



# Vertical changes in zooplankton abundance, biomass, and community structure at seven stations down to 3000 m in neighboring waters of Japan during the summer: Insights from ZooScan imaging analysis

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## ABSTRACT

The imaging device ZooScan is used to examine net-collected zooplankton samples. ZooScan has been applied to regional and seasonal changes in the zooplankton community, but it has rarely been used to characterize vertical changes, especially down to the deep sea. In this study, we report a ZooScan analysis of vertically stratified zooplankton samples collected by collected by Vertical Multiple Plankton Sampler down to 3000 m at seven stations near Japan in the Okhotsk Sea, Japan Sea, East China Sea, and subarctic, transitional, and subtropical North Pacific. Throughout the region, both abundance and biomass, as indicated by aggregate zooplankton volume decreased with increasing depths. ANCOVA analysis revealed that factors linked to vertical changes varied with location. Depth and region were the primary determinants of abundance and biomass, respectively. Cluster analysis based on abundance delineated 8 distinct zooplankton community groups. The occurrence of each group varied regionally and 3–5 groups were vertically stratified at each station. Across all stations, Normalized Biomass Size Spectra (NBSS) and size diversity showed pronounced change around 150–500 m depths. At shallower depths, the NBSS slope was steep, the intercept was high, and size diversity was low while, at deeper depths the opposite was true for each of those parameters. Generalized additive models showed that depth, temperature, and salinity had a significant effect on NBSS and size diversity. This study indicates that the ZooScan imaging approach may be useful in the analysis of deep-sea zooplankton communities.

## 1. Introduction

In aquatic ecosystems, zooplankton play a key role in mediating the transfer of energy as organic materials from primary producers to higher trophic levels (cf. Lalli and Parsons, 1997; Miller and Wheeler, 2012). In addition, zooplankton egests fecal pellets and performs diel vertical migration, which promote vertical material fluxes in a process termed the “Biological pump” (Ducklow et al., 2001; Steinberg et al., 2008a). Diet composition and feeding modes vary greatly across zooplankton taxa (cf. Lalli and Parsons, 1997; Miller and Wheeler, 2012). In turn, zooplankton size shape the community of vertebrate predators that target particular taxa (Nunn et al., 2012). Finally, zooplankton sizes also affect the fecal pellet sizes, which are directly related to the sinking rates of the fecal pellets (Stamieszkin et al., 2015). Thus, zooplankton size and

taxa are the two most important factors in determining their quantitative functional roles in marine ecosystems.

ZooScan is a device that allows simultaneous determination of size and taxonomic affinity of zooplankton (Gorsky et al., 2010; Irisson et al., 2022). ZooScan measurements can be used to obtain indices of zooplankton size spectra, and conduct analyses based on Normalized Biomass Size Spectra (NBSS) (Schultes and Lopes, 2009; Kwong and Pakhomov, 2021). Both the slope and intercept of NBSS are known to vary in response to bottom-up or top-down controls. Where high primary productivity induces a high abundance of the small-sized zooplankton (i.e., bottom-up conditions), the intercept and slope of NBSS are high and steep, respectively. On the other hand, under high predation pressure conditions on small zooplankton (i.e., top-down conditions), the intercept and slope of NBSS change to low and flat,

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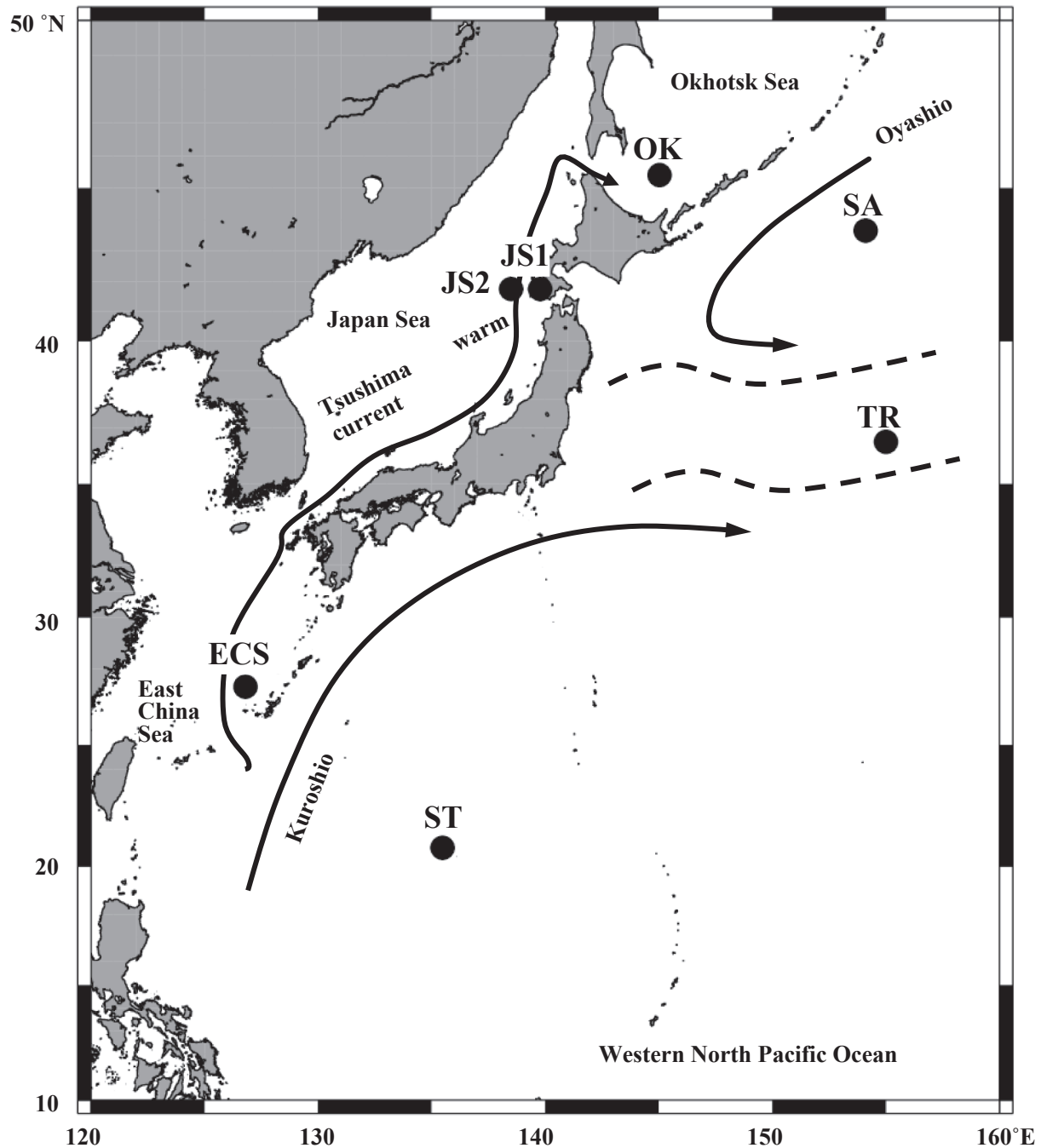
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respectively (Moore and Suthers, 2006; Suthers et al., 2006; Zhou, 2006; Zhou et al., 2009). The application of ZooScan data in NBSS studies has been limited to investigations on seasonal changes (Vandromme et al., 2012) and spatial changes in epipelagic depths (Naito et al., 2019; Kwong and Pakhomov, 2021). To date, few studies have used ZooScan to examine vertical changes in zooplankton size and community composition.

Japan's neighboring waters include subarctic, transitional, and subtropical regions of the western North Pacific and three marginal seas: Okhotsk Sea, Japan Sea, and East China Sea, all of them having different oceanographic characteristics. Studies on zooplankton size composition in the neighboring waters of Japan have focused on latitudinal differences (Yokoi et al., 2008; Shiota et al., 2013; Mishima et al., 2019),

inter-oceanic comparisons including marginal seas (Sato et al., 2015), and localized seasonal changes (Yamaguchi et al., 2014; Hikichi et al., 2018). These studies were based on measurements collected by Optical Plankton Counter (OPC; Herman, 1988), which does not produce taxonomic information. It also should be noted that they focused mainly on epipelagic depths. No attempt was made to characterize vertical changes in zooplankton size composition, especially down to the greater depths.

Studies of vertical changes in zooplankton community down to great depths in the neighboring waters of Japan have focused on latitudinal changes in zooplankton biomass in the subarctic, transitional, and subtropical regions of western North Pacific (Yamaguchi et al., 2002b, 2004, 2005), species-specific distributions of copepods (Yamaguchi et al., 2002a), and on chaetognath abundance and community



**Fig. 1.** Location of the seven sampling stations neighboring waters of Japan. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific. Approximate flow directions of the major currents are shown with the arrows in the panel.



mesh size (63 μm) used for field sampling We used smaller mesh size in field collections to avoid the effects of collection efficiency of smaller specimens due to the abundance of seston or detritus as reported in Makabe et al. (2012).

We performed regression analysis with abundance (*Abu*: ind. m<sup>-3</sup>) or biovolume (*Bio*: mm<sup>3</sup> m<sup>-3</sup>) as dependent variables and depth (*D*: m) as the independent variable to assess vertical changes in abundance and biovolume,. For regressions, we used log-log transformed values for each variable and perform the analyses using the relevant functions as implemented in MS-Excel:

$$\log_{10} Abu = a \times \log_{10} D + b$$

$$\log_{10} Bio = a \times \log_{10} D + b$$

where *a* is the slope and *b* is the intercept of the regression. We conducted an analysis of covariance (ANCOVA) by applying target variables such as abundance and biovolume and explanation variables such as depth and location to assess the relationship between these factors and the zooplankton assemblages.

We performed cluster analyses of zooplankton community for all 69 samples using Bray-Curtis similarities and mean-connecting methods based on values transformed to the fourth root of the abundance estimates (*Abu*: ind. m<sup>-3</sup>). Inter-group differences in zooplankton abundance were analyzed by one-way ANOVA and post hoc test (Tukey-

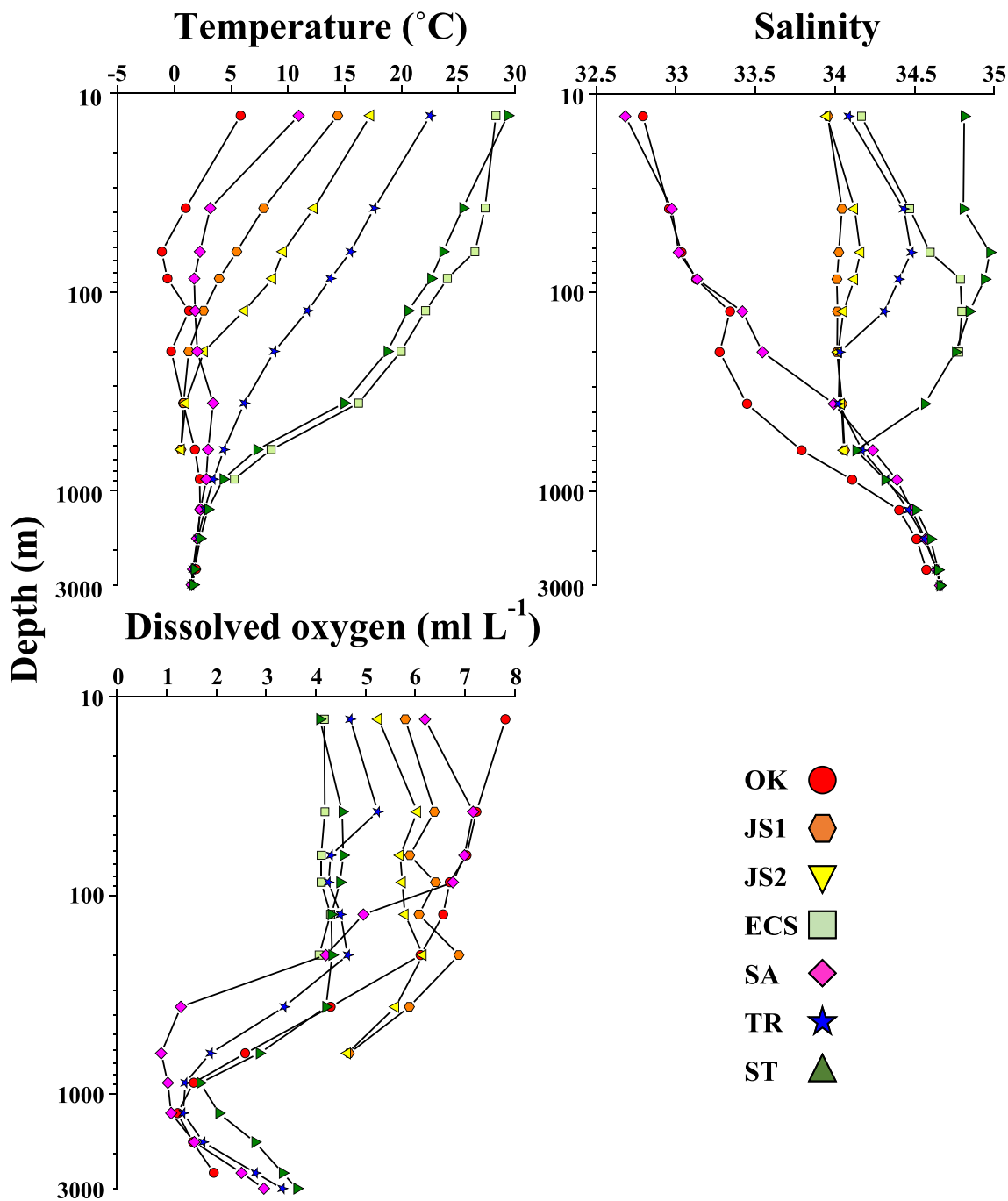


Fig. 2. Vertical changes in temperature, salinity and dissolved oxygen at the seven stations neighboring waters of Japan. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific. Symbols denote mean values for the sampling depths of VMPS at each station.



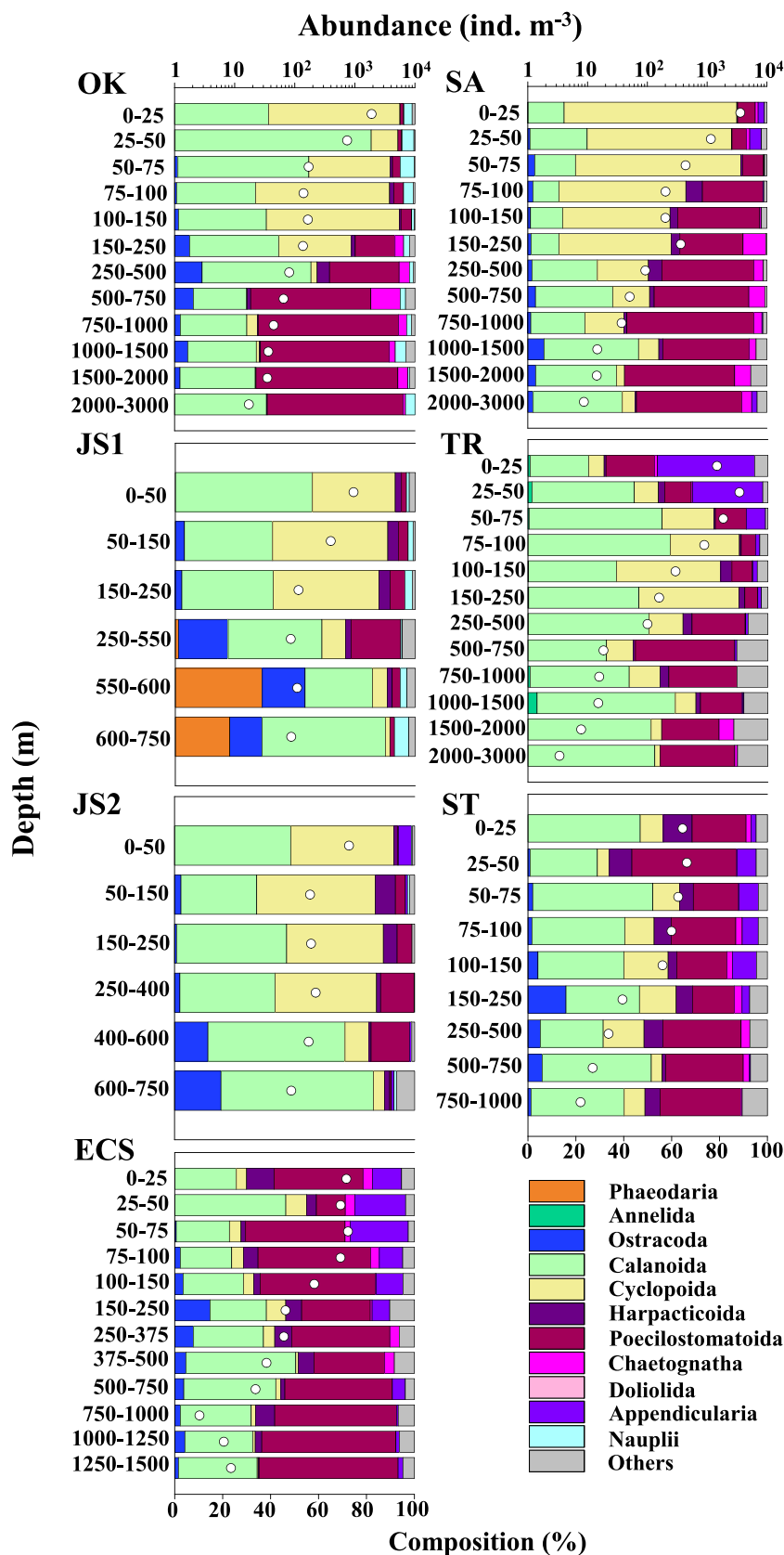


Fig. 4. Vertical changes in zooplankton abundance and their taxonomic composition at the seven stations neighboring waters of Japan. Note that abundance scales are in log-scales. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific.

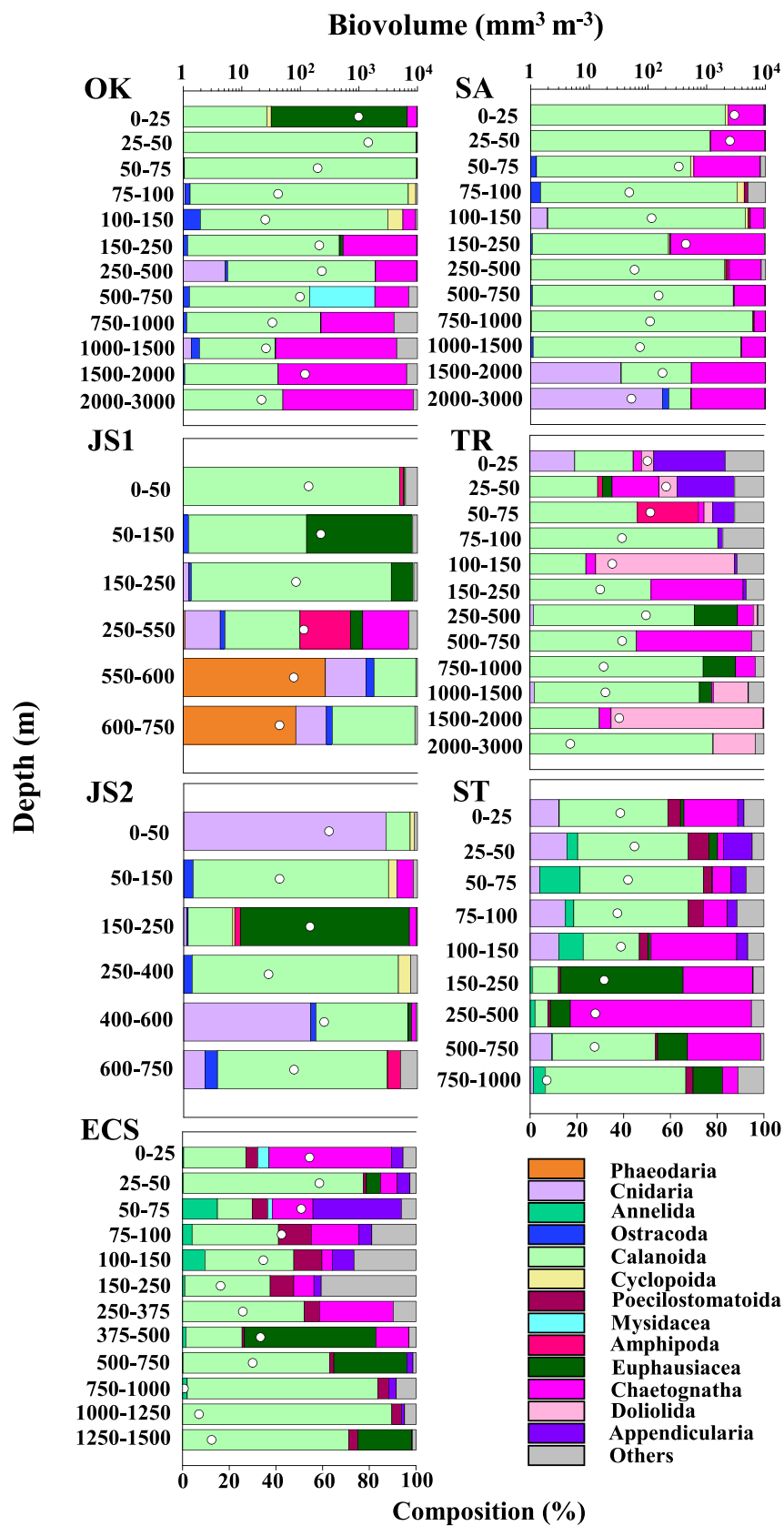


Fig. 5. Vertical changes in zooplankton biovolume and their taxonomic composition at the seven stations neighboring waters of Japan. Note that biovolume scales are in log-scales. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific.





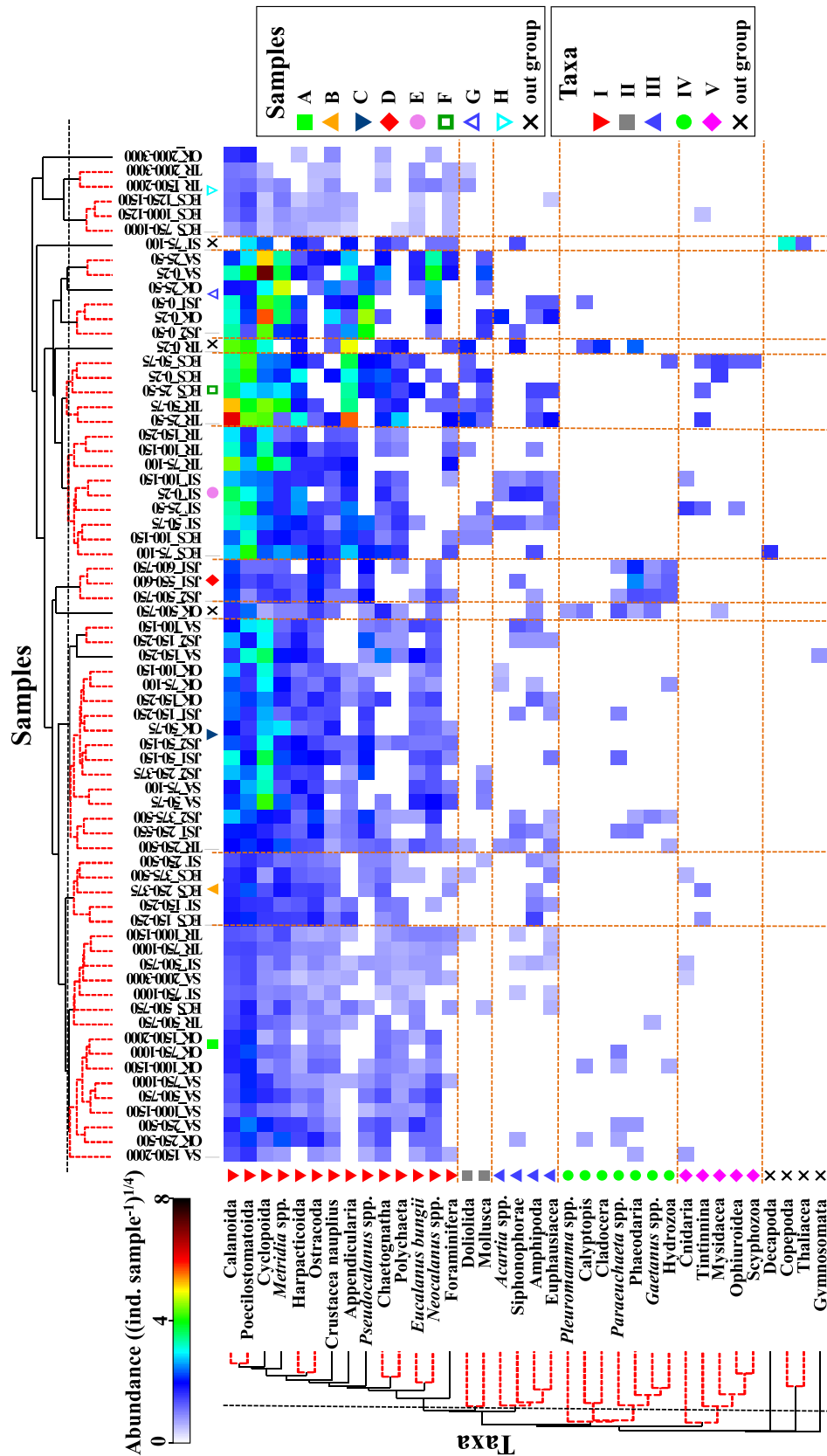
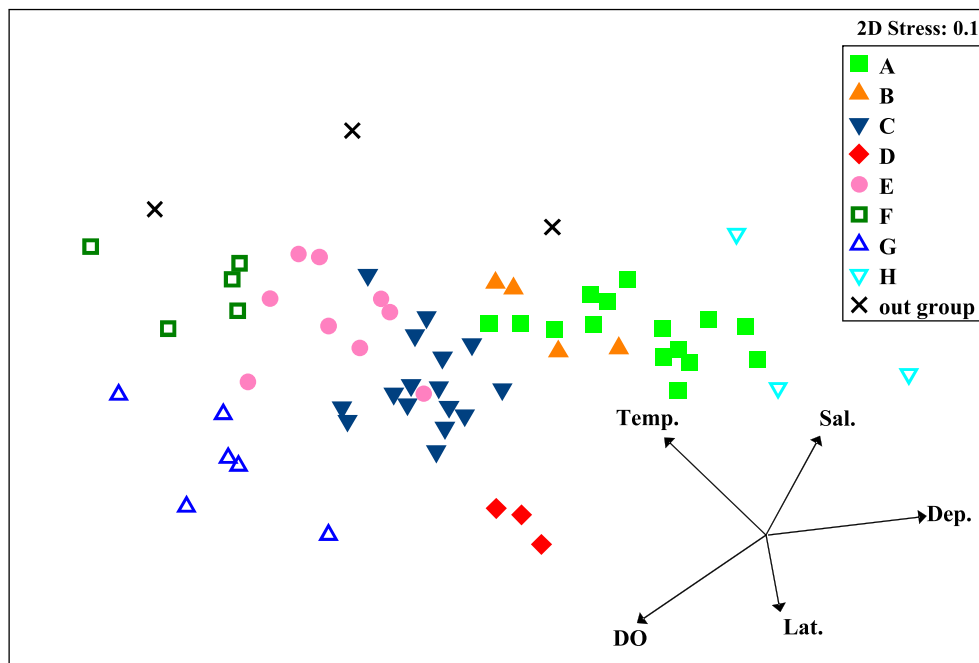


Fig. 7. Result of cluster analysis based on the mesozooplankton abundance of each sample collected from 0 to 3000 m strata of the seven stations neighboring waters of Japan. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific. For samples, numbers after underbar represent depth layers (m).



**Fig. 8.** Two-dimensional map by non-metric multidimensional scaling method (NMDS) of zooplankton communities specified by the depth-station complex data. Eight groups (group A-H) that clustered according to the Bray-Curtis similarity index (Fig. 7) are shown by the different symbols. Arrows indicate directions of significant environmental parameters. Lat.: latitude, Dep.: depth, Temp.: temperature, Sal.: salinity, DO: dissolved oxygen.

group F, Appendicularia was abundant, and dominance of calanoid copepod *Pseudocalanus* spp. was observed for zooplankton group G.

Occurrences (geographical and vertical distribution) of each zooplankton community are shown in Fig. 9. Each group occurred at consecutive regions and depths. Broadly, occurrences of each zooplankton group can be categorized into the subarctic stations (St. OK, JS1, JS2, SA) and transitional and subtropical stations (ECS, TR, ST). For the subarctic station, group G was seen at the shallower 0–50 m depths, then group C was seen at 50–500 m, and group A dominated below that layer (>500 m) (Fig. 9). Group D was only seen for the deep layer (>500 m) of the Japan Sea, and it should be noted that these depths correspond with the occurrence of “Japan Sea Proper Water” (Fig. 2). For stations in transitional and subtropical areas, group E and F were seen at the shallower 0–300 m depths, and group B was seen for 200–500 m depths, while groups A and H were present in the deepest layer (>500 m) (Fig. 9).

### 3.4. Zooplankton NBSS and size diversity

Results of NBSS based on zooplankton biovolume at each sampling layer of the seven sampling stations are shown in Fig. 10. Common for the whole region and depths, biovolume changes along with the sizes were generally smooth, and significant NBSS was obtained for all the samples. The vertical changes in slopes and intercepts of NBSS and size diversity of each sample are shown in Fig. 11. Slopes of NBSS were zero or positive for the surface layer (0–50 m) of the subarctic stations (St. OK and SA). It also should be noted that the prominent decrease of the slope, the intercept of NBSS, and size diversity were observed for subsequent 100–150 m depths. As the common patterns observed for the whole region, the three parameters: slope and intercept of NBSS, and size diversity showed great changes around 150–500 m depths. Thus, above 150–500 m depths, the slopes of NBSS were steep, intercepts of NBSS were high, and size diversity was low, while the moderate slope of NBSS and low intercept of NBSS, and high size diversity were the cases of below 150–500 m depths (Fig. 11). Such vertical changes in slope and intercept of NBSS, and size diversity were prominent, especially at St. TR, ST, and ECS. On the other hand, the slope of NBSS was moderate,

even in the surface layer of St. SA.

Scatter plots of the three parameters: slope and intercept of NBSS, and size diversity are shown in Fig. 12. Across stations, it is noted that the slopes of NBSS at 200–1000 m and 1000–3000 m depths are moderate and circumscribed to a subarea in the scatter plot. While plot area of the NBSS slope at 0–200 m depth was broad and varied with the station. Steep slopes of NBSS were seen at subtropical stations, while moderate slopes of NBSS were the case at subarctic stations.

Results of GAM analysis applying target variables as slope and intercept of NBSS, and size diversity and explanation variables as environmental parameters: depth, temperature, and salinity are shown in Fig. 13. The slope of NBSS had a significant relationship with temperature, with warm conditions linked to steep slopes and cold conditions associated with moderate slope. The intercept of NBSS had significant interactions with depth and salinity. The intercept of NBSS was high at shallower depths and low at the deeper depths. The intercept of NBSS was high in low salinity conditions and low in high salinity conditions. Size diversity had significant interaction with depth being low at shallower depths and increasing with depth. This relationship between depth and size diversity was highly significant ( $p < 0.001$ ).

Results of inter-group differences in slope and intercept of NBSS and size diversity tested by one-way ANOVA and post hoc test (Tukey-Kramer) are shown in Table 5. For the slope of NBSS, the groups E and F observed at the epipelagic zones of the subtropical stations (Fig. 9) were evaluated to have steep slopes. As groups having a high intercept of NBSS, groups F and G were prominent. These two groups were seen at surface 0–75 m of the subtropical (group F) or subarctic (group G) regions. As groups having high size diversity, groups A and D were present. These two groups were the deep-sea communities observed below 500 m depths. Thus, the three indices of zooplankton size: slope and intercept of NBSS, and size diversity varied greatly in the zooplankton communities examined.

**Table 4**

Mean abundance (ind. m<sup>-3</sup>) of each zooplankton taxon at eight clustered groups (A-H) identified by Bray-Curtis similarity analysis (cf. Fig. 7). The numbers in the parentheses indicate the number of samples included in each group. Differences between groups were tested by one-way ANOVA and post hoc Tukey-Kramer test. For the results of the Tukey-Kramer test, any groups not connected by the underlines are significantly different ( $p < 0.05$ ). -: no occurrence, \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ , NS: not significant. For abundance, the upper three most dominant taxa/species are shown by the bold and underlines.

Taxa/Species	Abundance (ind.m <sup>-3</sup> )								one-way ANOVA	Tukey-Kramer test
	A (16)	B (5)	C (16)	D (3)	E (9)	F (5)	G (6)	H (6)		
Phaeodaria	0.040	-	0.090	<b><u>20.630</u></b>	-	-	-	-	***	A C D
Foraminifera	0.110	0.130	0.480	0.210	2.310	4.310	3.470	0.120	*	Not detected
Tintinnina	-	0.310	-	-	0.250	1.950	-	0.010	***	H E B F
Cnidaria	0.030	0.020	-	-	0.730	-	-	-	NS	
Hydrozoa	0.010	-	0.060	2.090	-	0.500	-	-	***	A C F D
Scyphozoa	-	-	-	-	-	0.500	-	-	NS	
Siphonophorae	0.030	-	0.440	0.490	1.150	-	0.370	-	NS	
Amelida	0.320	0.460	0.240	0.150	2.930	16.820	-	0.000	***	H D C A B E F
Gymnosomata	-	-	0.030	-	-	-	-	-	NS	
Ostracoda	1.350	4.870	7.090	<b><u>15.900</u></b>	5.450	2.140	2.760	0.100	***	H A F G B E C D
Calanoida	<b><u>4.330</u></b>	<b><u>7.750</u></b>	<b><u>33.430</u></b>	<b><u>22.840</u></b>	<b><u>122.740</u></b>	<b><u>519.060</u></b>	76.340	<b><u>2.080</u></b>	***	H A B D C G E F
<i>Acartia</i> spp.	-	-	0.050	-	0.450	-	3.260	-	NS	
<i>Eucalanus bungii</i>	0.940	0.020	2.970	0.100	0.060	4.420	3.020	0.230	NS	
<i>Gaetanus</i> spp.	0.010	-	0.060	1.340	-	-	-	-	***	A C D
<i>Metridia</i> spp.	<b><u>3.640</u></b>	<b><u>5.550</u></b>	14.820	4.160	26.180	77.040	<b><u>200.350</u></b>	<b><u>0.460</u></b>	***	H A D B C E F G
<i>Neocalanus</i> spp.	1.310	0.040	3.440	2.450	-	0.920	74.020	0.190	***	B H F A D C G
<i>Paraeuchaeta</i> spp.	0.120	-	0.240	0.260	-	-	-	-	NS	
<i>Pseudocalanus</i> spp.	0.360	0.400	8.240	12.100	6.210	9.840	<b><u>157.350</u></b>	-	***	A B E C F D G
Cyclopoida	2.950	3.750	<b><u>91.840</u></b>	4.110	<b><u>67.140</u></b>	168.840	<b><u>844.580</u></b>	0.090	***	H A B D E C F G
Harpacticoida	0.840	3.200	6.480	1.370	19.780	44.820	9.650	0.080	***	H A D B C G E F
Poecilostomatoida	<b><u>13.180</u></b>	<b><u>14.230</u></b>	<b><u>27.060</u></b>	1.980	<b><u>93.320</u></b>	<b><u>253.090</u></b>	65.140	<b><u>3.770</u></b>	***	D H A B C G E F
Mysidacea	-	-	-	-	-	2.050	-	-	***	
Amphipoda	0.010	1.360	0.310	0.100	1.480	1.930	0.690	-	*	Not detected
Euphausiacea	0.030	0.290	0.250	-	0.450	3.570	2.320	0.010	*	H A C B E G F
Calyptopis	0.040	-	-	-	-	-	0.230	-	NS	
Chaetognatha	1.200	1.300	2.880	-	4.510	18.890	10.500	0.070	***	D H A B C E G F
Doliolida	0.000	0.020	0.010	-	0.230	5.500	-	0.090	**	A C B H E F
Appendicularia	0.120	1.280	0.640	0.310	21.280	<b><u>304.220</u></b>	35.650	0.050	***	H A D C B E G F
Ophiuroidea	-	-	-	-	0.080	0.500	-	-	NS	
Mollusca	0.010	0.030	0.130	-	0.310	3.130	7.060	-	***	A B E E F G
Decapoda	-	-	-	-	0.790	-	-	-	NS	
Crustacean nauplius	0.480	1.120	2.200	2.990	4.160	5.510	21.870	0.330	***	H A B C D E F G
Total	31.46	46.13	203.47	93.59	382.01	1449.56	1518.63	7.68	***	H A B D C E F G

## 4. Discussion

### 4.1. Abundance and biovolume

In abundance terms, three orders of Copepoda (Calanoida, Cyclopoida, and Poecilostomatoida) contributed significantly to community composition. Within them, Calanoida contains various feeding modes: particulate feeders, detritivores, and carnivores, and they have important roles as mediators of energy transfer to higher trophic levels and in vertical material flux (Mauchline, 1998). For the small-sized copepod, Cyclopoida was dominated at 0–250 m of the subarctic stations (Fig. 4). Cyclopoida feeds mainly on microzooplankton such as ciliates and are considered to have an important role in the transfer of the microbial production to the higher trophic levels (Nishibe et al., 2010). The other small-sized copepod Poecilostomatoida is considered to be a detritivore that feeds on detritus and is attached to the marine snow (Turner, 2004). Poecilostomatoida was abundant below 250 m of the subarctic stations and the whole water column of the subtropical stations. The dominance of Poecilostomatoida at the deep layer of the subarctic Pacific is well

documented (Yamaguchi et al., 2002a; Nishibe and Ikeda, 2004). In the subtropical Pacific, attachment of Poecilostomatoida to discarded appendicularian structures is reported (Nishibe et al., 2015).

In terms of biovolume, in addition to Calanoida, sporadic high contributions from Euphausiacea (Fig. 5) were observed. The dominant species of Euphausiacea in the western North Pacific, and their marginal seas are reported to be *Euphausia pacifica* and *Thysanoessa* spp. both of which are reported to perform diel vertical migration (DVM) (Iguchi et al., 1993; Taki, 2006, 2011). Stations where Euphausiacea was observed above 250 m depths corresponded night collections (Table 1). For the other prominent taxa contributing to overall biovolume: Phaeodaria, is important in deeper layers of the Japan Sea reportedly due to the prevalence of *Aulographis japonica* in the cold Japan Sea Proper Water (Nakamura et al., 2013).

To assess the depth decrease of zooplankton abundance and biomass, various regressions such as an exponential model ( $\log Y = a \text{Depth} + b$ ), power model ( $\log Y = a \log \text{Depth} + b$ ), and regression with an intercept at 100 m ( $Y = Y_{100} (\text{Depth}/100)^b$ ) have been reported (Yamaguchi et al., 2002a, 2002b, 2004, 2005). Here, we report power regression to both

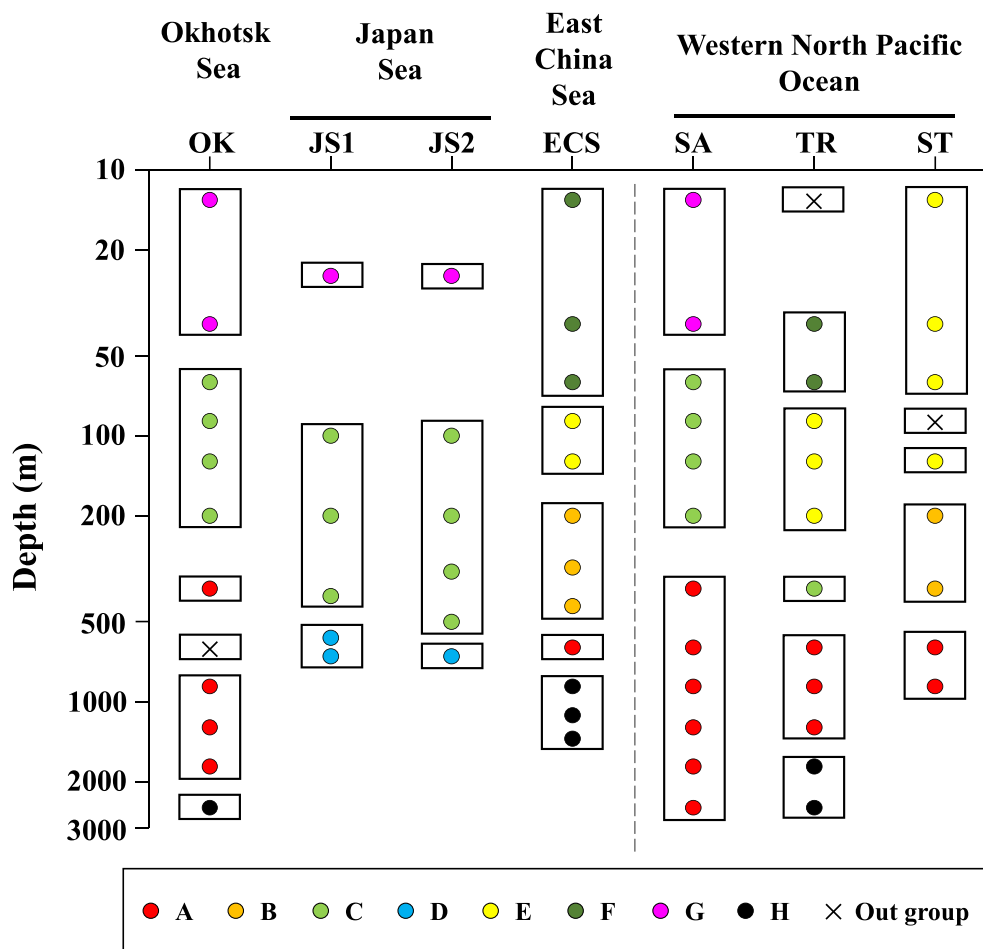


Fig. 9. Spatial and vertical distribution of zooplankton community groups identified by Bray-Curtis similarity index (cf. Fig. 7). Sampling depth at each station is shown by the symbols. Note that depth scale is in log-scale. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific.

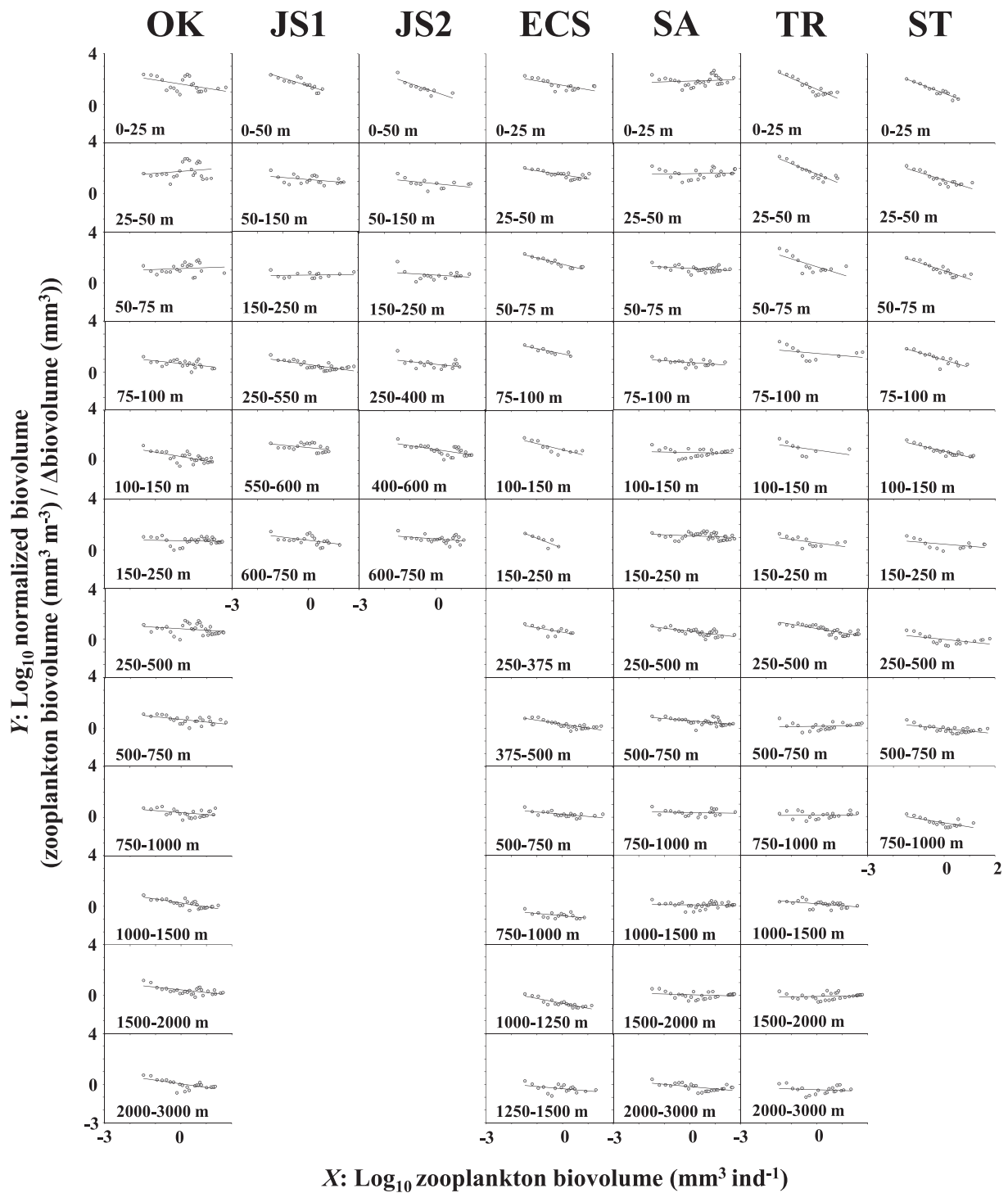
abundance and biovolume. Yamaguchi et al. (2002a) also employed power regressions to examine depth-decreasing rates of Copepoda in the western subarctic Pacific and reported that the slope (a) of the regression is steep (range  $-1.41$ – $-1.52$ ) for abundance and moderate for biomass (range  $-1.10$ – $-1.32$ ). A steeper regression slope for abundance than that of biomass (as biovolume) was also observed in this study (Table 2).

Biovolume decrease at the cold intermediate water at St. OK and SA was strong. The cold intermediate water is brine water that originated during ice-forming last winter and is characterized by extreme cold ( $<0$  °C) and the development of a strong pycnocline (Takizawa, 1982). At the intermediate cold water, the DVM of zooplankton is prevented, and the decrease of zooplankton biovolume at that layer has been well documented (Yamaguchi, 2015). These factors may have induced the abrupt decrease of biovolume at intermediate cold water observed for St. OK and SA (Figs. 5, 6b).

Taxonomic differences in rates of biomass decrease with depth were and the decreasing rates with more rapid rates for higher trophic level organisms than for those from lower trophic levels (Yamaguchi et al., 2002b, 2004). In this study, the depth-related decreasing rate and intercept of abundance were similar throughout all stations. This result in abundance contrasts the general patterns of zooplankton biomass: depth-decreasing rates are similar but intercepts vary (Vinogradov, 1968; Table 3 of this study). These differences would be due to the differences in the units of analysis (abundance or biomass [biovolume]). As a comparable study, Yamaguchi et al. (2015) conducted depth-decreasing rates of Copepoda of 0–2615 m depths based on the

vertically stratified samples collected at 16 stations covering tropical to subarctic regions ( $0$  to  $56$ N in latitude) of the North Pacific. In that expansive dataset, the abundance of Copepoda decreases with increasing depth throughout the stations, but differences in regressions were not observed (Yamaguchi et al., 2015). Thus, while comparable information concerning biomass is scarce, the depth-related decreasing rate and intercept of zooplankton abundance seem to be similar throughout the whole North Pacific and also the marginal seas.

For biovolume, regional (station-to-station) differences were prominent, while depth related changes were minor (Table 3). Rates of biomass decrease with depth are similar throughout the regions, while regional differences in intercept at the surface layer are found throughout the depths (Vinogradov, 1968; Yamaguchi et al., 2005). These patterns likely reflect the fact that the origin of energy for zooplankton starting from primary productivity centers at the sea surface. Thus, regions with high productivity and high biomass at the surface layer contain high values of both even in the deep layer, while the regions with low productivity and biomass at the surface layer have low values of both in the deep layer. Studies quantifying biogeochemical amounts and fluxes in the subarctic and subtropical Pacific indicate most of the parameters vary regionally approximately two-fold; however, mesozooplankton biomass is reported to be 10 times larger for the subarctic than that in the subtropical region (Steinberg et al., 2008b; Kitamura et al., 2016; Honda et al., 2017). Thus, the results on zooplankton biovolume in this study (regional differences were prominent and high in the subarctic region) correspond well with results of regional comparisons between the subarctic and subtropical Pacific.



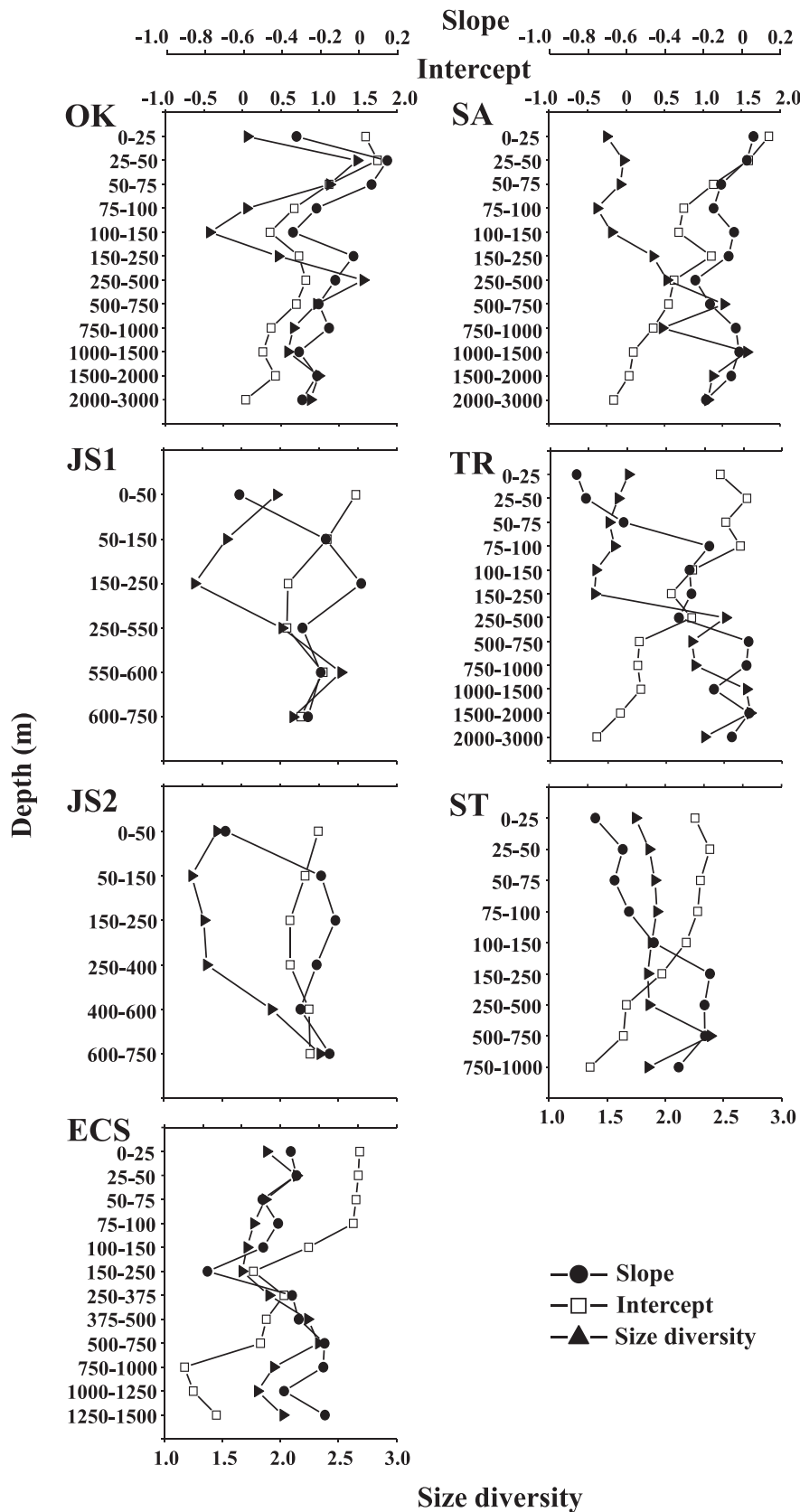
**Fig. 10.** Vertical changes in normalized biovolume size spectra (NBSS) at various depth strata of the seven sampling stations neighboring waters of Japan. Note that NBSS regressions are highly significant ( $r^2 = 0.15-0.9$ ,  $p < 0.05$ ) for all sampling depths. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific.

4.2. Zooplankton community

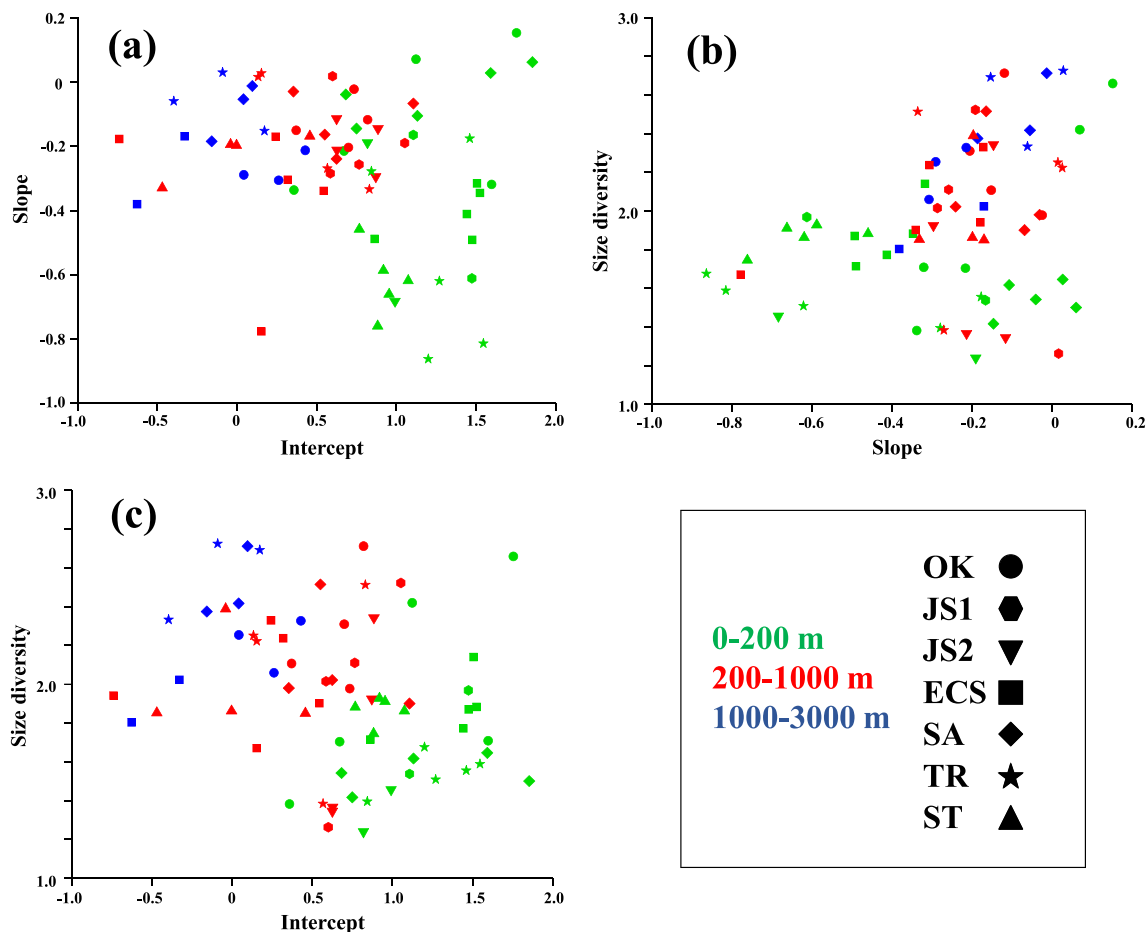
This study examines zooplankton from the sea surface down to 3000 m at seven stations covering the subarctic and subtropical Pacific and their three marginal seas. Because of the study targeting broader region and depth, zooplankton community was classified into eight groups (Fig. 7). Various environmental parameters are linked with the differentiation of zooplankton groups, (Fig. 8). Among zooplankton groups observed in high DO regions, group F was seen for the warm sea surface

of the subtropical region, and group G was seen for the cold surface layer of the subarctic region (Fig. 9). The same directions of depth and salinity in NMDS panel are interpreted that the salinity was high for deeper depths of most of the stations (Fig. 2). The zooplankton groups A and H which observed for high depth values in NMDS panel were restricted to deep layers (Fig. 9). Thus, plotted areas of each zooplankton group and directions of environmental parameters in NMDS are well corresponded with the regional and vertical distributions of each zooplankton group.

Beyond the dominant Copepoda (Calanoida, Cyclopoida, and



**Fig. 11.** Vertical changes in slope and intercept of the normalized biovolume size spectra (NBSS) and size diversity at various depth strata of the seven sampling stations neighboring waters of Japan. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific.



**Fig. 12.** Scatter plots between slope and intercept of NBSS (a), size diversity and slope of NBSS (b), and size diversity and intercept of NBSS (c) at seven stations neighboring waters of Japan. OK: Okhotsk Sea, JS1: Japan Sea station 1, JS2: Japan Sea station 2, ECS: East China Sea, SA: subarctic Pacific, TR: transitional Pacific, ST: subtropical Pacific. Differences in colors represent sampling depths (0–200, 200–1000, and 1000–3000 m).

Poecilostomatoida), *Metridia* spp., the large-sized calanoid copepod genus, were notably abundant for the zooplankton groups A, B, G, and H (Table 4). Within these groups, group G was seen for the surface layers of the subarctic Pacific, Japan Sea, and Okhotsk Sea (Fig. 9). *Metridia* is known to perform DVM (Padmavati et al., 2004) and *M. okhotensis* is the most common species in the Okhotsk Sea (Yamaguchi, 2015; Arima et al., 2016), *M. pacifica* in the Japan Sea (Hirakawa and Imamura, 1993), and *M. okhotensis* and *M. pacifica* in the subarctic Pacific (Padmavati et al., 2004; Takahashi et al., 2009). The boreal large-bodied copepod species are known to be transported to the deeper layers of the transitional and subtropical regions through the submergible cold-water Oyashio (Omori and Tanaka, 1967; Kobari et al., 2008). The dominance of the deep-sea *Metridia* species (*M. venusta*) in deep layers at lower latitudes (<30N) has been reported (Yamaguchi et al., 2015). Thus, in the transitional and subtropical regions, the groups dominated by *Metridia* spp. (groups A, B, H) were seen only for the deeper layers.

For the other zooplankton groups, with particular dominant zooplankton taxa/species, Phaeodaria and Ostracoda primarily comprised group D (Table 4), which was seen in the deeper layers of the Japan Sea representing cold Japan Sea Proper Water (Fig. 9). In the Japan Sea Proper Water *A. japonica* has been well documented and their biomass is reported to be second to that of copepods at these layers (Nakamura et al., 2013). For the Japan Sea Proper Water, the dominance of the ostracod *Conchoecia pseudodiscophora* has also been reported (Ikeda, 1990; Ikeda and Imamura, 1992). The distinct zooplankton community in the cold Japan Sea Proper Water is confirmed by our findings.

For the other zooplankton groups dominated by the specific

zooplankton taxa, group F, dominated by Appendicularia, was seen at the surface layers of the ECS and TR (Table 4, Fig. 9). Appendicularia filter feeds on pico- and nano-sized particle, reproduces asexually, and is known to show outbreaks at the surface layer of the transitional region (Yokoi et al., 2008). Appendicularia creates a “house” structure for filter feeding, which it sheds frequently, and Poecilostomatoida is known to attach to the discarded “houses” of Appendicularia and use them as feeding and living places (Nishibe et al., 2015). For zooplankton group F, Appendicularia and Poecilostomatoida are the dominant groups (Table 4). This suggests that Appendicularia dominated zooplankton communities at surface layers of ECS and TR where it feeds on small-sized particles, then Poecilostomatoida would attach on the discarded appendicularian houses.

Here we examined geographical and vertical distribution of zooplankton communities from the sea surface to the deep sea, including subarctic to subtropics of the western North Pacific (Fig. 9). In this region, vertical distribution of planktonic communities has been reported for the pelagic copepods (Yamaguchi et al., 2015) and chaetognaths (Ozawa et al., 2007). Copepod communities were segregated into surface and deep sea vertically and into subarctic and subtropics horizontally (Yamaguchi et al., 2015), a pattern corroborated in this study. Chaetognath deep-sea communities have been reported to be the same from the Bering Sea to the subtropics, while those in the Japan Sea have been reported to be markedly distinct from other regions (Ozawa et al., 2007). These substantial differences in the zooplankton community of the deep sea of the Japan Sea characterized by the Japan Sea Proper Water were confirmed in this study (Fig. 9). The basin area of the Japan Sea is deep (maximum at 3700 m and mean 1350 m), while depths of its

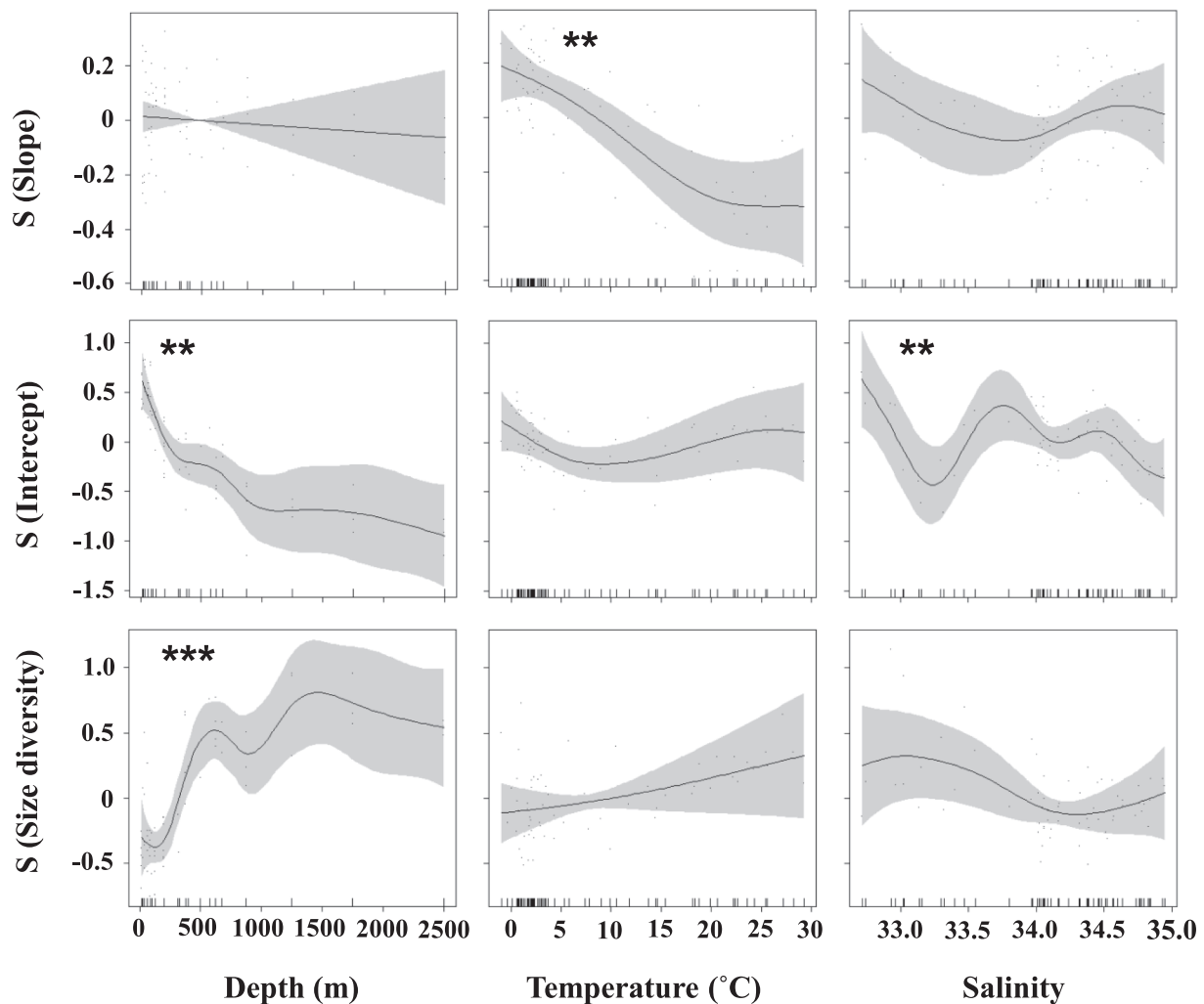


Fig. 13. Result of GAMs based on anomalies of the slope and intercept of NBSS and size diversity with environmental parameters (depth, temperature and salinity). \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

Table 5

Inter-group differences in zooplankton size related variables (slopes and intercepts of NBSS and size diversities) evaluated for zooplankton samples collected from 0 to 3000 m depths of the seven sampling stations at neighboring waters of Japan. For details of the location of the stations and distribution of each zooplankton community clustered by the zooplankton abundance data, see Figs. 1 and 9, respectively. For detailed data of NBSS and size diversity see Figs. 10 and 11, respectively.

Parameters	Zooplankton community group								one-way	
	A (16)	B (5)	C (16)	D (3)	E (9)	F (5)	G (6)	H (6)	ANOVA	Tukey-Kramer test
NBSS Slope	-0.143	-0.358	-0.153	-0.198	-0.458	-0.518	-0.229	-0.175	***	F E B G D H C A
NBSS Intercept	0.224	0.295	0.789	0.901	0.984	1.465	1.544	-0.356	***	H A B C D E F G
Size diversity	2.310	1.904	1.698	2.325	1.692	1.798	1.823	2.180	***	E C F G B H A D

connections other outer oceans are shallow (<130 m), which leads to a disconnection of the waters in the deep layer with the neighboring North Pacific, East China Sea, and Okhotsk Sea, and forming the Japan Sea Proper Water, and thus the presence of a specialized deep-sea fauna (Zenkevitch, 1963; Vinogradov, 1968).

#### 4.3. NBSS and size diversity of zooplankton

We measured slopes and intercepts of NBSS and size diversity of all the sampled examined in this study. The slopes of NBSS are expected to have a negative value (e.g. low biomass at the large-sized higher trophic organisms) and a value of  $-1$  expected in stable marine ecosystems

(Moore and Suthers, 2006; Suthers et al., 2006; Zhou, 2006; Zhou et al., 2009). In this study, NBSS slopes had positive values for certain stations and depth combinations: 25–75 m of OK and 0–75 m of SA (Fig. 10). This was the result of higher biomass of the large-sized zooplankton in those samples. These stations/depths clustered in groups C and G in the zooplankton community mentioned before (Fig. 9). The groups C and G are characterized by the dominance of the large-body-sized copepod *Neocalanus* spp. (Table 4) suggesting that the positive slopes of NBSS of these stations/depths may be due to the smaller size ranges of the sampled zooplankton, as pointed out for the zooplankton community in the eastern North Pacific by Kwong and Pakhomov (2021). Since we have abundance and biovolume data of each taxon, added to slopes and



intercepts of NBSS, we can discuss the causes of the unexpected NBSS values in detail.

The slopes of NBSS observed in this study were between  $-0.143$  and  $-0.51$  for the mean values of each zooplankton community (Table 5). An NBSS analyses by OPC was conducted on zooplankton samples collected from 0 to 150 m using 335  $\mu\text{m}$  mesh NORPAC net on the same cruise on which this study is based (Sato et al., 2015). In that study, the NBSS slope were reported as  $-0.90$  for the areas dominated by large-sized copepod *Neocalanus* spp. and as  $-1.11$ – $-1.24$  for other regions such as subtropical Pacific (Sato et al., 2015). On the other hand, the samples of this study were collected by the vertically stratified samplings of VMPS down to 3000 m equipped with a smaller mesh of 63  $\mu\text{m}$ , then measured by ZooScan. Thus, greater differences were available between the two studies (Sato et al., 2015 and this study) in terms of the target depth (0–150 m vs. 0–3000 m), applied mesh size (335  $\mu\text{m}$  vs. 63  $\mu\text{m}$ ), and measurement devices (OPC vs ZooScan).

The differences in mesh sizes of the plankton net would provide differences in net clogging or filtering efficiencies. However, the filtering efficiencies measured by the flowmeter reading were high ( $>85\%$ ) for both mesh sizes (Electronic Supplement 1). Thus, the differences in net filtering efficiency are not considered to cause the differences in NBSS slopes between the two studies (Sato et al., 2015 and this study). Since this study applied smaller mesh sizes (63  $\mu\text{m}$ ), it may allow us to collect smaller-sized zooplankters and broader target size ranges for NBSS analysis and then produce steeper slopes of NBSS than those quantified by the large mesh size (335  $\mu\text{m}$ ) samples. But the results were the opposite: NBSS slopes of this study were more moderate than those by Sato et al. (2015). Thus, the differences in net mesh size are not considered to be a cause of the differences in NBSS slopes. These facts suggest that the different instruments (OPC vs. ZooScan) led to differences in NBSS.

OPC quantifies all the particles contained in a sample, while ZooScan can differentiate zooplankton based imagery. Thus, ZooScan can distinguish zooplankton from non-living particles such as fecal pellet, fragment, and detritus, and not include those non-living particles in subsequent analyses as was the case in the present study (Vandromme et al., 2012). NBSS derived from OPC includes all the particles, living and non-living. Because the non-living particles (fecal pellet, fragment, detritus) may be altered by fragmentation, coprophagy, and coprorhexy by zooplankton and bacterial decomposition, their sizes are generally smaller than the zooplankton (Turner, 2002, 2015). Thus, when measuring the same zooplankton samples, data from OPC contains small-sized non-living particles, and their intercept and slope of NBSS would be higher and steeper, respectively, than those from ZooScan which calculated only on zooplankton data.

Several studies have compared ZooScan with other instruments, including ZooScan with LOPC (Schultes and Lopes, 2009) and ZooScan with OPC (Naito et al., 2019). Since LOPC and OPC include small-sized non-living particles, their NBSS slope tended to be steep, while for ZooScan, the biovolumes of the large-sized gelatinous zooplankton (e.g. jellyfishes, doliolids, and salps) have been reported to be overestimated, thus their NBSS slope tends to be more moderate (Schultes and Lopes, 2009; Gorsky et al., 2010; Vandromme et al., 2012; Naito et al., 2019; Kwong and Pakhomov, 2021). Regardless of instrumental biases, when measuring the samples with a common methodology it should be possible to detect and test for community structure changes with geographical, horizontal, or spatial factors (Schultes and Lopes, 2009, 2012; Naito et al., 2019). Thus, in this study, we will make a comparison of the values of the NBSS slope or intercept obtained from this study only. For the other studies, we will make comparisons on the geographical patterns and not include NBSS values for the inter-study comparison.

For the latitudinal changes of NBSS slope of zooplankton in the subarctic-subtropical North Pacific, there are several studies based on OPC analyses, and the NBSS slope has been reported to moderate for the subarctic region where dominated by the large-sized *Neocalanus*

copepods (Fukuda et al., 2012; Shiota et al., 2013; Sato et al., 2015; Mishima et al., 2019). Within the region, seasonal changes in NBSS slope have also been reported, and moderate NBSS slopes in summer when development for the late copepodite stages have been observed for the large-sized *Neocalanus* copepods (Yamaguchi et al., 2014; Hikichi et al., 2018). Zooplankton biomass in the subarctic Pacific is predominated by the large-sized *Neocalanus* copepods (Ikeda et al., 2008). These facts suggest that moderate NBSS slopes are available for the region or season where and when dominated by the large-sized *Neocalanus* copepods.

Significant relationships were observed between NBSS slope and temperature, with moderate slopes under low temperature, and steep slopes under high temperature (Fig. 13). The moderate NBSS slope of cold condition is due to the dominance of the large-sized copepods *Neocalanus* spp. especially in the epipelagic zones of the subarctic Pacific (Ikeda et al., 2008). Even for the subtropical region, the temperature of the deep-sea is low, and the deep-sea copepods inhabiting under such condition contain lipids in their body, have long longevity, and large-body sizes (Mauchline, 1998). Thus, under low-temperature conditions, NBSS may tend to have moderate slopes. On the other hand, under warm conditions, acceleration and high metabolism of zooplankton would occur, and large-sized copepods with diapause phases in their life history are absent (Mauchline, 1998). The steepest slopes of NBSS of this study were seen from the groups E and F which were observed for the epipelagic zones of the subtropical region (Table 5). These facts suggest that high temperatures under these conditions may prevent the occurrence of large-sized zooplankton there.

Depth and salinity had significant negative relationship with the NBSS intercept (Fig. 13). Intercept of NBSS is reported to reflect primary productivity at the given region and depth (Moore and Suthers, 2006; Zhou, 2006; Zhou et al., 2009; Gomez-Canchong et al., 2013). Since primary productivity centers at sea surface, the NBSS intercept would be high at the shallower depth. Since zooplankton biovolume decreased with increasing depth (Fig. 6), the NBSS intercept would be decreased with increasing depth. These depth trends of primary productivity and zooplankton biovolume induce negative relationships of NBSS intercept and depth mentioned above. For the interaction of NBSS intercept and salinity, the NBSS intercept was high (=high biovolume) under low salinity conditions, while the NBSS intercept was low (=low biovolume) under high salinity conditions (Fig. 13). In this study, low salinity conditions were seen for two stations in the subarctic Pacific and Okhotsk Sea (Fig. 3). The zooplankton biovolume of the epipelagic zones of these stations was high, especially at the near surface (Fig. 6b). These high zooplankton biovolumes there would produce high NBSS intercept under low salinity conditions. Salinity increased with increasing depths throughout the stations (Fig. 3). The decreasing NBSS intercept with increasing salinity would be analogous to the NBSS intercept decrease with increasing depths, as described above.

Depth had a strong significant effect on size diversity, and the size diversity was low at the shallower depths and increased with increasing depths (Fig. 13). In terms of the zooplankton community, size diversity was high for groups A and D (Table 5) which were observed in the deep layer of the subarctic region (Fig. 9). These facts suggest that size diversity would be high at depths where zooplankton covering the broader size ranges occur.

In the present study, all parameters on zooplankton size spectra: intercept and slope of NBSS, and size diversity showed large geographical and vertical changes. Especially, vertical change was detected at 150–500 m depths for all parameters, and these shifts were most prominent in the transitional region and subtropical North Pacific, and East China Sea (Fig. 11). For these regions, depths of 150–500 m were serve as the boundaries to separate epipelagic zooplankton community and deep-sea zooplankton community, and below that layer, since zooplankton community was characterized with the that in the cold condition, intercept of NBSS would be lower, high size diversity due to dominance of the large-sized zooplankton (Fig. 13), then the moderate slope of NBSS may present (Fig. 11). While the narrower treated

size ranges should be noted (Kwong and Pakhomov, 2021), NBSS and size diversity of this study clearly showed reflect of geographical and vertical changes in zooplankton community in the subarctic, transitional, and subtropical regions of the western North Pacific, and its three marginal seas: Okhotsk Sea, Japan Sea, and East China Sea.

## 5. Conclusions

Based on the vertically stratified net samples collected down to the deep layer (3000 m), regional and vertical changes in zooplankton abundance, biovolume, community structure, NBSS, and size diversity were evaluated at seven stations covering subarctic, transitional, and subtropical regions of western North Pacific and its marginal seas: Okhotsk Sea, Japan Sea, and East China Sea. Both abundance and biovolume decreased with increasing depths. Their depth-decreasing rates were more rapid for abundance than those in biovolume. The most important environmental determinant of zooplankton abundance was depth, while region was the most prominent for their biovolume. Based on the abundance data, zooplankton communities were clustered into eight groups. Each group was distributed in adjacent regions and depths, and the occurrence of a distinct community dominated by Phaeodaria and Ostracoda was seen for the deep layer of the Japan Sea. NBSS and size diversity showed clear vertical changes around 150–500 m depths. Above that layer, the intercept and slope of NBSS were high and steep, respectively, and linked with low size diversity there. On the other hand, contrasting patterns: low NBSS intercept, moderate NBSS slope, and high size diversity were seen below that layer. This study showed regional and vertical changes in zooplankton abundance, biovolume, community structure, NBSS, size diversity, and its governing environmental parameters clearly.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2023.103155>.

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