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Vertical variations in zooplankton size spectra down to 3,000 m depth and significant effects of the sizes of Calanoida and Ergasilida across the subarctic, transitional, and subtropical regions of the western North Pacific

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ABSTRACT

Zooplankton size spectra are crucial for evaluating marine ecosystem structure, with copepods being the predominant taxa within the marine zooplankton communities. Among copepods, Calanoida and Ergasilida are the two numerically dominant taxa. Despite their importance, limited information exists regarding the effects of these two taxa on the overall zooplankton size spectra. This study aimed to comprehensively evaluate the regional and vertical changes in zooplankton size spectra, normalised biomass size spectrum (NBSS), and size diversity across subarctic, transitional, and subtropical regions of the western North Pacific Ocean. Additionally, the study aimed to investigate the effects of size variations in two dominant copepod taxa, Calanoida and Ergasilida, on the overall zooplankton size spectra. To achieve this, vertically stratified zooplankton samples were collected from 12 layers, ranging from the sea surface to a depth of 3000 m, at five stations across the subtropical to subarctic western North Pacific. The samples were analysed using ZooScan to assess the overall zooplankton size spectra and the effects of Calanoida and Ergasilida on it. Across all stations, the NBSS slopes became moderate, and the size diversity increased with increasing depth, particularly evident for the oxygen minimum layer (OML) at approximately 1000 m depth. These patterns reflect a high proportion of large-sized zooplankton in the deeper layers and a lower predation pressure from micronektonic fish around the OML. Calanoida and Ergasilida accounted for 43.3% and 24.6% of the mean zooplankton abundance, respectively. Among the two taxa, Calanoida exhibited significant changes in body size depending on the station and depth, being larger in the subarctic region and deeper layers. Ergasilida showed minimal changes in body size relative to location and depth. The body size of Calanoida significantly influenced the overall zooplankton size spectra. Therefore, the dominance of large-sized Calanoida induced a moderate NBSS slope and high size diversity in the overall zooplankton size spectra. The results of this study indicate that the size of Calanoida, the dominant taxon in the zooplankton community, primarily governs the size spectra of the overall zooplankton community.

1. Introduction

In marine ecosystems, zooplankton play a vital role in the biological pump, which transports organic materials produced by primary producers from the surface to deeper ocean layers. This transport occurs through two primary mechanisms: the egestion of large-sized faecal pellets, which sink rapidly (passive transport), and diel vertical migration, which connects the epi- and mesopelagic layers (active transport) (Ducklow et al., 2001). Copepods represent the most dominant taxa in marine zooplankton communities, characterised by their substantial abundance and biomass, which are essential to the biological pump (Kobari et al., 2013; Yokoi et al., 2018; Sun et al., 2019). The quantitative role of zooplankton in the material flux of marine ecosystems varies with the size and composition of the zooplankton communities (Ducklow et al., 2001). For example, in the subarctic region, large-sized copepods dominate the zooplankton community (Omori, 1967; Oh et al.,

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Abbreviations: ANCOVA, analysis of covariance; T-S, temperature-salinity; ESD, equivalent spherical diameter; NBSS, normalised biomass size spectra; OML, oxygen minimum layer; OPC, optical plankton counter; VMPS, vertical multiple plankton sampler.

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1991). The higher transport efficiencies to the deeper layers in this region result from the large-sized faecal pellets egested by these large copepods and their seasonal and ontogenetic vertical migrations (OVMs). This contrasts with the subtropical region, which is dominated by small-sized zooplankton (Steinberg et al., 2008b; Kobari et al., 2013; Yokoi et al., 2018). Therefore, zooplankton size spectra are important for evaluating the structure of marine ecosystems (Suthers et al., 2006; Zhou et al., 2009).

The normalised biomass size spectrum (NBSS) serves as a valuable index for assessing zooplankton size composition (Zhou, 2006). The NBSS represents a regression between zooplankton biomass and body size, with the intercept indicating the amount of productivity and the slope denoting the energy transfer efficiency to higher trophic levels (Zhou, 2006; Zhou et al., 2009). A steep NBSS slope implies a dominance of small-sized zooplankton, high productivity, and low transfer efficiency to higher trophic levels. Conversely, a moderate NBSS slope indicates dominance of large-sized zooplankton and high transfer efficiency to higher trophic levels (Zhou, 2006; Heneghan et al., 2016). Another index for assessing zooplankton size spectra is size diversity. High size diversity indicates the presence of zooplankton across broader size ranges (Sun et al., 2021; Yamamae et al., 2023). However, most studies on these zooplankton size spectra indices (i.e., NBSS and size diversity) have primarily focused on surface layer zooplankton communities (Moore and Suthers, 2006; Herman and Harvey, 2006; Chen et al., 2020). Consequently, information regarding zooplankton size spectra extending to the deeper layers remains extremely limited despite their importance in vertical material flux.

In the western North Pacific Ocean, two distinct current systems, the cold Oyashio and warm Kuroshio, occur adjacent to each other. These regions are divided into subarctic, transitional, and subtropical regions, each characterised by varying zooplankton communities and marine ecosystems (Yamaguchi et al., 2002b, 2004). Differences in zooplankton communities lead to variations in the extent of vertical material transport across regions (Mauchline, 1998; Turner, 2015). Within the western North Pacific, studies have been conducted on zooplankton communities and carbon fluxes in the subarctic and subtropical regions (Kobari et al., 2013; Kitamura et al., 2016); latitudinal changes in zooplankton community structure and biomass across the subarctic, transitional, and subtropical regions (Yamaguchi et al., 2002b, 2004, 2005); and latitudinal and vertical changes in the stable isotopes (δ^{13}C and δ^{15}N) of zooplankton communities in the subarctic, transitional, and subtropical regions (Kim et al., 2023). Conversely, research on zooplankton size spectra has focused on the surface waters of neighbouring waters around Japan, including the western North Pacific (Sato et al., 2015), deep layers in the subtropical region (Dai et al., 2017), and deep layers of the marginal seas (Yamamae et al., 2023). However, no studies have been conducted on regional comparisons extending to deeper layers in the western North Pacific.

Two copepod taxa, Calanoida and Ergasilida (Poecilostomatoida), are dominant in the zooplankton communities of the western North Pacific (Yamaguchi et al., 2002a; Steinberg et al., 2008b; Sun et al., 2019). However, the effects of the sizes of these two copepod taxa on the overall zooplankton size spectra have not been evaluated. Vertical changes in physical and chemical environments substantially affect copepod-size structures and their effects on vertical material transport (Stamieszkin et al., 2015). However, studies addressing these aspects in the western North Pacific are currently lacking.

This study aimed to comprehensively evaluate the regional and vertical changes in zooplankton size spectra, normalised biomass size spectrum (NBSS), and size diversity across subarctic, transitional, and subtropical regions of the western North Pacific Ocean. Additionally, the study aimed to investigate the effects of size variations in two dominant copepod taxa, Calanoida and Ergasilida, on the overall zooplankton size spectra.

2. Materials and methods

2.1. Field sampling

Stratified sampling was conducted during a cruise of R/V *Hakuho-Maru*, operated by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), using a vertical multiple plankton sampler (VMPS; Tsurumi Seiki Co. Ltd., Japan; Terazaki and Tomatsu, 1997). The VMPS was equipped with a 63-μm mesh and had a mouth-opening area of 0.25 m^2. Sampling was conducted across twelve layers from the sea surface to a depth of 3000 m (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–500, 500–750, 750–1,000, 1000–1,500, 1500–2,000, and 2000–3000 m) at five stations: one in the subarctic (St. 41N: 40°57′ N, 146°52′ E), one in the transitional (St. 37N: 36°59′ N, 149°39′ E), and three in the subtropical (St. 33N: 32°58′ N, 148°10′ E, St. 31N: 31°00′ N, 147°40′ E, and St. 29N: 29°00′ N, 147°12′ E) regions (Fig. 1) in the western North Pacific from 19 October to November 7, 2017 (Kim et al., 2023). Notably, sampling at one station (St. 29N) occurred during the daytime, whereas sampling at the other four stations (Sts. 41N, 37N, 33N, and 31N) occurred at night. Stratification at 1500 m failed at one station (St. 33N), yielding only 11 layer samples for that station. The collected zooplankton samples were immediately split onboard the vessel using a Motoda splitter (Motoda, 1959). One half of each sample was frozen for analysing carbon-nitrogen stable isotope ratios (Kim et al., 2023), while the other half was preserved in 5% borax-buffered formalin seawater. This study utilised the formalin-preserved samples. Hydrographic data, including water temperature, salinity, and dissolved oxygen (DO), were measured using a conductivity, temperature, and depth (CTD) oceanographic research tool (SBE 911 Plus, Sea-Bird Electronics Inc., WA, USA).

2.2. ZooScan measurement

Imaging data of the formalin-preserved zooplankton samples were obtained using ZooScan (Hydroptic Inc., France) following the protocol established by Gorsky et al. (2010). First, the ZooScan scanning cell was filled with distilled water to perform a background scan. Subsamples (1/2–1/32 of the total) were subsequently poured into the scanning cell of

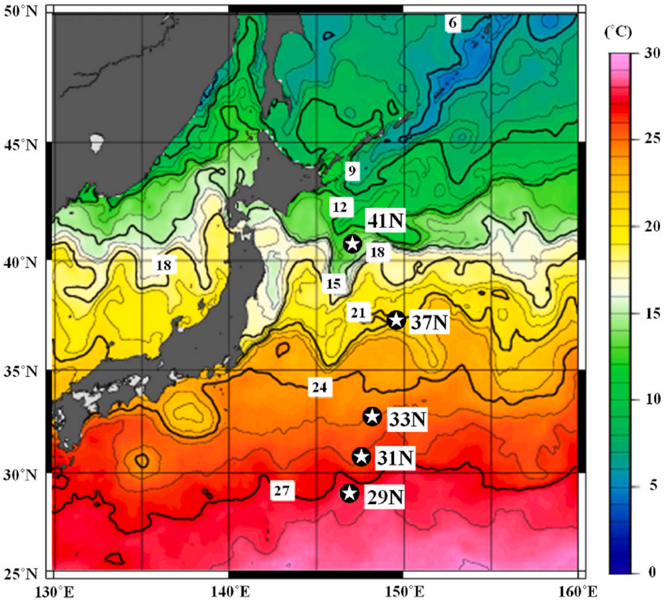

Fig. 1. Locations of the five sampling stations in the western North Pacific from October to November 2017. The mean sea surface temperature data from satellites during the study period are presented as the background (data derived from the Japan Meteorological Agency).

the ZooScan for analysis. The samples were divided using a Motoda splitter according to the sample amount. The obtained images were separated into individual images using ZooProcess in ImageJ software. The images were digitised at a resolution of 2400 dpi, corresponding to 10.6 μm per pixel. Images were uploaded to EcoTaxa (https://ecotaxa.obs-vlfr.fr/) using FileZilla software for the web-based identification of each taxon.

The taxonomic groups identified in this study included the following categories: protozoans (Phaeodaria and Foraminifera), copepods (Calanoida, Ergasilida, Harpacticoida, and Oithonida), and other metazoans (Amphipoda, Appendicularia, Chaetognatha, Decapoda, Doliolida, Echinodermata, Euphausiacea, Hydrozoa, Mollusca, Ostracoda, Polychaeta, nauplii, fish larvae, and detritus). Detritus was excluded from subsequent analyses owing to its non-living status.

The size of each individual was calculated using the area excluded (AE; mm^2) obtained using EcoTaxa, and the equivalent spherical diameter (ESD; mm) was calculated using the following equation:

$$ESD = 2\sqrt[2]{\frac{AE}{\pi}} \tag{1}$$

Using the ESD, the volume ($Volume$; mm^3) was calculated with the following equation:

$$Volume = \frac{4}{3}\pi\left(\frac{ESD}{2}\right)^3 \tag{2}$$

The abundance (A; ind. m^{-3}) was based on the number of particles (n) and volume of filtered water (F; m^3). The biovolume (B; mm^3 m^{-3}) was determined from the $Volume$ (mm^3) and volume of filtered water (m^3) using the following equations:

$$A = \frac{n}{F \times s} \tag{3}$$

$$B = \frac{Volume}{F \times s} \tag{4}$$

where s is the sample split factor (1/2–1/32) for the ZooScan measurement.

2.3. Data analysis

The biovolume (B: mm^3 m^{-3}) integrated at each 0.05-mm interval between 0.2 and 5.0 mm ESD was used to calculate the NBSS for this study. The X-axis of the NBSS represents the biovolume of each size class, expressed in normal logarithm [X: log$_{10}$ zooplankton biovolume (mm^3)]. The Y-axis indicates the biovolume of each size class divided by the difference in biovolume between adjacent size classes [Δbiovolume (mm^3)], also expressed in normal logarithm [Y: log$_{10}$ zooplankton biovolume (mm^3 m^{-3})/Δbiovolume (mm^3)]. Based on these X- and Y-axis values, a linear regression of the NBSS was performed using the solver function in Microsoft Excel to obtain the following linear equation:

$$Y = aX + b \tag{5}$$

where a is the slope of the NBSS and b is the intercept.

Zooplankton size diversity was determined by calculating H' values (Morishita, 1996) using the following equation:

$$H' = -\sum_{i=1}^{S} pi \times \ln(pi) \tag{6}$$

where S is the number of size classes (96 = [5.0–0.2]/0.05) and pi is the relative proportion of size class i in each sample. The NBSS and size diversity were computed for each sample.

To determine the factors affecting the NBSS slope, intercept, and size diversity of each sample, we examined the effects of the ESD values of Calanoida and Ergasilida, which were both numerically dominant taxa of the zooplankton community throughout the samples. The mean and standard deviation of the ESD for these two taxa were calculated, and the effects of station and depth on the changes in the ESD of each taxon were tested using an analysis of covariance (ANCOVA). Because only the ESD of Calanoida showed significant changes with station and depth (refer to Section 3.3), the effects of these changes on the NBSS slope, NBSS intercept, and size diversity of the overall zooplankton community, were tested using correlation analyses aided by scatter plots. Statistical analyses were performed using StatView software (SAS Institute, NC, USA).

3. Results

3.1. Hydrography

The temperature, salinity, and DO vertical profiles and temperature-salinity (T-S) diagrams at the five stations used in this study are presented in Fig. 2. Temperatures ranged from 1.5 to 26.3 °C across all stations (Fig. 2A). Warm waters were observed in the subtropical region (Sts. 33N, 31N, and 29N), cold waters in the subarctic region (St. 41N), and intermediate waters in the transitional region (St. 37N). The regional temperature differences diminished below depths of 2000 m.

Salinity ranged from 32.8 to 35.1 across all stations (Fig. 2B). Station-specific differences in salinity were apparent above 2000 m depths and could be categorised into three types, similar to temperature. In the subarctic region (St. 41N), salinity was low near the surface and increased with increasing depth. In the subtropical region (Sts. 33N, 31N, 29N), salinity formed a subsurface maximum at 68–108 m depth, then decreased with increasing depth, reaching a minimum at 638–717 m depth, and finally increased again with increasing depth below those layers. In the transitional region (St. 37N), the salinity above 300 m showed vertical changes similar to those in the subtropical region but with lower values. In contrast, the salinity below 300 m at the transitional station was consistent with that at the subarctic station (St. 41N).

Across all stations, DO ranged from 0.70 to 6.66 ml L^{-1} (Fig. 2C). A common trend across all stations was high DO levels near the sea surface layer that decreased with increasing depth. Minimum DO values ranged from 0.70 to 0.97 ml L^{-1} across all stations. The depths of the oxygen minimum layers (OMLs) were shallow (620–930 m) for the subarctic (St. 41N) and transitional (St. 37N) stations and deep (1150–1300 m) for the subtropical stations. Below the OML, DO levels increased gradually with increasing depth across all stations.

In the T-S diagram, the plotted areas for each station varied and were classified into three types: subarctic, transitional, and subtropical regions (Fig. 2D). In the subarctic region, vertical density changes were mainly due to salinity variations. In the transitional and subtropical regions, vertical density changes were largely governed by temperature changes.

3.2. NBSS and size diversity of the overall zooplankton community

The NBSS values of overall zooplankton communities at all depth stations are presented in Fig. 3. Significant NBSS values were obtained for all samples ($r^2 = 0.15$–0.90, $p < 0.05$). Vertical changes in the slopes and intercepts of the NBSS, as well as size diversity at each station, are depicted in Fig. 4. Across all stations and depths, the NBSS slopes ranged from −0.745 to −0.128, the intercept ranged from −2.744 to 0.779, and the size diversity ranged from 0.865 to 2.293. The NBSS intercepts were higher at the subarctic station than at the subtropical stations. The NBSS intercept decreased with increasing depth across all stations. In contrast, the vertical changing patterns of the NBSS slope and size diversity varied by station. For the middle latitudes (Sts. 37N, 33N, and 31N), the NBSS slope became moderate, and the size diversity exhibited higher values with increasing depth. For the northern and southern end stations (Sts. 41N and 29N), the most moderate NBSS slope and highest size diversity were observed at 1000 m depth. For other depths, steeper NBSS slopes

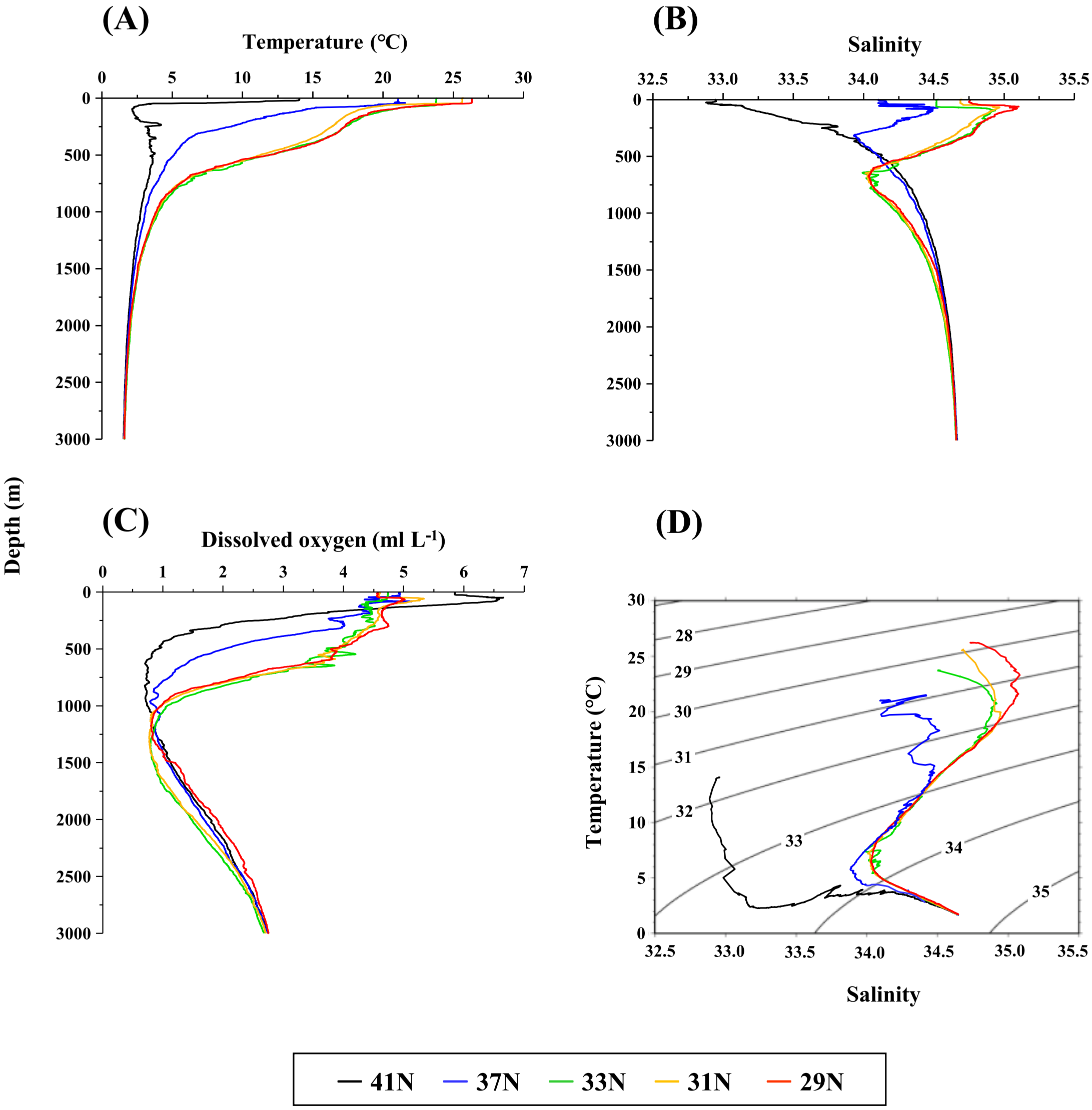

Fig. 2. Vertical changes in (A) temperature, (B) salinity, (C) dissolved oxygen, and (D) T-S diagram at five stations in the western North Pacific from October to November 2017.

and lower size diversity were observed in the shallower layers, with both indices showing irregular vertical changes.

Scatter plots depicting the relationships between the three indices for the overall zooplankton size spectra (e.g., NBSS slope and intercept and size diversity) are shown in Fig. 5. Among the three indices, a significant relationship was found only between size diversity and NBSS slope, characterised by high size diversity under flat NBSS slope conditions ($r^2 = 0.292$, $p < 0.001$).

3.3. *ESD of two dominant copepod taxa (Calanoida and Ergasilida)*

Vertical changes in the taxonomic composition of the overall zooplankton abundance at each station are shown in Fig. 6. The numerically dominant taxa at all stations and depths were Calanoida and Ergasilida. Calanoida comprised 38.1–50.7% of the overall zooplankton abundance (mean ± 1SD: 43.3 ± 10.7%), while Ergasilida accounted for 15.7–33.0% of the overall zooplankton abundance (24.6 ± 9.6%) (Fig. 6).

Vertical changes in the ESDs of Calanoida and Ergasilida at each station are shown in Fig. 7. Across all stations, the mean ESDs of Calanoida and Ergasilida ranged from 291 to 840 μm and 251–401 μm, respectively. In most samples, the ESD of Ergasilida was smaller than that of Calanoida. The ESD of Calanoida varied greatly in terms of station and depth compared to that of Ergasilida. The ESD of Calanoida was larger at depths below 100 m at the subarctic station and at depths of approximately 1000 m at the other stations. Although the ESD of Calanoida increased with increasing depth, peaking at approximately 1000 m, the ESD of Ergasilida remained stable, showing minimal change with station or depth.

The ANCOVA results on the effects of station and depth on the ESDs of Calanoida and Ergasilida are presented in Table 1. These results revealed that the effects of station and depth were significant only for the ESD of Calanoida ($p < 0.01$–0.001). The interactions of station or depth × station were also present for the ESD of Calanoida. However, the ESD of Ergasilida showed only slight effects of depth ($p < 0.05$), with no changes across stations or the interaction of station or depth × station. Therefore, among the two numerically dominant taxa (Calanoida and Ergasilida), the body size of large-sized Calanoida exhibited greater differences with station and depth.

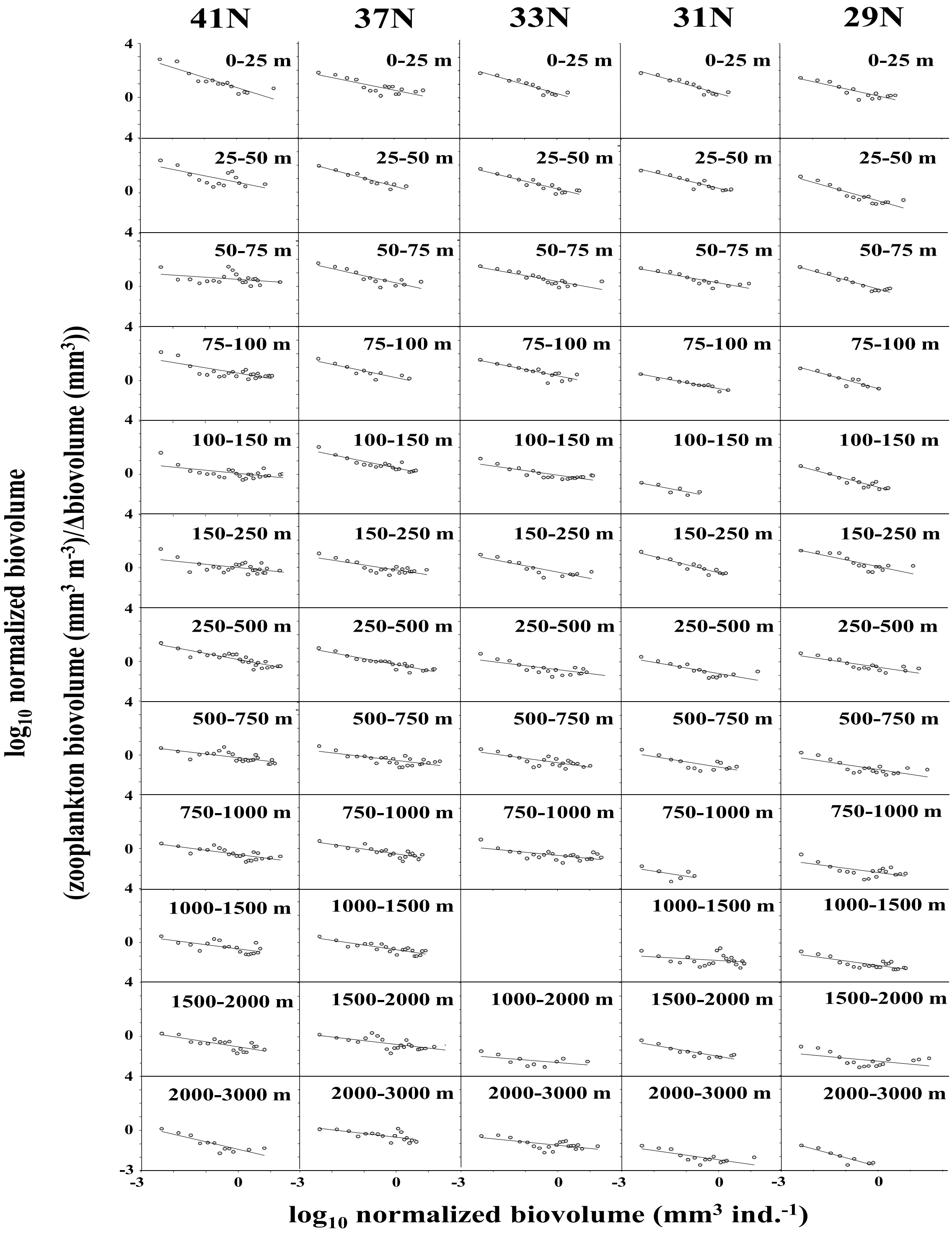

Fig. 3. Normalised biovolume size spectra (NBSS) results at various depth strata of the five stations in the western North Pacific from October to November 2017. Note that NBSS regressions were significant (r^2 = 0.15–0.90, p < 0.05) for all sampling depths.

3.4. Effect of calanoid body size on the overall zooplankton size spectra

To evaluate the effect of calanoid ESD on the overall zooplankton size spectra, scatter plots with calanoid ESD as the *X*-axis and NBSS slope, intercept, and size diversity as the *Y*-axes are shown in Fig. 8. While calanoid ESD showed no interaction with the NBSS intercept, it had highly significant relationships with the other two indices: NBSS slope and size diversity (r^2 = 0.467–0.567, p < 0.001). These interactions indicated that the large-sized calanoid ESD induced a flatter NBSS slope and greater size diversity (Fig. 8A–C).

The relationship between the overall zooplankton size spectra and DO is shown in Fig. 9. Significant correlations were observed between DO and all three parameters of the overall zooplankton size spectra. These relationships revealed that zooplankton in the OML exhibited a moderate NBSS slope, a low NBSS intercept, and a high degree of size diversity (Fig. 9).

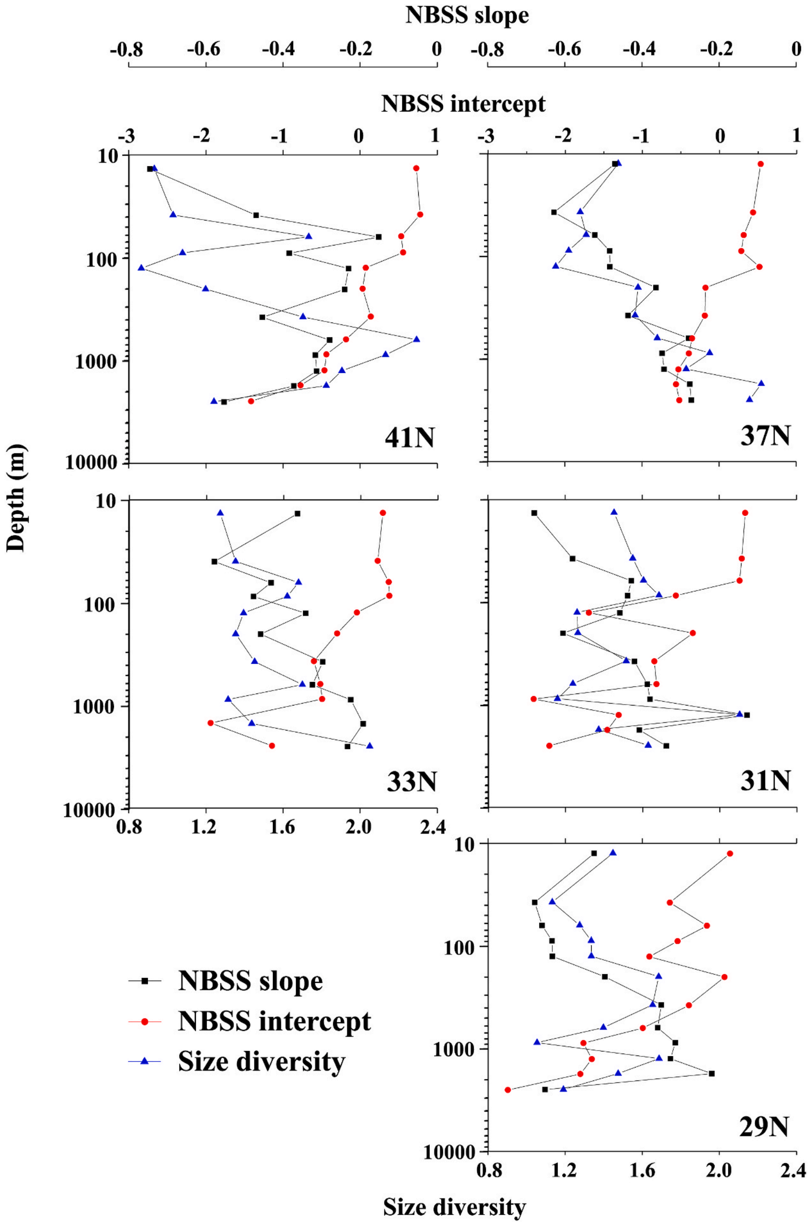

Fig. 4. Vertical changes in slope and intercept of the normalised biovolume size spectra (NBSS) and size diversity across various depth strata at five stations in the western North Pacific from October to November 2017. Note that the depth scales are represented in log-scales.

4. Discussion

4.1. Advantages of this study

In this study, significant NBSS were detected in all samples across all stations and depths, with slopes ranging from −0.745 to −0.128 (Fig. 3). These values are moderate compared to those reported in previous studies targeting nearby geographical locations, such as −1.24 to −1.11 for the neighbouring tropical waters of Japan (Sato et al., 2015), −1.11 to −0.25 in the western North Pacific (Dai et al., 2017), and −1.03 to −0.65 in the northern South China Sea (Chen et al., 2020). Extremely steep NBSS slopes or lack of significant NBSS regression are often attributed to collecting limited amounts of zooplankton or a narrow size range of samples (Moore and Suthers, 2006; Suthers al., 2006; Zhou et al., 2009; Gomez et al., 2013; Kwong and Pakhomov, 2021). The zooplankton community size range used for NBSS calculations in this study was 0.2–5.0 mm ESD, which was wider than previously reported ranges, such as 0.2–0.6 mm (Moore and Suthers, 2006), 0.2–2.0 mm (Herman and Harvey, 2006), and 0.3–4.0 mm (Chen et al., 2020). Given that we used fine mesh nets (63 μm) for sampling, the results of this study can effectively quantify the zooplankton biomass across a wide size range. Notably, this study, along with the aforementioned studies, focuses exclusively on mesozooplankton. The size range used to calculate the slope and intercept data was limited to two orders of magnitude. Previous literature indicates that data covering more than three orders of magnitude are necessary for accurate size spectrum analysis (Zhou, 2006; Heneghan et al., 2016; Kwong and Pakhomov, 2021). Therefore, it is unsurprising that the overall slope in this study was less than −1. We acknowledge this as a limitation of this study.

In previous studies, difficulties in obtaining significant NBSS regression have been reported because of the inability of the optical plankton counter (OPC) to separate detritus from zooplankton (Moore and Suthers, 2006; Zhou et al., 2006; Marcolin al., 2013; Huntley et al., 2006). In addition, the limited size ranges of quantified plankton have hindered accurate zooplankton biomass calculations (Zhou et al., 2004; Yamaguchi et al., 2014). Given these challenges, our study improved on

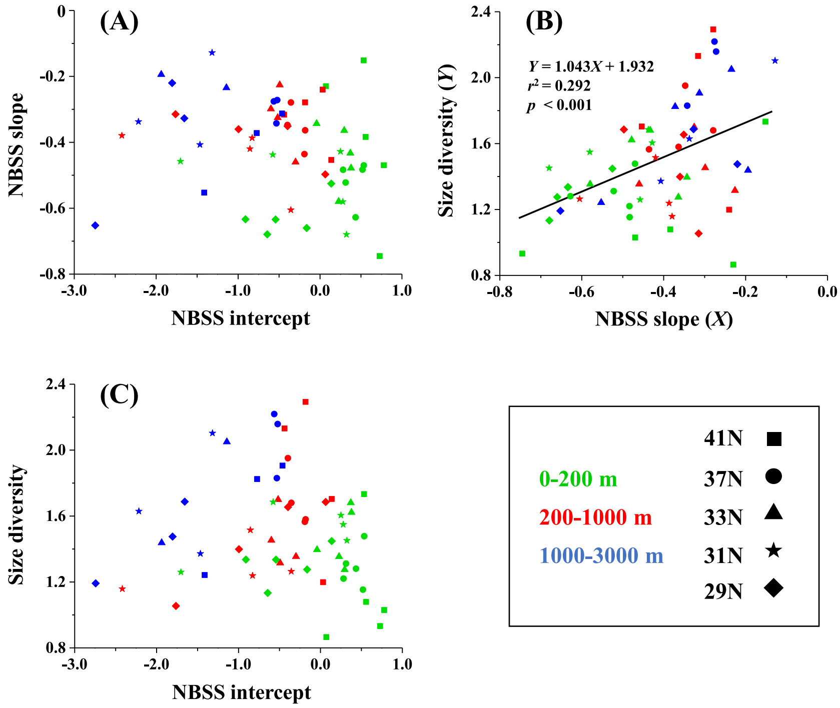

Fig. 5. Scatter plots between (A) slope and NBSS intercept, (B) size diversity and normalised biovolume size spectra (NBSS) slope, and (C) size diversity and NBSS intercept across various depth strata at five stations in the western North Pacific. Differences in colours represent differences in sampling depths (0–200, 200–1000, and 1000–3000 m). The regression was only shown for the significant interaction (B).

previous research by conducting ZooScan measurements on zooplankton samples collected using a fine mesh net (63 μm). This approach allows for more accurate zooplankton identification based on imaging data and covers a broader size range across different stations and depths.

Most previous studies have used major and minor axes to calculate zooplankton volume and applied these measurements to NBSS calculations (Herman and Harvey, 2006; Moore and Suthers, 2006; Dai et al., 2017; Chen et al., 2020). In contrast, we used the *Area excluded* (mm^2) data as the zooplankton volume data in this study. Because the *Area excluded* represents the surface area of each organism excluded from the background pixel, a more accurate volume can be calculated compared to the volumes based on the Feret diameter or major and minor elliptical axes (Gorsky et al., 2010).

Theoretically, the NBSS slope in a general marine ecosystem is −1, whereas a moderate NBSS slope is less than −1. This condition suggests low productivity coupled with high energy transfer efficiency for higher trophic levels (Zhou, 2006; Marcolin et al., 2013). Notably, the size range in this study (spanning two orders of magnitude) is inadequate for accurately determining the appropriate NBSS slope (Zhou, 2006; Heneghan et al., 2016; Kwong and Pakhomov, 2021). However, the observed moderate NBSS slope, ranging from −0.745 to −0.128, indicates a low productivity level and stable ecosystem structure in the oceanic deep layer, extending down to 3000 m. This indicates a consistently high energy transfer efficiency at higher trophic levels (Dai et al., 2017).

As an important aspect of this study, we performed NBSS analyses from the sea surface to a depth of 3000 m at five stations. Most previous studies on zooplankton NBSS have primarily focused on surface layers, with limited studies targeting deep layers (Dai et al., 2017; Yamamae et al., 2023). Moreover, few studies have focused on latitudinal changes (Zhou et al., 2006; Sun et al., 2021; Yamamae et al., 2023). Under these conditions, we collected zooplankton samples from five oceanic stations covering three domains (subarctic, transitional, and subtropical regions), allowing us to evaluate latitudinal or regional comparisons.

4.2. Overall zooplankton size spectra

Based on physical oceanographic parameters, the study area was categorised into three regions: subarctic, transitional, and subtropical (Fig. 2). This classification aligns with that of previous studies conducted in the western North Pacific (Yamaguchi et al., 2002b, 2004, 2017; Kim et al., 2023). Regional differences in environmental conditions result in both quantitative and qualitative changes in primary productivity, which in turn influence zooplankton size spectra (Herman and Harvey, 2006; Marcolin et al., 2013). Expatriated or transported zooplankton from other regions also represent an alternative factor affecting zooplankton size spectra (Marcolin et al., 2015; Sun et al., 2021). The sampling period of this study (October and November) corresponds to the peak of the descent OVM of large-sized subarctic copepods that enter the diapause phase in deeper layers (Ikeda et al., 2008). Therefore, in addition to the aforementioned environmental factors, seasonal effects may shape zooplankton size spectra.

The NBSS intercepts of the three parameters, representing the overall zooplankton size spectra, decreased with increasing depth across all stations (Fig. 4). This trend indicates a decrease in food resources for zooplankton, resulting in decreased zooplankton biomass with increasing depth, as documented in various previous studies (Yamaguchi et al., 2002b, 2004; Turner, 2015; Yamamae et al., 2023). The NBSS intercept values at the subarctic station were higher than those at the subtropical stations, reflecting regional patterns throughout the depths (Fig. 4). In the western North Pacific, the standing stocks of zooplankton in the subarctic region are much higher than those in the subtropical region (Kitamura et al., 2016; Honda et al., 2017). The

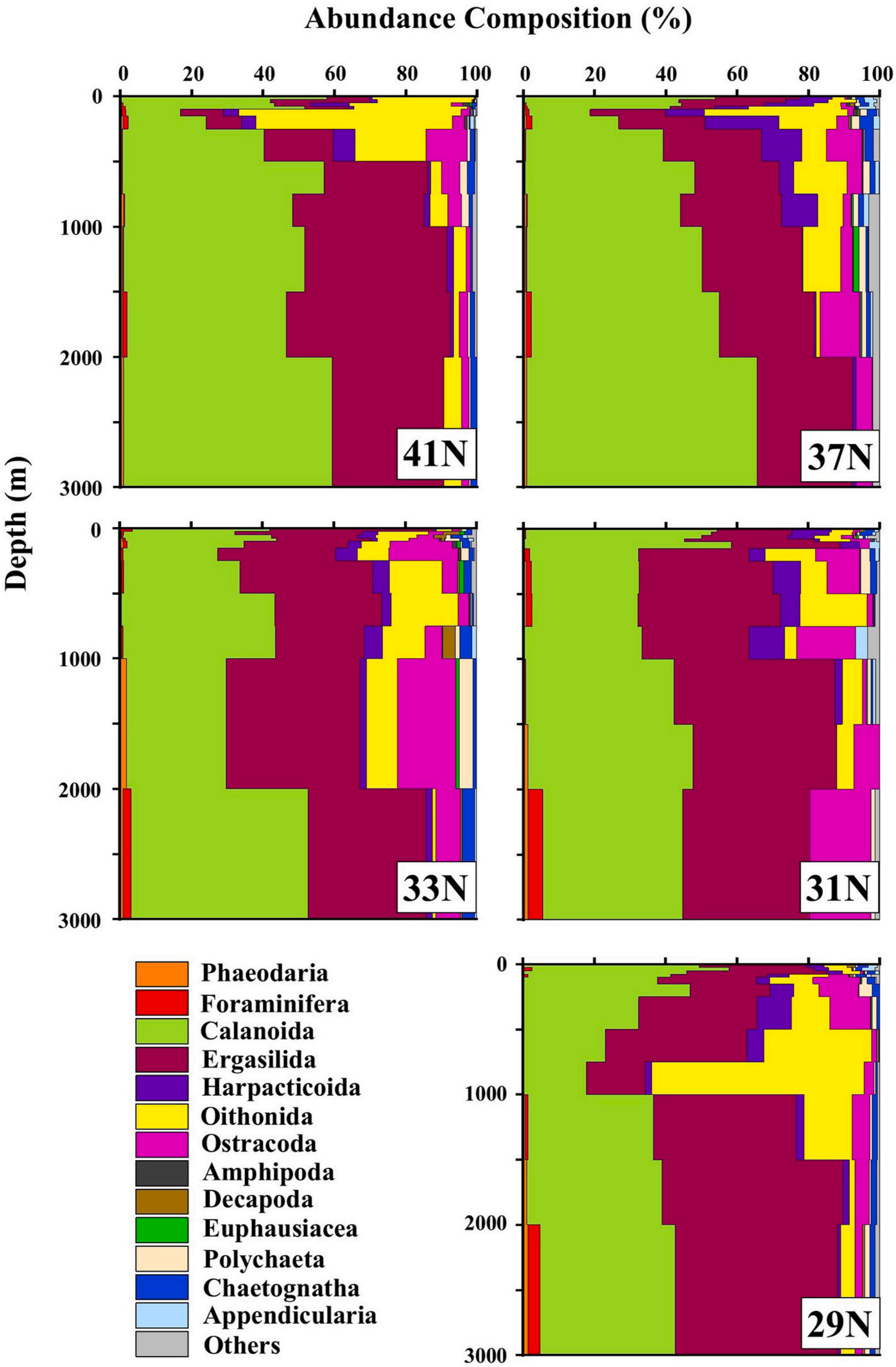

Fig. 6. Vertical changes in taxonomic composition of zooplankton abundance at five stations in the western North Pacific from October to November 2017.

predominance of large copepods contributes to the high zooplankton biomass in subarctic regions (Yamaguchi et al., 2004, 2005; Sato et al., 2015; Kitamura et al., 2016). The dominance of large-sized copepods results in the egestion of large-sized faecal pellets characterised by a rapid sinking rate and high vertical energy efficiency to deeper layers (Steinberg et al., 2008a, 2008b; Kobari et al., 2013).

The prevalence of small zooplankton in the subtropical region indicates limited vertical energy transport and flux (Kitamura et al., 2016; Yokoi et al., 2018). In the western subtropical North Pacific, the dominance of heterotrophic bacteria and protozooplankton within the overall plankton biomass indicates a low sinking particle flux to deeper layers (Yamaguchi et al., 2004). Reductions in zooplankton reproduction and growth rates occur in seasons other than spring or summer, alongside fewer vertical material fluxes to the deep layers (Huntley et al., 2006; Stamieszkin et al., 2015). Therefore, the observed low NBSS intercept for the deep layer of the subtropical region in this study (Fig. 4) may also be a seasonal effect, given that the study was conducted during the low-productivity autumn season. Notably, productivity in subtropical regions is lower than that in subarctic regions (Ikeda and Motoda, 1978; Yamaguchi et al., 2017). Lower productivity in subtropical regions may also contribute to the low NBSS intercept observed in this area.

Clear vertical changing patterns in NBSS slope and size diversity were observed in the transitional region and northern stations of the subtropical region (Sts. 37N, 33N, and 31N). At these stations, as depth increased, the NBSS slope exhibited a moderate trend and size diversity increased (Fig. 4). The observed vertical changing patterns in NBSS

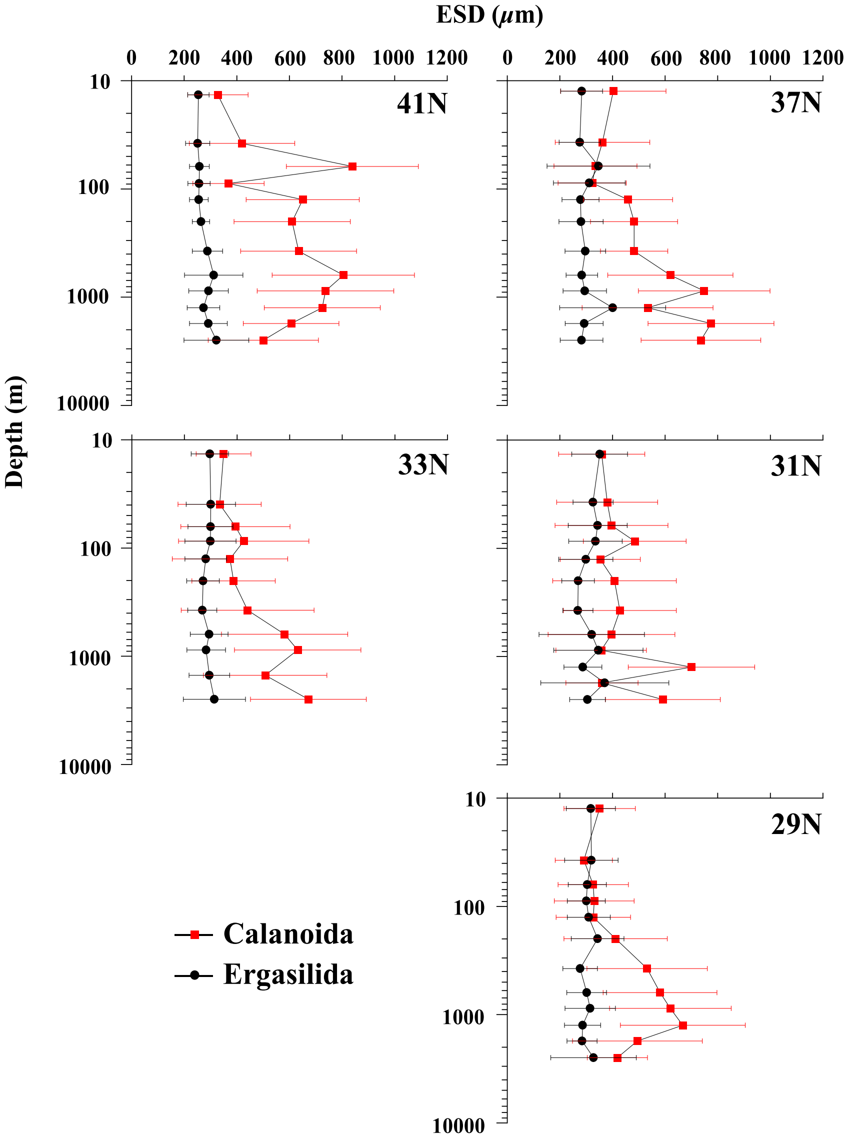

Fig. 7. Vertical changes in the equivalent spherical diameter (ESD) of calanoid and ergasilid copepods across various depth strata at five stations in the western North Pacific from October to November 2017. Symbols and bars represent means and standard deviations, respectively. Note that the depth scales are represented in log-scales.

Table 1
ANCOVA results on equivalent spherical diameter (ESD) of calanoid and ergasilid copepods, with the sampling depth (m) and station (cf. Fig. 1) applied as the independent variables. *df*: degree of freedom, *SS*: sum of squares.

Unit	Parameter	*df*	*SS*	*F*-value	*p*-value
Calanoida					
	Depth	4	240,448	4.063	0.0064
	Station	1	184,200	12.451	0.0009
	Depth × Station	4	155,505	2.628	0.0456
	Error	50	724,880		
Ergasilida					
	Depth	4	13,274	4.688	0.0282
	Station	1	1746	2.468	0.1226
	Depth × Station	4	2825	0.998	0.4177
	Error	50	34,683		

slope and size diversity can be attributed to OVM and the horizontal transportation and advection of large-sized copepods (*Neocalanus* spp.), which enter a dormant resting phase in the deeper layers of the subarctic region. This process, termed the 'submerged Oyashio' (Omori, 1967; Oh et al., 1991), transports large-sized subarctic copepods to the deep layers of the transitional region, resulting in similar zooplankton biomass levels as those in the subarctic region (Yamaguchi et al., 2004, 2005). Notably, the hydrographic conditions below 300 m in the transitional region were also similar to those in the subarctic region (Fig. 2B).

This study was conducted in autumn (October–November), a period when large-sized subarctic copepods perform OVM and spend their resting phase in the deeper layers (Ikeda et al., 2008). The low productivity in the epipelagic layer and high zooplankton biomass resulting from OVM and the horizontal transport of large-sized copepods in deeper layers contributed to a more moderate NBSS slope and increased size diversity with increasing depth. Kim et al. (2023) provided direct evidence based on the same samples, indicating that the stable isotope ratios ($\delta^{15}N$) of the overall zooplankton at the subarctic and transitional

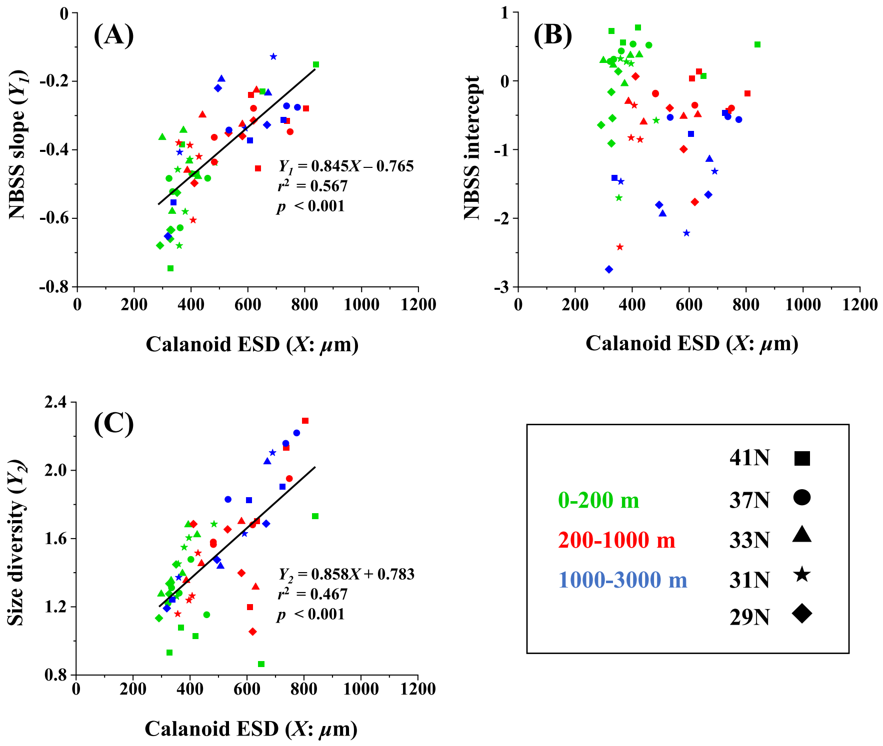

Fig. 8. Scatter plots between zooplankton size parameters: (A) slope, (B) intercept of the normalised biovolume size spectra (NBSS), (C) size diversity and the mean equivalent spherical diameter (ESD) of Calanoida at various depth strata of the five stations in the western North Pacific from October to November 2017. Differences in colours represent variations in sampling depths (0–200, 200–1000, and 1000–3000 m). The regressions for significant interactions are also shown.

stations exhibited similar values across the water column. This uniformity is attributed to the dominance of the same large-sized subarctic copepods (e.g., *Neocalanus* spp.) from surface to deep water via their OVM.

From the comparison of the three parameters (NBSS intercept, NBSS slope, and size diversity) that represent the overall zooplankton size spectra, a significant correlation was detected between the NBSS slope and size diversity (Fig. 5B). Similar significant correlations between the NBSS slope and size diversity have been reported for 0–3000 m depths in the transitional and subtropical regions of the western North Pacific (Yamamae et al., 2023) and 0–3000 m depths of the subtropical region of the western North Pacific (Dai et al., 2017). These results suggest that an increase in large-sized zooplankton with increasing depth is a common phenomenon in this region. This finding is a crucial observation of this study. The question arises whether this phenomenon is because of the OVM of large calanoid copepods or if it is a general phenomenon. The effect is notable in the subarctic and transitional regions. However, subtropical observations (Dai et al., 2017; this study) exhibiting the same pattern may suggest a general pattern. This novel finding serves as validation of this study. Although this may be a generalised pattern, the mechanisms across different domains may differ. In subarctic and transitional regions, the dominance of large-sized dormant copepods in the deeper layers contributes to this phenomenon, especially during their dormant season (autumn and winter). In the subtropical region, the absence of inter-zonal copepods results in changes in taxonomic composition with increasing depth, potentially linked to their feeding modes.

In the entire western North Pacific, a correlation has been observed between increasing depth and increasing taxonomic proportions of carnivorous gelatinous zooplankton, polychaetes, and hydrozoans relative to zooplankton biomass (Steinberg et al., 2008a, 2008b; Dai et al., 2017). The dominance of large-sized zooplankton has been reported to accelerate the vertical material flux due to the egestion of large-sized faecal pellets (Stamieszkin et al., 2015). The cold deep-sea environment (cf. Fig. 2) reduces zooplankton metabolic rates, resulting in higher energy accumulation, slow growth rates, extended generation lengths, and decreased risk from visual predation. These factors contribute to the large body sizes of zooplankton in the deeper layers (Mauchline, 1998). In deep-sea energy acquisition, organisms feed on passive sinking particles, notably faecal pellets (coprophagy), through a process known as repacking. This method facilitates multiple feedings on the same substances, elevating trophic levels with increasing depth (Steinberg et al., 2008b; Kitamura et al., 2016; Kim et al., 2023). Vertical changes in the trophic level (particularly in deeper environments) indicate increased body size with increasing depth. For example, in the western subarctic Pacific, large-sized carnivorous copepods, such as *Paraeuchaeta* spp., are primarily distributed in deep waters (Homma and Yamaguchi, 2010). Vertical changes in zooplankton feeding modes have been documented, revealing that the proportion of carnivores increases with increasing depth (Vinogradov, 1968). The large body sizes of these carnivores suggest that vertical changes in zooplankton feeding modes, particularly the dominance of carnivores in deeper layers, increase body size with increasing habitat depth.

DO was a prominent environmental factor affecting the overall zooplankton size spectra (Fig. 9). Consequently, the NBSS slope was moderate, and the size diversity was high at a depth of approximately 1000 m (Fig. 4), coinciding with the minimum DO levels in the OML (Fig. 2C). Within the OML, the distribution of species adapted to low DO conditions and the zooplankton community structure, especially that of copepods, has been reported to vary with vertically adjacent layers (Homma and Yamaguchi, 2010; 2011). A possible explanation for the moderate NBSS slope in the OML observed in this study is the decrease in

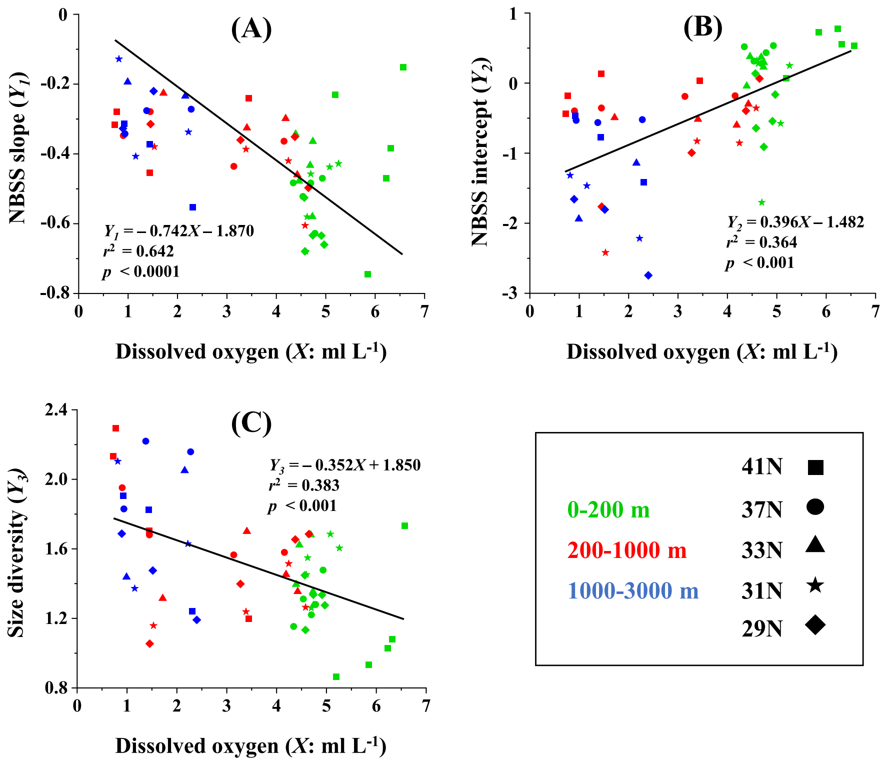

Fig. 9. Scatter plots between zooplankton size parameters: (A) slope, (B) normalised biovolume size spectra (NBSS) intercept, (C) size diversity and dissolved oxygen at various depth strata of five stations in the western North Pacific from October to November 2017. The regressions for significant interactions are also shown.

predation pressure from higher trophic level organisms at this depth. Consequently, most mesopelagic micronektonic fish avoid low DO conditions, producing low predation pressure by fish on large-sized zooplankton at the OML (Herman and Harvey, 2006). In the OML of the western subtropical North Pacific, the dominance of large-sized chaetognaths has been reported, suggesting that their high predation impacts small-sized copepods, which serve as prey for the chaetognaths (Dai et al., 2017). Most mesopelagic invertebrate and vertebrate predators avoid the OML (Vinogradov, 1968). Consequently, the decrease in predation pressure facilitates the dominance of large-sized zooplankton in this area, leading to a moderate slope in the NBSS and greater size diversity (Figs. 2, 4 and 9). However, the dominance of large-sized zooplankton, particularly carnivorous species, exerts predation pressure on smaller copepods in the OML (cf. Dai et al., 2017). Notably, the OML affects the vertical distribution of copepods (cf. Vinogradov, 1968). Therefore, copepods are likely to concentrate on at least the uppermost OML. This suggests that both mechanical concentration and reduced predation contribute to the zooplankton size spectra around the OML. Both factors are interlinked and contribute to the observed patterns.

Biological information on depths below the OML is scarce. In this study, the DO increased with increasing depth below the OML, while the NBSS slope and size diversity became steep and high, respectively, particularly at Sts. 41N and 29N (Figs. 2 and 4). These results can be interpreted as increased predation pressure on large-sized zooplankton below the OML. Vertical changes in plankton communities below the OML have shown increases in the taxonomic composition of the overall plankton biomass for heterotrophic bacteria, while metazooplankton composition decreased steadily with increasing depth in the subarctic Pacific (Yamaguchi et al., 2002b, 2004, 2005). As a comparable study, Dai et al. (2017) reported that the proportion of large carnivorous zooplankton was highest at the OML, whereas the NBSS slope exhibited minimal variation at depths below the OML in the western subtropical North Pacific. Although this information is interesting, the differences in mesh sizes used in each study should be acknowledged. The mesh size of the plankton net employed by Dai et al. (2017) was 200 μm, whereas we collected the samples using a finer mesh size (63 μm). Given these differences, underestimating the small fraction is inevitable when applying a coarse mesh (Dai et al., 2017). This study used a fine mesh (63 μm), enabling the evaluation and quantification of the biomass in the small-sized fraction. Yamamae et al. (2023) used the same mesh net size (63 μm) as that used in this study, targeting depths of up to 3000 m for various stations in the western North Pacific. Unfortunately, they did not collect samples from depths below 1000 m in the subtropical region. Therefore, a comparison with our study is not feasible. Moreover, the steepening of the NBSS slope and reduction in size diversity at depths below the OML should be confirmed in future studies. Despite the identified shortcomings, the results of this study, which encompass depths of up to 3000 m in subarctic, transitional, and subtropical regions, support the assertion that the copepod size spectra indicate that higher predation below the OML results in steeper NBSS slopes and higher diversity.

4.3. ESDs of the two dominant copepod taxa

At all stations and depths, the overall zooplankton abundance was dominated by two copepod taxa, Calanoida and Ergasilida (Fig. 6). The dominance of Calanoida, followed by Ergasilida, in overall zooplankton abundance has been reported in various studies across various depths: 0–3000 m in the northern North Pacific and Bering Sea (Homma and Yamaguchi, 2010; Homma et al., 2011), 0–1000 m in the subtropical North Pacific (Sun et al., 2019), 0–4000 m in the subarctic Pacific (Yamaguchi et al., 2002a), 0–3000 m in the neighbouring waters of Japan including the western North Pacific (Yamamae et al., 2023), and 0–1000 m in the subtropical region off Hawaii (Steinberg et al., 2008b). This suggests that the dominance of Calanoida, followed by Ergasilida, in overall zooplankton abundance is a common phenomenon in the

North Pacific. In contrast, Oithonida showed a composition similar to that of Calanoida and Ergasilida at relatively shallower depths (Fig. 6); however, their proportion decreased substantially with increasing depth. Moreover, the proportions of the two dominant copepod taxa (Calanoida and Ergasilida) in the overall zooplankton abundance have been reported to be high throughout the layers at various locations (Yamaguchi et al., 2002a, 2015; Homma and Yamaguchi, 2010; Homma et al., 2011; Yamamae et al., 2023). This suggests that the body sizes of the two dominant copepod taxa greatly impacted the overall zooplankton size spectra at various depth ranges and geographical locations.

The dominance of the small-sized Ergasilida in the overall zooplankton abundance at all depths and stations in this study can be attributed to the use of fine mesh nets (63 μm) for sample collection. The dominance of Ergasilida (Poecilostomatoida) has been reported in several studies using fine mesh nets for sample collection (Yamaguchi et al., 2002a; Homma and Yamaguchi, 2010; Böttger-Schnack and Schnack, 2023).

The ESD of Calanoida was larger than that of Ergasilida and elevated at higher latitudes (Fig. 7). The copepod communities of Calanoida differ between subarctic and subtropical regions, with subarctic copepods generally exhibiting larger body sizes compared to subtropical copepods (Yamaguchi et al., 2015; Yokoi et al., 2018). The dominance of large-sized copepods, such as *Neocalanus* spp., in subarctic regions and their transportation to the deeper layers of transitional regions by the submerged Oyashio have been well documented (Omori, 1967; Oh et al., 1991; Kobari et al., 2008). Although these regional patterns were present for the ESD of Calanoida, the ESD of Ergasilida exhibited only minor depth variations and remained consistent across stations (Fig. 7, Table 1). These observed taxa-specific differences in ESD changes across regions and depths are attributed to ecological differences, particularly the distinct feeding modes of these two taxa.

Ergasilida exhibits ecological characteristics that allow it to attach to large detritus, such as marine snow and discarded appendicularian houses, to feed on them (Nishibe and Ikeda, 2007; Steinberg et al., 2008b; Nishibe et al., 2015). Because Ergasilida attaches to large-sized detritus, their body sizes are typically less than 1 mm, characterised by a Reynolds number of less than 1. In their environment, dominated by intermolecular forces of attraction, they do not perform diel vertical migration and have low respiration rates. These adaptations allow them to thrive in food-limited deep-sea environments (Nishibe and Ikeda, 2008; Steinberg et al., 2008b; Böttger-Schnack and Schnack, 2023). Ergasilida feeds on large detritus, including appendicularian houses, and some species are recognised as carnivores (Ohtsuka and Nishida, 1997). Their feeding modes remain consistent across various depths, indicating that their weight-specific respiratory rates do not fluctuate with depth (Nishibe and Ikeda, 2008). This results in a stable ergasilid ESD throughout depths ranging from 0 to 3000 m and across various regions, including the subarctic, transitional, and subtropical zones.

Calanoida exhibits diverse feeding modes and ecological characteristics that can vary considerably across species or their developmental stages (Ohtsuka and Nishida, 1997; Mauchline, 1998; Turner, 2004; Yamaguchi et al., 2015). For example, Calanoida can function as suspension feeders, detritivores, or carnivores (Ohtsuka and Nishida, 1997). The ecological adaptation of Calanoida is reflected in their varied swimming behaviour and the occurrence of diel vertical migration, which is an adaptation to environmental parameters, such as water temperature, DO, and day/night differences (Mauchline, 1998; Stamieszkin et al., 2015). Lower temperatures at greater depths may result in the dominance of larger-bodied Calanoida in these deep layers. The dominance of large Calanoida observed around the OML in this study (Fig. 7) indicates a correlation between environmental parameters and the body size of Calanoida.

Interestingly, the latitudinal and vertical change patterns of the calanoid ESD were similar to those of the NBSS slope and size diversity of the overall zooplankton community (Figs. 4 and 7). The calanoid ESD was highly significantly correlated with the NBSS slope and size diversity of the overall zooplankton community ($p < 0.001$, Fig. 8). As mentioned above, the two parameters of the overall zooplankton size spectra, namely NBSS slope and size diversity, were closely related (Fig. 5B). Within the zooplankton community, the two numerically dominant taxa, Calanoida and Ergasilida, exhibited contrasting effects on the overall zooplankton size spectra. From the perspective of trophic guilds, coprophagous species (Ergasilida) appear to have no impact on size spectra with depth, whereas suspension feeders (Calanoida) do influence it. The divergence of the calanoid trophic guilds, along with depth, greatly affected the vertical changes in the overall zooplankton size spectra, especially in the subtropical region.

The close relationships between the calanoid ESD and the overall zooplankton size spectra suggest that changes in the overall zooplankton size spectra are ultimately determined by the size spectra of Calanoida. Calanoida are recognised for their role in influencing the quality and quantity of phytoplankton stocks via feeding and ingestion. Variations in the qualitative and quantitative relationships between phytoplankton and Calanoida result in differences in energy flow within marine ecosystems across various oceanic regions (Ohtsuka and Nishida, 1997; Mauchline, 1998). Most of the zooplankton production in the deeper layers is derived from primary productivity in the surface layer (Steinberg et al., 2008b; Yamaguchi et al., 2015). Because all stations and depth ranges of the overall zooplankton abundance examined in this study were dominated by Calanoida, size changes in Calanoida had a considerable impact on the ecology and material transport of zooplankton from the surface to the deep layers at all stations. Furthermore, in contrast to Ergasilida, the highly diverse behaviours and ecological characteristics of Calanoida, which varied with environmental parameters, might significantly influence changes in the overall zooplankton size spectra.

5. Conclusion

This study examined changes in zooplankton size spectra relative to latitude and depth, using vertically stratified samples collected with a fine mesh (63 μm) from the sea surface to a depth of 3000 m in the subarctic, transitional, and subtropical regions of the western North Pacific. Because of the fine mesh size, this study focused only on mesozooplankton within a limited range (two orders of magnitude). Significant NBSS regressions were obtained for the overall zooplankton samples; however, their NBSS slopes, ranging from −0.745 to −0.128, were somewhat lower than the theoretical value of −1. This discrepancy may be attributable to the limited size range examined in this study. Some studies have suggested that data spanning over three orders of magnitude are necessary for an accurate size spectral analysis.

Despite this limitation, this study revealed several key findings. With increasing depth, the NBSS intercept decreased, the NBSS slope became more moderate, and size diversity increased. The observed low NBSS intercept in the subtropical region may have resulted from lower productivity in this area. The more moderate NBSS slope and increased size diversity in the deeper layers of the subarctic and northern transitional regions appear to be influenced by large-bodied boreal copepods (e.g. *Neocalanus* spp.) at those depths. The deep layers in the subtropical region also exhibited a similar moderate NBSS slope and significant size diversity, likely owing to the dominance of large-bodied carnivorous copepods.

Temperature and DO in the OML were identified as environmental factors influencing the overall zooplankton size spectra. Calanoida significantly influenced the size spectra of the overall zooplankton community, suggesting that variations in their vertical distribution within the trophic guild might influence the size spectra of the overall zooplankton community.

Overall, the study's findings contribute to a better understanding of zooplankton dynamics, the factors influencing their distribution, and their role in marine ecosystems. This knowledge is essential for predicting and mitigating the impacts of environmental changes on marine biodiversity and ecosystem services.

CRediT authorship contribution statement

Dongwoo Kim: Writing – original draft, Investigation. **Sota Komeda:** Resources, Methodology. **Kohei Matsuno:** Writing – review & editing, Supervision. **Atsushi Yamaguchi:** Resources, Investigation, Data curation.

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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Data availability

Data will be made available on request.

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