Comparisons between POC and zooplankton swimmer flux from sediment traps in the subarctic and subtropical North Pacific

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ARTICLE INFO

ABSTRACT

Seasonal changes in zooplankton swimmer (ZS) abundance, biomass and community structure were evaluated based on samples collected by moored sediment traps at a depth of 200 m in the subarctic (SA) and subtropical (ST) western North Pacific. Based on these samples, we made comparisons on two topics: 1) latitudinal (subarctic vs. subtropical) changes in ZS abundance, biomass and community and 2) quantitative differences between the ZS and particle organic carbon (POC) fluxes based on data from moored or drifting sediment traps. The results showed that the ZS flux was greater in the SA (annual mean: 311 ind. m^{-2} day^{-1} or 258 mg C m^{-2} day^{-1}) than in the ST (135 ind. m^{-2} day^{-1} or 38 mg C m^{-2} day^{-1}). The peak ZS flux was observed from July–August in the SA and from April–May in the ST. The dominant taxa were Copepoda and Chaetognatha in the SA and Ostracoda and Mollusca in the ST. These latitudinal differences are likely related to the dominance of large-sized Copepoda in the SA, regional differences in the timing of the spring phytoplankton bloom, and the magnitude and size structure of primary producers. The percent composition of ZS to the total C flux (= ZS + POC flux) varied by region: 85–95% in the SA and 47–75% in the ST. These differences between the ZS composition and the total C flux are most likely caused by the dominance of large-sized Copepoda (*Neocalanus* spp. and *Eucalanus bungii*) in the SA.

1. Introduction

A sediment trap is an oceanographic observation device that is moored at a certain depth in the water column and used to collect sinking particles. Since the 1970s, various studies have been conducted on sinking particles using sediment traps. For example, the relationships between particle organic carbon (POC) flux and primary production (Silver and Gowing, 1991) as well as the major components of POC flux (biogenic opal and $CaCO_3$) have been studied (Honda et al., 2016). Regarding these topics, various aspects of sinking POC flux have been reported in different oceans (cf. Lohrenz et al., 1992; Buesseler et al., 2000, 2007). Most studies using sediment traps collected zooplankton, called "swimmers", in their samples, and these were not treated as sinking particles; therefore, the swimmers were removed from the POC flux measurements (Knauer et al., 1979; Silver and Gowing, 1991). Sometimes, it is estimated that the contribution of the swimmers and larvacean houses could be as much as 96% of the measured carbon flux, quantified by sediment traps at shallower depths in the upper few 100 m (Michaels et al., 1990).

Several more recent studies, however, have focused on zooplankton swimmers (ZS). For example, the flux caused by Copepoda carcasses is reported to be greater than their fecal pellets in oligotrophic oceans (Frangoulis et al., 2011). In the Arctic region, seasonal changes in the population structure of Mollusca *Limacina helicina* and Copepoda *Metridia longa* can be evaluated by the data collected through sediment traps (Makabe et al., 2016). Considering the results from these previous studies, the usefulness of sediment traps for plankton ecological studies has been reconsidered. For studying ZS, sediment traps have the advantage of being able to collect high-resolution time-series samples in regions where access is difficult (e.g., oceanic regions or ice-covered oceans). Recently, seasonal changes in zooplankton communities and the life cycles of dominant zooplankton species in oceanic or ice-covered oceans have been evaluated based on analyses of ZS samples collected using sediment traps (Ota et al., 2008; Ohashi et al., 2011; Matsuno et al., 2014, 2015). Although zooplankton swimmers have been studied based on data collected from sediment traps, several problems remain unsolved. Thus, little information is available for regional patterns in ZS (subarctic vs. subtropical) and for quantitative comparisons between sinking POC flux and ZS flux (Buesseler et al., 2007).
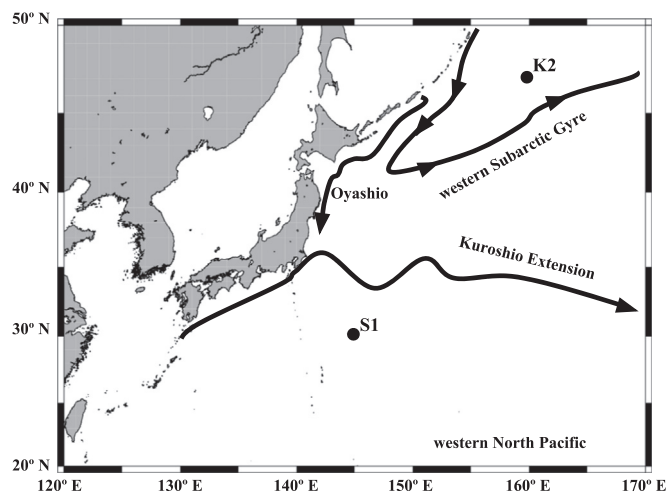

Fig. 1. Location of sampling stations: K2 is in the subarctic and S1 is in the subtropical western North Pacific. The approximate directions of current flows are shown with arrows (cf. Yasuda, 2003).

Table 1

Sampler rotation timings of moored sediment traps (MSTs) and deployed timings of drifting sediment traps (DSTs) at the St. K2 (47°N, 160°E) in the subarctic and the St. S1 (30°N, 145°E) in the subtropical western North Pacific. Dates were arranged according to the order of the Julian day. Parentheses indicates deployed durations (days) for DSTs.

K2		S1	
MST	DST	MST	DST
25 July 2013	1 July 2011 (5.0)	18 July 2013	25 July 2011 (4.3)
1 Aug. 2013		5 Aug. 2013	
8 Aug. 2013		23 Aug. 2013	
15 Aug. 2013		10 Sep. 2013	
22 Aug. 2013		28 Sep. 2013	
5 Sep. 2013		16 Oct. 2013	
19 Sep. 2013		3 Nov. 2013	8 Nov. 2010 (3.1)
3 Oct. 2013		21 Nov. 2013	
17 Oct. 2013		9 Dec. 2013	
31 Oct. 2013	28 Oct. 2010 (3.0)	27 Dec. 2013	
14 Nov. 2013		14 Jan. 2014	
28 Nov. 2013		23 Jan. 2014	30 Jan. 2010 (3.0)
12 Dec. 2013		1 Feb. 2014	
26 Dec. 2013		10 Feb. 2014	
9 Jan. 2014		19 Feb. 2014	15 Feb. 2011 (3.0)
23 Jan. 2014	23 Jan. 2010 (1.9)	28 Feb. 2014	
6 Feb. 2014		9 Mar. 2014	
20 Feb. 2014	25 Feb. 2011 (4.0)	18 Mar. 2014	
6 Mar. 2014		27 Mar. 2014	
20 Mar. 2014		5 Apr. 2014	
3 Apr. 2014		23 Apr. 2014	28 Apr. 2011 (3.1)
10 Apr. 2014	19 Apr. 2011 (3.0)	11 May 2014	
17 Apr. 2014		29 May 2014	
24 Apr. 2014		16 June 2014	
1 May 2014		4 July 2014	28 June 2012 (3.0)
8 May 2014	11 June 2012 (3.0)		

In this study, we evaluated seasonal changes in ZS abundance, biomass and community structure based on samples collected by moored sediment traps at 200 m (the bottom of the epipelagic zone) in the subarctic and subtropical western North Pacific. These data were compared with the POC flux, which was quantified based on data collected from moored and drifting sediment traps (Honda et al., 2016). Regarding these comparisons, we focus on the following two topics: 1) latitudinal (subarctic vs. subtropical) changes in ZS abundance, biomass and community and 2) quantitative differences between the ZS and POC fluxes based on data collected by moored or drifting sediment traps.
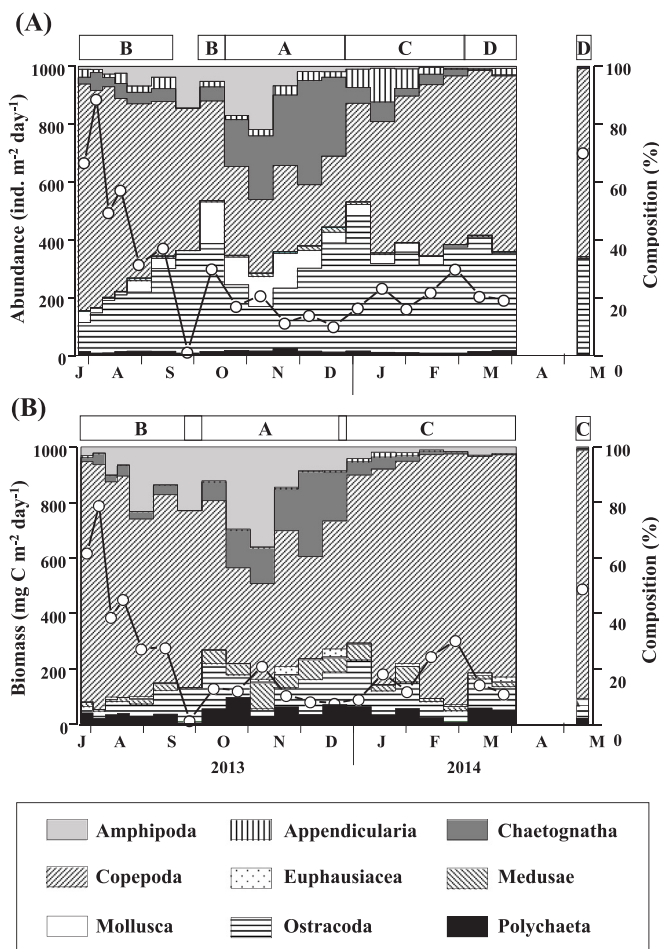

Fig. 2. Zooplankton swimmer abundance (A) and biomass (B) collected at 200 m of the St. K2 in the western subarctic Pacific from July 25, 2013 to May 8, 2014. The line with an open circle indicates the total zooplankton swimmer abundance or biomass, and the fills indicate the percentage composition of the different taxa. Note that the samples were unavailable from April 3 to May 1, 2014. Based on cluster analyses, the samples were separated into four (A–D, abundance) or three (A–C, biomass) groups (cf. Fig. 3).

2. Materials and methods

2.1. Field sampling

Samples were collected using time-series sediment traps (SMD26S-26 with 26 collecting cups, conical-shaped, and an open mouth area of $0.5 \, m^2$; Nichiyu Giken Kogyo Co., Ltd., Kawagoe, Japan) moored at a depth of 200 m in the subarctic station K2 (47°00′ N, 160°00′E, bottom depth: 5200 m) and subtropical station S1 (30°00′ N, 145°00′E, bottom depth: 5700 m) of the western North Pacific from July 25, 2013 to May 15, 2014 (St. K2) and July 18, 2013 to July 4, 2014 (St. S1), respectively (Fig. 1, Table 1). The traps were anchored with rope to the sea bottom at each station. Within the trap cup, 10% buffered formalin seawater was added before deployment. After the traps were recovered, the samples were gently sieved with a 1 mm mesh. We treated all samples < 1 mm as POC and samples > 1 mm as ZS. It should be noted that the 1 mm mesh size would certainly allow smaller swimmers (e.g., young stages of copepods) to pass through the mesh into the POC fraction. While it is a source of error, microscopic observation confirmed that the volume of swimmers was a minor component of the < 1 mm fraction (data not shown).

2.2. Sample treatment

ZS samples were sorted for taxa and counted using a
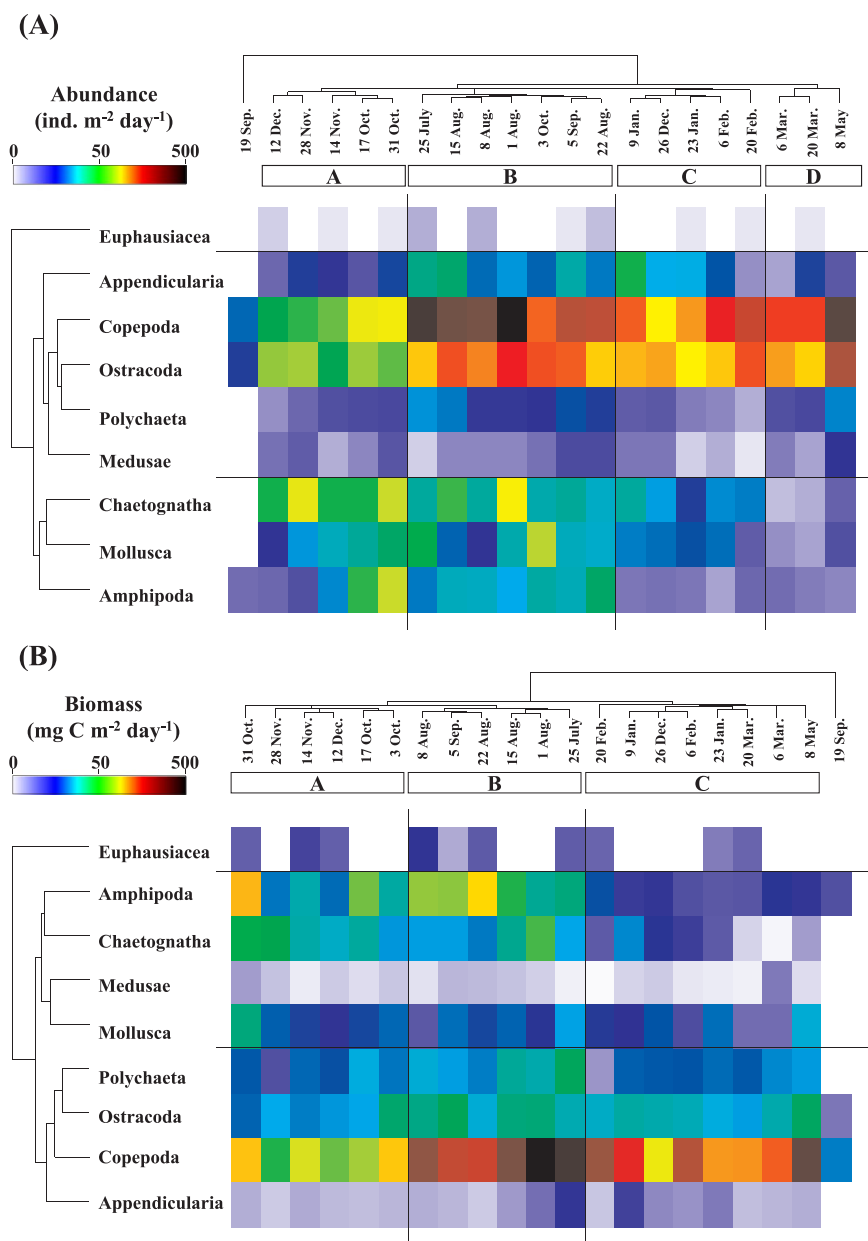
(A)

(B)

Fig. 3. Results of cluster analyses of the zooplankton swimmer abundance (ZSA, A) and biomass (ZSB, B) at 200 m at the St. K2 in the western subarctic Pacific from July 25, 2013 to May 8, 2014. Four and three groups were identified for the ZSA and the ZSB, respectively. The ZSA and the ZSB of each taxon are shown with colored bars.

stereomicroscope; then, the wet mass (WM) was weighed with a precision of 0.1 mg by an electric balance (AE100, Mettler-Toledo International Inc.). WM data were converted to dry mass (DM) using water content (WC) that varied by taxon (80% for Amphipoda, Copepoda, Euphausiacea, Mollusca, Ostracoda and Polychaeta; 90% for Chaetognatha; and 96% for Appendicularia and Medusae) (DM = WM × [1 - WC × 0.01]) (Postel et al., 2000). Finally, DM data were converted to carbon mass using carbon content that varied by taxon (Amphipoda: 37.2% DM, Appendicularia: 56.4% DM, Chaetognatha: 10.9% DM, Copepoda: 52.8% DM, Euphausiacea: 43.0% DM, Medusae: 7.2% DM, Mollusca: 25.0% DM, Ostracoda: 42.5% DM and Polychaeta: 29.9% DM) (Kitamura et al., 2016).

The zooplankton swimmer abundance (ZSA, ind. m^{-2} day^{-1}) and biomass (ZSB, mg C m^{-2} day^{-1}) were calculated using the following equations:

$$ZSA = A/0.5/D \tag{1}$$

$$ZSB = B/0.5/D \tag{2}$$

where A is abundance (ind. $sample^{-1}$) and B is biomass (mg C $sample^{-1}$)

per sample, 0.5 is the mouth area (m^2) of the sediment trap and D is the rotation interval of the trap sample (day). The rotation interval was 7–14 days at St. K2 and 9–18 days at St. S1 (Table 1).

For the POC flux collected by moored sediment traps (MSTs), samples with < 1 mm were filtered through a GF/F filter and dried. Elemental analyses (2400 CHN/O, PerkinElmer, Inc.) were made on the dried samples, and the results on organic carbon were expressed as the POC flux (mg C m^{-2} day^{-1}).

For the POC flux collected by drifting sediment traps (DSTs), traditional, surface-tethered particle interceptor traps (PITs) (Knauer et al., 1979), constructed of eight cylinders with a collection area and an aspect ratio of 0.0038 m^2 and 8.27 (620 mm length/75 mm width), respectively, were deployed for several days on six occasions at each station (Table 1).

Detailed methods for MSTs and DSTs were presented in Honda et al. (2016). Data on the POC flux using MSTs and DSTs were sourced from the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) database, which has data collected from the K2 and S1 time-series stations (netCDF format for OceanSITES; https://ebcrpa.jamstec.go.jp/k2s1/en/index.html).
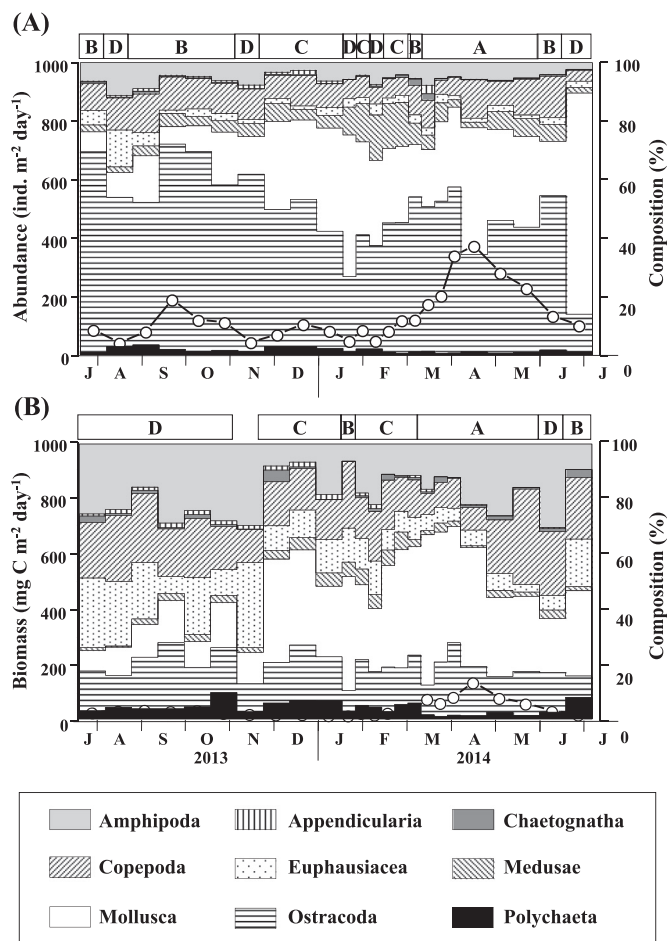
(A)

(B)

Fig. 4. The zooplankton swimmer abundance (A) and biomass (B) collected at 200 m at the St. S1 in the western subtropical Pacific from July 18, 2013 to July 4, 2014. The line with an open circle indicates the total zooplankton swimmer abundance or biomass, and the fills indicate the percentage composition of the different taxa. Based on the cluster analysis, the samples were separated into four (A–D) groups (cf. Fig. 5).

2.3. Statistical analysis

To evaluate the seasonal changes in ZS, the ZSA and ZSB data were log transformed (log[ZSA + 1] or log [ZSB + 1]) prior to analyses to reduce their variability bias. After that, similarities between samples were identified using the Bray-Curtis method (Bray-Curtis, 1957). To group the samples, similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method (unweighted pair group method using arithmetic mean, UPGMA; Field et al., 1982). We evaluated the differences in the ZSA and the ZSB of each taxon between groups using one-way ANOVA.

To evaluate the regional differences in ZS, the ZSA and ZSB data and their taxonomic composition were compared between the subarctic (K2) and subtropical (S1) regions using a *U*-test.

For quantitative comparison between the ZS and POC fluxes, we calculated the total C flux (= ZSB + POC flux) and the percentage composition of the ZSB in the total C flux. All statistical analyses were made using PRIMER v7 (PRIMER-E Ltd.) and Stat View v5.0.

3. Results

3.1. Subarctic region (K2)

At the subarctic K2, the ZSA ranged from 11.9 to 887.6 ind. m^{-2} day^{-1}, and the annual mean was 310.7 ± 48.5 ind. m^{-2} day^{-1} (mean ± SD) (Fig. 2A). The dominant taxon in the ZSA was Copepoda

(50 ± 4%), followed by Ostracoda (28 ± 2%) and Chaetognatha (9 ± 2%). The cluster analysis results classified the ZSA samples into four groups (A–D) (Fig. 3A). A comparison between the groups showed that four taxa (Chaetognatha, Copepoda, Ostracoda and Polychaeta) had significant inter-group differences in the ZSA (one-way ANOVA, $p < 0.05$). Temporally, group B, which is characterized by a high ZSA dominated by Copepoda, was observed from late July to mid-October 2013 (Fig. 2A). Group A, with a low ZSA that was dominated by Chaetognatha, was found from mid-October to late December 2013 (Fig. 2A).

The ZSB in K2 ranged from 11.3 to 787.9 mg C m^{-2} day^{-1} with a mean of 258.3 ± 44.1 mg C m^{-2} day^{-1} (mean ± SD) (Fig. 2B). The dominant taxon in the ZSB was Copepoda (68 ± 4%), followed by Amphipoda (9 ± 2%) and Chaetognatha (6 ± 2%). The results from a cluster analysis classified ZSB samples into three groups (A–C) (Fig. 3B). Comparisons between groups indicated that five taxa (Amphipoda, Chaetognatha, Copepoda, Ostracoda and Polychaeta) had significantly different ZSBs (one-way ANOVA, $p < 0.05$). From late July to mid-October 2013, group B was observed and was characterized by a high ZSB dominated by Copepoda (mean composition in the ZSB for group B accounted for 78%). From mid-October to late December, group A was observed and had a low ZSB that was dominated by Chaetognatha (Fig. 2B).

3.2. Subtropical region (S1)

At the subtropical S1, the ZSA ranged from 40.4 to 372.7 ind. m^{-2} day^{-1} with a mean of 134.9 ± 18.3 ind. m^{-2} day^{-1} (mean ± SD) (Fig. 4A). The dominant taxon in the ZSA was Ostracoda (48 ± 3%), followed by Mollusca (26 ± 3%) and Copepoda (9 ± 1%). The results from a cluster analysis classified ZSA samples into four groups (A–D) (Fig. 5A). Comparisons between groups showed that there were six taxa (Amphipoda, Copepoda, Euphausiacea, Medusa, Mollusca and Ostracoda) that had significantly different ZSAs (one-way ANOVA, $p < 0.05$). Temporally, group A, which was characterized by a high ZSA for all taxa, was observed from early March to May 2013 (Fig. 5A).

The ZSB in S1 ranged from 13.4 to 133.5 mg C m^{-2} day^{-1}, and its mean was 37.8 ± 5.9 mg C m^{-2} day^{-1} (mean ± SD) (Fig. 4B). The dominant taxon in the ZSB was Mollusca (29 ± 3%), followed by Amphipoda (18 ± 2%) and Copepoda (18 ± 1%). The results from a cluster analysis classified ZSB samples into four groups (A–C) (Fig. 5B). Comparisons between groups showed that there were six taxa (Amphipoda, Chaetognatha, Copepoda, Medusa, Mollusca and Ostracoda) with a significantly different ZSB (one-way ANOVA, $p < .05$). Temporally, group A, which had a high ZSB for all taxa, was observed from March to May 2013 (Fig. 5B).

3.3. Comparison between K2 and S1

Regional comparisons (K2 vs. S1) in the ZSA and the ZSB yielded significant regional differences for several taxa (Table 2). Common patterns in the ZSA and the ZSB were observed for Chaetognatha and Copepoda. Thus, both taxa had significantly greater values in the subarctic K2 (Table 2).

Regional differences in taxonomic composition were also detected for seven taxa in both the ZSA and the ZSB (*U*-test, $p < 0.05$, Fig. 6). For both the ZSA and the ZSB, Copepoda (K2: 50–68%, S1: 9–18%) and Chaetognatha (K2: 6–9%, S1: 0–1%) had significantly higher percentage compositions among all taxa found in the subarctic region (Fig. 6). In contrast, Euphausiacea (K2: 0–1%, S1: 3–11%), Medusa (K2: 0–1%, S1: 3–6%), Mollusca (K2: 3–4%, S1: 26–29%) and Ostracoda (K2: 8–28%, S1: 16–48%) had significantly higher percentage compositions among all taxa observed in the subtropical region (Fig. 6).
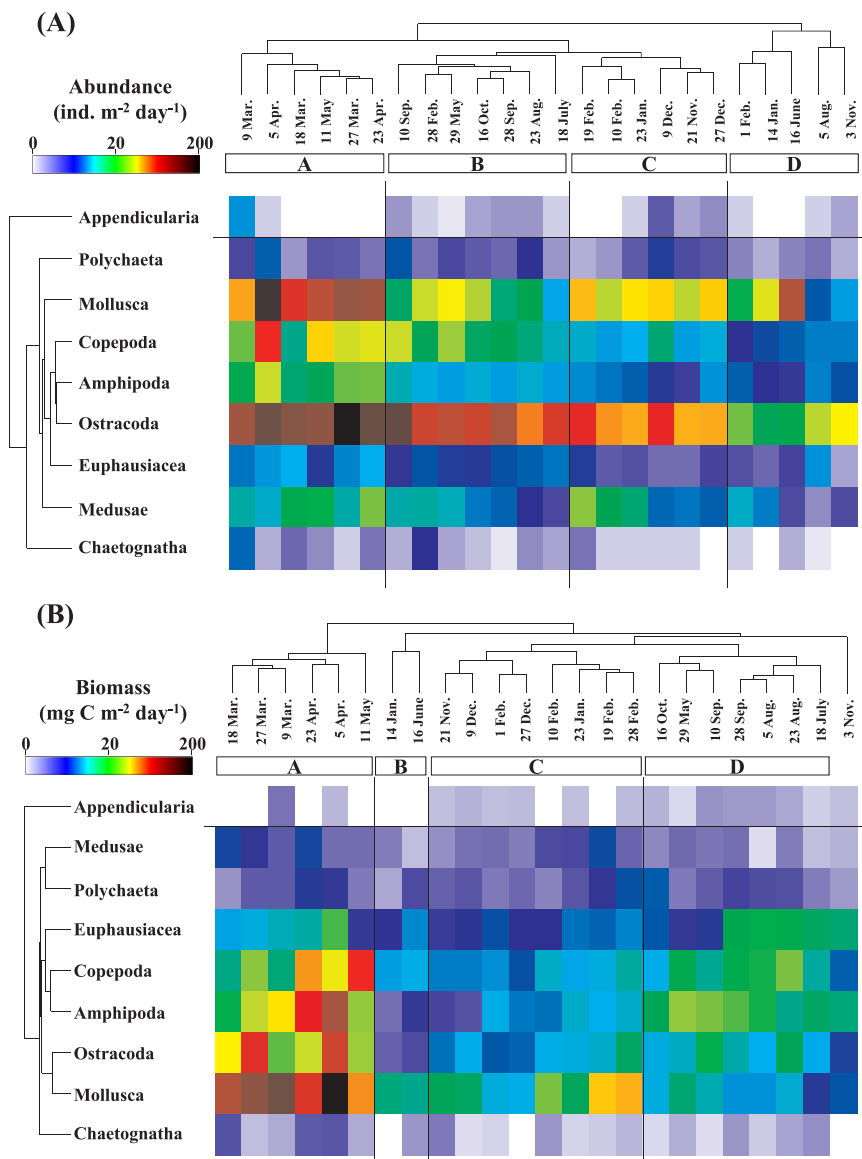
(A)

(B)

Fig. 5. Results of the cluster analysis on the zooplankton swimmer abundance (ZSA, A) and biomass (ZSB, B) at 200 m at the St. S1 in the western subtropical Pacific from July 18, 2013 to July 4, 2014. For both the ZSA and the ZSB, four groups (A–D) were identified. The ZSA and the ZSB of each taxon are shown with colored bars.

Table 2

Results of inter-regional comparison in the zooplankton swimmer abundance (ZSA) and biomass (ZSB) collected at 200 m depths between the subarctic K2 and the subtropical S1 in the western North Pacific. Inter-regional differences were tested using *U*-test. *: $p < 0.05$, **: $p < 0.01$, ns: not significant.

Taxon	ZSA	ZSB
Amphipoda	ns	ns
Appendicularia	* (K2 > S1)	ns
Chaetognatha	** (K2 > S1)	** (K2 > S1)
Copepoda	** (K2 > S1)	** (K2 > S1)
Euphausiacea	* (S1 > K2)	ns
Medusae	ns	ns
Mollusca	ns	ns
Ostracoda	ns	ns
Polychaeta	ns	ns

3.4. Comparison between the POC flux and ZS

From POC flux data at each station (Honda et al., 2016), the total C flux (= POC flux + ZSB) was calculated. At K2, the annual mean POC flux collected using MSTs was 15.0 mg C m^{-2} day^{-1} (Table 3). Since the annual mean ZSB was 258.3 ± 44.1 mg C m^{-2} day^{-1} at K2, the ZSB was higher than the POC flux throughout the year; the ZSB accounted for 94.5% of the total C flux. At the same station, the POC flux collected using DSTs was 45.2 mg C m^{-2} day^{-1}, and the ZSB accounted for 85.1% of the total C when the POC flux was evaluated using DSTs.

At S1, the annual mean POC flux collected by moored sediment traps was 12.5 mg C m^{-2} day^{-1} (Table 3). The annual mean of ZSB at the same station was 37.8 ± 5.9 mg C m^{-2} day^{-1}; the ZSB accounted for 75.1% in the total C flux. The annual mean POC flux collected using DSTs at the same station was 42.1 mg C m^{-2} day^{-1}; thus, the percent composition of the ZSB of total C was 47.3% when the POC flux was evaluated using DSTs.

4. Discussion

4.1. Comparison between subarctic and subtropical regions

In this study, regional ZS differences between the subarctic K2 and the subtropical S1 were observed in three ways. First, both the ZSA and the ZSB at K2 were higher than those at S1. At K2, the ZSA (ind. m^{-2} day^{-1}) was 2.3 times higher (= 310.7/134.9) and the ZSB (mg C m^{-2} day^{-1}) was 6.5 times higher (= 246.0/37.8) than those at S1 (Figs. 2 and 4). Second, the seasonal peak timings of the ZSA and the ZSB varied by region: July–August for K2 and April–May for S1 (Figs. 2 and 4).
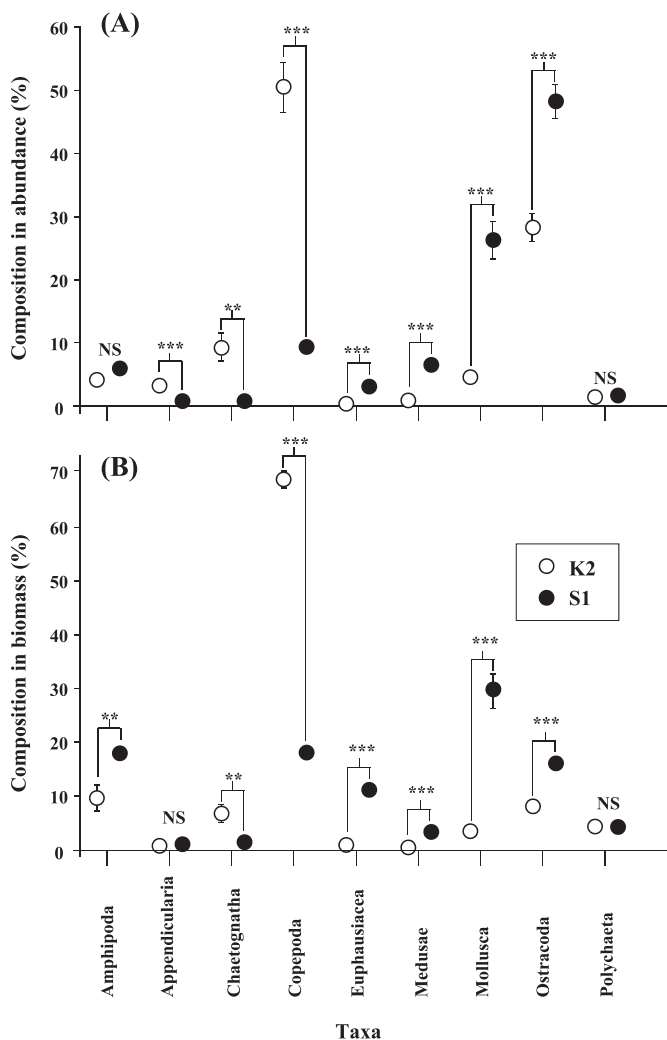
Fig. 6. Inter-regional comparison of taxonomic composition regarding zooplankton swimmer abundance (A) and biomass (B) collected at 200 m depths for the subarctic K2 (○) and the subtropical S1 (•) in the western North Pacific. The symbols and bars indicate annual means and standard deviations for each station. The inter-regional differences were tested using the *U*-test. **: $p < 0.01$, ***: $p < 0.001$, NS: not significant.

Table 3

Comparisons of the flux of particulate organic carbon (POC), the zooplankton swimmer biomass (ZSB) and the total carbon (total C) at 200 m depths of the subarctic K2 and the subtropical S1 in the western North Pacific. The POC fluxes were quantified by the two trap types—moored sediment traps (MSTs) and drifting sediment traps (DSTs)—while the ZSB was quantified using only MSTs. Note that the total C flux using DSTs was calculated using ZSB data from the MSTs. Values are the means ± sd. All POC flux data were cited by Honda et al. (2016).

| Station | Type of sediment trap | Flux (mg C m^{-2} day^{-1}) | | | |
		(A) POC	(B) ZSB	Total C (A + B)	Composition of the ZSB to the total C flux (%)
K2	MST	15.0	258.3 ± 44.1	273.3	94.5
	DST	45.2		303.5	85.1
S1	MST	12.5	37.8 ± 5.9	50.3	75.1
	DST	42.1		79.9	47.3

Third, the taxonomic composition varied by region; Copepoda and Chaetognatha dominated at K2, while Ostracoda and Mollusca dominated at S1 (Fig. 6). We discuss each of these three major differences below.

The regional differences in the ZSA and the ZSB can likely be

explained by the regional differences in the pelagic zooplankton community. Zooplankton biomasses at 0–200 m and 0–1000 m depths are higher at the subarctic K2 throughout the year by a factor of 8.5–14.0 times more than at S1 (Kitamura et al., 2016). The regional differences in the zooplankton biomass between the subarctic and subtropical regions correspond well to the ZS differences observed in this study. For the regional differences in hydrography, sea surface temperature was higher and chlorophyll *a* (Chl. *a*) was lower for the subtropical region than for the subarctic region (Longhurst, 2006; Honda et al., 2016; Kitamura et al., 2016). For the zooplankton biomass, the composition of herbivores varied by region: 80% for the subarctic region and as low as 30% for the subtropical region (Taniguchi, 1973). Latitudinal differences for the zooplankton community would be caused by the occurrence of large-bodied Copepoda in the subarctic region (Yamaguchi et al., 2004; Steinberg et al., 2008).

Regarding seasonal changes, the regional differences in the timing of the phytoplankton bloom should be considered. The phytoplankton bloom period varies between K2 and S1: June for K2 and March for S1 (Fujiki et al., 2014; Siswanto et al., 2015). The factors controlling the initiation of the phytoplankton bloom vary by region; iron supplied through atmospheric dust is important in the subarctic region, while nutrients supplied to the surface layer from vertical water mixing are more important for the subtropical region (Longhurst, 2006; Fujiki et al., 2014, 2016). Compared with the timing of those phytoplankton blooms, both the ZSA and the ZSB at K2 and S1 peaked 1–2 months after the phytoplankton blooms at each region (July–August at K2, April–May at S1) (Figs. 2 and 4). Thus, the seasonal timing of the primary production may affect the temporal patterns of the ZSA and the ZSB for both regions.

Regarding the taxonomic composition, the occurrence of large-sized Copepoda, which undergo seasonal vertical migration from the surface to the deep layers, is highly important. Copepoda dominates the ZSB in the subarctic region throughout the year (68% in annual mean, Fig. 2B), in particular, large-sized Copepoda, including *Eucalanus bungii, Neocalanus cristatus, N. flemingeri* and *N. plumchrus* (77% ZSA and 84% ZSB of the total Copepoda observed, Table 4). These species have long generation lengths (more than a year), spend diapause at deep layers, and perform seasonal ontogenetic vertical migrations (Miller et al., 1984; Kobari et al., 2003). The seasonal timings of their downward migrations from surface to deep layers correspond with the peak timings of the ZSA and the ZSB (July–August) in the subarctic K2. In winter, these Copepoda undergo diapause in the deep layers; therefore, their composition in the ZSA and the ZSB may be low (Fig. 2).

In the subtropical region, these large-sized Copepoda do not occur (Taniguchi, 1973; Yamaguchi et al., 2004; Steinberg et al., 2008). Because of the regional differences in zooplankton fauna, the percentage composition of Copepoda in the ZSA and the ZSB are relatively low in the subtropical region; alternatively, the percentage compositions of Ostracoda and Mollusca are high (Fig. 4). In the subtropical region, Chl. *a* is low and is mainly composed of pico-sized phytoplankton, such as the *Prochlorococcus* and *Synechococcus* spp. (Longhurst, 2006). Most of the picophytoplankton are consumed by small protozooplankton, such as flagellates, and they are fed by ciliates; thus, most of the energy flow may enter the microbial loop in the subtropical region (Longhurst, 2006; Fujiki et al., 2016). Most of the Mollusca in this study were shelled Gastropoda (N. Yokoi, unpublished data). The feeding mechanism of shelled Gastropoda is to collect food particles using a mucoid net (Glimer and Harbison, 1986). Because the body size of Ostracoda is relatively small, they can feed effectively on small particles. These feeding mechanisms of Mollusca and Ostracoda may allow them to dominate the ZS community at the subtropical S1 (Fig. 4).

4.2. Comparison between the POC flux and ZS

Concerning the POC flux, the MSTs collected less than the DSTs for both locations (Table 3). From the measurements of ^{230}Th, ^{231}Pa and

Table 4
List of calanoid copepods for zooplankton swimmers at 200 m at the St. K2 in the western subarctic Pacific from 25 July 2013 to 8 May 2014. Values are the mean ± SD for the annual mean zooplankton swimmer abundance (ZSA, ind. m^{-2} day^{-1}) and biomass (ZSB, mg C m^{-2} day^{-1}). Parentheses indicate percentage composition. •: large-sized suspension-feeding copepods that undergo seasonal ontogenetic vertical migration.

Species	ZSA	ZSB
Eucalanus bungii •	99.5 ± 29.5 (51.5)	105.8 ± 32.1 (53.5)
Neocalanus cristatus •	18.9 ± 4.3 (9.8)	43.0 ± 10.6 (21.7)
Paraeuchaeta elongata	25.1 ± 3.0 (13.0)	22.9 ± 3.0 (11.6)
Neocalanus plumchrus •	29.5 ± 10.3 (15.2)	16.0 ± 6.3 (8.1)
Gaetanus simplex	4.4 ± 0.7 (2.3)	2.1 ± 0.3 (1.1)
Racovitzanus sp.	6.6 ± 1.2 (3.4)	1.8 ± 0.3 (0.9)
Metridia pacifica	4.7 ± 0.6 (2.5)	1.7 ± 0.2 (0.8)
Neocalanus flemingeri •	0.6 ± 0.3 (0.3)	1.3 ± 0.7 (0.6)
Candacia bipinnata	1.0 ± 0.1 (0.5)	1.0 ± 0.2 (0.5)
Gaetanus variabilis	1.4 ± 0.5 (0.7)	0.8 ± 0.4 (0.4)
Pleuromamma scutullata	1.0 ± 0.3 (0.5)	0.5 ± 0.1 (0.3)
Heterorhabdus tanneri	0.5 ± 0.2 (0.2)	0.3 ± 0.1 (0.2)
Other Copepoda	0.4 ± 0.1 (0.2)	0.5 ± 0.1 (0.2)

the Th/Pa ratio, the trapping efficiency of the MSTs in shallower waters (< 1200 m depth) is low (Yu et al., 2001). At shallower depths (150–200 m) in the Southern Ocean, the DSTs collected a higher POC flux than the MSTs by a factor of 6.6–20 times (Sweeney et al., 2000; Buesseler et al., 2010). Flow fields in cylindrical and conical sediment traps vary greatly, and the effects of tilt toward and away from the flow also varied with the shape of the sediment trap (Gardner, 1985, 2000). Differences in the POC flux between DSTs and MSTs were also reported for the Sts. K2 and S1. Thus, the DSTs collected three to four times more mean POC flux than the MSTs (Honda et al., 2016). Based on ^{210}Pb flux measurements, Honda and Kawakami (2014) reported that the trapping efficiency of MSTs at 500 m was only approximately 20% at K2. Thus, the POC flux at 200 m is likely an underestimate of the true flux, and the flux collected using DSTs is considered closer to the true POC flux than that collected by the MSTs (Honda et al., 2016).

If we apply POC flux data using DSTs, the composition of the ZSB to the total C flux (= POC flux + ZSB) was 85.1% at K2 and 47.3% at S1 (Table 3). Thus, ZS constituted a large proportion of the total C flux for both locations. From oceans worldwide, the mean contribution of the ZSB to the total C flux for shallow traps (< 200 m) is reported to be 30–90%, while for deeper traps (450–1000 m depth), it ranges from 24% to 47% (Buesseler et al., 2007). In the subtropical Bermuda Atlantic Time-series Study (BATS), the ZSB composed 49% of the total C flux (Owens et al., 2013). This value is close to our subtropical S1 value (47.3%). Screening and wet-picking are two methods for removing ZS from sediment trap samples. For the subtropical BATS, the ZSB contribution to the total C flux was small at less than 350 µm, and differences were not detected between screening by 350 µm mesh and wet-picking on whole samples (Owens et al., 2013). In this study, since we applied 1 mm mesh to separate the POC flux (< 1 mm) and ZS (> 1 mm), small ZS (under < 1 mm) may cause an underestimation of the ZSB, especially for the subtropical S1. For the subarctic K2, the high composition of large-sized Copepoda in the ZSB (Fig. 2B, Table 4) suggests that ZSB underestimation would be minor.

Acknowledgements

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