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SPECIAL SECTION: ORIGINAL ARTICLE

K2S1 project

Seasonal changes in the mesozooplankton biomass and community structure in subarctic and subtropical time-series stations in the western North Pacific

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Abstract Seasonal changes in mesozooplankton biomass and their community structures were observed at time-series stations K2 (subarctic) and S1 (subtropical) in the western North Pacific Ocean. At K2, the maximum biomass was observed during the spring when primary productivity was still low. The annual mean biomasses in the euphotic and 200- to 1000-m layers were 1.39 (day) and 2.49 (night) g C m^{-2} and 4.00 (day) and 3.63 (night) g C m^{-2}, respectively. Mesozooplankton vertical distribution was bimodal and mesopelagic peak was observed in a 200- to 300-m layer; it mainly comprised dormant copepods. Copepods predominated in most sampling layers, but euphausiids were dominant at the surface during the night. At S1, the maximum biomass was observed during the spring and the peak timing of biomass followed those of chlorophyll *a* and primary productivity. The annual mean biomasses in the euphotic and 200- to 1000-m layers were 0.10 (day) and 0.21 (night) g C m^{-2} and 0.47 (day) and 0.26 (night) g C m^{-2}, respectively. Copepods were dominant in most sampling layers, but their mean proportion was lower than that in K2. Mesozooplankton community characteristics at both sites were compared with those at other time-series stations in the North Pacific and with each other. The annual mean primary productivities and sinking POC fluxes were equivalent at both sites; however, mesozooplankton biomasses were higher at K2 than at S1. The difference of biomasses was probably caused by differences of individual carbon losses, population turnover rates, and trophic structures of communities between the two sites.

Keywords Mesozooplankton community · Seasonal change · Subarctic · Subtropical · Western North Pacific

1 Introduction

The mesozooplankton community plays a crucial role in ocean ecosystems and biogeochemical cycles. For example, mesozooplankton influence the fate of primary production and they are the main trophic link that connects primary producers with larger predators. Biogeochemical research has focused on their roles in the biological pump such as fecal pellet production, vertical carbon transport via diel/ontogenetic vertical migration, respiratory remineralization of organic material into carbon dioxide, and repackaging of sinking particles (e.g., Giering et al. 2014; Kobari et al. 2003; Willson et al. 2008). However, despite the presumed importance of the mesozooplankton community, we know comparatively little about their ecological role in epipelagic waters as well as mesopelagic waters in oceanic waters. This is partly due to the limited availability of basic information on its biomass, distribution, composition, variability and other feature of its biology and ecology. For example, seasonal changes in the mesozooplankton biomass have not been described adequately in the central part of the western subarctic gyre of the North Pacific Ocean. Many mesozooplankton species may be influenced by a changing

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ocean due to warming, higher acidity, areal expansion of suboxic zones, and growing human footprint (e.g., Cripps et al. 2014; Hoegh-Guldberg and Bruno 2010; Richardson 2008), and thus, the ecological interactions among biota or material cycles could also be changed. In order to predict the impact of environmental changes on mesozooplankton, we need an improved understanding of their current biology/ecology and the temporal changes in their community. Thus, we conducted biological observations of mesozooplankton at two time-series stations, K2 (47°N, 160°E) and S1 (30°N, 145°E), which were located in the western subarctic gyre and subtropical gyre of the North Pacific Ocean, respectively.

In the western subarctic gyre of the North Pacific, time-series observations has been carried out since 1998 at the KNOT station (44°N, 155°E) located at the southwestern edge of the subarctic gyre which improved the understanding of the carbon cycle (Saino et al. 2002). The occasional intrusion of a subtropical water mass was observed at KNOT, so K2 was established as a new time-series station in 2001. Biological findings based on observations at KNOT and K2 have been reported, including the primary productivity, phytoplankton standing stock, phytoplankton community, and Fe limitations on primary productivity (Fujiki et al. 2014; Imai et al. 2002; Matsumoto et al. 2014; Mochizuki et al. 2002). There have been reports of the vertical distributions of the copepod and mesozooplankton standing stocks in summer (Yamaguchi et al. 2002, 2004; Steinberg et al. 2008b), the mesopelagic mesozooplankton community and their feeding ecology in summer (Kobari et al. 2008; Steinberg et al. 2008a, b; Willson et al. 2008, 2010), and the active carbon fluxes by mesozooplankton in summer and winter (Kobari et al. 2008, 2013). Station S1 was established in 2010 as a counterpart of K2. Previously, the downward active carbon transport by diel vertical migratory mesozooplankton was reported to be 2 mg C m^{-2} day^{-1} during winter at S1 (Kobari et al. 2013). However, these mesozooplankton studies were only snapshots and no information is available on their seasonality at both stations. Thus, we report the seasonal variability in the mesozooplankton community (biomass, vertical distribution, major taxa compositions, individual body weight, and carbon:nitrogen ratios) at these two stations. Among them, the carbon:nitrogen ratios are used as proxy for lipid content in mesozooplankton because lipids contains mostly carbon and little to no nitrogen, increases in the ratio closely track increases in lipid content (Logan et al. 2008; Schmidt et al. 2003).

To characterize the two mesozooplankton communities, each community was compared with other mesozooplankton time-series from the Oyashio region (off Japan), as well as stations P (Alaskan Gyre) and ALOHA (off Hawaii). Both communities were also compared each other. Our zooplankton samples were obtained through the 0- to 1000-m water column during the day and night in all four seasons. The overall mesozooplankton taxa were considered in the analysis. The use of a large net system (1.5-m^2 mouth opening) reduced net avoidance by larger zooplankton such as euphausiids. This study was also a part of a research program “K2S1 project” that aimed to clarify the material cycles via biological activity (overviewed by Honda et al. 2015); thus, environmental properties and biogeochemical processes such as the sinking particulate organic carbon (POC) flux were also observed at the two stations. This is another advantage of the present study.

2 Materials and methods

The sampling sites were located in the central area of the western subarctic gyre (Station K2; 47°N, 160°E) and about 500 km northeast of Ogasawara Archipelago (Station S1; 30°N, 145°E). Mesozooplankton were collected using the multiple opening/closing net system, IONESS (Intelligent Operative Net Sampling System, SEA Corporation), during seven cruises of R/V “Mirai” (Table 1). The system was equipped with nine nets of 0.33-mm mesh, which had a 1.5-m^2 mouth opening area when towed at 45°. The net system was towed obliquely at about 2 knots (ship speed) and at discrete depth intervals from 0 to 1000 m (every 50 m between 0 and 200 m, and every 100 m between 200 and 1000 m in the cruise MR08-05; 0–50, 50–100, 100–150, 150–200, 200–300, 300–500, 500–750, and 750–1000 m in other cruises), where the samples were obtained on the upcast during the day and night. The net tow sample was split after sorting contaminated fishes and large Decapoda on board. One-sixteenth was frozen at −20 °C after removing excess water by filtration for mesozooplankton biomass analysis, and the remaining subsamples were fixed in 5 % formalin-seawater for taxon analysis. The water temperature and salinity were measured with a CTD/Carousel system (SBE 911 plus; Sea-Bird Electronics). The chlorophyll *a* concentrations at depths shallower than 200 m were measured by the acidification method and ^{13}C uptake experiments were conducted to measure the primary productivity (Matsumoto et al. 2015).

In the land laboratory, the frozen subsamples were dried for 24 h at 60 °C and then weighed. After weighing, the dried samples were pulverized and analyzed to determine their carbon and nitrogen contents using elemental analyzers (NC2500, CE Instruments or Vario EL III; Elementar Analysensysteme). The biomass on a carbon weight basis of the mesozooplankton was determined by multiplying the dry mass by the carbon content. The vertically integrated biomasses were calculated through the 0- to 1000-m and euphotic layers. The integrated biomass in the euphotic

Table 1 Summary of scientific cruises and mesozooplankton samplings for the K2S1 project, showing the observed sea surface temperature (*SST*, °C), euphotic layer depth (m), vertically integrated chlorophyll *a* (mg m^{-2}), and primary productivity (mg C m^{-2} day^{-1}) at the two time-series stations, K2 and S1, in the northwestern Pacific Ocean

Cruise	Station	Season	Net samplings		SST (°C)	Euphotic layer (m)	Chl. *a* (mg m^{-2})	PP (mg C m^{-2} day^{-1})
			Date	Number of net tows				
MR08-05	K2	Autumn	25–29 Oct, 2008	4	8.3	50	34.9	212
MR10-01	K2	Winter	15–16 Feb, 2010	2	1.6	70	43.9	94
	S1		31 Jan–10 Feb, 2010	5	19.2	85	37.1	420
MR10-06	K2	Autumn	29 Oct–1 Nov, 2010	3	8.6	55	30.9	248
	S1		8–12 Nov, 2010	4	25.2	110	18.6	108
MR11-02	K2	Winter	26 Feb, 2011	2	1.9	75	40.6	125
	S1		15–19 Feb, 2011	3	18.6	75	72.5	847
MR11-03	K2	Spring	20–23 Apr, 2011	4	1.8	60	35.1	200
	S1		30 Apr–2 May, 2011	4	19.5	55	35.9	296
MR11-05	K2	Summer	2–3 July, 2011	4	6.7	40	59.9	689
	S1		26–29 July, 2011	4	27.2	94	24.6	224
MR12-02	K2	Summer	12–14 June, 2012	4	5.2	75	51.2	570
	S1		29 June–2 July, 2012	4	23.4	76	25.5	243

The cruises were assigned to the following meteorological seasons according to Matsumoto et al. (2014): winter (December–February), spring (March–May), summer (June–August), and autumn (September–November)

Table 2 Conversion factors from dry weight to carbon weight for 13 major taxonomic groups of mesozooplankton

Taxa	Carbon weight (% of dry weight)	References
Hydromedusae	7.2	Beers (1966)
Ctenophore	3.0	Larson (1986)
Caetognatha	10.9	Omori (1969)
Mollusca	25.0	Larson (1986)
Polychaeta	29.9	Beers (1966)
Copepoda	52.8	Omori (1969)
Euphausiacea	43.0	Omori (1969)
Mysidacea	42.4	Omori (1969)
Ostracoda	42.5	Kitamura, unpublished
Amphipoda	37.2	Omori (1969)
Cladocera	42.9	Hirota (1981)
Taliacea	7.0	Larson (1986)
Appendicularia	56.4	Schneider (1989)

layer was computed by multiplying the biomass density (mg C m^{-3}) by the depth of the euphotic layer. The subsamples preserved in formalin were split again. To determine the major taxa composition during both the day and the night, the mesozooplankton were sorted from specific aliquots (ranging from 1/8 to 1/64) into 13 major taxonomic groups (Table 2). The animals sorted in each taxon were counted, dried for 24 h at 60 °C after removing the interstitial water by filtration, and then weighed. The biomass values by dry weight were converted to the carbon weight using the conversion factors listed in Table 2. Individual body weights were also calculated for the dominant four taxa (copepods, euphausiids, chaetognaths, and ostracods) using the numbers and weights of the sorted animals. Exoskeletons of crustaceans that lacked recognizable inner tissues, which were assumed to be carcasses or molts, were excluded from the analysis. The major taxa compositions and individual body weights were only analyzed for eight net tow sample series collected during four sequential cruises that covered all four seasons (from autumn 2010 to summer 2011). During the autumn survey at K2, many specimens of dormant *Neocalanus cristatus* were collected from shallower depths than the overwintering depths known previously for this species in the Oyashio region (Kobari and Ikeda 1999) or Alaskan Gyre (Miller et al. 1984). *Neocalanus cristatus* is one of the dominant mesozooplankton in the western subarctic North Pacific (Kobari and Ikeda 1999), so we also analyzed the vertical distribution of the dormant stage (copepodite V) of *N. cristatus* during autumn at K2 using formalin-preserved subsamples.

To quantify the diversity of the mesozooplankton community in each depth layer, we calculated Simpson's index of diversity (SID), which considers both the richness and evenness, where we used the biomass data for the 13 major taxa collected during the four sequential cruises in the calculation. SID was calculated by:

$$\mathrm{SID} = 1 - \Sigma(b/B)^2,$$

where b is the biomass (carbon weight) of a particular taxon and B is the total biomass (carbon weight) of the mesozooplankton community. The value of this index ranges between 0 and 1, where the sample diversity is greater when the value is higher.

3 Results

3.1 Hydrographic properties and primary production

At K2, the sea surface temperature (SST) ranged from 1.6 to 8.6 °C during the seven cruises. Winter mixing reached to 130 m in February 2010. The Intermediate Cold Water was observed at around 100 m from summer to autumn and the minimum temperatures in this water mass ranged between 1.2 and 1.5 °C. A prominent seasonal thermocline was located above the minimum temperature layer in summer and autumn. Permanent thermo- and haloclines were detected between 100 and 200 m. The temperature decreased below 200 m, whereas the salinity gradually increased with depth. The primary productivities ranged from 109 (winter) to 629 mg C m^{-2} day^{-1} (summer), and the annual mean was 292 mg C m^{-2} day^{-1} (Fig. 1b). The vertically integrated chlorophyll *a* in the euphotic layer ranged from 32.9 (autumn) to 55.5 (summer) mg m^{-2} and the annual mean was 41.5 mg m^{-2}. This seasonal pattern did not correspond with the primary productivity (Fig. 1a).

By contrast, SST ranged from 18.6 to 27.2 °C during the six cruises at S1. Winter mixing reached up to 200 m, which was deeper than that in K2. The seasonal thermo- and haloclines were detected between 25 and 60 m in summer and autumn, whereas the permanent ones were located from 300 to 600 m. The Subtropical Mode Water was observed between 100 and 250 m in summer and autumn, and the temperature and salinity ranges were 17–18 °C and 34.6–34.7, respectively. The North Pacific Intermediate Water characterized by low salinity was detected in the mesopelagic layer and its minimum salinity layer was at 600–700 m. The primary productivities ranged from 108 (autumn) to 634 mg C m^{-2} day^{-1} (winter), and the annual mean was 318 mg C m^{-2} day^{-1} (Fig. 1g). The subsurface chlorophyll *a* maximum occurred at around 100 m during summer and autumn, whereas higher chlorophyll *a* concentrations were observed in the upper 100 m and upper 50 m during winter and spring, respectively. The vertically integrated chlorophyll *a* in the euphotic layer ranged from 18.6 (autumn) to 54.8 mg m^{-2} (winter), and the annual mean was 33.6 mg m^{-2} at S1 (Fig. 1f).

3.2 Vertically integrated biomass

Seasonal composites of the depth integrated mesozooplankton biomass (g C m^{-2}) at K2 and S1 are shown in Table 3 and Fig. 1c–e, h–j. At K2, the 0- to 1000-m biomasses exhibited no seasonal trend, although the biomasses in the euphotic and 200- to 1000-m layers exhibited opposite seasonal patterns each other. The seasonality in the euphotic layer did not correspond to that of the primary productivity and the maximum biomass was observed earlier than the peak in primary productivity. A prominent seasonal change in biomass was detected in the euphotic layer, i.e., the maximum biomasses (observed in spring) were 48- and fourfold higher than the minimum biomasses (winter) during the day and night, respectively. High year-to-year variability in the biomasses was found in the euphotic layer during summer, i.e., the biomasses in summer 2012 were 9.9- and 3.6-fold higher than those in 2011 during the day and night, respectively, although the primary productivities in the two summers were almost at the same level. Nighttime biomasses in the euphotic layer were higher than the daytime ones over the four seasons (Fig. 1d); it suggested the presence of diel vertical migrants at K2 through the four seasons.

At S1, the seasonal changes in the mesozooplankton biomass integrated through the 0- to 1000-m, euphotic, and mesopelagic layers shared the same pattern, i.e., high in spring but low in autumn (Table 3; Fig. 1). The peak timing of the mesozooplankton biomass followed those of chlorophyll *a* and primary productivity. Higher seasonal variability in the biomass was detected in the euphotic layer, i.e., the maximum biomasses (observed in spring) were 5.7- and 3.8-fold higher than the minimum biomasses (autumn) during the day and night, respectively. The coefficients of variation indicated lower seasonal variability in the biomasses of the euphotic layer at S1 compared with those at K2 (Table 3). In terms of the year-to-year variability, the twofold difference in the winter biomasses in the euphotic layer (0.14 and 0.29 g C m^{-2} during the night in 2010 and 2011, respectively) corresponded to that in the primary productivity (420 and 847 mg C m^{-2} day^{-1} in 2010 and 2011, respectively). Higher biomasses in euphotic layer during the night through the four seasons (Fig. 1i) suggested that diel vertical migratory species occurred over the four seasons at S1. The annual mean biomasses at S1 were one order of magnitude lower than those at K2 in both the euphotic and mesopelagic layers.

3.3 Vertical distribution

Figure 2 shows the vertical distributions of the mesozooplankton biomass at K2. Two cruises were conducted during each season except spring, and the vertical distribution patterns of the two results in each season were similar to each other. A prominent peak in terms of biomass was observed between 0 and 50 m in both the day (5.5–75.8 mg C m^{-3}, except in winter) and night (16.3–97.5 mg C m^{-3}). During winter, the daytime biomasses in the winter mixing layer (0–100 m) were quite low (<0.1 g C m^{-2}), whereas

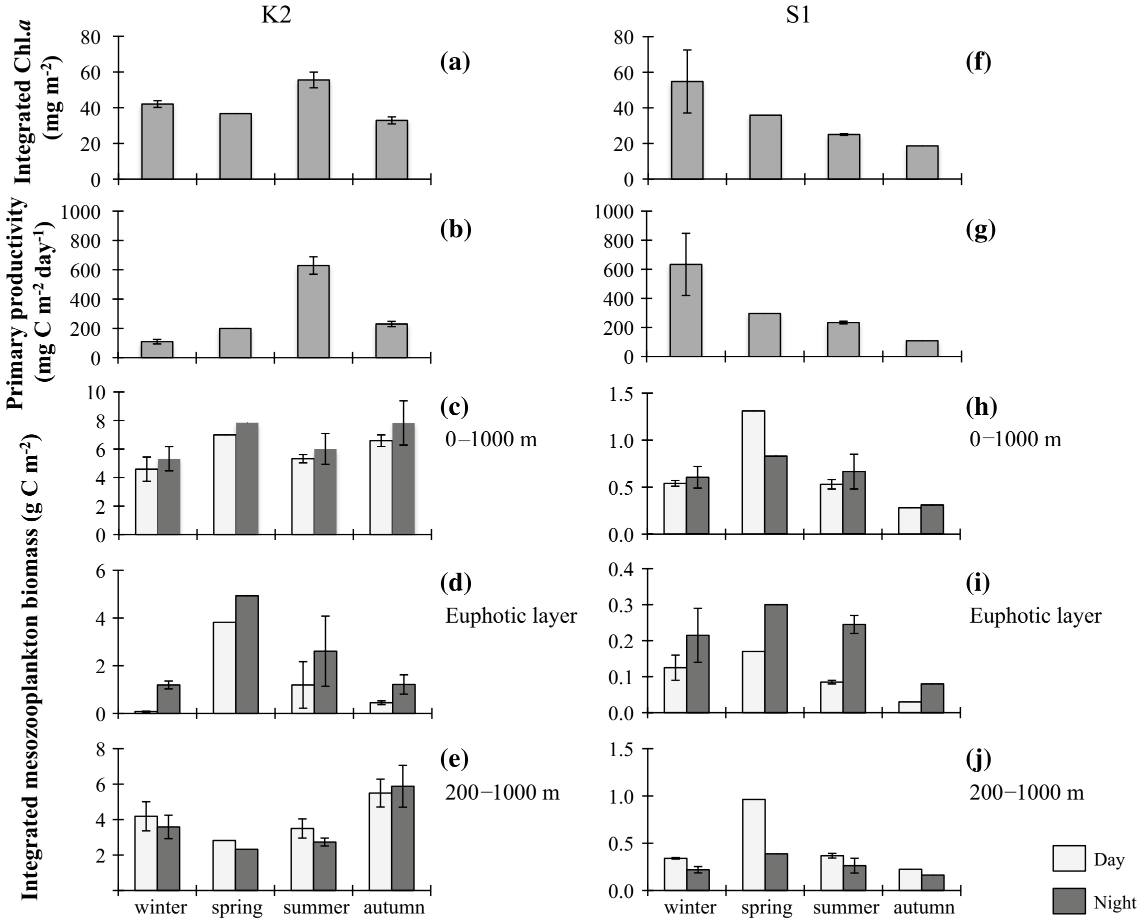


Fig. 1 Seasonal composite showing the depth-integrated chlorophyll *a* (mg m^{-2}) (**a**, **f**), primary productivity (mg C m^{-2} day^{-1}) (**b**, **g**), and mesozooplankton biomasses (mg C m^{-2}) between 0 and 1000 m (**c**, **h**), in the euphotic (**d**, **i**), and mesopelagic layers (**e**, **j**) during the day and night at the two time-series stations, i.e., K2 and S1, in the western North Pacific Ocean. The euphotic layer was defined as depths between light levels of 100 and 0.5 % of surface photosynthetically active radiation. Each *bar* represents the mean value of the cruise means and the *error bar* indicates the range (minimum and maximum) of the cruise means. Note: the *vertical axes* are on different scale between K2 and S1

Table 3 Seasonal composite showing the depth-integrated mesozooplankton biomasses (g C m^{-2}) at subarctic (*K2*) and subtropical (*S1*) time-series stations in the western North Pacific Ocean

Site and sampling depth		Day/night	Winter	Spring	Summer	Autumn	Annual mean ± SD	CV
K2	Euphotic layer	Day	0.08	3.82	1.20	0.45	1.39 ± 1.7	1.2
		Night	1.20	4.93	2.61	1.22	2.49 ± 1.8	0.7
	200–1000 m	Day	4.19	2.82	3.50	5.50	4.00 ± 1.1	0.3
		Night	3.59	2.32	2.73	5.88	3.63 ± 1.6	0.4
S1	Euphotic layer	Day	0.13	0.17	0.09	0.03	0.10 ± 0.1	0.6
		Night	0.22	0.30	0.25	0.08	0.21 ± 0.1	0.4
	200–1000 m	Day	0.34	0.96	0.37	0.22	0.47 ± 0.4	0.7
		Night	0.22	0.39	0.26	0.16	0.26 ± 0.1	0.4

The mesozooplankton biomass in each season is the mean value of the cruise mean biomasses

CV coefficient of variation

the night-time biomasses were higher (0.4–1.1 g C m^{-2}), mainly due to euphausiids. In April 2011, the mesozooplankton biomass was considerably high between 0 and 50 m due to the mass occurrence of a large copepod species, *N. cristatus*. During summer and autumn, the mesozooplankton biomasses in the Intermediate Cold Water

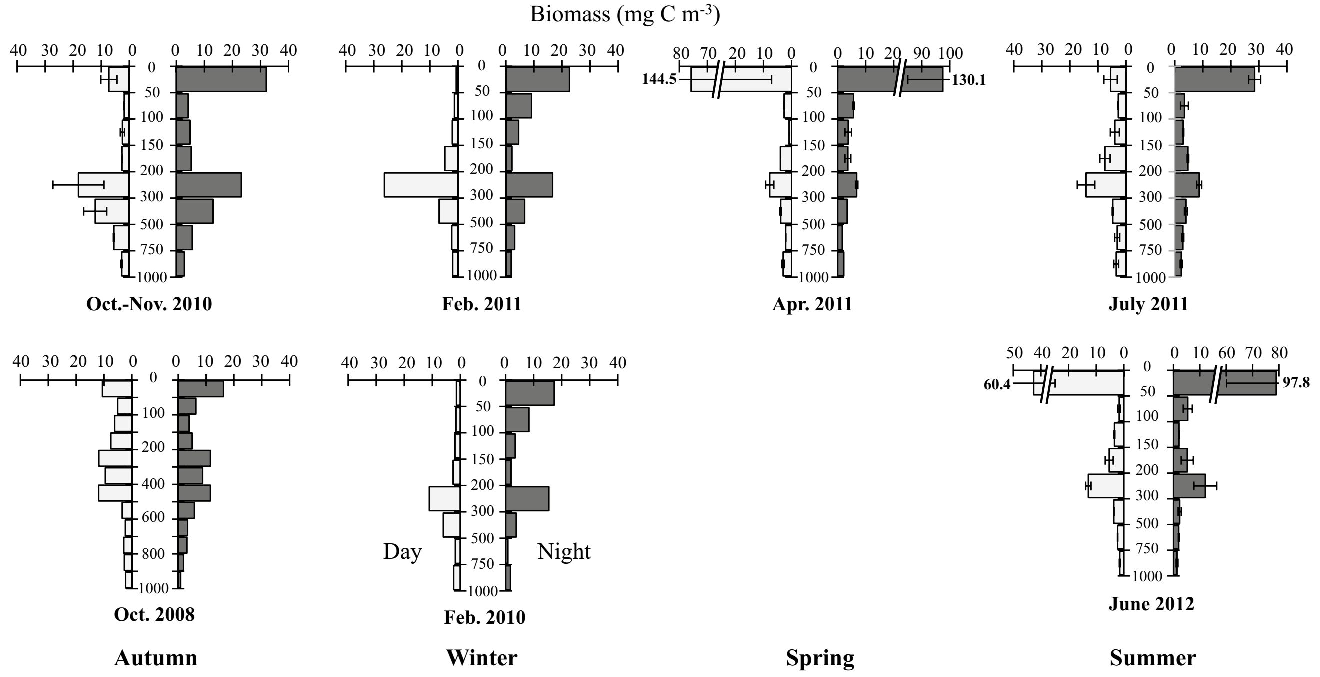


Fig. 2 Diel and seasonal changes in the vertical distributions of the mesozooplankton biomass (mg C m^{-3}) at subarctic time-series station K2 in the western North Pacific Ocean. The results of the sequential four cruises from autumn 2010 to summer 2011 are shown in the *top row* and the three results from other cruises are depicted in the *bottom row*. The *error bars* represent the minimum and maximum values of the biomasses

(50–150 m) were relatively low compared with those in the neighboring depth layers. In the mesopelagic layer, another biomass peak was also detected from 200 to 300 m during the day and night throughout the four seasons, where the biomasses changed seasonally (high in winter, low in spring). Ontogenetic migratory copepods (*N. cristatus* and *Eucalanus bungii*) and a diel vertical migratory copepod, *Metridia pacifica*, accounted for high proportions in this layer (Fig. 3). For *N. cristatus,* the copepodite 5th stage was abundant between 200 and 500 m (Fig. 4), where 75–87 % of their total abundance throughout the water column (0–1000 m) was distributed in this layer. Higher mesozooplankton biomasses in surface layers during the night compared with daytime ones (Fig. 2) suggested intrusions of diel vertical migratory species into surface layer during the night. Among the 13 major taxonomic groups, euphausiids showed clear diel vertical migratory behavior through the four seasons (Fig. 5).

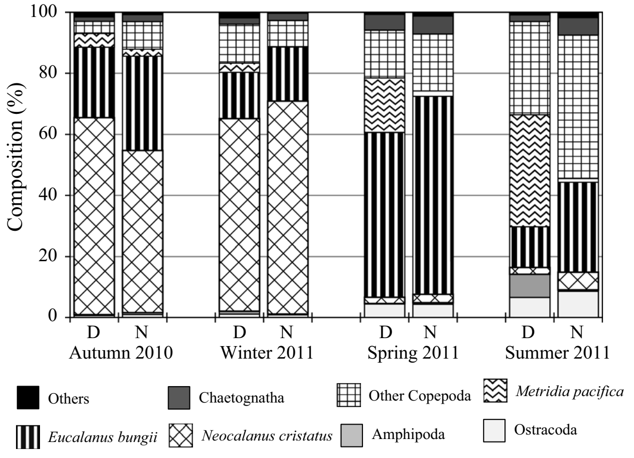


Fig. 3 Diel and seasonal changes in the species compositions of mesozooplankton between 200 and 300 m at K2, where the mesozooplankton biomass formed a mesopelagic peak. The compositions are based on the carbon masses. *D* day, *N* night

At S1, a bimodal distribution was observed during the day, although the surface peak in the biomass was unclear during autumn (Fig. 6). The daytime mesopelagic peak was observed in upper mesopelagic zone (200–500 m) during winter and spring, although it was distributed in deeper depths (500–750 m) during summer and autumn. At night, relatively high values were observed throughout the euphotic layer compared with the mesopelagic zone. In all the four seasons, a peak in the biomass was not recognized in the mesopelagic layer at night. Euphausiids showed clear diel vertical migratory behavior through the four seasons as K2 (Fig. 5). Their mesopelagic peaks in biomass during the day were observed in depth layers corresponded to peak depths of mesozooplankton through the four seasons.

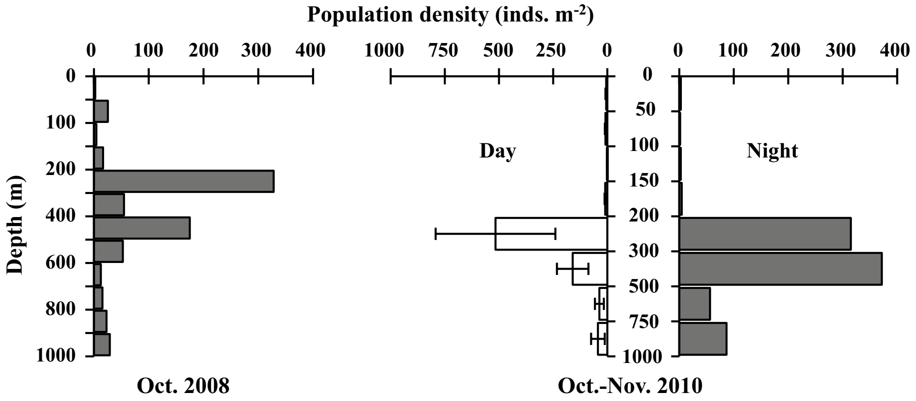


Fig. 4 Vertical distributions of *Neocalanus cristatus* copepodite 5th stage during autumn at K2. Each *bar* represents the mean population density integrated within a depth layer (individuals m^{-2}) and the *error bars* indicate the minimum and maximum values of the population densities

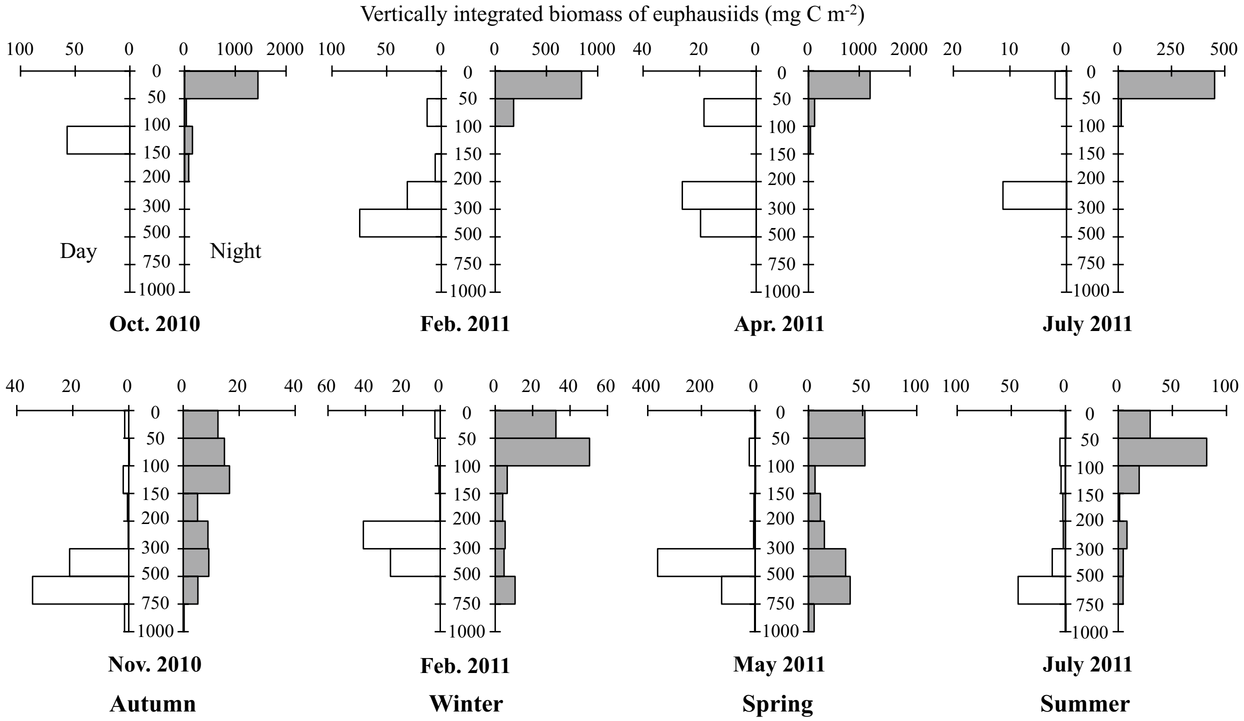


Fig. 5 Vertical distributions of euphausiids (mg C m^{-2}) at subarctic station K2 (*top row*) and subtropical station S1 (*bottom row*) obtained from the four sequential cruises from autumn 2010 to summer 2011

The vertical changes in the seasonal variability of the mesozooplankton biomass at K2 and S1, represented by the coefficients of variation, are shown in Fig. 7. High seasonal variability was detected at 0–50 m in the two sites and the highest one was recorded at 0–50 m during the day at K2. In the mesopelagic layers, the vertical profiles of the coefficients had an another peak between 300 and 500 m, and the profiles showed same pattern during the day and night at K2. On the other hand, a mesopelagic peak was also shown between 300 and 500 m only during the day at S1. The vertical profiles showed prominent difference between day and night due to higher daytime coefficients in the mesopelagic layer except between 750 and 1000 m. Furthermore, a coefficient of variation in 300–500 m layer during the day exceeded the surface values at S1. The coefficients of variation between 300 and 750 m at K2 were equivalent to that at 0–50 m during the night. The presence of high variability in the mesopelagic layers was notable.

3.4 Major taxa composition, diversity, individual body weights, and C:N ratios

Copepoda was predominant in most of the sampling layers at both sites (Fig. 8), although the mean proportion of this taxon in each layer at S1 (58.9 %) was lower than that at K2 (73.5 %). The relative biomasses of Euphausiacea during the

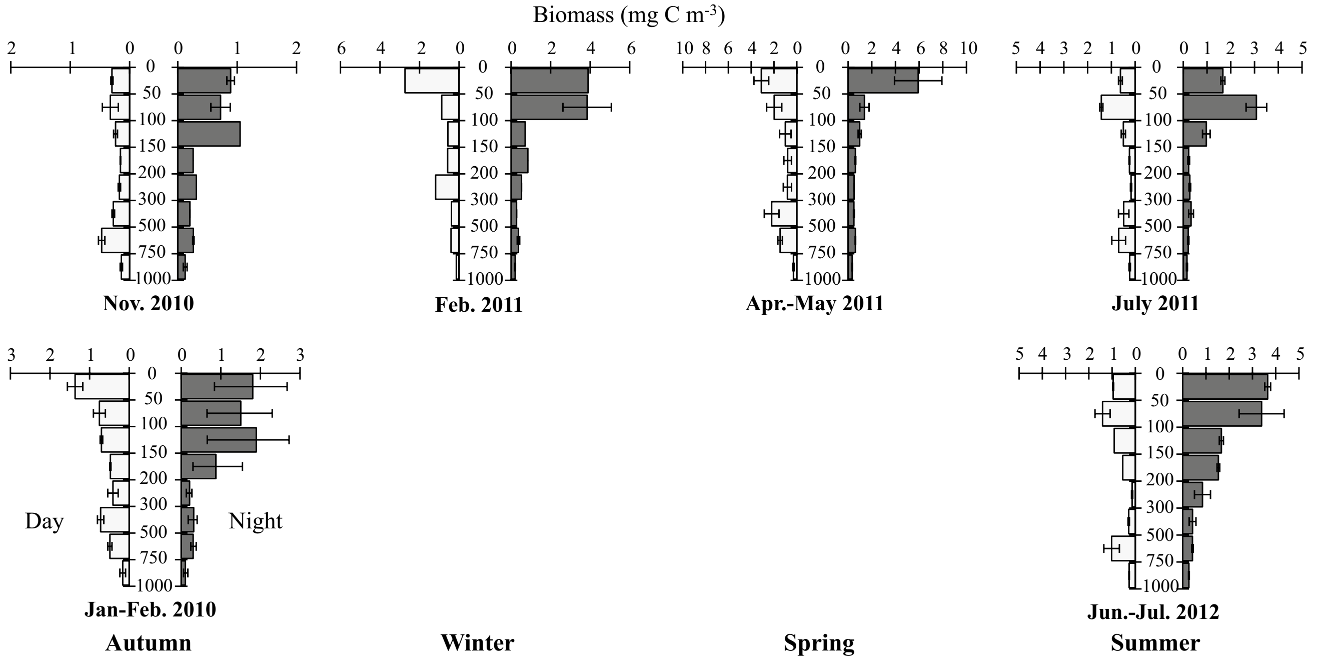
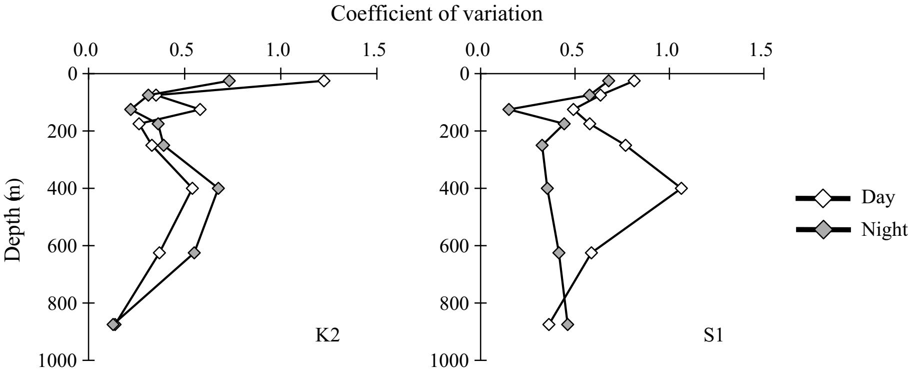


Fig. 6 Diel and seasonal changes in the vertical distributions of the mesozooplankton biomass (mg C m^{-3}) at subtropical time-series station S1 in the western North Pacific Ocean. The results of the four sequential cruises from autumn 2010 to summer 2011 are shown in the top row and the two results from other cruises are depicted in the bottom row. The *error bars* indicate the minimum and maximum values of the biomasses

Fig. 7 Seasonal variability in the mesozooplankton biomass expressed as the coefficient of variation versus depth (center of each sampling layer)



night were high above 200 m at K2 (up to 90.2 %), but they were still high in the deeper layers at S1. The daytime biomasses of Euphausiacea were quite low throughout the water column at K2, whereas high proportions of this taxon (up to 63.7 %) were detected below 100 m during the day at S1. Chaetognatha was also dominant at K2, particularly between 50 and 200 m (up to 35.7 %, mean 13.7 %), whereas the relative biomasses were generally low throughout the water column at S1 (up to 26.3 %, mean 5.1 %). The relative biomasses of Ostracoda were high in several layers above 300 m at S1 (up to 27.1 %, mean 10.0 %) but low throughout the water column at K2 (up to 16.4 %, mean 2.9 %).

The major taxa diversities were high in the subsurface layer (50–200 m) at K2 (Fig. 9). At S1, there were diel changes in the vertical profiles, i.e., the diversities were high at around 200 m during the day, whereas high values were obtained in the upper 300 m during the night (Fig. 9). The vertical patterns in the major taxa diversity did not change drastically over all four seasons at both sites. A comparison of the indices at the two sites showed that the diversities at S1 were higher than those at K2, except in the 50- to 100-m layer.

Figure 10 shows the vertical distributions of the annual mean and the seasonal range in the individual body weight (μg C ind.$^{-1}$) during the night for four dominant taxa: Copepoda, Euphausiacea, Ostracoda, and Chaetognatha. Larger copepods occurred at K2 (35–147 μg C ind.$^{-1}$) compared with S1 (9–67 μg C ind.$^{-1}$). Prominent seasonal

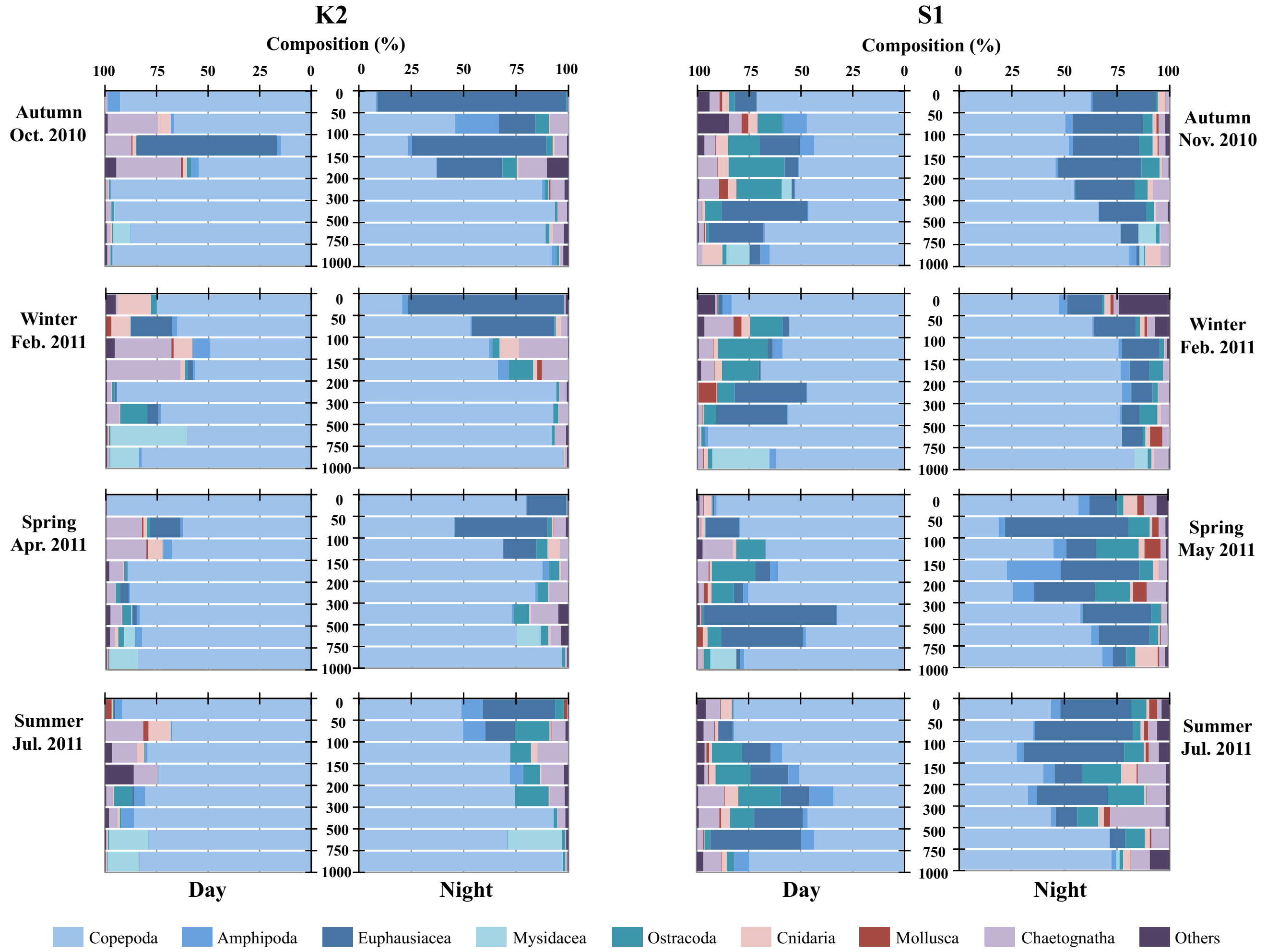


Fig. 8 Vertical/diel/seasonal changes in the major mesozooplankton taxa compositions based on the carbon mass at the two time-series stations, i.e., K2 and S1, in the western North Pacific Ocean. The *vertical axes* show the sampling depth (m)

variations in the depth layers were recognized at 0–50 m (heavier in spring) and at 200–500 m (lighter in spring) for copepods at K2, which appeared to be influenced by the seasonal occurrence of ontogenetic migrants such as *N. cristatus*. The euphausiids and chaetognaths that occurred at K2 were also larger than those at S1 whereas the ostracods collected from the two sites were approximately equivalent to each other.

Vertical, diel, and seasonal changes of carbon:nitrogen ratio (C:N ratio, wt/wt) of mesozooplankton in the two stations were shown in Fig. 11. At K2, the C:N ratios between 0 and 50 m showed prominent seasonal change; it was low in autumn and winter and high in spring and summer. Day/night difference of the C:N ratios in this layer was also shown; the nighttime ratios were lower than the daytime ones. The C:N ratios observed in mesopelagic layers were higher than those between 50 and 200 m. Diel and seasonal variations of the C:N ratios below 50 m were small comparing with those above 50 m. On the other hand, the C:N ratios at S1 showed small vertical variations between 0 and 500 m although the ratios increased with depth below 500 m. The C:N ratios at S1 were significantly lower than those at K2 through the four seasons (Wilcoxon signed-rank test: $p < 0.01$). The seasonal variability of the ratio in each depth layer at S1 was smaller than that at K2.

4 Discussion

4.1 Mesozooplankton biomass at K2 compared with other zooplankton time-series in the North Pacific Ocean

In this study, the maximum mesozooplankton biomass at K2 was observed during spring when the chlorophyll *a* and primary productivities were still low. Because the carbon demand of the surface mesozooplankton community exceeded the primary productivity during April 2011

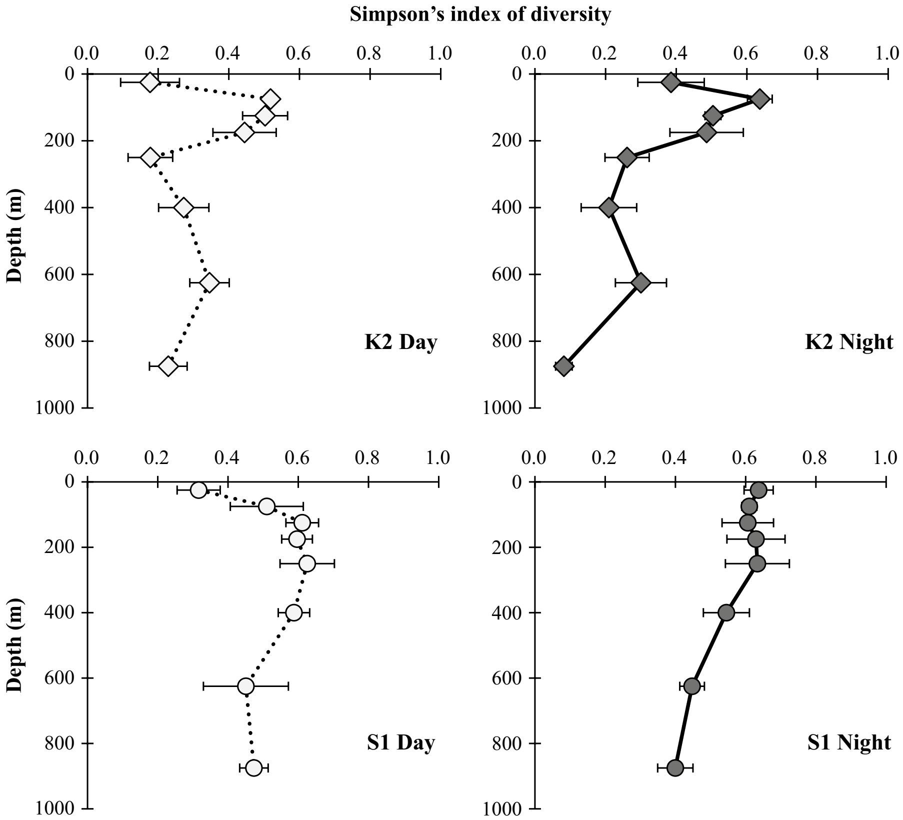


Fig. 9 Vertical distributions of the annual mean Simpson's Index of Diversity at the two time-series stations, i.e., K2 and S1. The *error bars* represent the minimum and maximum values of the indexes over the four seasons

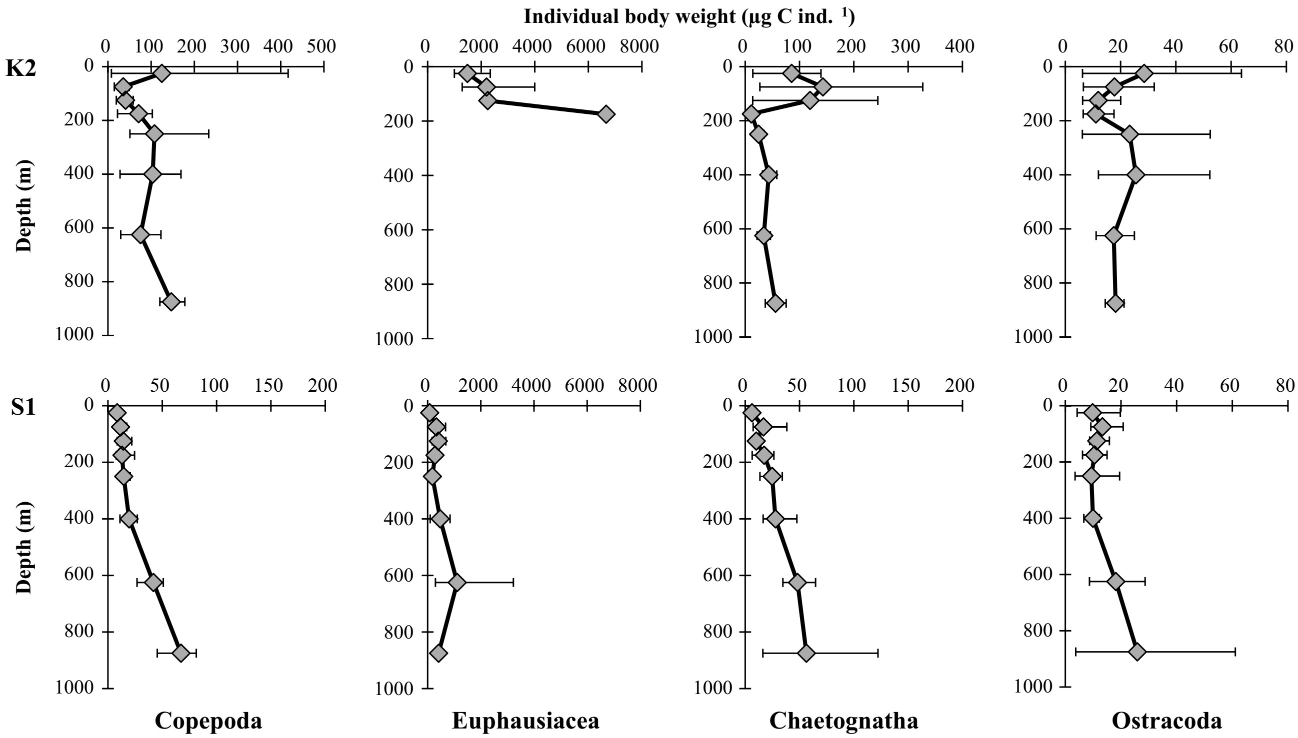


Fig. 10 Vertical distributions of the annual mean individual body weight for the four dominant mesozooplankton taxa: Copepoda, Euphausiacea, Chaetognatha, and Ostracoda. The *error bars* represent the minimum and maximum values of individual body weights over the four seasons

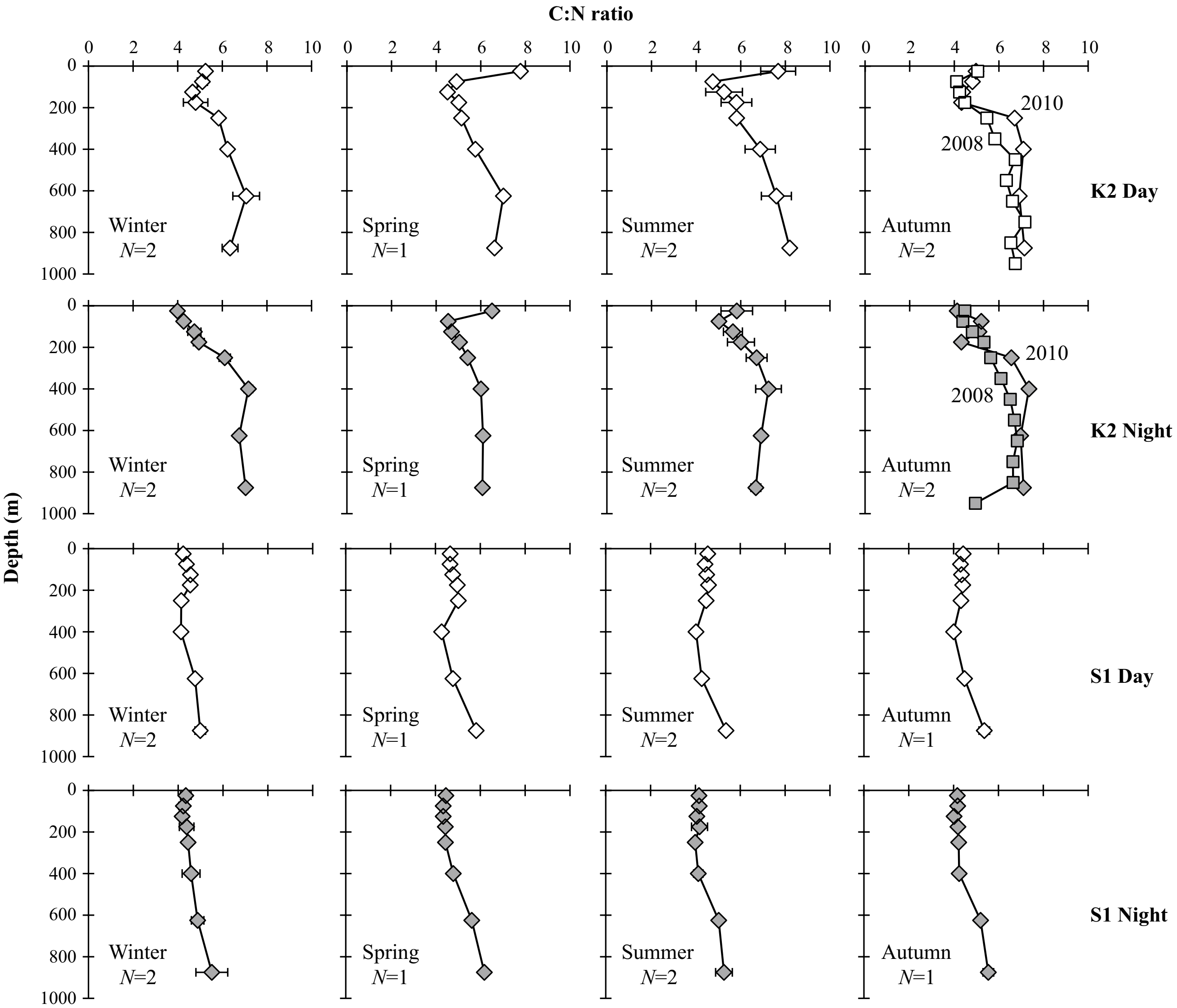


Fig. 11 Vertical distributions of the C:N ratio (wt/wt) of mesozooplankton both during the day and night in the four seasons at the two time-series stations, i.e., K2 and S1. The *error bars* represent the minimum and maximum values of the ratios

(Kobari et al. 2015), it is unlikely that the mesozooplankton increase was attributable only to grazing phytoplankton around K2. Mass occurrence of *N. cristatus* in the 0- to 50-m layer was contributed to the highest biomass during the spring. And *Neocalanus* are known to feed on protozoa (Gifford, 1993). Microzooplankton was probably important as a food source for the mesozooplankton during the spring. In addition, we consider that horizontal advection of the coastal mesozooplankton population into K2 may have been important. Phytoplankton blooms have often been observed in the Kamchatka/northern Kuril regions in April (Goes et al. 2004; Sasaoka et al. 2002), and higher chlorophyll *a* concentrations were observed in these regions compared with that in K2 during April 2011 according to satellite investigations. Although the seasonal occurrence of mesozooplankton is not known in the Kamchatka/northern Kuril regions, the coastal population may have been enhanced when the phytoplankton increased in April 2011, part of which may have been transported to K2. In fact, Lam and Bishop (2008) suggested the presence of lateral advection from the Kamchatka/Kuril margin to the K2 area based on the chemical characteristics of Mn and Fe at K2. Satellite images also showed that a chlorophyll-rich coastal plume occasionally spread southward from the Kuril Islands (Sasaoka et al. 2002). Neritic diatoms were observed at KNOT and in the central part of the western subarctic gyre (Mochizuki et al. 2002; Tsuda et al. 2007). Recently, the horizontal transport of materials from coastal regions to station P (50°N, 145°W) by a mesoscale eddy was also reported in the Gulf of Alaska (Whitney et al.

2005). Thus, interactions between the coastal and central areas of the western subarctic gyre require greater consideration in terms of biological and environmental aspects.

In contrast to our expectation, the annual mean mesozooplankton biomass in the surface layer observed at K2 (0–200 m; 1.9 and 3.1 g C m^{-2} during the day and night, respectively) was approximately equivalent to that in the Oyashio region (0–250 m; 2.4 g C m^{-2}; Ikeda et al. 2008), although the primary productivity at K2 (annual mean: 292 mg C m^{-2} day^{-1}) was lower than that in the Oyashio region (annual mean: 400 mg C m^{-2} day^{-1}; Kasai 2000). This was probably related to the underestimation of the euphausiid biomass in the Oyashio region because the samples were collected using a small net (60 cm mouth diameter). In fact, the annual mean mesozooplankton biomasses, excluding euphausiids, at K2 were calculated as 1.5 and 1.9 g C m^{-2} during the day and night, respectively (using data from only four cruises between autumn 2010 and summer 2011), which were 68 and 86 % of the levels in the Oyashio region (2.2 g C m^{-2}), respectively. The biomass of Euphausiacea integrated for 0–200 m during the night ranged from 0.5 to 1.7 g C m^{-2} (high in autumn but low in summer), and their relative biomasses were high during the autumn and winter at K2 when large ontogenetic migratory copepods migrated down into the mesopelagic layers.

Subarctic mesozooplankton dynamics has been studied at station P in the Alaskan Gyre. In general, seasonal biomass peaks were observed in May or June, although sometimes in July (Goldblatt et al. 1999; Mackas et al. 1998; Marlowe and Miller 1975). The seasonal variability in the primary productivity was relatively low but the primary productivity was increased during spring and summer (Harrison et al. 1999), and the mesozooplankton biomass peaks were observed during the season with higher productivity at station P. The vertically integrated mesozooplankton biomasses in 0–150 m at station P were <0.5 (winter), ca 3 (spring), and >2.3 (early summer) g C m^{-2} (calculated from Fig. 1 in Goldblatt et al. 1999). The integrated biomasses in 0–150 m at K2 were slightly higher (1.8–3.1 times) than those at station P, although the annual mean primary productivity at K2 was lower than that at station P (384–589 mg C m^{-2} day^{-1}; Harrison et al. 2004). Many mesozooplankton species showed feeding preference for larger phytoplankton (Jang et al. 2010; Liu et al. 2005; Takahashi and Ide 2011) or diatom (Schnetzer and Steinberg 2002), although mesozooplankton is able to feed nano- and picoplankton (Motwani and Gorokhova 2013; Uitto and Hällfors 1997). Larger phytoplankton such as diatoms dominated at K2 compared with station P (Harrison et al. 2004); thus, the food sources probably matched the herbivorous/omnivorous mesozooplankton at K2.

As shown in Fig. 4, the dormant depth of *N. cristatus* was shallower than that in the Oyashio region (below 500 m; Kobari and Ikeda 1999). This difference was probably attributable to hydrographic features. Although the physical environment below the permanent pycnocline (100–200 m) was stable in K2, a short-term variability in temperature and salinity due to the passage of a mesoscale eddy, or the intrusion of different water masses, was observed in the upper mesopelagic layers of the Oyashio region (Itoh et al. 2011; Sato et al. 2013). These disturbances may have made the dormant individuals in this layer spread out. The dormant stage of *Neocalanus flemingeri* also occurred in shallower depths at K2 (200–500 m; Kobari et al. 2008) compared with the Oyashio region (about 600 m; Kobari and Ikeda 2001). At station P in the Gulf of Alaska, Miller et al. (1984) reported that the dormant stages of *N. cristatus* were distributed below 250 m and over half of them occurred below 500 m. The physical environment was also stable below the pycnocline (100–125 m) but the water temperature was slightly higher at P (4–6 °C between the pycnocline and 400 m, 3–4 °C between 400 and 1000 m; Miller et al. 1984) than at K2 (3–4 °C between 200 and 500 m). The shallower distribution of the dormant *N. cristatus* at K2 was possibly influenced by the lower water temperature. Regional differences in the *Neocalanus* life cycle such as the life span and the period of downward migration are known in the subarctic Pacific and its marginal seas (Harrison et al. 2004), so it is not surprising that there was a regional difference in their dormant depths.

4.2 Seasonality of mesozooplankton biomasses at S1

The mesozooplankton community in the North Pacific Subtropical Gyre has been well studied based on the Hawaii Ocean Time-series (HOT) at the ALOHA station (e.g., Landry et al. 2001; Huntley et al. 2006). We compared the characteristics of the mesozooplankton community at S1 with that at ALOHA. The annual means of the standing stocks in the euphotic layer at S1 (103 and 210 mg C m^{-2} during the day and night, respectively) were comparable to those at ALOHA (183 and 314 mg C m^{-2}; Landry et al. 2001); however, the seasonal signals of the standing stocks differed. Thus, the maximum standing stock was observed in spring at S1 but in summer at ALOHA (Landry et al. 2001). Shallow winter mixing (Dore et al. 2002) rarely penetrates the top of the nitracline, so mesoscale eddy activity and N_2 fixation may be major sources of nutrients in the surface waters at ALOHA (Calil et al. 2011; Karl et al. 1997; Vaillancourt et al. 2003). A regular pattern of enhanced production and higher abundances of large phytoplankton species is associated with the bloom of nitrogen-fixing organisms during the summer (Landry et al. 2001; Calil et al. 2011). Therefore, the seasonal mesozooplankton maximum may depend on the enhanced production during the summer period (Landry et al. 2001). However, wintertime convection reached to 200 m and the nitrate concentration was increased in the surface waters (Honda et al. 2015), and this nutrient delivery made the primary production increase during the winter at S1 (Matsumoto et al. 2015). The increased mesozooplankton biomass during the winter and spring probably depended on the higher primary productivity during winter at S1. The response speeds of the biomass increases to temporal changes in primary productivity were also different at the two sites, where the maximum biomass was observed during the spring after enhanced primary productivity at S1, whereas the increases in the mesozooplankton biomass and primary production corresponded with each other at ALOHA. The biomass increase at ALOHA was associated with that of small copepods such as *Macrosetella gracilis* (Landry et al. 2001; Huntley et al. 2006). By contrast, larger mesozooplankton such as euphausiids had high biomasses at S1. The intra-specific growth rate may decrease with increasing body weight, and thus larger individuals grow more slowly than smaller individuals (Hirst and Sheader 1997). Therefore, the slower response of the biomass increase at S1 was probably influenced by larger body sizes.

It is not entirely surprising that mesozooplankton communities exhibit seasonal variation in the subtropical oceans because the seasonality of mesozooplankton standing stocks is a well-documented feature at ALOHA as well as in the Sargasso Sea (Deevey 1971; Roman et al. 1995). The biomass increase derived from deep winter mixing at S1 was similar to the seasonality of the mesozooplankton biomass in the Sargasso Sea. In the western subtropical Pacific, the penetration of deep wintertime convection (>150 m) into the nitracline (≈100 m) was observed between the Kuroshio Current and approximately 29°N (Inoue et al. 2015). Thus, the enhanced mesozooplankton biomass observed during the winter/spring at S1 may occur widely in this area. In fact, the epipelagic mesozooplankton biomass peaked in April, and a time lag between the chlorophyll *a* and mesozooplankton biomass peaks was also observed about 1000 km west of S1 (Limsakul et al. 2002).

The mesopelagic biomass peak was observed only during the day, which suggests that the majority of the diel vertical migrants swim down to the peak depth. The peak occurred at a shallower depth during the winter when primary productivity was high but at deeper depths in lower productivity seasons, i.e., summer and autumn. The vertical shift in the peak depths was probably due to the sensitivity of migrants to different light environments because light penetration increased during the seasons with lower productivity. This result is consistent with that reported by Andersen et al. (1997), who found that mesozooplankton migrated deeper at an oligotrophic site compared with meso- and eutrophic sites in the tropical Atlantic Ocean. Correlation between daytime depth distribution of copepods and light intensity was also reported by Buskey et al. (1989) and Takahashi et al. (2009) in subtropical and subarctic areas, respectively. Mesopelagic biomass peaks were also observed between 400 and 750 m during the day in the summer at ALOHA (Steinberg et al. 2008b). The depth range of the biomass peak was similar to that in the present study, although the species compositions differed. The peak mainly comprised copepods, ostracods, and chaetognaths at ALOHA, whereas copepods and euphausiids dominated in the peak at S1.

4.3 Comparison of the mesozooplankton communities of K2 and S1

A major difference between the two sites was the higher biomass at K2 compared with S1. A difference in the mesozooplankton biomasses of subarctic and subtropical stations was observed previously during the summer (Steinberg et al. 2008b; Yamaguchi et al. 2004), which was explained by differences in the primary productivity, sinking particles, and diel vertical migration (Steinberg et al. 2008b). However, the annual mean mesozooplankton biomasses at K2 were one order of magnitude higher than those at S1, although the annual means of the primary productivity and sinking POC flux into the mesopelagic layer were approximately equivalent at K2 and S1 (Honda et al. 2015; Matsumoto et al. 2015). Even during the winter, when the primary productivity at K2 was lower than that at S1, the night-time mesozooplankton biomass in the euphotic layer at K2 was 5.6-fold higher than that at S1. It is possible that the mesozooplankton biomass is also influenced by other factors in addition to the primary productivity or downward particle flux, which we discuss in the following.

As a general rule, large organisms have lower respiration and excretion rates per unit biomass than small ones (Hirst and Sheader 1997). Thus, the respiratory and excretory carbon losses per unit biomass by large organisms are lower than those by small ones. As shown in Fig. 10, the mesozooplankton collected at K2 were much larger than those at S1. The lower water temperature at K2 also let mesozooplankton decrease respiratory carbon loss. These probably contributed to the higher biomass at K2. Similarly, an ecological advantage of lower respiratory loss compared with other copepod species has been discussed for *Oithona* copepods (Almeda et al. 2011). Body sizes also affect population growth. The rate of turnover at a steady state is negatively correlated with body size (Brown et al. 2007). The higher turnover rates of small organisms at S1 may have allowed their snapshot biomasses to be maintained at low levels. Furthermore, the trophic structures of mesozooplankton communities may also influence their standing stocks. The transfer efficiency of energy to the next trophic level is approximately 10–15 % (Iverson 1990; Lalli and

Parsons 1997). The relative biomasses of herbivores were reported to be 80 and 30 % in the subarctic and subtropical areas of the western North Pacific Ocean, respectively (Taniguchi 1973); thus, the energy loss from primary producers to mesozooplankton community at K2, in which primary consumers were probably dominant, was considered to be lower than that to the community at S1.

In this study, advection of the coastal community into K2 probably masked the correlation among the seasonal changes, primary productivity, and mesozooplankton biomass at K2, as discussed in "Mesozooplankton biomass at K2 compared with other zooplankton time-series in the North Pacific Ocean". The higher lipid content of the mesozooplankton at K2 was indicated by their higher C:N ratios compared with that at S1. Greater lipid storage, which allows mesozooplankton to tolerate starvation, probably enhanced the survival of organisms advected from coastal to open oceans. By contrast, the mesozooplankton biomasses at S1 were sensitive to changes in primary productivity, which were possibly affected by the shorter turnover rates of the mesozooplankton population. Geographical features also affected their dynamics, i.e., the advection of the coastal community is limited because the Kuroshio Current passes between the marginal area of the Pacific and S1. Episodic physical events such as the advection or passage of mesoscale eddys may affect mesozooplankton biomasses not only in subarctic but also in subtropical areas. Samplings at shorter intervals, which will provide us more accurate dynamics and annual mean biomass, are required for future studies. Mooring observations using acoustical devices (e.g., Jiang et al. 2007) are probably effective for them.

The mean proportion of copepods in the carbon-based compositions at K2 was higher than that at S1 (Fig. 7). Thus, the evenness of the major taxa in each depth layer at K2 was lower than that at S1. Therefore, the diversity of the major taxa levels at K2 was lower than that at S1 (Fig. 9), which is similar to the latitudinal differences in species diversity (e.g., Angel et al. 2007; Tittensor et al. 2010). In general, diversified communities, which have a diversity of interaction types (e.g., antagonism and mutualism), can stabilize community dynamics (Mougi and Kondoh 2012). However, the effect of diversity on the stability of the communities was still unclear at the two sites because of the high environmental seasonality or the possible effects of advection. Thus, further studies of the ecological importance of diversity for the plankton community are needed.

The contributions of euphausiids to the mesozooplankton biomass also differed between the two sites (Fig. 8). During the day, a few euphausiids were collected throughout the water column at K2 (annual mean day/night biomass ratio of 0.07) but the mean ratio was 1.19 at S1. The extremely low biomass during the day at K2 was probably due to the higher efficiency of net avoidance because of their larger body size. Furthermore, the night-time distributions of euphausiids were concentrated in the surface layer at K2, whereas they were collected from a broad range of depths during the night at S1. According to our preliminary results, the species richness of euphausiids at S1 (17 species) was higher than that at K2 (five species). The vertically broad distribution and the higher species richness at S1 might suggest vertical space partitioning by euphausiid species to utilize different food sources, as shown by Barange et al. (1991) in the Benguela Current.

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