Contents lists available at ScienceDirect

Deep-Sea Research Part I

Vertical, spatial, size, and taxonomic variations in stable isotopes (δ^{13}C and δ^{15}N) of zooplankton and other pelagic organisms in the western North Pacific

Dongwoo Kim [a],[*], Kanako Amei [a],[1], Sota Komeda [a],[2], Koki Tokuhiro [a],[3], Maki Noguchi Aita [b], Fujio Hyodo [c], Atsushi Yamaguchi [a]

[a] *Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1 Minato-cho, Hakodate, Hokkaido, 041–8611, Japan*
[b] *Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2–15, Natsushima-cho, Yokosuka, Kanagawa, 237–0061, Japan*
[c] *Research Core for Interdisciplinary Sciences, Okayama University, 3–1–1, Tsushimanaka, Okayama, 700–8530, Japan*

A B S T R A C T

Stable isotopes (δ^{13}C and δ^{15}N) of zooplankton and other marine organisms are useful for evaluating trophic levels and the food web structure of marine ecosystems. Further, taxonomic variations and regressions between δ^{15}N and δ^{13}C can provide details of regional differences in the food web structure. Despite their ecological importance, information on the taxonomic differences in the stable isotopes of various pelagic biota and vertical, latitudinal, and size variations in the stable isotopes of the mesozooplankton are scarce in the western North Pacific. In this study, we compared regional differences in the taxonomic variations of the stable isotopes of the all pelagic organisms collected by gillnets and various plankton nets in the subarctic and transitional domains (37–44°N) of the western North Pacific during spring. Additionally, we evaluated the vertical, size, and latitudinal variations in the stable isotopes of mesozooplankton in the western North Pacific. Regressions between δ^{15}N and δ^{13}C were highly significant for the subarctic and transitional domains, while they varied significantly between the two regions ($P < 0.0001$, ANCOVA). These regional differences in the stable isotopes were characterised by the high δ^{15}N and low δ^{13}C values in the subarctic region, whereas the opposites trend was observed in the transitional domains. Vertical observations from the sea surface to a depth of 3000 m at five stations (29°, 31°, 33°, 37°, and 41°N) showed that there were no significant changes in the δ^{13}C stable isotope of mesozooplankton with depth across the stations. However, for δ^{15}N, the significance of regressions increased with increasing depths at the subtropical stations (29°, 31°, and 33°N), while no significant trends with depth were observed for the subarctic and transitional domain stations (37°, 41°N). The dominance of interzonal copepods (e.g., *Neocalanus* spp.) in the mesozooplankton biomass in the subarctic and transitional region may mask the vertical changes in δ^{15}N values in that region. Further, δ^{13}C varied neither with size nor latitude. In contrast, δ^{15}N showed clear size and latitudinal patterns. Thus, δ^{15}N values increased with increasing zooplankton size (112 μm < 407 μm < 925 μm), and significant regressions increased with increasing latitude for all three size classes ($P < 0.001$). Subsequent ANCOVA revealed that the regression did not vary with organism size. Thus, the changing latitudinal patterns in δ^{15}N values (higher for high latitude) had much greater effects than the size differences for mesozooplankton.

1. Introduction

In marine ecosystems, zooplankton play two main ecological roles: 1) first, they serve as a mediator of the organic materials and energy from primary producers to the higher trophic level organisms (fisheries viewpoint) and 2) second, as an accelerator of the biological pump (oceanographic viewpoint); they are responsible for vertical material

Abbreviations

ANCOVA analysis of covariance
ANOVA analysis of variance
POM particulate organic material
SVM seasonal vertical migration
VMPS Vertical Multiple Plankton Sampler

Abbreviations
particulate organic matter (POM)
optical plankton counter (OPC)
analysis of covariance (ANCOVA)
North Pacific Standard net (NORPAC net)
Vertical Multiple Plankton Sampler (VMPS)
Conductivity Temperature Depth profiler (CTD)
Temperature vs. Salinity (T-S)

transport from the sea surface to the deep sea via egestion of faecal particles or vertical migration (Miller and Wheeler, 2012).

Stable isotope ratios (δ^{15}N and δ^{13}C) are useful indices for evaluating food web structure in marine ecosystems (Aita et al., 2011). It is well known that δ^{15}N increases by approximately 3.4‰ each trophic level. Thus, it is a useful indicator for the trophic level of each taxon within a marine ecosystem (Minagawa and Wada, 1984). On the contrary, δ^{13}C is an indicator of the differences in carbon sources at the origin of primary production (Hobson et al., 2002). It has been reported that there is a common regression slope between δ^{15}N and δ^{13}C in terrestrial and marine environments: δ^{15}N = (1.6 ± 0.2) × δ^{13}C + intercept (Aita et al., 2011). The constant values of $\Delta\delta^{15}$N/$\Delta\delta^{13}$C for these various taxa (1.6 ± 0.2) are thought to be a reflection of deamino- and decarbonizing metabolic systems that are common throughout terrestrial and marine environments (Wada and Noguchi, 2017). While it is interesting, testing and confirmation of this hypothesis are needed. Spatial changes in the stable isotope ratios of zooplankton present, two dimensions: vertical and horizontal. For vertical changes, δ^{15}N has been reported to increase with increasing depth in various oceanic regions (Saino and Hattori, 1980; Koppelmann et al., 2003, 2009; Williams et al., 2014; Bode et al., 2015). This is because the frequency of repacking particulate organic matter (POM) increases with depth (Williams et al., 2014; Richards et al., 2020). For horizontal, δ^{15}N has been reported to be low at low latitudes in various oceanic regions (Koppelmann et al., 2003, 2009; Williams et al., 2014). This is thought to be due to a lower δ^{15}N baseline in the marine food web because the phytoplankton community at lower latitudes is dominated by cyanobacteria (*Trichodesmium* spp.) which possess nitrogen-fixation capabilities (Koppelmann et al., 2003, 2009; Williams et al., 2014).

A study on the stable isotope ratio of zooplankton in the subarctic Pacific and its neighbouring waters, was conducted to evaluate $\Delta\delta^{15}$N/$\Delta\delta^{13}$C for the various zooplankton taxa (e.g. copepods, euphausiids, amphipods, chaetognaths) mentioned above (Aita et al., 2011). As large-sized interzonal copepods (e.g., *Neocalanus* spp.) dominate the subarctic Pacific, various studies have focused on them: east-west, geographical changes, and interannual variations (Chiba et al., 2012), regional and interannual variations in the Gulf of Alaska (Kline, 2009, 2010), and interannual variations in the British Columbia fjord (El-Sabaawi et al., 2009). Regarding vertical changes, studies have investigated the effects of hydrothermal plumes on the Pacific coast of Canada (Burd et al., 2002) and also revealed the vertical changes with depth at one station each in the subarctic and subtropical western North Pacific (Kobari et al., 2022). Regarding latitudinal variations, Pomerleau et al. (2014) investigated the epipelagic zooplankton from the Gulf of Alaska to the western Arctic Ocean. While these studies have revealed important findings, studies on the stable isotope ratios from zooplankton to the

higher trophic level organisms such as fishes and squids in the same region and period remain scarce. Regarding vertical changes, the study regions were limited, and little comparable information is available on the vertical changes in the stable isotope ratio in the subarctic, transitional, and subtropical regions. Regarding latitudinal changes, few attempts have been made based on north–south transects (Richoux and Froneman, 2009; Williams et al., 2014; Horii et al., 2018) and more detailed studies are needed to accurately evaluate latitudinal changes in the stable isotopes of zooplankton. Since water masses vary with region, evaluating their effects on stable isotope ratios is also important.

Historically, for the subarctic and transitional domain of the western North Pacific, several studies have been conducted on the whole biota, from zooplankton to fish and squids, by applying both plankton nets and gillnets in latitudinal transect (155°E, 170°E, and 175°E longitudes) (Pearcy et al., 1996; Takagi et al., 1997; Yamaguchi et al., 2005a). Regarding vertical changes in zooplankton communities, some studies have analysed vertically-stratified net zooplankton samples from the sea surface to great depths (maximum 5800 m) at four stations (44°N, 39°N, 30°N, and 25°N latitudes in the western North Pacific) to determine community structure from bacteria to mesozooplankton (Yamaguchi et al., 2002a, 2004), and access vertical changes in community structure for specific taxa such as copepods and chaetognaths (Yamaguchi et al., 2002b; Ozawa et al., 2007). Vertical changes in biomass and chemical composition (C/N ratio) from the surface to the deep sea were also evaluated based on the same zooplankton samples (Yamaguchi et al., 2005b).

For the latitudinal variations in zooplankton communities, studies compared changes in community structure along north–south transects covering the subarctic, transitional, and subtropical regions (Saito et al., 2011; Yamaguchi et al., 2017). Latitudinal variations in zooplankton community is also characterised by many studies investigating zooplankton size composition evaluated by the optical plankton counter (OPC), along these transects (Yokoi et al., 2008; Matsuno and Yamaguchi, 2010; Shiota et al., 2013; Mishima et al., 2019). Although these studies have presented important insights, they have not analysed stable isotope ratios, and our knowledge on this topic in the western North Pacific remains limited.

To this end, the currents study aimed to investigated the following three topics: (1) evaluate the $\Delta\delta^{15}$N/δ^{13}C of the pelagic organisms from zooplankton to fishes and squids, collected by both plankton nets and gillnets in the subarctic and the transitional domain of the western North Pacific; (2) evaluate vertical changes in δ^{15}N and δ^{13}C from the sea surface to a depth of 3000 m at fixed stations located between 29°00′N–42°40′N, and (3) evaluate latitudinal and size changes based on the size-fractionated (925 μm, 407 μm, 112 μm) zooplankton samples collected from the epipelagic zones of stations along the north–south transect, covering the subarctic to subtropical regions. The results were compared with those of studies on stable isotope ratios from various oceans, and the general patterns of stable isotope ratios of pelagic biota have been discussed. In particular, $\Delta\delta^{15}$N/$\Delta\delta^{13}$C, a comparison was made with findings from previous studies conducted in this region (western North Pacific) (Aita et al., 2011; Kobari et al., 2022). The factors causing spatial variations in stable isotope ratios (vertical and latitudinal changes) are also discussed from the perspective of zooplankton communities in the western North Pacific.

2. Materials and methods

2.1. Field sampling

During cruises of the T.S. *Oshoro-Maru*, zooplankton, fishes, and squids were collected using several sampling methods at depths of 0–150 m at six stations along the north–south transect (located 37°15′N–44°00′N) along 155°E longitude in the western North Pacific Ocean from 14 to 20 May 2016 (Fig. 1). Zooplankton was collected by vertically stratified sampling using VMPS (mouth opening areas and
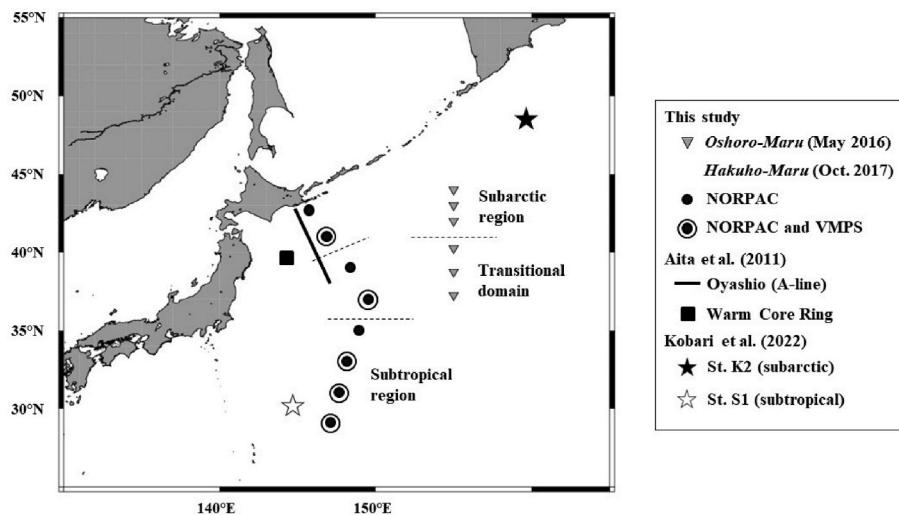
Fig. 1. Sampling stations where the pelagic organisms used in this study were collected, and those of the other comparable studies (Aita et al., 2011; Kobari et al., 2022). For the *Oshoro-Maru* cruise, we targeted zooplankton and nekton (pelagic fishes and squids) by using plankton net and gillnet, respectively, at the latitudinal transect along 155°E during May 2016 (gray triangles). For the *Hakuho-Maru* cruise, vertical changes in mesozooplankton were evaluated down to 3000 m by using VMPS, and size and latitudinal changes in mesozooplankton were conducted by NORPAC net from 0 to 200 m along a north–south transect in the western North Pacific during October 2017 (solid and with circled symbols). Dashed lines indicate approximate positions of differences in water masses (subarctic, transitional domain, and subtropical region) evaluated by T-S diagrams in this study (cf. Fig. 2). For the reference studies, the solid line and solid square indicate the sampling locations of the Oyashio and Warm Core Ring of Aita et al. (2011), respectively. Solid and open stars represent the subarctic St. K2 and subtropical St. S1 of Kobari et al. (2022). The results of these two comparable studies are shown in Fig. 7.

mesh sizes were 0.25 m^2 and 63 μm) and, vertical tows of a NORPAC net (45 cm mouth diameter, 335 μm mesh size) from 0 to 150 m, and horizontal towing with a Bongo net (60 cm mouth diameter, 500 μm mesh size) at depth of 5 m. Fishes and squids were collected by horizontal towing with a larva net (1.3 m mouth diameter, 500 μm mesh size) from the sea surface at speed of two knots for 10 min, fishing and a 2500-m-long gillnet deployed overnight. The collected specimens were identified as species on board, and the whole body of the small species or muscle parts of the large species were cut out, placed in a plastic bag or vial, and frozen, and stored at −20 °C.

During the cruise of R.V. *Hakuho-Maru*, vertically stratified sampling by VMPS equipped with a 63 μm mesh was made from 12 layers down to 3000 m (0–25, 25–50, 50–75, 75–100, 100–150, 150–250, 250–500, 500–750, 750–1000, 1000–1500, 1500–2000, 2000–3000 m) at 5 stations along the north–south transect (29°00′N–42°40′N, 145°45′E−149°40′E) from 19 October to 7 November 2017. Along the transect, the NORPAC net equipped with a 100 μm mesh was also towed vertically from 0 to 200 m at eight stations. VMPS samples were gently filtered through a 50-μm mesh under a weak vacuum and then frozen and stored at −20 °C. NORPAC net samples were gently sieved through three meshes (925 μm, 407 μm, and 112 μm) within a large bucket filled with seawater. The zooplankton samples at each fraction were filtered onto a 50 μm mesh under a weak vacuum, then frozen and stored at −20 °C. For both cruises of *Oshoro-Maru* and *Hakuho-Maru*, water temperature and salinity were measured by CTD (Sea-Bird Electronics, Bellevue, USA) at each station, T-S diagrams were drawn, then the water mass classification was performed using the criteria of Anma et al. (1990). For references on inorganic nitrogen, we provided the data as an electronic supplement (Electronic Supplement 1).

2.2. Stable isotope analyses

In the land laboratory, samples were first freeze-dried, and then oven-dried at 60 °C for more than 24 h; subsequently, they were powdered using a mortar and pestle and the, lipids were then extracted using a 2:1 chloroform: methanol solution. After lipid extraction, the samples were dried at 60 °C for 24 h. The powdered samples were placed in a tin cup, and the stable isotope ratios of carbon and nitrogen were measured using a continuous flow–isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific Inc., Waltham, MA, USA) connected to an elemental analyser. The natural abundance of ^{13}C or ^{15}N is expressed in per mil (‰) deviation from international standards using

the following equation,

$$\delta^{13}C \text{ or } \delta^{15}N = (R_{sample}/R_{standard} - 1) \tag{1}$$

where, R_{sample} and $R_{standard}$ are the isotopic ratios (^{13}C/^{12}C or ^{15}N/^{14}N) of the sample and standard, respectively. The standards used were Vienna Pee Dee belemnite and atmospheric nitrogen for carbon and nitrogen, respectively. The standard deviation of the repeated measurements of multiple working standards was less than 0.2‰ for both isotope ratios.

2.3. Statistical analysis

To clarify the effects of various factors (δ^{13}C, sea area, depth, and size) on the nitrogen stable isotopic ratio (δ^{15}N), we created scatter plots with δ^{15}N as the dependent variable (Y) based on the data from each cruise. For the data of the *Oshoro-Maru* cruises, the regression equation (2) was used for the two regions (subarctic and transitional domain),

$$Y = a\,X + b \tag{2}$$

where, Y is δ^{15}N (‰), X is δ^{13}C, and a and b are constants. To evaluate the differences in the regressions between regions, an analysis of covariance (ANCOVA) was performed.

For the data based on VMPS samples from the *Hakuho-Maru* cruise, the vertical changes in δ^{15}N (Y) were determined using the linear regression equation,

$$Y = a\,X + b, \tag{3}$$

where, X is the mid-point depth (m) of the sampling layer, and a and b are fitted constants. Differences in the regressions between stations, were tested using ANCOVA. For the NORPAC net samples of the *Hakuho-Maru* cruise, the linear regression equation (4) was used to analyse each size fraction (925 μm, 407 μm, 112 μm),

$$Y = a\,X + b \tag{4}$$

where, Y is δ^{15}N, X is latitude (°N), and a and b are fitted constants. Differences in the regressions were tested using by ANCOVA, with size and latitude as independent variables. Statistical analyses were performed using MS Excel or StatView (SAS Institute).
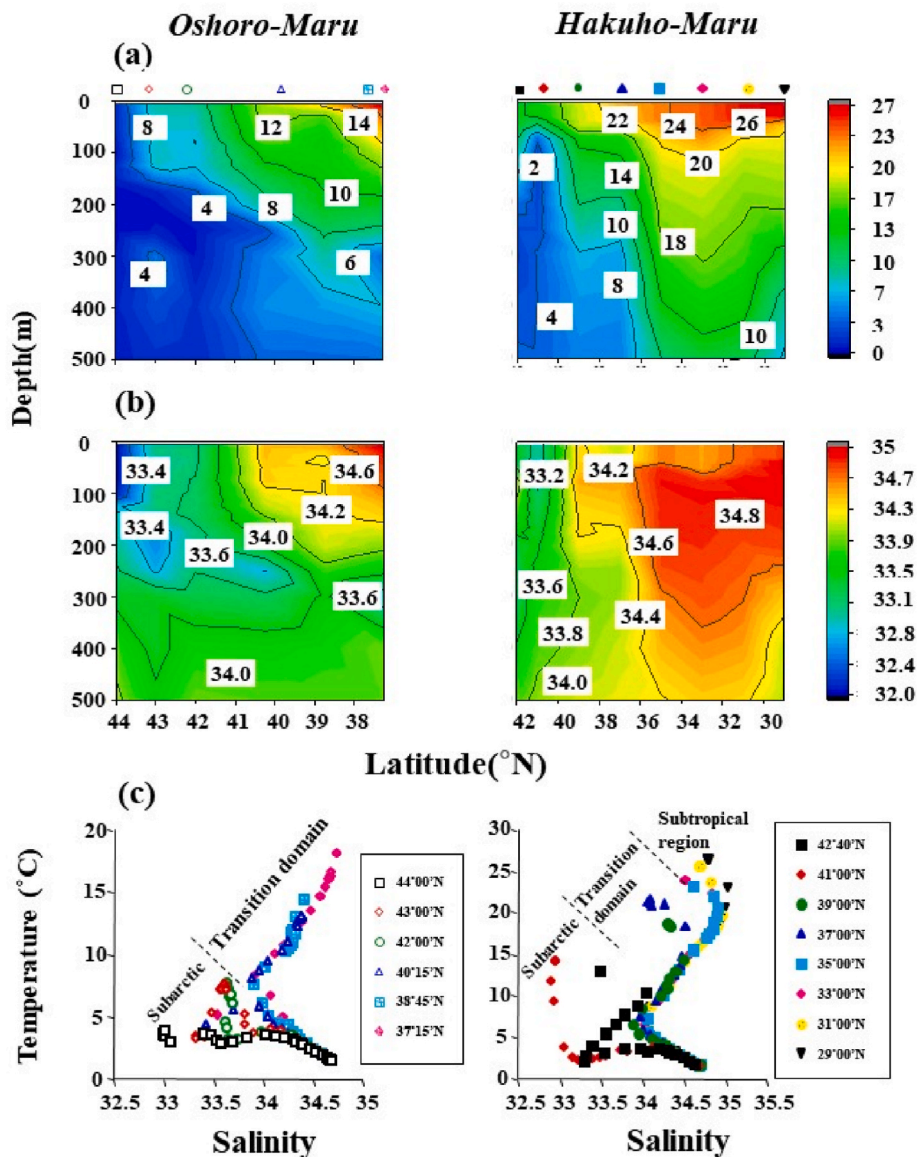
Fig. 2. Vertical and latitudinal changes in temperature (a), salinity (b), and T-S diagrams (c) based on the *Oshoro-Maru* cruise (left) and *Hakuho-Maru* cruise (right). Differences in symbols denote stations in each cruise. Dashed lines represent the separation of the water masses (subarctic, transition domain, and subtropical region) (cf. Anma et al., 1990).

3. Results

3.1. Hydrography

The vertical section contour plot and T-S diagrams of the water temperature and salinity at each station for each cruise are shown in Fig. 2. For the 155°E line observations by the *Oshoro-Maru* cruises in May 2016, the sea surface temperature and salinity ranged from 3.0 °C to 18.1 °C and from 33.0 to 34.7, respectively. The plot of each station in the T-S diagram showed discontinuity around a salinity of 34.0 and was divided into three stations with lower salinity at higher latitudes (42–44°N: subarctic region), and three stations with higher salinity at lower latitudes (37°15′N–40°15′N: transitional domain). For the north–south observation line by the *Hakuho-Maru* in October 2017, the plotted areas of the deep layer in the T-S diagram showed similar temperature and salinity values for all stations. On the contrary, the plotted areas of sea surface waters in the T-S diagram were largely divided into three groups: two stations with cold and fresh waters (42–44°N, subarctic), four stations with hot and saline waters (29–35°N, subtropical),

and two geographically intermediate stations (37–39°N) forming the transitional domain.

3.2. Regional differences in carbon and nitrogen stable isotope ratios

A scatter plot of the stable isotope ratio between $\delta^{15}N$ and $\delta^{13}C$ of the samples collected in the subarctic region of the *Oshoro-Maru* cruise is shown in Fig. 3. We found that $\delta^{13}C$ ranged from −25.5‰ to −19.0‰ and $\delta^{15}N$ ranged from 3.2‰ to 12.0‰, and a significant linear regression was obtained between them; $\Delta\delta^{15}N/\Delta\delta^{13}C$ was 1.210 ($r^2 = 0.76$, $P < 0.0001$).

A scatter plot of $\delta^{15}N$ and $\delta^{13}C$ in the transitional domain is shown in Fig. 4. The plotted areas of $\delta^{13}C$ and $\delta^{15}N$ varied greatly from those of the subarctic region described above, with the plotted areas of $\delta^{13}C$ on the right (high $\delta^{13}C$ values) and those of $\delta^{15}N$ starting at a lower $\delta^{15}N$ value. A significant linear regression between $\delta^{13}C$ and $\delta^{15}N$ was also obtained for the transitional domain, with $\Delta\delta^{15}N/\Delta\delta^{13}C$ being 2.112 ($r^2 = 0.650$, $P < 0.0001$).

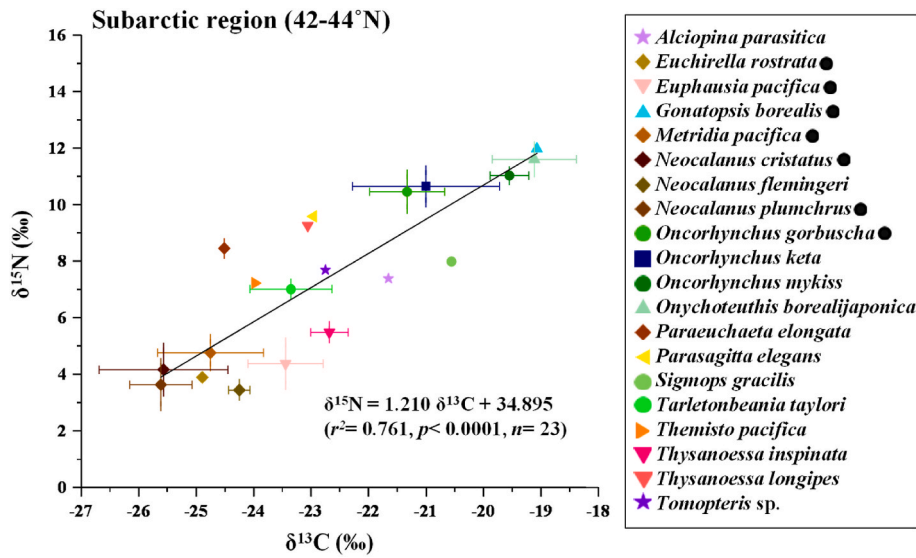The seven species that commonly occurred in both areas were the

Fig. 3. Scatter plots between $\delta^{15}N$ (Y) and $\delta^{13}C$ (X) for various pelagic organisms collected at the epipelagic level (0–150 m) of the western subarctic Pacific (42–44°N, 155°E) during 14–17 May 2016. Symbols and bars denote means and standard deviations, respectively. The regression line was analysed based on the whole dataset plotted in the panel.

Fig. 4. Scatter plots between $\delta^{15}N$ (Y) and $\delta^{13}C$ (X) for various pelagic organisms collected at the epipelagic level (0–150 m) of the transitional domain of the western North Pacific (37°15′–40°15′N, 155°E) from 14 to 17 May 2016. Symbols and bars denote means and standard deviations, respectively. The regression line was analysed based on the whole dataset plotted in the panel.
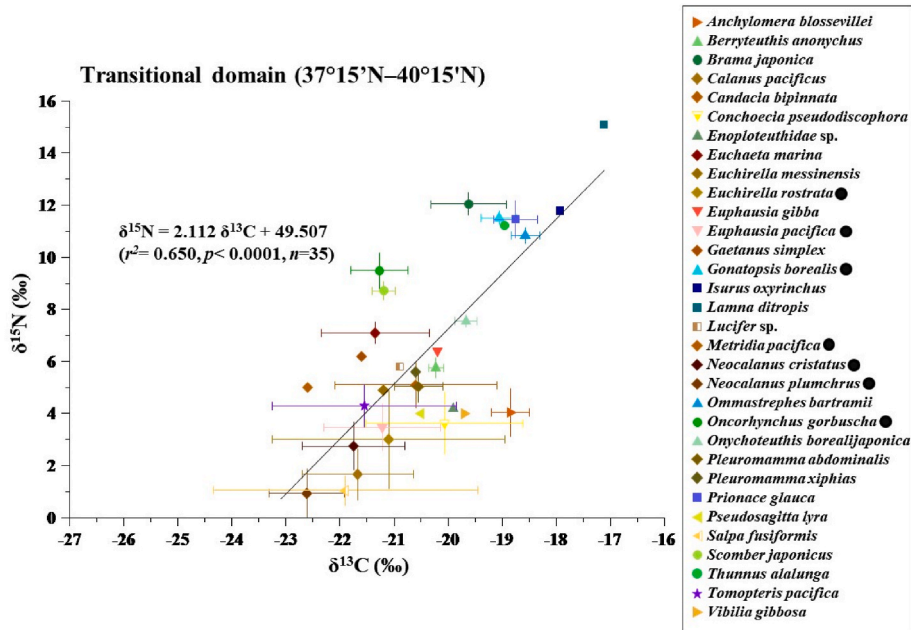
copepods: *Euchirella rostrata* (Claus 1866), *Metridia pacifica* Brodsky 1950, *Neocalanus cristatus* (Krøyer 1848), and *N. plumchrus* (Marukawa 1921); the euphausiid: *Euphausia pacifica* Hansen 1911; the squid: *Gonatopsis borealis* Sasaki 1923, and the fish: *Oncorhynchus gorbuscha* (Walbaum 1792) (Figs. 3 and 4). A common pattern between regions was observed in the stable isotope ratios of these species. Thus, high $\delta^{15}N$ and low $\delta^{13}C$ in the subarctic region and low $\delta^{15}N$ and high $\delta^{13}C$ in the transitional domain were common patterns observed across the taxa (Table 1).

ANCOVA for the linear regressions between $\delta^{13}C$ and $\delta^{15}N$ in the subarctic and transitional domains showed a significant interaction between area and $\delta^{13}C$ ($P < 0.01$, Table 2), indicating that the regression

equation in both areas varied. Comparing the linear regressions for both regions, the zooplankton value at the lower left end of the regression varied substantially, whereas the values of the fish and squid at the upper right end of the regression were similar (Figs. 3 and 4). Thus, the differences in the regressions could be derived from the differences in zooplankton values.

3.3. Vertical changes in $\delta^{13}C$ and $\delta^{15}N$ of zooplankton

Vertical changes in $\delta^{13}C$ and $\delta^{15}N$ of zooplankton down to a depth of 3000 m at five stations obtained during the cruise of *Hakuho-Maru* are shown in Fig. 5. The $\delta^{13}C$ values showed large variations in the

Table 1

Regional comparison of $\delta^{15}N$ and $\delta^{13}C$ of the commonly occurring species in the subarctic (SA: 42–44°N) and transitional domains (TR: 37°15′–40°15′N) along 155°E of the western North Pacific from 14 to 20 May 2016. Values are means ± standard error. The numbers of measurements are shown in parentheses. Regional differences were tested by Mann-Whitney U test. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, ns: not significant, -: not applicable. TL: total length, ML: mantle length, FL: fork length.

TaxaSpecies/stage or length	$\delta^{15}N$			$\delta^{13}C$		
	SA	TR	U test	SA	TR	U test
Copepoda						
Euchirella rostrata	3.90	3.00 ± 0.96	–	−24.89	−21.10 ± 0.77	–
C6F	(1)	(6)		(1)	(6)	
Metridia pacifica	4.76 ± 0.53	4.10 ± 1.32	ns	−24.75 ± 0.28	−21.27 ± 0.78	**
C6F	(4)	(3)		(4)	(3)	
Neocalanus cristatus	5.21 ± 0.39	3.09 ± 0.64	**	−24.26 ± 0.49	−22.43 ± 0.31	*
C5	(19)	(8)		(19)	(8)	
Neocalanus plumchrus	3.63 ± 0.24	1.70 ± 0.32	**	−25.62 ± 0.84	−22.36 ± 0.74	***
C5	(6)	(14)		(6)	(14)	
Euphausiacea						
Euphausia pacifica	4.37 ± 0.66	3.52 ± 0.52	ns	−23.44 ± 0.76	−20.99 ± 0.96	*
TL: 4–5 mm	(3)	(7)		(3)	(7)	
Cephalopoda						
Gonatopsis borealis	11.98	11.52 ± 0.37	–	−19.07	−19.06 ± 0.11	–
ML: 152–200 mm	(1)	(5)		(1)	(5)	
Salmonidae						
Oncorhynchus gorbuscha	10.46 ± 0.68	9.49 ± 0.64	*	−21.33 ± 0.64	−21.27 ± 0.64	ns
FL: 340–435 mm	(15)	(3)		(15)	(3)	

Table 2

Results of ANCOVA for $\delta^{15}N$ of the various pelagic organisms collected by plankton net tows and gillnet surveys in the subarctic and transitional domain of the western North Pacific from 14 to 20 May 2016. For this analysis, area and $\delta^{13}C$ were applied as independent variables. *df*: degrees of freedom, *SS*: sum of squares, ***: $P < 0.001$, ****: $P < 0.0001$.

	df	SS	F-value	P
Area	1	71	13.9	***
$\delta^{13}C$	1	1586	308.7	****
Area x $\delta^{13}C$	1	126	24.4	****
Error	192	987		

epipelagic zone (0–200 m), but settled around −21 to −19‰ at depths below 200 m, showing little difference with depth and between stations. In contrast, the $\delta^{15}N$ showed lower values near the sea surface and increased with increasing depth, especially for the three stations in the subtropical region (29°, 31° and 33°N), where significant linear regressions were observed. The significance of vertical changes in $\delta^{15}N$ with increasing depth was more pronounced at lower latitudes (29°N: $r^2 = 0.698$, $P < 0.001$), moderate at higher latitudes (33°N: $r^2 = 0.495$, $P < 0.05$) and intermediate between the two stations (31°N: $r^2 = 0.668$, $P < 0.01$). There were no significant vertical changes in $\delta^{15}N$ with depth in the transitional (37°N) and subarctic (41°N) domains. Especially at 41°N, there were few vertical changes in $\delta^{15}N$ from the surface to a depth of 3000 m.

ANCOVA was performed for the linear regressions obtained for the three stations in the subtropical region. Although a difference by latitude ($P < 0.05$) was observed, no interactions were detected for latitude × depth (Table 3). These results indicate that the intercepts of the regressions for $\delta^{15}N$, at the surface layer varied between the stations, while their slopes remained the same.

3.4. Latitudinal and size changes in stable isotopes of zooplankton

Latitudinal changes in the stable isotopes of the size-fractionated zooplankton samples at 0–200 m depth during the cruise of the *Hakuho-Maru* are shown in Fig. 6. For $\delta^{13}C$, no variations with latitude or size were observed. In contrast, for $\delta^{15}N$, increases with increasing latitude were observed for all size classes ($r^2 = 0.787$–0.826, $P < 0.001$).

Among the size classes, the largest, intermediate, and smallest values of $\delta^{15}N$ were observed for regressions of the largest (925 μm), intermediate (407 μm), and smallest size classes (112 μm), respectively. The differences in $\delta^{15}N$ between the size classes were at a factor of 1.06–1.49. ANCOVA showed no significant differences in size or size × latitude interactions (Table 4), indicating that the linear regressions for the three size classes could be treated as the same line.

4. Discussion

4.1. Regional differences in $\Delta\delta^{15}N/\Delta\delta^{13}C$

In this study, significant linear regressions were observed between $\delta^{15}N$ and $\delta^{13}C$ in both the subarctic and transitional domains, which reflect the high correlations of the stable isotope ratios in each region (Figs. 3 and 4). This indicates the trophic accumulation effects of ^{15}N (Kline, 1999; Hobson et al., 2002), and the single carbon source of the primary products supporting marine ecosystems (Fanelli et al., 2011; Williams et al., 2014). In general, low $\delta^{15}N$–$\delta^{13}C$ correlations have been reported for marine ecosystems where the original primary production sources have various origins, such as marine snow, phytodetritus, regenerated POM, and the effects of river plumes (Fanelli et al., 2011).

Seasonal differences also affect the correlations between $\delta^{15}N$ and $\delta^{13}C$ (Aita et al., 2011). High $\delta^{15}N$–$\delta^{13}C$ correlations were found for pulses from fresh organic matter based on primary production by phytoplankton blooms, and high $\delta^{13}C$ of zooplankton was observed when the surface chlorophyll-α concentration was high (Fanelli et al., 2011). In the eastern subarctic Pacific, there are seasonal changes in the correlation coefficients of the $\delta^{15}N$–$\delta^{13}C$ regressions of the dominant large-sized copepod *N. cristatus*, and their isotope ratios are reported to be divergent after the end of the spring phytoplankton bloom (Kline, 1999). As the present study was conducted in May with high phytoplankton productivity in the western North Pacific (Longhurst, 2007), high correlation coefficients between the stable isotope ratios were obtained for both the subarctic and transitional region. While the regressions between $\delta^{15}N$ and $\delta^{13}C$ of various taxonomic groups (copepods, euphausiids, amphipods, and chaetognaths) were significant from March–October, substantial changes in the slopes of the regressions were reported within the 2-month intervals (Aita et al., 2011).

As notable characteristics observed in this study, greater differences in the linear regressions for $\delta^{15}N$ and $\delta^{13}C$ were present between the subarctic and transitional domains even within the same season (Fig. 3
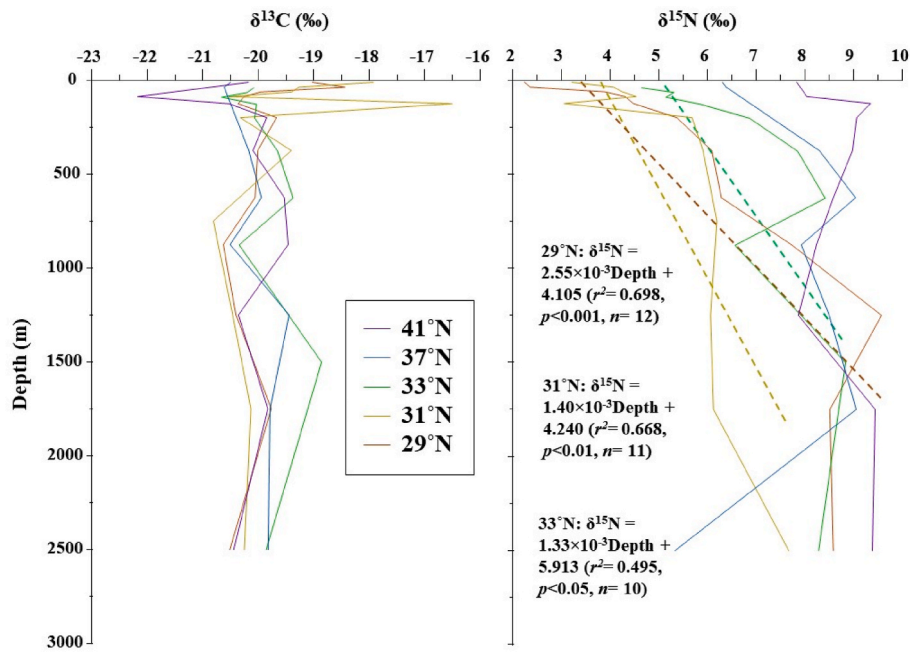
Fig. 5. Vertical changes in $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of mesozooplankton down to a depth of 3000 m collected by 63-μm mesh VMPS at five latitudinal stations in the western North Pacific from 25 October to November 7, 2017. Linear regressions were analysed for each station and dashed lines showed those showing a significant relationship.

Table 3
Results of ANCOVA for $\delta^{15}N$ of zooplankton samples collected by VMPS to a depth of 3000 m at five stations along a north–south transect (29–41°N) in the western North Pacific. For this analysis, latitude and depth were applied as independent variables. *df*: degrees of freedom, *SS*: sum of squares, *: $P < 0.05$, ****: $P < 0.0001$, ns: not significant.

	df	SS	*F*-value	P
Latitude	2	12.4	4.54	*
Depth	1	61.0	44.34	****
Latitude x Depth	2	6.4	2.32	ns
Error	27	37.1		

and, 4). The presence of common regressions for $\delta^{15}N$ and $\delta^{13}C$ of zooplankton has been reported in four different oceanic regions (Southern Ocean, Oyashio, Gulf of Alaska, and the warm-core ring off Sanriku) (Aita et al., 2011). For this reason, as the amino acid metabolic systems are identical throughout the species and regions, shared $\Delta\delta^{15}N/\Delta\delta^{13}C$ values of approximately 1.6 are present across the regions (Wada and Noguchi, 2017). In this study, the $\Delta\delta^{15}N/\Delta\delta^{13}C$ values in the subarctic and transitional domains were 1.210 and 2.112, respectively, which varied substantially from the reported values (1.6). According to Aita et al. (2011), $\Delta\delta^{15}N/\Delta\delta^{13}C$ values fluctuate seasonally, even within the same region. For example, they reported the same $\Delta\delta^{15}N/\Delta\delta^{13}C$ values (1.23) in March and October, 0.61 in May and 1.39 in June for zooplankton in the Oyashio region. These results suggest that $\Delta\delta^{15}N/\Delta\delta^{13}C$ values vary greatly from May to June, during this region's productive season. As the present study was also conducted in May, the presence of large spatio-temporal variations in $\Delta\delta^{15}N/\Delta\delta^{13}C$ corresponded well with the results of Aita et al. (2011). According to Aita et al. (2011), water temperature increased and nitrate concentrations decreased from May–June, and subsequently, zooplankton $\delta^{15}N$ decreased and $\delta^{13}C$ increased simultaneously. While the actual values were varied, the results of Aita et al. (2011) in May (low $\Delta\delta^{15}N/\Delta\delta^{13}C$) matched the results of the cold subarctic region of this study closely. In contrast, the results of June (high $\Delta\delta^{15}N/\Delta\delta^{13}C$) in Aita et al. (2011) were consistent with the results of the warm transitional domain in this study (Figs. 3 and 4). These similarities may be due to the earlier onset of

warming and start of the phytoplankton bloom in the transitional domain. These hydrographic characteristics may correspond to the condition in June reported by Aita et al. (2011). Such latitudinal and seasonal variations in stable isotope ratios were observed for species that occurred in both regions, especially for zooplankton species (Table 1).

Our study's treatment of $\Delta\delta^{15}N/\Delta\delta^{13}C$ values adds to the data of Aita et al. (2011) and, Kobari et al. (2022) from the same region. For comparison, the regressions between $\delta^{15}N$ and $\delta^{13}C$ from these two studies and those from our study are shown in Fig. 7. From this figure, it is recognised that the plotted areas of this study were broader than those of the other two. This is partly because the previous studies included only the zooplankton, while our study included organisms ranging from zooplankton to the higher trophic levels, such as fishes and squids collected by gillnetting. Compared to those of previous studies, the regressions of the subarctic and transitional domains in this study are close to those of St. K2 in the subarctic and St. S1 in the subtropical regions by Kobari et al. (2022), respectively. Common patterns observed in both studies are that $\delta^{13}C$ has high values at low latitudes, whereas $\delta^{15}N$ has high values at high latitudes (Fig. 7). It is also notable that such regional differences in the stable isotope ratios were mostly caused by zooplankton, and few regional differences were observed in the higher trophic level organisms mentioned. These facts (small regional differences in higher trophic levels) are considered to be a reflection of the generation length of each taxon. For shorter-lived zooplankton, their isotope ratios would have large fluctuations that vary with region and season, whereas those of fishes and squids would be more stable around the values mentioned before ($\delta^{15}N$: $\delta^{13}C = 1.6$) in both regions, because they have comparatively long generation lengths.

Higher $\delta^{13}C$ values of zooplankton have been attributed to the faster growth rate of the phytoplankton community (Pomerleau et al., 2014; Henschke et al., 2015). In the northern Gulf of Alaska, the $\delta^{13}C$ of *N. cristatus* is reported to be lower in different seasons and regions, characterised by smaller phytoplankton cell sizes (Kline, 2009). Phytoplankton growth rates are positively affected by, higher water temperatures (Sherman et al., 2016). As the water temperature was high in the transitional domain (Fig. 2), the growth rate of the phytoplankton community is expected to be faster than that of the subarctic region, which would be expected to produce high $\delta^{13}C$ values for
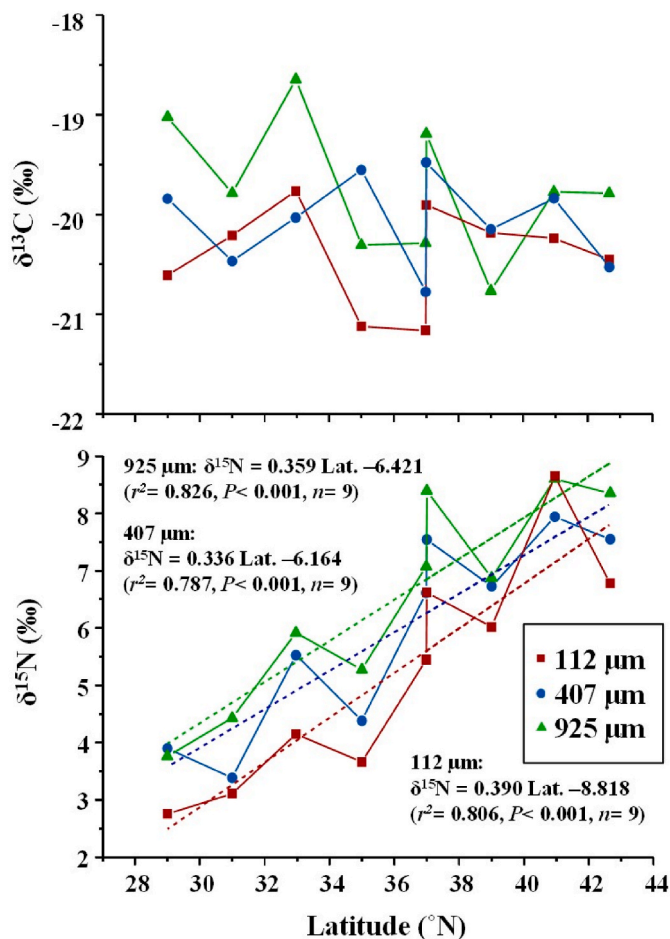
Fig. 6. Latitudinal changes in $\delta^{13}C$ (upper) and $\delta^{15}N$ (lower) of size-fractionated (925, 407, and 112 μm) mesozooplankton samples collected by 150-μm mesh NORPAC net at depths of 0–200 m between 29°00′–42°40′N, 147°12′–145°44′E in the western North Pacific Ocean from 25 October to November 7, 2017. Linear regressions were analysed for each size fraction and dashed lines indicate significant sizes ($P < 0.05$).

phytoplankton, consequently inducing high $\delta^{13}C$ values in zooplankton.

For the $\delta^{15}N$ of the large copepods *Neocalanus* spp., predation pressure is high under cold conditions because of the weak development of the thermocline, which may present phytoplankton blooms, and induce the dominance of microbial organisms. This has been proposed as an explanation for high $\delta^{15}N$ values in *Neocalanus* spp. under cold conditions before (Chiba et al., 2012). The nitrate concentration also affects $\delta^{15}N$ (Chiba et al., 2012; Pomerleau et al., 2014). Thus, low nitrate concentrations and high $\delta^{15}N$ values may enhance the uptake of heavier $\delta^{15}N$ by the phytoplankton, increasing $\delta^{15}N$ of food phytoplankton and also for *Neocalanus* (Chiba et al., 2012; Pomerleau et al., 2014). Thus, the high $\delta^{15}N$ and low $\delta^{13}C$ values observed in the subarctic region in this study may be due to differences in phytoplankton growth rates caused by cold water temperatures. Temperature conditions strongly affected both $\delta^{13}C$ and $\delta^{15}N$ values. In this study, while significant regressions were observed for both the subarctic and transitional domain, the $\Delta\delta^{15}N/\Delta\delta^{13}C$ values varied substantially (1.210 and 2.112, respectively, Figs. 3 and 4) from the theoretical value (about 1.6, Wada and Noguchi, 2017). This is attributed to changes in the stable isotope ratios of the organisms in response to environmental changes mainly due to the water temperature (Fig. 2) and nitrate concentration in each region (Electronic Supplement 1).

4.2. Vertical changes in stable isotope ratios

In the present study, there was no significant relationship between $\delta^{13}C$ and depth at all stations (Fig. 5). Such phenomena have been reported in studies of various zooplankton taxa from depths of 0–2500 m in the north–eastern Pacific off the coast of Vancouver (Burd et al.,

Table 4
Results of ANCOVA for $\delta^{15}N$ of zooplankton samples collected by NORPAC net from depths of 0–200 m at eight stations along the latitudinal transect (29°00′N–42°40′N) in the western North Pacific. For this analysis, size and latitude were applied as independent variables. *df*: degrees of freedom, *SS*: sum of squares, ****: $P < 0.0001$, ns: not significant.

	df	SS	*F*-value	*P*
Size	2	0.53	0.36	ns
Latitude	1	64.36	87.52	****
Size x Latitude	2	0.24	0.16	ns
Error	21	15.45		

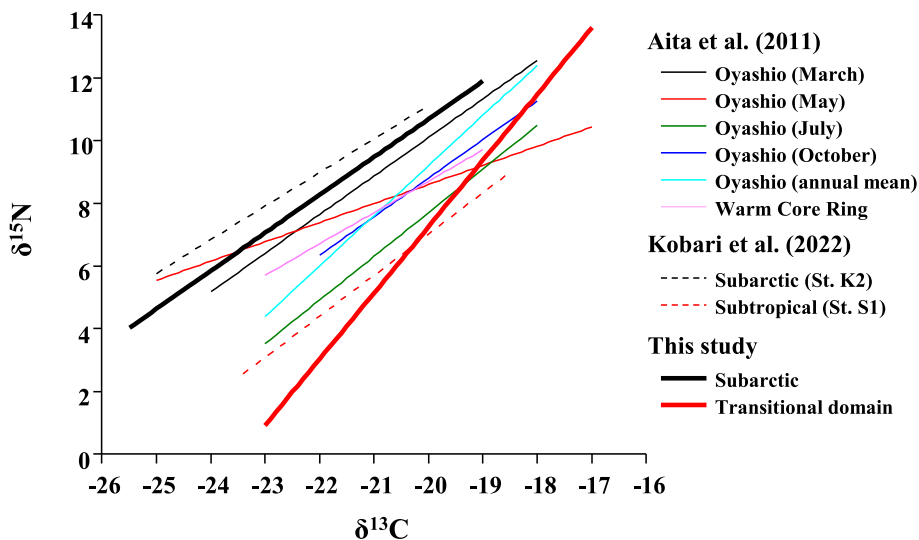**Fig. 7.** Inter-study comparison of the regressions between $\delta^{15}N$ and $\delta^{13}C$ evaluated during various studies in the western North Pacific Ocean. Comparable data for the present study were sourced from Aita et al. (2011) and Kobari et al. (2022), which were also conducted in this region. For sampling locations of each study, see Fig. 1.

2002), zooplankton between 0 and 2000 m in the eastern Atlantic Ocean at 37°N to 21°S (Bode et al., 2015), and zooplankton at 0–1200 m in the eastern tropical North Pacific (Williams et al., 2014). In this study, large fluctuations were observed in $\delta^{13}C$ at shallower depths of 0–200 m (Fig. 5). A similar situation (large fluctuations in $\delta^{13}C$ values at shallower depths) was reported off the coast of Vancouver (Burd et al., 2002). The high $\delta^{13}C$ value, the high growth rate of phytoplankton has been reported as the cause of high $\delta^{13}C$ values (Pomerleau et al., 2014; Henschke et al., 2015). Thus, the high fluctuations in $\delta^{13}C$ values in the surface layer are thought to reflect spatiotemporal changes in the growth rate of phytoplankton. In contrast, in the deep layer (>200 m), the $\delta^{13}C$ value was in a narrow range (−21 to −19) and did not change vertically (Fig. 5). This is thought to indicate that the labile component of the POM decomposes first, then the persistent components remain in the deep layers and settle, resulting in the constant stable isotope values of $\delta^{13}C$ in the deeper layer (Burd et al., 2002). Thus, the $\delta^{13}C$ value can fluctuate at the sea surface layer where phytoplankton actively reproduce, while in the deep layer, $\delta^{13}C$ likely remains at constant values throughout the layer. This is because of the distance separating it from the sea surface, where primary production occurs, and the aging of the utilisation of the material fluxes may occur, causing stabilization of the $\delta^{13}C$ values.

A trend of increasing zooplankton $\delta^{15}N$ values with increasing depth was observed in the subtropical region of this study (Fig. 5). The same trend is well known to occur at the lower latitudes in the temperate to tropical regions, including depths of 0–4200 m in the Mediterranean Sea (Koppelmann et al., 2003, 2009), 0–2000 m depths at 37°N–21°S in the eastern Atlantic Ocean (Bode et al., 2015), and 0–1200 m in the tropical Eastern North Pacific (Williams et al., 2014). For the western North Pacific, the depth-increasing trend of $\delta^{15}N$ has also been reported in the subarctic and subtropical regions (Kobari et al., 2022). The vertical change in POM is considered to be a factor causing the increase in $\delta^{15}N$ with increasing depth. Thus, during the biodegradation of POM by microbial consumption, bonds containing ^{14}N are preferentially broken, and the remaining isotopically heavier $\delta^{15}N$ connection results in higher $\delta^{15}N$ in POM in the deep layer (Koppelmann et al., 2009; Laakmann and Auel, 2010; Richards et al., 2020). Consumption of POM by zooplankton in the mesopelagic zone, repacking of POM by fecal pellet egestion, and its coprophagy also contribute to the higher $\delta^{15}N$ in the deeper layer (Williams et al., 2014; Richards et al., 2020). As depth increases may induce additional feeding and predation by various zooplankton, the $\delta^{15}N$ values of zooplankton in the deep sea are thought to be higher than those near the sea surface (Bode et al., 2015). Thus, the increasing $\delta^{15}N$ values with increasing depth observed in the subtropical region are thought to be caused by the repacking of POM that, originated from the sea surface layer, during sinking to the deep layer.

In contrast, no vertical changes in $\delta^{15}N$ values were observed in the transitional domain and subarctic regions (Fig. 5). It should also be noted that the significance of the regressions between $\delta^{15}N$ and depth at the three stations in subtropical regions was low at higher latitudes. In the western subarctic Pacific, large-sized copepods (*Neocalanus* spp. and *Eucalanus bungii* Giesbrecht 1893) that perform seasonal ontogenetic vertical migration to the deep, considered a diapause phase in their life cycles, dominate the zooplankton biomass (Ikeda et al., 2008). As the sampling in this study was conducted from October–November, when the copepods migrate down to the deep sea to start diapause, they are estimated to contribute 8–67% (mean ± SD: 31 ± 19%) of the total zooplankton biomass between depths of 200 and 3000 m in the western subarctic Pacific during summer (Yamaguchi et al., 2004). The dominance of the diapausing copepods was also the case for the deep layer samples in the subarctic and transitional regions (Kim, unpublished data). As feeding of these copepods occurs at the sea surface layer and does not occur in the deep layer (Tsuda et al., 2004), their $\delta^{15}N$ values are expected to be similar throughout the layers. It should also be noted that the diapausing copepods are transported southwards by submerged Oyashio water, and their occurrence in the deep layer extends to 1000–2000 m at 30°N (Yamaguchi et al., 2004; Kobari et al., 2008). Due

to the large-body sizes of subarctic copepods, their occurrence in the deep layer only may affect the $\delta^{15}N$ value of the transitional domain and northern subtropical regions, which may reduce the significance of the $\delta^{15}N$ regressions with increasing depth. Thus, the decreasing significance of the regressions between $\delta^{15}N$ and depth at the higher latitudes is thought to be due to the dominance of these large subarctic copepods in the deep layer.

4.3. Latitudinal and size changes in stable isotopes

For all organism sizes, we found no significant latitudinal changes in $\delta^{13}C$ values (Fig. 6). Such results have been reported for zooplankton from various oceanic regions, including the Southern Ocean, Oyashio, Gulf of Alaska, and warm-core rings off Sanriku (Aita et al., 2011), and in the southern Indian Ocean (Richoux and Froneman, 2009). For copepods, no latitudinal changes in $\delta^{13}C$ have been reported in the eastern Atlantic Ocean (Bode et al., 2015), and the Greenland and Barents Seas (Sato et al., 2002). No differences in $\delta^{13}C$ with size were reported in a study on capelin in the Arctic Ocean (Ogloff et al., 2020). A reason for the lack of latitudinal and size changes in $\delta^{13}C$ may lie in the almost identical major metabolic pathways such as amino acid synthesis in animals resulting in the absence of differences in stable isotope ratios even in different regions (Aita et al., 2011), in addition to the effects of carbon sources. For example, there are no changes in the $\delta^{13}C$ value of copepods at high latitudes during the winter season because they feed primarily during a phytoplankton bloom from spring to summer and do not feed during the rest of the year. Consequently, their $\delta^{13}C$ values are stable, because they derived from the same phytoplankton carbon sources (Sato et al., 2002). In this study, sampling was not conducted during phytoplankton bloom season, as the samples were collected at depths of 0–200 m, thus, they may not have contained diapausing copepods. According to Richoux and Froneman (2009), the $\delta^{13}C$ values of euphausiids, amphipods, and copepods were not related to external variables (salinity, temperature, chl. *a*, size, etc.). Thus, there are many examples showing that $\delta^{13}C$ values do not change with region, corresponding with the pattern in this study.

In this study, across all size classes, the $\delta^{15}N$ value was higher at higher latitudes (Fig. 6). This patterns in $\delta^{15}N$ of various zooplankton taxa have been reported in the eastern tropical North Pacific (Williams et al., 2014) and eastern Mediterranean Sea (Koppelmann et al., 2003, 2009). As reason for this pattern of $\delta^{15}N$ (low at low latitudes) is partly due to the nitrogen fixation ability of phytoplankton. Thus, cyanobacteria, having a nitrogen fixation ability with a low $\delta^{15}N$ value (1–4‰) among the epipelagic plankton of the eastern Mediterranean, caused by atmospheric nitrogen, is the dominant primary producer and responsible for the extremely low $\delta^{15}N$ baseline in the region (Koppelmann et al., 2003, 2009). The abundance of cyanobacteria is high at lower latitudes (Shiozaki et al., 2015; Wang et al., 2021). These factors induce low $\delta^{15}N$ values in zooplankton at lower latitudes. Furthermore, a low nitrate concentration is available (Electronic Supplement 1). As $^{14}NO_3^-$ is abundant and is utilized preferentially by phytoplankton, incomplete utilisation of nitrate creates POM with low a $\delta^{15}N$ values (2–3‰) in the tropical regions (Williams et al., 2014). In the sea off Western Australia, the cold upwelled water contains a high $\delta^{15}N$ value because of the dominance of upwelled nitrate in the nutrients available for primary production, while a low $\delta^{15}N$ occurs in the normal warm region, which is due to the dominance of regenerated nitrogen sources for primary production (Waite et al., 2007). Such latitudinal changes in nitrate concentrations are also present in the western North Pacific (Shiozaki et al., 2015; Wang et al., 2021; Electronic Supplement 1), where the present study was conducted.

The $\delta^{15}N$ value is known to increase by approximately 3.4‰ by increasing one trophic level, thus indicating their trophic level in each ecosystem (Minagawa and Wada, 1984). In the present study, the $\delta^{15}N$ value of zooplankton was higher for larger organism size classes. However, the differences in $\delta^{15}N$ values with size were less than 2‰

(Fig. 6), indicating that the differences could not have been caused by trophic level differences. Generally, it is well known that the small-sized organisms tend to be herbivores with low $\delta^{15}N$ values, whereas large-sized organisms tend to be carnivores with high $\delta^{15}N$ values (Koppelmann et al., 2003; Richoux and Froneman, 2009; Hiwatari et al., 2011). Within the same species, it has also been reported that the diet shifts to carnivory as the organism grows, inducing higher $\delta^{15}N$ values in older specimens (Hop et al., 2006; Waite et al., 2007; Ogloff et al., 2020). Common to all size classes, a significant linear regression between the $\delta^{15}N$ values and latitude was observed, with $\delta^{15}N$ increasing with increasing latitude (Fig. 6). The subsequent ANCOVA revealed no interactions with size, or size × latitude (Table 3), indicating that the regressions observed for the three size classes can be treated as the same. Thus, within the taxonomic category of zooplankton, differences in $\delta^{15}N$ values are much greater for latitudinal changes than those caused by the differences in sizes.

5. Conclusion

Here, we conducted three analyses on the stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of zooplankton in the western North Pacific. Different $\Delta\delta^{15}N/\Delta\delta^{13}C$ values were obtained for the subarctic and transitional domains, which could be attributed to changes in the zooplankton community composition, to species with shorter generation lengths. For vertical changes, the significance of regressions increased with increasing depth, but only in the subtropical regions. The cause of the absence of vertical changes in $\delta^{15}N$ values in the subarctic region may be the dominance of large-sized interzonal copepods that perform an ontogenetic vertical migration from the sea surface to the deep sea to undergo diapause in their life cycle. Thus, the dominance of interzonal copepods in the zooplankton biomass may mask the vertical changes in their $\delta^{15}N$ values. On the contrary, the scarcity of such interzonal copepods in the subtropical region caused an accumulation of the effect of repacking by zooplankton on the sinking particles, especially for the deeper layer, which may have induced higher $\delta^{15}N$ values here. The $\delta^{15}N$ of zooplankton in the size fraction was higher for the larger size classes, but the differences in $\delta^{15}N$ caused by size were much smaller than those caused by latitudinal changes. A high $\delta^{15}N$ value of zooplankton at higher latitudes was observed for all size classes. As a limitation of this study, since this study conducted only one each occasion or year, yearly changes in the stable isotope ratios could not be evaluated. For future study, evaluation of such issues (yearly changes) would be needed.

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.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2023.104045.

References

Aita, M.N., Tadokoro, K., Ogawa, N.O., Hyodo, F., Ishii, R., Smith, S.L., Saino, T., Kishi, M.J., Saitoh, S., H, Wada, E., 2011. Linear relationship between carbon and nitrogen isotope ratios along simple food chains in marine environments. J. Plankton Res. 33, 1629–1642.

Anma, G., Masuda, K., Kobayashi, G., Yamaguchi, H., Meguro, T., Sasaki, S., Ohtani, K., 1990. Oceanographic structures and changes around the transition domain along 180° longitude, during June 1979-1988. Bull. Fish. Sci. Hokkaido Univ. 41, 73–88.

Bode, M., Hagen, W., Schukat, A., Teuber, L., Fonseca-Batista, D., Dehairs, F., Auel, H., 2015. Feeding strategies of tropical and subtropical calanoid copepods throughout the eastern Atlantic Ocean-Latitudinal and bathymetric aspects. Prog. Oceanogr. 138, 268–282.

Burd, B.J., Thomson, R.E., Calvert, S.E., 2002. Isotopic composition of hydrothermal epiplume zooplankton: evidence of enhanced carbon recycling in the water column. Deep-Sea Res. I 49, 1877–1900.

Chiba, S., Sugisaki, H., Kuwata, A., Tadokoro, K., Kobari, T., Yamaguchi, A., Mackas, D. L., 2012. Pan-North Pacific comparison of long-term variation in *Neocalanus* copepods based on stable isotope analysis. Prog. Oceanogr. 97, 63–75.

El-Sabaawi, R., Dower, J.F., Kainz, M., Mazumder, A., 2009. Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar. Biol. 156, 225–237.

Fanelli, E., Cartes, J.E., Papiol, V., 2011. Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: insight from stable isotopes. J. Mar. Syst. 87, 79–89.

Henschke, N., Everett, J.D., Suthers, I.M., Smith, J.A., Hunt, B.P., Doblin, M.A., Taylor, M.D., 2015. Zooplankton trophic niches respond to different water types of the western Tasman Sea: a stable isotope analysis. Deep-Sea Res. I 104, 1–8.

Hiwatari, T., Koshikawa, H., Nagata, R., Suda, Y., Hamaoka, S., Kohata, K., 2011. Trophic relationships in early spring along the Okhotsk coast of Hokkaido, Japan, as traced by stable carbon and nitrogen isotopes. Plankton Benthos Res 6, 56–67.

Hobson, K.A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J.M., Fortier, M., 2002. A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Res. II 49, 5131–5150.

Hop, H., Falk-Petersen, S., Svendsen, H., Kwasniewski, S., Pavlov, V., Pavlova, O., Søreide, J.E., 2006. Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog. Oceanogr. 71, 182–231.

Horii, S., Takahashi, K., Shiozaki, T., Hashihama, F., Furuya, K., 2018. Stable isotopic evidence for the differential contribution of diazotrophs to the epipelagic grazing food chain in the mid-Pacific Ocean. Global Ecol. Biogeogr. 27, 1467–1480.

Ikeda, T., Shiga, N., Yamaguchi, A., 2008. Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific. J. Oceanogr. 64, 339–354.

Kline Jr., T.C., 1999. Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. Can. J. Fish. Aquat. Sci. 56, 94–117.

Kline Jr., T.C., 2009. Characterization of carbon and nitrogen stable isotope gradients in the northern Gulf of Alaska using terminal feed stage copepodite-V *Neocalanus cristatus*. Deep-Sea Res. II 56, 2537–2552.

Kline Jr., T.C., 2010. Stable carbon and nitrogen isotope variation in the northern lampfish and *Neocalanus*, marine survival rates of pink salmon, and meso-scale eddies in the Gulf of Alaska. Prog. Oceanogr. 87, 49–60.

Kobari, T., Moku, M., Takahashi, K., 2008. Seasonal appearance of expatriated boreal copepods in the Oyashio-Kuroshio mixed region. ICES J. Mar. Sci. 65, 469–476.

Kobari, T., Nakamura, R., Aita, M.N., Kitamura, M., 2022. Mesopelagic community supported by epipelagic production in the western North Pacific Ocean based on stable isotope ratios of carbon and nitrogen. Deep-Sea Res. I 182, 103722.

Koppelmann, R., Weikert, H., Lahajnar, N., 2003. Vertical distribution of mesozooplankton and its $\delta^{15}N$ signature at a deep-sea site in the Levantine Sea (eastern Mediterranean) in April 1999. J. Geophys. Res. C108, 8118.

Koppelmann, R., Böttger-Schnack, R., Möbius, J., Weikert, H., 2009. Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. J. Plankton Res. 31, 669–686.

Laakmann, S., Auel, H., 2010. Longitudinal and vertical trends in stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of omnivorous and carnivorous copepods across the South Atlantic Ocean. Mar. Biol. 157, 463–471.

Longhurst, A.R., 2007. Ecological Geography of the Sea, second ed. Academic Press, Cambridge.

Matsuno, K., Yamaguchi, A., 2010. Abundance and biomass of mesozooplankton along north-south transects (165°E and 165°W) in summer in the North Pacific: an analysis with an optical plankton counter. Plankton Benthos Res 5, 123–130.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochem. Cosmochim. Acta 48, 1135–1140.

Mishima, K., Matsuno, K., Yamaguchi, A., 2019. Zooplankton size structure in the summer western North Pacific Ocean: analysis by optical plankton counter. Bull. Fish. Sci. Hokkaido Univ. 69, 37–45.

Miller, C., Wheeler, P., 2012. Biological Oceanography, second ed. Wiley-Blackwell, Hoboken.

Ogloff, W.R., Ferguson, S.H., Tallman, R.F., Davoren, G.K., 2020. Diet of capelin (*Mallotus villosus*) in the Eastern Canadian Arctic inferred from stomach contents and stable isotopes. Polar Biol. 43, 1273–1285.

Ozawa, M., Yamaguchi, A., Ikeda, T., Watanabe, Y., Ishizaka, J., 2007. Abundance and community structure of chaetognaths from the epipelagic through abyssopelagic zones in the western North Pacific and its adjacent seas. Plankton Benthos Res 2, 184–197.

Pearcy, W.G., Fisher, J.P., Anma, G., Meguro, T., 1996. Species associations of epipelagic nekton of the north Pacific ocean, 1978–1993. Fish. Oceanogr. 5, 1–20.

Pomerleau, C., Nelson, R.J., Hunt, B.P., Sastri, A.R., Williams, W.J., 2014. Spatial patterns in zooplankton communities and stable isotope ratios (δ^{13}C and δ^{15}N) in relation to oceanographic conditions in the sub-Arctic Pacific and western Arctic regions during the summer of 2008. J. Plankton Res. 36, 757–775.

Richards, T.M., Sutton, T.T., Wells, R.J., 2020. Trophic structure and sources of variation influencing the stable isotope signatures of meso-and bathypelagic micronekton fishes. Front. Mar. Sci. 7, 876.

Richoux, N.B., Froneman, P.W., 2009. Plankton trophodynamics at the subtropical convergence, Southern Ocean. J. Plankton Res. 31, 1059–1073.

Saino, T., Hattori, A., 1980. ^{15}N natural abundance in oceanic suspended particulate matter. Nature 283, 752–754.

Saito, R., Yamaguchi, A., Saitoh, S.I., Kuma, K., Imai, I., 2011. East-west comparison of the zooplankton community in the subarctic Pacific during summers of 2003–2006. J. Plankton Res. 33, 145–160.

Sato, M., Sasaki, H., Fukuchi, M., 2002. Stable isotopic compositions of overwintering copepods in the arctic and subarctic waters and implications to the feeding history. J. Mar. Syst. 38, 165–174.

Sherman, E., Moore, J.K., Primeau, F., Tanouye, D., 2016. Temperature influence on phytoplankton community growth rates. Global Biogeochem. Cycles 30, 550–559.

Shiota, T., Abe, Y., Saito, R., Matsuno, K., Yamaguchi, A., Imai, I., 2013. Spatial changes in mesozooplankton community structure in the North Pacific : analyses by optical plankton counter. Bull. Fish. Sci. Hokkaido Univ. 63, 13–22.

Shiozaki, T., Takeda, S., Itoh, S., Kodama, T., Liu, X., Hashihama, F., Furuya, K., 2015. Why is *trichodesmium* abundant in the kuroshio? Biogeosciences 12, 6931–6943.

Takagi, S., Sakurai, Y., Kamei, Y., Miyoi, T., Sakaoka, K., Shiga, N., 1997. Oceanographic conditions and distribution of pelagic nekton in the Northwestern North Pacific Ocean during the summer and fall in 1995 and 1996. Bull. Fish. Sci. Hokkaido Univ. 48, 13–28.

Tsuda, A., Saito, H., Kasai, H., 2004. Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (copepoda: calanoida) in the western subarctic Pacific Ocean. Fish. Oceanogr. 13, S10–S20.

Wada, E., Noguchi, M., 2017. A new aspect on food chain analyses using N/C isotope ratios. Radioisotopes 66, 331–342.

Waite, A.M., Muhling, B.A., Holl, C.M., Beckley, L.E., Montoya, J.P., Strzelecki, J., Thompson, P.A., Pesant, S., 2007. Food web structure in two counter-rotating eddies based on δ^{15}N and δ^{13}C isotopic analyses. Deep-Sea Res. II 54, 1055–1075.

Wang, Y., Kang, J., Sun, X., Huang, J., Lin, Y., Xiang, P., 2021. Spatial patterns of phytoplankton community and biomass along the Kuroshio Extension and adjacent waters in late spring. Mar. Biol. 168, 1–17.

Williams, R.L., Wakeham, S., McKinney, R., Wishner, K.F., 2014. Trophic ecology and vertical patterns of carbon and nitrogen stable isotopes in zooplankton from oxygen minimum zone regions. Deep-Sea Res. I 90, 36–47.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M.M., 2002a. Structure and size distribution of plankton communities down to the greater depths in the western North Pacific Ocean. Deep-Sea Res. II 49, 5513–5529.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Takahashi, M.M., 2002b. Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific (WEST-COSMIC). Deep-Sea Res. I 49, 1007–1025.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T., Mac Takahashi, M., 2004. Latitudinal differences in the planktonic biomass and community structure down to the greater depths in the western North Pacific. J. Oceanogr. 60, 773–787.

Yamaguchi, A., Shiga, N., Ikeda, T., 2005a. Variabilities in zooplankton biomass and its community structure as the prime food source for pelagic fishes/squids in the subarctic Pacific Ocean. Kaiyo Monthly 37, 596–604.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Maeda, M., Ishizaka, J., Ikeda, T., Takahashi, M.M., 2005b. Biomass and chemical composition of net-plankton down to greater depths (0–5800 m) in the western North Pacific Ocean. Deep-Sea Res. I 52, 341–353.

Yamaguchi, A., Matsuno, K., Abe, Y., Arima, D., Imai, I., 2017. Latitudinal variations in the abundance, biomass, taxonomic composition and estimated production of epipelagic mesozooplankton along the 155°E longitude in the western North Pacific during spring. Prog. Oceanogr. 150, 13–19.

Yokoi, Y., Yamaguchi, A., Ikeda, T., 2008. Regional and inter-annual changes in the abundance, biomass and community structure of mesozooplankton in the western North Pacific in early summer; as analyzed with an optical plankton counter. Bull. Plankton Soc. Jpn. 55, 79–88.