minor</i>	1645	8.9
3	<i>Metridia pacifica</i>	35,539	295.3	30	<i>Acartia longiremis</i>	97	0.1	56	<i>Scolecithricella ovata</i>	997	11.8
4	<i>Pseudocalanus</i> spp. (C1–C3)	25,058	62.3	31	<i>Pseudochirella polyspina</i>	57	8.3	57	<i>Racovitzanus antarcticus</i>	352	7.5
5	<i>Eucalanus bungii</i> ^a	14,358	1519.7	32	<i>Calanus glacialis</i> ^a	43	6.2	58	<i>Scaphocalanus magnus</i>	95	13
6	<i>Pseudocalanus newmani</i>	12,663	84.9	33	<i>Spinocalanus similis</i>	41	0.1	59	<i>Amalothrix inornata</i>	56	4.7
7	<i>Pseudocalanus minutus</i> ^a	11,153	198.6	34	<i>Aetideus pacificus</i>	41	1.5	60	<i>Scaphocalanus medius</i>	25	0.5
8	Harpacticoida	5399	5.8	35	<i>Spinocalanus pseudospinipes</i>	33	0.2	61	<i>Scaphocalanus subelongatus</i>	25	0.6
9	<i>Pseudocalanus mimus</i>	5388	38.3	36	<i>Euchirella messinensis</i>	33	1.4	62	<i>Amalothrix valida</i>	23	2
10	<i>Neocalanus plumchrus</i> ^a	3917	249.4	37	<i>Lucicutia ellipsoidalis</i>	24	0.5	63	<i>Xanthocalanus kurilensis</i>	16	0.6
11	<i>Neocalanus flemingeri</i> ^a	2997	442.6	38	<i>Cornucalanus indicus</i>	17	2	64	<i>Amalothrix paravalida</i>	9	0.2
12	<i>Gaetanus simplex</i>	1619	37	39	<i>Pseudochirella pacifica</i>	17	6.7	65	<i>Scaphocalanus affinis</i>	7	0.3
13	<i>Neocalanus cristatus</i> ^a	1395	584.3	40	<i>Metridia ornata</i>	16	1.2		Carnivores		
14	<i>Lucicutia ovaliformis</i>	958	10.3	41	<i>Pseudochirella spinifera</i>	16	2.2	66	<i>Paraeuchaeta elongata</i>	699	64.5
15	<i>Metridia asymmetrica</i>	747	67.3	42	<i>Chiridiella abyssalis</i>	9	0.2	67	<i>Heterorhabdus tanneri</i>	516	24.7
16	<i>Calanus marshallae</i> ^a	678	73.8	43	<i>Lucicutia pacifica</i>	9	0.3	68	<i>Heterostylites major</i>	334	44.2
17	<i>Pleuromamma scutullata</i>	559	54.6	44	<i>Aetideopsis rostrata</i>	9	0.7	69	<i>Paraeuchaeta birostrata</i>	294	56.8
18	<i>Spinocalanus stellatus</i>	546	15.3	45	<i>Lucicutia grandis</i>	9	7.1	70	<i>Paraeuchaeta rubra</i>	123	23.6
19	<i>Pseudocalanus moulti</i>	360	7.3	46	<i>Spinocalanus magnus</i>	9	0.5	71	<i>Haloptilus pseudoxycephalus</i>	58	8.3
20	<i>Gaidius variabilis</i>	290	16	47	<i>Temorites brevis</i>	9	0.2	72	<i>Haloptilus longicirrus</i>	17	0.9
21	<i>Gaidius brevispinus</i>	287	22.1	48	<i>Gaetanus brevicornis</i>	8	1.3	73	<i>Pachyptilus pacificus</i>	9	1
22	<i>Metridia similis</i>	251	5	49	<i>Mimocalanus distinctocephalus</i>	8	0.4	74	<i>Heterorhabdus compactus</i>	8	0.7
23	<i>Metridia curticauda</i>	221	10.5	50	<i>Onchocalanus magnus</i>	8	0.9	75	<i>Candacia columbiae</i>	8	0.2
24	<i>Calanus pacificus</i> ^a	179	3.6	51	<i>Spinocalanus polaris</i>	8	0.1	76	<i>Candacia parafalcifera</i>	7	0.2
25	<i>Gaidius tenuispinus</i>	166	2.4	52	<i>Cephalophanes frigidus</i>	7	0.3				
26	<i>Pseudogaetanus robustus</i>	140	12.7	53	<i>Lucicutia longifurca</i>	7	2.6				

^a These species indicate that their late copepodid stages below 250 m are treated as suspension feeders in diapause.

were greater (Fig. 7b). Interestingly, the occurrence of some families was restricted by depth. Thus, Heterorhabdidae were only found below 250 m and Lucicutiidae, Phaennidae and Spinocalanidae were only found below 500 m (Fig. 7b).

3.3. Community structure

The number of genera and species of calanoid copepods occurring in each sampling layer is shown in Fig. 8a. The vertical distribution patterns of the number of genera and species were separated into 4 groups: ca. 10 species at 0–100 m depth, then species number increased around 100–500 m depth, to more than about 25 species at 500–1500 m and then decreased

around 2000–3000 m (Fig. 8a). The maximum number of species was at 1500–2000 m depth (33 species). Vertical changes in the species diversity index (H') based on abundance or biomass also showed similar patterns to the number of species (Fig. 8b). H' was low in the epipelagic layer (0–200 m), and was high around 500–1500 m depth, had a peak at 1500–2000 m, then decreased between 2000 and 3000 m.

Based on the Q-mode analysis the calanoid copepod community was classified into 5 groups at a 43% dissimilarity level (Fig. 8c). Each group was vertically well separated from each other, and the depth range of each group was 0–75 m (group A), 75–500 m (B), 500–750 m (C), 750–1500 m (D) and 1500–3000 m (E). To clarify indicator species for each group, one-way ANOVA and Fisher's PLSD test were applied to the abundance data of

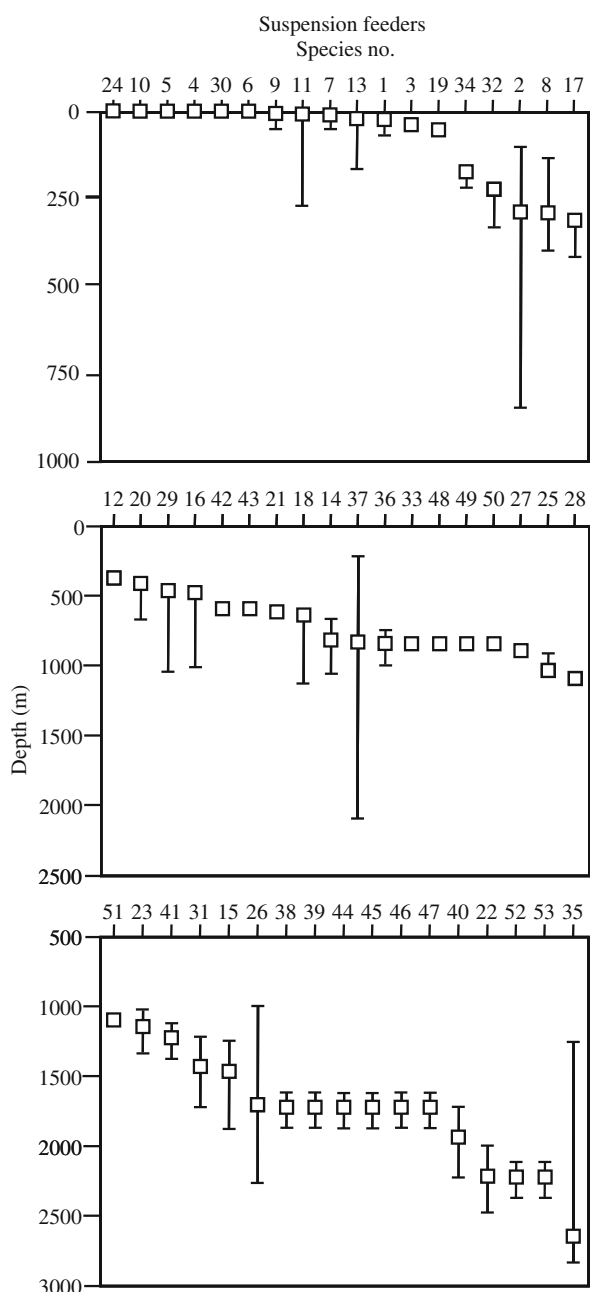


Fig. 5. Vertical distribution of suspension feeding copepods at St. AB in the southern Bering Sea, 14 June 2006. Of each species, symbols indicate 50% distribution depth ($D_{50\%}$). Vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population were distributed. For species number see Table 2. Note that the vertical depth scales are not the same among panels.

dominant species/taxa. The indicator species 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 3). Since low abundances were present below 1500 m, no indicator species was detected for group E.

Using the R-mode analysis calanoid copepod abundance associations were separated into 4 groups (1–4) at a 79% dissimilarity level (Fig. 9). Group 1 consisted of bathypelagic species except *C. marshallae*, group 2 contained mesopelagic species except two *Neocalanus* species, group 3 contained epipelagic species and group 4 consisted of species with wide vertical distribution ranges.

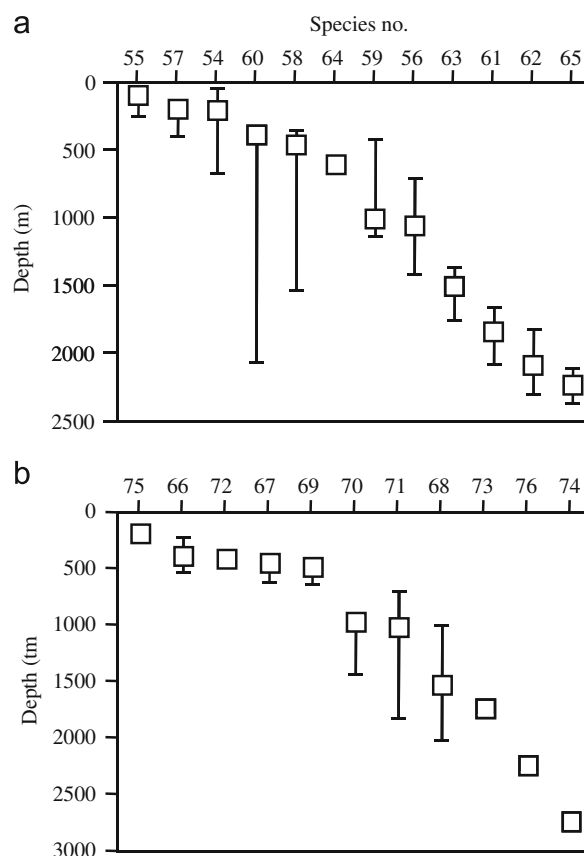


Fig. 6. Vertical distribution of detritivorous (a) and carnivorous (b) copepods at St. AB in the southern Bering Sea, 14 June 2006. Symbols indicate 50% distribution depth ($D_{50\%}$), and vertical bars indicate depth ranges where 25% ($D_{25\%}$) and 75% ($D_{75\%}$) of the population was distributed. For species number see Table 2. Note that the vertical depth scales are not the same among panels.

4. Discussion

4.1. Abundance and biomass

Abundances of copepods were compared with previous reports from various regions (Table 4). Within the southern Bering Sea, Minoda (1971) reported copepod abundance based on large-mesh (330 μm) nets. Since fine-mesh (60 μm) nets were used in this study, the abundance of copepods is 10–14 times greater than that of Minoda (1971). Smaller copepods are caught more efficiently by fine-mesh nets (cf. Böttger-Schnack et al., 2008). For instance, small Poecilostomatoida composed 30–78% of the total copepod abundance in the present study (Fig. 4a), while only 4% of the total copepods in Minoda (1971). Böttger-Schnack (1996) applied 55 μm mesh nets in the epi- to mesopelagic zone of the Arabian Sea and noted that the Poecilostomatoida contributed 60–80% of total copepod abundance. Yamaguchi et al. (2002) also used 90 μm mesh net in the western subarctic Pacific, and reported that the composition of Poecilostomatoida was 47–93% of total copepod abundance. To evaluate accurate abundance of small copepods (Cyclopoida and Poecilostomatoida), use of fine-mesh size nets (< 100 μm) is needed.

Comparison within the fine-mesh net studies showed that the ratio in abundance of copepods in 0–200 m was: southern Bering Sea:western subarctic Pacific:Arabian Sea=3.1:1.5:1 (Table 4). In the 200–1000 m layer, the ratios of copepod abundance of southern Bering Sea:western subarctic Pacific:Arabian Sea was 1.9:2.0:1 in abundance ratio (nearly equal in the southern Bering Sea and western subarctic Pacific). This discrepancy between

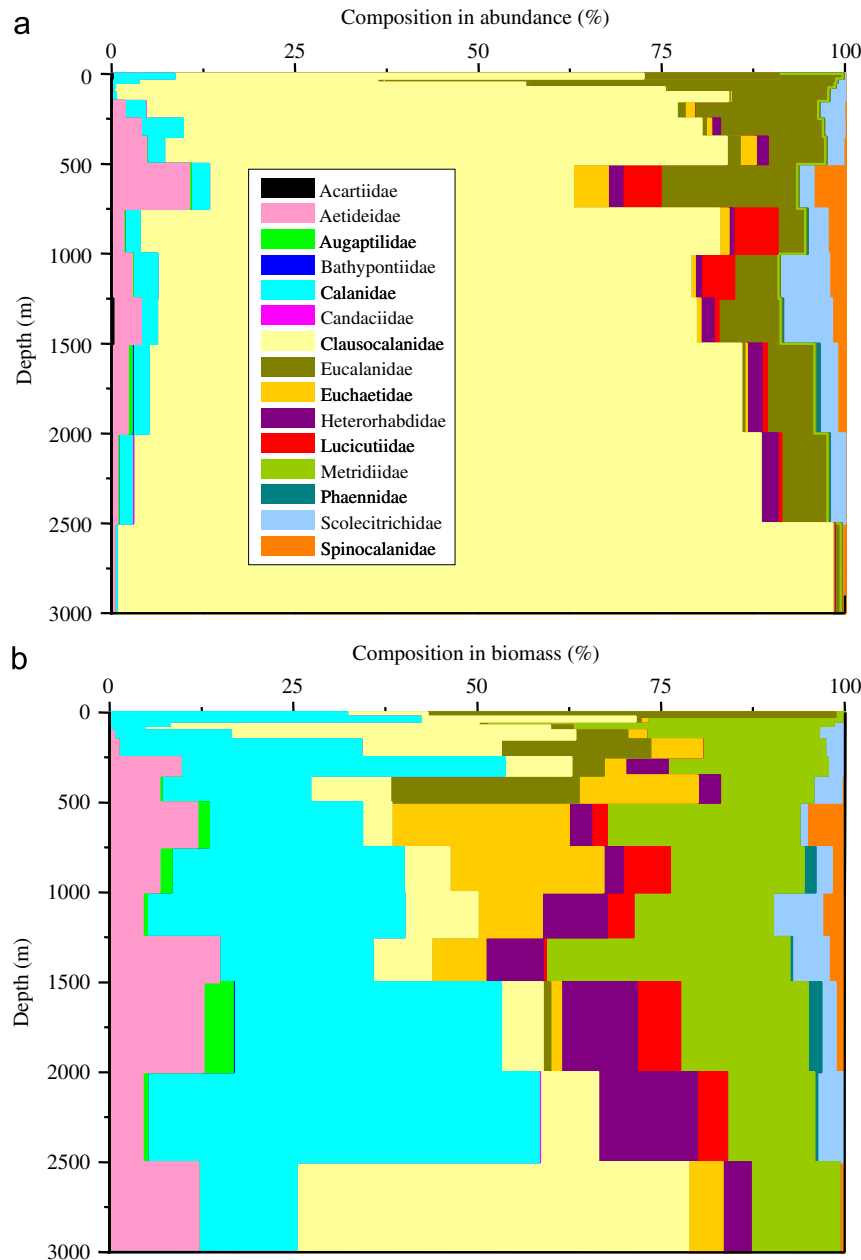


Fig. 7. Vertical changes in the composition of families of calanoid copepods in terms of abundance (a) and biomass (b) at St. AB in the southern Bering Sea, 14 June 2006.

0–200 and 200–1000 m may be partly because of the small copepods which dominated in the near surface layer and could be collected more efficiently by the 60 μm mesh in this study than the 90 μm mesh of Yamaguchi et al. (2002) (Table 4).

Both abundance and biomass of copepods decreased with increase in depth, but their depth-decreasing rates 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 ($\text{Log}_{10} Y = a + bX$, where a and b are fitted constants) by Vinogradov (1968), and the other is a power model ($\text{Log}_{10} Y = a' + b' \text{Log}_{10} X$, where a' and b' are fitted constants) by Koppelman and Weikert (1992). Abundance and biomass data in this study showed a better fit to the power model ($r^2 = 0.94\text{--}0.97$) than that of the exponential model ($r^2 = 0.67\text{--}0.75$) (Table 5). The higher depth-decreasing rate of abundance ($b' = -1.40$) over biomass ($b' = -1.15$) may be caused by the dominance of

small-sized Cyclopoida and Nauplii near the surface layer (they composed 83% of the total abundance in the 0–25 m layer) (Fig. 4a).

The ratio of carcasses to living specimens showed a prominent maximum at 750–1000 m (carcass:living specimen ratio of abundance was 2.3, Fig. 3a). Although abundance of living specimens was greatest in the surface 0–25 m layer, abundance of carcasses had a minimum at that layer (3.5 inds. m^{-3}). Abundance of carcasses showed a maximum in the 25–50 m layer (402 inds. m^{-3}) (Fig. 3a). This ambivalent result in the two adjacent layers suggests that the copepod carcasses had been ingested and removed by visual predators (fishes) in the surface 0–25 m layer. Below 1000 m, the abundance ratio of carcasses to living specimens increased with increase in depth (Fig. 3a). The abundance of copepod carcasses may therefore reflect the predation pressure of fishes. The abundance of copepod carcasses

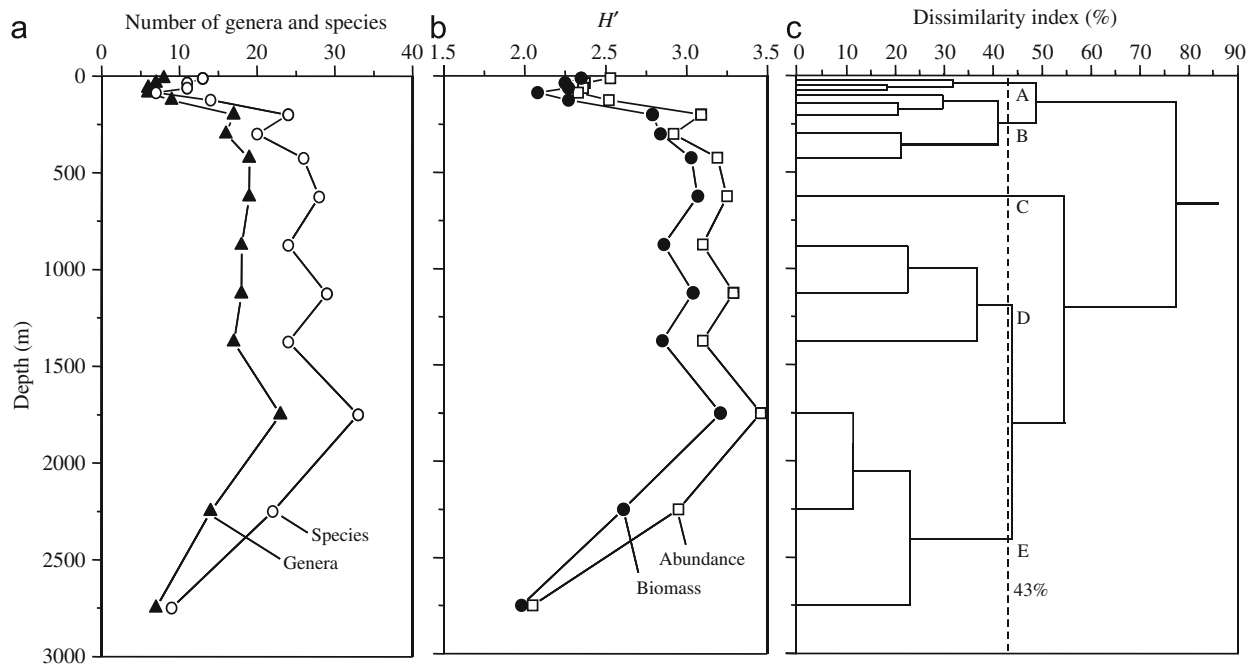


Fig. 8. Vertical distribution of the number of genera and species of calanoid copepods (a), species diversity indices (H') based on abundance and biomass data (b) and results of cluster analysis based on Bray–Curtis dissimilarity index (%) (c) at St. AB in the southern Bering Sea, 14 June 2006. Five groups (A–E) were recognized at 43% dissimilarity by cluster analysis (c).

Table 3

Mean abundance of dominant calanoid copepod species in each group, derived from cluster analysis (cf. Fig. 8c). Differences between communities were tested by one-way ANOVA and Fisher's PLSD. Numbers underlined are significantly greater than those of the other groups

Species	Abundance ($\text{Log}_{10} [\text{inds. m}^{-3} + 1]$)						Results of one-way ANOVA
	A	B	C	D	E	F	
<i>Calanus marshallae</i>	0	0.12	0.18	0.13	0.01	0.74	ns
Cyclopoida	<u>3.63</u>	2.07	0.83	0.47	0.31	19.57	***
<i>Eucalanus bungii</i>	<u>1.39</u>	0.32	0	0	0.01	3.68	*
<i>Gaetanus simplex</i>	0	0.36	0.45	0	0.002	2.64	ns
Harpacticoida	0.78	0.83	0	0.05	0.12	2.44	ns
<i>Lucicutia ovaliformis</i>	0	0	<u>0.38</u>	0.23	0.01	10.23	**
<i>Metridia asymmetrica</i>	0	0	0.07	0.15	0.09	3.2	ns
<i>Metridia pacifica</i>	<u>2.57</u>	1.43	0.76	0.06	0.16	33.35	***
<i>Microcalanus pygmaeus</i>	2.07	<u>2.14</u>	1.17	1.17	0.98	11.75	***
Nauplii	<u>3.46</u>	2.2	1.01	1.09	0.32	10.57	**
<i>Neocalanus flemingeri</i>	<u>1.06</u>	0.33	0.02	0.03	0.02	4.03	*
<i>Pleuromamma scutullata</i>	0	0.21	0.03	0.02	0	1.13	ns
Poecilostomatoida	1.79	<u>2.2</u>	0.43	0.78	0.74	3.12	*
<i>Pseudocalanus mimus</i>	<u>1.65</u>	0.41	0	0	0	15	***
<i>Pseudocalanus minutus</i>	<u>1.93</u>	0.62	0.07	0.05	0.03	24.5	***
<i>Pseudocalanus newmani</i>	<u>1.67</u>	0.23	0	0	0.02	8.37	**
<i>Pseudocalanus</i> spp.	<u>1.93</u>	0.2	0	0	0	10.97	**
<i>Scolecithricella ovata</i>	0	0.08	0.16	<u>0.27</u>	0.02	6.23	**

ns: not significant.

* $p < 0.05$;

** $p < 0.01$;

*** $p < 0.001$.

was low in the high predation pressure layer (sea-surface) and was greater in the low predation pressure layer (below 1000 m). As the other alternative cause, dead copepods inevitably sink; according to the hydrographical data the water column appeared to be strongly stratified at 50–100 m (Fig. 2), which may “trap” carcasses causing the higher carcass abundance.

The layer where the contribution of carcasses had a pronounced peak (750–1000 m, Fig. 3a) was corresponded well to the oxygen minimum layer (Fig. 2). It is well known that the micronektonic

fishes avoid the oxygen minimum layer (Sameoto, 1986; Herring et al., 1998). So, the possible cause of the pronounced maximum of carcasses to living specimens in the 750–1000 m layer (Fig. 3a) is low predation pressure by micronektonic fishes because they avoid the oxygen minimum layer. As the other alternative cause, since abundance of living copepods in the 750–1000 m layer was lower than the subsequent layers (Fig. 3a), live copepods may actively avoid the oxygen minimum layer therefore inflating the carcass to living specimen ratio (Fig. 3a).

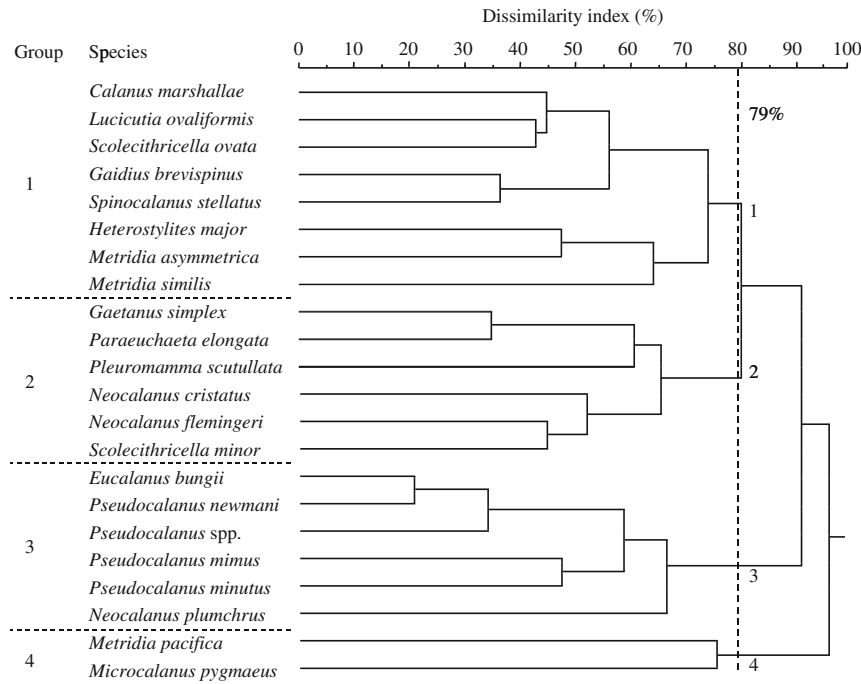


Fig. 9. Cluster diagram of dominant species (>2% of total abundance on any sampling layer) based on Bray–Curtis dissimilarity index (%) of their association of the occurrence. Four species groups (1–4) were recognized at 79% dissimilarity index (dashed line).

Table 4

Regional comparison in abundance of copepods (inds. m^{-2}) within the southern Bering Sea (A, B) and the other regions which are based on the fine mesh-size nets (C, D). To clarify regional characteristics, abundance ratios were calculated with A:C:D.

Region Mesh size (μm) References	Abundance (inds. m^{-2})				A:C:D
	(A) Southern Bering Sea	(B) Southern Bering Sea	(C) Western Subarctic Pacific	(D) Arabian Sea	
60		330	90	55	
This study		Minoda (1972)	Yamaguchi et al. (2002)	Böttger-Schnack (1996)	
Depth (m)					
0–200	1,165,990	79,860	568,580	379,200	3.1:1.5:1
200–1000	154,106	15,950	165,507	80,843	1.9:2.0:1
1000–3000	65,920		89,672		

Table 5

Regression statistics of abundance/biomass of copepods on depth. 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. $1000 m^{-3}$) or biomass ($\mu g C m^{-3}$), X is depth in m, and a , b , a' and b' are fitted constants.

Exponential model	a	b	r^2	p
Abundance	6.30	-9.42×10^{-4}	0.67	0.0002
Biomass	3.82	-8.31×10^{-4}	0.75	<0.0001
Power model	a'	b'	r^2	p
Abundance	9.09	-1.40	0.97	<0.0001
Biomass	6.07	-1.15	0.94	<0.0001

4.2. Community structure

Details of community structure of copepods down to greater depths have been studied in the Arctic Ocean (Kosobokova and Hirche, 2000), Greenland Sea (Richter, 1994), North Atlantic (Roe, 1972), Red Sea (Weikert, 1982), Mediterranean Sea (Weikert and Trinkaus, 1990) and western North Pacific (Yamaguchi et al., 2002; Shimode et al., 2006; Steinberg et al., 2008). A special well-

known feature of copepod communities in high latitude regions is the presence of suspension feeders in diapause. They ingest and grow actively in the epipelagic zone during the spring phytoplankton bloom and store lipid in their body, then they sink to deep layers at a late copepodid stage (Kobari et al., 2003). In terms of biomass, their contribution is known to be great (Vinogradov, 1968; Yamaguchi et al., 2004). Downward carbon flux by seasonal vertical migration of copepods has been calculated as nearly equal to passive POC flux (Kobari et al., 2003, 2008). In the present study, suspension feeders in diapause included *C. pacificus*, *C. glacialis*, *C. marshallae*, *E. bungii*, *N. cristatus*, *N. plumchrus*, *N. flemingeri* and *P. minutus* below 250 m (Table 2). The contribution of suspension feeders in diapause to the total copepod biomass was 10–45% between 250 and 3000 m ($28.5 \pm 12.6\%$ [mean \pm 1sd], Fig. 4d). This contribution was lower than those in the western subarctic Pacific (200–2000 m, $62.8 \pm 10.3\%$ [mean \pm 1sd], Yamaguchi et al., 2002). This difference may be attributed to the studied season. Yamaguchi et al. (2002) studied in August, while this study was conducted in June when suspension feeders in diapause were assumed to be about to descend to the deep layer for seasonal vertical migration.

The species of each feeding group had species-specific restricted depth ranges (Figs. 5 and 6). To determine the causes of this

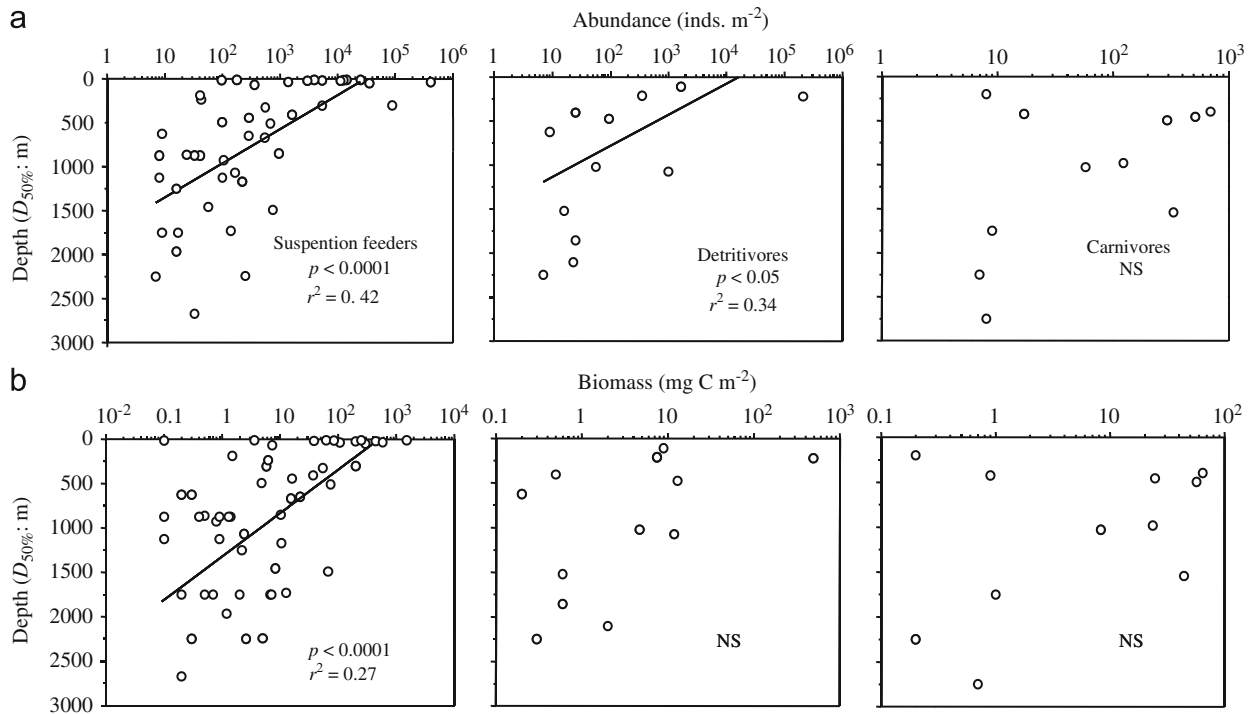


Fig. 10. Relationships between distribution depth ($D_{50\%}$) and abundance (a) and biomass (b) of suspension feeding (left), detritivorous (middle) and carnivorous (right) copepods in the southern Bering Sea. Regression lines are showed only for significant relationships. NS: non-significant.

species-specific depth distribution, we compared the abundance and biomass with the depth where the 50th percentile of the population resided ($D_{50\%}$) (Fig. 10). For suspension feeders, both abundance and biomass significantly decreased with depth, and this was also the case with the abundance of detritivores (Fig. 10). The depth-decreasing abundance and biomass of suspension feeders and detritivores may be caused by the depth-related decrease in their food, particulate organic flux. For instance, Poecilostomatoida, which dominated the abundance of detritivores, were reported to ingest and grow on the surface of the giant larvacean houses (Ohtsuka et al., 1993; Steinberg et al., 1994; Steinberg, 1995). Decreases in abundance of detritivores with increase in depth (Fig. 10) may reflect the reduction in detritus with increase in depth. The lack of a correlation of carnivorous abundance and biomass with depth might be due to the fact that the food availability for carnivores did not greatly vary with depth as shown by copepod abundance below 1000 m in Fig. 3a.

Based on the cluster analysis, calanoid copepod community in the Bering Sea was classified into 5 groups (Fig. 8c). It should be noted that the categories are somewhat pre-determined by the selection of the depth strata for sampling (Table 1). Although this shortcoming, vertical changes in the number of genera, species and species diversity index (H') also showed similar patterns to the cluster analysis. Thus, the species number and H' were low at 0–75 m, while high at 500–1500 m, then decreased with increase in depth to 1500–3000 m (Fig. 8a–c). In the following section we compare the characteristics of the copepod community in each depth layer.

For R-mode (species association) analysis, the genus *Pseudocalanus* spp. and *E. bungii* belonging to group C (Fig. 9) corresponded to the indicator species at 0–75 m of Q-mode analysis (Table 3). In the 75–500 m layer, the contribution of *E. bungii* (Eucalanidae) increased in biomass (Fig. 7b), while the contribution of other families was similar to that in 0–75 m.

Between 500–1500 m, the contribution of Spinocalanidae, Lucicutiidae, Euchaeiidae and Scolecitrichidae increased (Fig. 7b).

The indicator species in this oxygen minimum layer (500–1500 m, group C and D, Fig. 8c) were *Lucicutia ovariformis* and *S. ovata* (Table 3). *Lucicutia* species (*L. grandis*) in the Arabian Sea is known to inhabit the oxygen minimum layer and is the indicator species of the layer (Gowing and Wishner, 1998; Wishner et al., 2000; Koppelman and Weikert, 2005). Thuesen et al. (1998) have reported that this is due to high lactate dehydrogenase activities in the tricarboxylic acid cycle of *L. grandis* under anoxic conditions; thus *Lucicutia* species could adapt to the oxygen minimum layer.

At 1500–3000 m depths, *M. pygmaeus* and *M. asymmetrica* dominated the suspension feeder group and *Heterostylites major* dominated in carnivores (Figs. 5 and 6b). Between 1500–3000 m, the contribution of small *M. pygmaeus* increased with increase in depth (Clausocalanidae in Fig. 7), while the contribution of the other species decreased with depth, thus the number of species and H' decreased through this layer (Fig. 8a, b). The fact that species number and H' decreased with depth between 1500 and 3000 m, it suggests that copepods could not sustain a particular community due to the limited food supply in the deep sea. Vinogradov (1968) has reported that the carnivorous Euchaetidae, Heterorhabdidae and Lucicutiidae have a wide distribution depth range between 2000 and 6000 m. Also in this study, $D_{50\%}$ of carnivores was deeper than those of suspension feeders and detritivores (Figs. 5 and 6), and abundance and biomass of carnivores did not decrease with increase in depth (Fig. 10).

Yamaguchi et al. (2002) have reported that copepod community in the western subarctic Pacific was vertically classified into 3 groups (0–200, 200–1000 and 1000–4000 m). In the Greenland Sea, Richter (1994) also has reported that copepod community was classified into 3 groups (0–300, 300–1000 and 1000–3000 m). Generally, the zooplankton is known to be classified vertically into epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–3000 m) and abyssopelagic (> 3000 m) communities (Vinogradov, 1968). In the present study the copepod community was classified into 5 groups (0–75, 75–500, 500–750, 750–1500 and 1500–3000 m) at 43% dissimilarity or 3 groups (0–500,

500–750 and 750–3000 m) at 53% dissimilarity (Fig. 8c) levels. Both classifications showed that the community structure in the oxygen minimum layer (500–750 m) is a very special characteristic of the southern Bering Sea. This strong effect of the oxygen minimum layer is considered to be the feature of the Bering Sea basin where oxygen minimum layer is well developed (Fig. 2).

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