ORIGINAL ARTICLE

Biology

Geographical differences in the stable isotope ratios of Pacific saury in the North Pacific Ocean

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Abstract

We collected samples of Pacific saury *Cololabis saira* (249–331 mm in knob length; ages 0 and 1) in the North Pacific Ocean from 154°E to 165°W during their northward migration in the early summers of 2013, 2014, and 2015, and measured the stable nitrogen and carbon isotope ratios (δ^{15}N and δ^{13}C) of their muscle tissues. A hierarchical cluster analysis based on δ^{15}N and δ^{13}C yielded three groups (G1–G3). G1 (mean δ^{15}N: 12.9%; mean δ^{13}C: –20.3%) had the highest δ^{15}N and occurred only in the eastern area of 170° W in 2013 and 2015. G2 (δ^{15}N: 9.3%; δ^{13}C: −20.1%) and G3 (δ^{15}N: 7.3%, δ^{13}C: −20.9%) occurred in all years mainly in eastern and western areas of 170° W, respectively. The latter two groups presented reasonable δ^{15}N and δ^{13}C considering the trophic enrichment and potential prey such as *Neocalanus* copepods that exist in each area. In contrast, the substantially enriched δ^{15}N of G1 was characteristic of organisms at higher trophic levels in the same area. Thus, this group is most likely an immigrant from outside the survey area. This study showed that Pacific saury utilize different ecosystems east and west of 170° W during their northward migration.

Keywords Stable isotope ratios · Geographical variation · Small pelagic fish · North pacific ocean · Pacific saury

Introduction

The Pacific saury *Cololabis saira* is one of the most commercially important migratory small pelagic fish distributed from the coastal to the open waters of the North Pacific Ocean (Hubbs and Wisner 1980). Pacific saury fishing grounds are formed in the western part of the North Pacific Ocean in the summer and autumn (Kosaka 2000). The species is fished commercially by Japan, Russia, Korea, China, Taiwan, and Vanuatu, with total landings fluctuating from 180,973 tons in 1998 to 631,094 tons in 2014 over last 30 years (FAO website. http://www.fao.org/fishery/species/3001/en; accessed 30 April 2021). The stock assessment and management of Pacific saury have been undertaken by the North Pacific Fisheries Commission (NPFC). Stocks of small pelagic fishes such as Pacific saury fluctuate dynamically in response to changes in ocean productivity (Yatsu 2019). It is necessary to clarify biological information such as feeding habits, growth, migration and maturation to understand the mechanism of resource fluctuation and to achieve better stock management.

This fish feeds mainly on zooplankton including copepods and euphausiids throughout its life (Odate 1977; Sugisaki and Kurita 2004; Miller et al. 2010; Miyamoto et al. 2020) and is one of the main prey species of tuna, sea birds, and marine mammals (Minami et al. 1995; Minami and Ogi 1997; Gould et al. 2000; Mitani et al. 2006; Davies et al. 2009; Madigan et al. 2012; Glaser et al. 2015). Thus, Pacific saury links organisms of lower and higher trophic levels in

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the pelagic ecosystems of the North Pacific Ocean (Madigan et al. 2012). During its 2-year lifespan (Suyama et al. 2006), Pacific saury seasonally migrates between subarctic and subtropical areas (Fukushima 1979). It spawns over a wide range of subtropical areas from autumn to spring (Iwahashi et al. 2006; Fuji et al. 2020). The larvae and juveniles migrate northward while growing during spring and reach the subarctic area by the end of the summer (Kosaka 2000). Pacific saury then migrate southward towards their spawning grounds in the subtropical area and arrive there by wintertime (Miyamoto et al. 2019). In their second year of life, their migration pattern is nearly identical to that of the first (Fukushima 1979). However, age-1 fish migrate towards the southwest after summer (Nagasawa et al. 1984; Kosaka et al. 1985; Watanabe et al. 1985; Suyama et al. 2012a; Miyamoto et al. 2019). Similar patterns of north–south migration also occur in the eastern part of the North Pacific Ocean (Baitaliuk et al. 2013). The migration pattern of Pacific saury is summarized in Fig. 1.

Northward migration during the spring and summer is important for Pacific saury because they need to feed on the abundant subarctic zooplankton available during these seasons to gain enough energy to grow and mature (Kurita et al. 2004; Sugisaki and Kurita 2004). During this period, their main distributional area ranges extensively between 155° E and 165° W (Miyamoto et al. 2019), and they show longitudinal variation in feeding habits regardless of age; *Neocalanus plumchrus* and *N. flemingeri* tend to be important prey species in areas west of ca 175° E, whereas Pacific saury feed mainly and selectively on *N. cristatus* in eastern areas (Miyamoto et al. 2020). In addition, Pacific saury show longitudinal variation in their growth and maturity, with a higher rate of growth and maturity observed in the western area than in the eastern
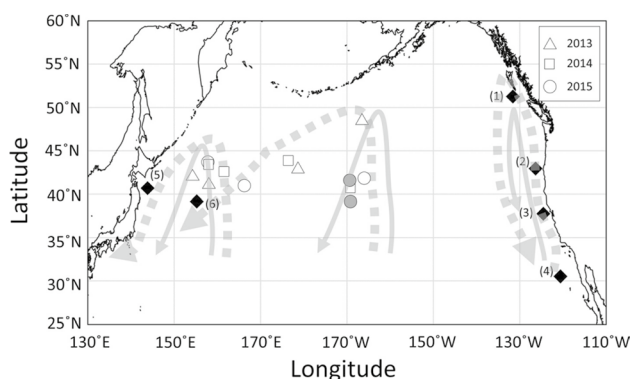
area (Watanabe et al. 1988; Suyama et al. 2012b, 2019). Such geographical variation in biological indices might stem from the geographical variation in the ecosystems to which the species belongs. For example, Shiomoto and Hashimoto (2000) reported differences in phytoplankton size composition and standing stock between the western and eastern parts of the North Pacific Ocean in early summer. Demonstrating the spatial variation in the ecosystems experienced by Pacific saury during its northward migration is essential for understanding the spatial variation observed in its growth and maturity.

Carbon and nitrogen stable isotope ratios (δ^{13}C and δ^{15}N, respectively) of organisms reflect those of their prey (Minagawa and Wada 1984; Post 2002). These values may be indicative of the feeding ecology of organisms and/or basal ecosystem differences (Tanaka et al. 2008; Miller et al. 2011; Navarro et al. 2013). In general, the stable isotope ratios of plankton at the base of oceanic ecosystems change geographically because of the heterogeneity in biogeochemical processes, such as nitrogen metabolism and phytoplankton production (Saino and Hattori 1987; Minagawa et al. 2001). The stable isotope ratios of small organisms at lower trophic levels, such as Pacific saury, could be good indicators of the ecosystems and prey environments these organisms have encountered (Takai et al. 2000).

Previous studies have examined δ^{13}C and δ^{15}N of Pacific saury distributed in coastal areas in the North Pacific Ocean (Table 1). Markedly higher δ^{15}N values were reported for populations within the eastern distribution area (~ 14%; Davies et al. 2009; Miller et al. 2010; Madigan et al. 2012; Carle et al. 2015) than those in the western North Pacific Ocean (~ 9%; Minami et al. 1995; Mitani et al. 2006). These differences imply that the prey environments and ecosystems where Pacific saury grew up differ by intraspecies. However, no previous studies have focused on the spatial variations in δ^{13}C and δ^{15}N of Pacific saury in its main distributional area of the west-central North Pacific Ocean in early summer. The δ^{13}C and δ^{15}N of Pacific saury in this area could provide fruitful information to understand the geographical variation of Pacific saury growth and maturity as well as its feeding habits during its northward migration.

The objectives of this study are therefore to describe the geographical patterns of δ^{13}C and δ^{15}N in Pacific saury in the west-central North Pacific Ocean during the early summer season and to identify the geographical differences in the energy resources it utilizes during its northward migration.

Fig. 1 Locations of the sampling stations in the North Pacific Ocean at which fish were collected in 2013, 2014, and 2015. Filled circles: stations at which Pacific saury gut contents were collected for stable isotope analysis. Black diamonds: locations where stable isotope ratios for Pacific saury were reported (Table 1). Gray arrows with solid and broken lines indicate schematic images of migration routes of age-0 and age-1 Pacific saury from spring to winter, respectively

Materials and methods

Field sampling

The Pacific saury were collected from stations between 154° E and 165° W in the central and western North Pacific

Table 1 Published $\delta^{15}N$ and $\delta^{13}C$ data for muscle tissue of Pacific saury collected in the North Pacific Ocean

Location	n	$\delta^{15}N$ (%)		$\delta^{13}C$ (%)		Body length (mm)	Year/Month	Remarks	Reference
		Mean	SD/SE	Mean	SD/SE				
1	10	14.31	0.23 SE	−20.36	0.30 SE		2002/late Mar–late Aug		Davies et al. (2009)
2	41	12.8	0.1 SE	–	–		2000 and 2002/Jun and Aug		Miller et al. (2010)
3	10	13.98	1.1 SD	−19.12	0.7 SD	84–145	2012/Jun–Jul	From bird gut contents	Carle et al. (2015)
4	20	13.21	0.76 SD	−18.85	0.26 SD	92 ± 31 (mean ± SD)	2007–2010/Jun–Oct	From bird gut contents	Madigan et al. (2012)
5	15	9.3	1.4 SD	−19.6	0.6 SD		1996/Aug	From whale gut contents	Mitani et al. (2006)
6	15	9.2	0.58 SD	−18.5	0.58 SD		1986,1989 and 1990/ Apr–Jun		Minami et al. (1995)

Numbers in the "Location" column correspond to those in Fig. 1. Note that the definitions of body length in these references were different from this study.

SD standard deviation, *SE* standard error, *n* sample size

Ocean by a towing sea surface trawl net (NST-99; Nichimo Co. Ltd.) at a speed of ca. 5 kn for 1 h (Ueno et al. 2004, 2017) behind the training vessel *Hokuho-Maru* (Hokkaido Board of Education Management for Training Ships, Hokkaido, Japan) and the research vessel *Hokko-Maru* (Fisheries Research and Education Agency, Japan) in June and July of 2013, 2014, and 2015 (Table 2, Fig. 1). Four or five stations were set widely in a west–east direction each year to investigate mainly the longitudinal variation in the stable isotope ratios. Net widths during trawling on *Hokuho-Maru* and *Hokko-Maru* were 24.0 m and 34.7 m, respectively, footline depth varied between 20 and 25 m, net length was 90 m, and maximum and minimum stretched mesh sizes were 15.2 m and 16.7 mm, respectively. Twenty individuals of Pacific saury were randomly selected for each station and, in total, 260 individuals were provided for stable isotope ratio analysis. They were frozen onboard for transport to the laboratory and subsequent measurement and analysis. The water temperature at 100 m depth (T_{100}) was obtained at each station using a conductivity temperature depth profiler (CTD, Seabird SBE 911plus). T_{100} indicated latitudinal variations in the water domain including the subarctic water and the transition domain (Favorite et al. 1976). Sea surface temperature (SST, °C) was measured with a bar thermometer.

Laboratory analysis

Prior to stable isotope analysis, knob lengths (KnL, distance from the tip of the lower jaw to the posterior end of the muscular knob on the caudal peduncle; Kimura 1956) were measured in the laboratory to the nearest millimeter. Then, otoliths were extracted from all individuals to determine the age. The right otolith of each individual was embedded in epoxy resin and examined under a light microscope. The age (0 or 1 year) was determined from the absence or presence of annual rings (Suyama et al. 2006). The lateral muscle anterior to the dorsal fin was excised for stable isotope analysis. The gut contents were also extracted from 17 individuals of both ages (251–312 mm KnL) used for muscle stable isotope analysis at two stations in 2015 (Table 2). The gut contents were applied to stable isotope analysis without prey species identification. The stations where gut samples were collected were located east of 170° W at different latitudes (Fig. 1). The lipids of the fish tissues and gut contents were extracted by drying the material at 60 °C overnight and re-grinding it in a 2:1 chloroform:methanol mixture. Stable isotope ratios were measured with a stable isotope ratio mass spectrometer (DELTA V Advantage; Thermo Fisher Scientific, Waltham, MA, USA) and calculated as parts per thousand (%) deviations from the international standard using the following equation:

$$\delta X = 1000 \times \left(R_{\text{sample}} - R_{\text{standard}} \right) / R_{\text{standard}}, \qquad (1)$$

where X represents ^{15}N or ^{13}C and R is the $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio for either the sample or the standards. The standards used in these analyses were Pee Dee Belemnite for C and air for N. Glycine, *L*-alanine, *L*-histidine or acetanilide were used as secondary standards. Each had a standard deviation of <0.2%.

Data analysis

A hierarchical cluster analysis based on Euclidean distance and Ward's minimum variance method was performed to identify groups of individuals according to their $\delta^{13}C$ and

Table 2 Sample results of stable isotope ratio analyses

Year	Date	Latitude	Longitude	Temperature (°C) 0 m	Temperature (°C) 100 m	Sample	n	Knob length (mm)	δ¹⁵N (‰) Median	Max	Min	δ¹³C (‰) Median	Max	Min
2013	June 24	41°26'N	159°00'E	13.8	11.0	Pacific saury (age-1)	20	303–322	7.4	8.3	6.7	−21.3	−20.7	−21.6
	June 28	42°18'N	154°58'E	11.8	7.7	Pacific saury (age-1)	20	290–320	7.7	8.3	6.9	−21.0	−20.4	−21.3
	June 28	43°16'N	179°58'W	10.2	8.6	Pacific saury (age-1)	18	269–317	7.0	8.7	6.1	−21.5	−20.6	−21.9
						Pacific saury (age-0)	2	266–273	6.4	6.9	5.9	−20.4	−20.1	−20.6
	July 13	48°34'N	165°01'W	10.4	4.2	Pacific saury (age-1)	20	273–317	11.7	13.5	7.8	−20.1	−19.5	−21.3
2014	June 24	42°29'N	162°58'E	9.9	5.5	Pacific saury (age-1)	20	291–329	6.8	8.2	5.6	−20.9	−20.2	−21.4
	June 28	42°02'N	169°00'W	13.6	10.1	Pacific saury (age-1)	18	286–323	8.9	9.7	7.0	−20.2	−20.0	−20.7
						Pacific saury (age-0)	2	278–287	7.7	8.5	6.9	−20.6	−20.4	−20.7
	June 29	43°01'N	158°57'E	11.4	6.2	Pacific saury (age-1)	20	285–327	6.8	8.0	5.6	−21.2	−20.2	−22.0
	July 15	43°46'N	177°58'E	13.1	6.7	Pacific saury (age-1)	18	275–325	8.0	9.0	6.7	−20.5	−19.7	−21.0
						Pacific saury (age-0)	2	255–273	6.8	7.0	6.6	−20.9	−20.6	−21.2
2015	June 10	41°02'N	166°57'E	12.8	12.1	Pacific saury (age-1)	20	282–322	7.5	8.3	6.8	−20.9	−20.4	−21.4
	June 28	43°31'N	158°51'E	11.8	8.4	Pacific saury (age-1)	20	277–306	8.1	8.7	7.1	−20.6	−20.2	−21.4
	July 2	39°08'N	168°58'W	14.4	10.5	Pacific saury (age-1)	5	288–331	9.2	10.2	8.3	−19.9	−19.4	−20.3
						Pacific saury (age-0)	15	249–287	7.9	9.0	6.4	−20.0	−19.6	−20.5
						Gut contents	10	–	5.1	6.0	3.8	−19.2	−18.9	−20.0
	July 3	41°33'N	169°02'W	12.8	8.7	Pacific saury (age-1)	17	293–317	9.6	13.7	8.8	−20.0	−19.5	−20.7
						Pacific saury (age-0)	3	268–274	7.7	8.0	7.6	−19.9	−19.8	−20.1
						Gut contents	7	–	5.0	5.7	4.1	−21.8	−21.2	−22.5
	July 7	41°54'N	164°59'W	12.8	8.4	Pacific saury (age-1)	19	285–326	12.7	14.0	9.2	−20.6	−19.7	−20.9
						Pacific saury (age-0)	1	273	8.8	8.8	8.8	−20.2	−20.2	−20.2

n sample size

δ^{15}N. The number of groups was arbitrarily selected based on its interpretability. Analysis of variance (ANOVA) was used to determine significant differences in KnL among groups of age-1 individuals. ANOVA was not performed for age-0 individuals because their sample was too small for statistical analysis. Linear models were constructed for each group to evaluate the relationship between δ^{15}N ratio and KnL. All analyses were done using the R statistical program.

Results

Hydrological conditions

The SST ranged from 9.9 to 14.4 °C (Table 2). In general, the higher the latitude, the lower the SST. T_{100} ranged from 4.2 to 12.1 °C. The lowest T_{100} was observed at the northeastern-most station in 2013. These values correspond to a transition domain based on the water mass criteria of Favorite et al. (1976).

Stable isotope ratios of Pacific saury and its gut contents

Two hundred and thirty-five individuals out of 260 (90.4%) were identified as age-1 and ranged from 269 to 331 mm KnL. Twenty-five individuals (9.6%) were identified as age-0 and ranged from 249 to 287 mm KnL (Table 2).

The δ^{15}N of the age-1 individuals sampled from the stations west of 170° W ranged from 5.6 to 9.0% (Table 2). The median for those stations ranged from 6.8 to 8.1%. The δ^{13}C ranged from −22.0 to −19.7% and the median ranged from −21.5 to −20.5% (Table 2). The frequency distributions of δ^{15}N and δ^{13}C were unimodal west of 170° W (Fig. 2). In contrast, a bimodal distribution was observed for δ^{15}N of the individuals east of 170° W (mode values of ~ 9.5% and ~ 13.0%; Fig. 2). In this area, the range of median δ^{13}C for the age-1 individuals was higher (−20.6 to −19.9%) than that for the same age of individuals in the stations west of 170° W (−21.5 to −20.5%; Table 2). A histogram plotting δ^{13}C as a function of longitude showed a unimodal pattern (Fig. 2). A declining trend in the mode values of both stable isotope ratios against latitude was observed from 38° N to 44° N, followed by a slight increase in 48° N to 50° N (Fig. 3). The range of δ^{15}N was specifically wide in 40° N–42° N and 48° N–50° N.

Age-0 individuals also exhibited increasing trends in δ^{15}N and δ^{13}C from west to east. Nevertheless, the mode of the δ^{15}N for age-0 individuals east of 170° W was lower than that for the age-1 individuals in the same area (Fig. 2, Table 2). Age-0 individuals did not present high δ^{15}N (~ 13.0%), unlike age-1 individuals (Fig. 2, Table 2). The δ^{15}N and δ^{13}C of age-0 individuals appear to decrease with latitude (Fig. 3).

The gut contents of Pacific saury caught east of 170° W were near 5.0% in δ^{15}N regardless of station position (Table 2). However, there was a greater variation in gut content for δ^{13}C, ranging from −22.5 to −18.9% (Table 2).

Characteristics of Pacific saury groups identified by cluster analysis

A cluster analysis based on individual δ^{13}C and δ^{15}N yielded three major groups by the Euclidean distance cutoff at 100 characterized mainly by their δ^{15}N (Fig. 4). Hereafter, these groups are referred to as G1 (δ^{15}N, 12.9 ± 0.6%; δ^{13}C, -20.3 ± 0.4‰ in mean ± standard deviation), G2 (δ^{15}N, 9.3 ± 0.8%; δ^{13}C, -20.1 ± 0.3%), and G3 (δ^{15}N, 7.3 ± 0.6‰; δ^{13}C, -20.9 ± 0.4%) in descending order of the mean δ^{15}N (Fig. 4). G1 comprised only age-1 individuals, and all age-0 individuals were included in G2 and G3 (Fig. 5). The δ^{15}N of each group remained constant as KnL increased (Fig. 5). No significant correlation was detected between δ^{15}N and KnL for any group ($P > 0.01$). There were no significant differences in the KnL of the age-1 individuals among the three groups ($P > 0.01$). The unique distribution patterns of each cluster are represented by the cluster composition at each sampling station (Fig. 6). G1 occurred only in the area east of 170° W in 2013 and 2015. The proportions of G1 were 0–70% in the area east of 170° W and 0% in the western area. G2 predominated in the area east of 170° W (30–75%), whereas G3 mainly occupied the area west of 170° W (70–100%).

Discussion

This study shows that stable isotope ratios, especially δ^{15}N, tended to differ between the western and eastern sides of 170° W of the North Pacific Ocean (Fig. 2). Based on these results, hereafter, we divide the study area into the areas east (EA) and west (WA) of 170° W.

It is important to evaluate tissue turnover in order to interpret the feeding history reflected in the stable isotope values. However, no turnover rate data is currently available for Pacific saury. For this reason, we applied the allometry equation proposed by Zanden et al. (2015), which associates individual body weight with muscle tissue half-life. We took 150 g as the general body weight of age-1 Pacific saury (Kosaka 2000) and obtained a half-life of 69 days. Therefore, the stable isotope ratios of Pacific saury reflect smooth feeding habit data within a half-year and focus around the nearest 1–2 months. According to the calculated half-life value, the δ^{15}N and δ^{13}C of Pacific saury are indicative of its feeding habits during its northward migration, which starts in spring,

Fig. 2 Histograms of δ^{15}N and δ^{13}C of age-1 (above) and age-0 (below) Pacific saury in each ten-degree longitudinal area

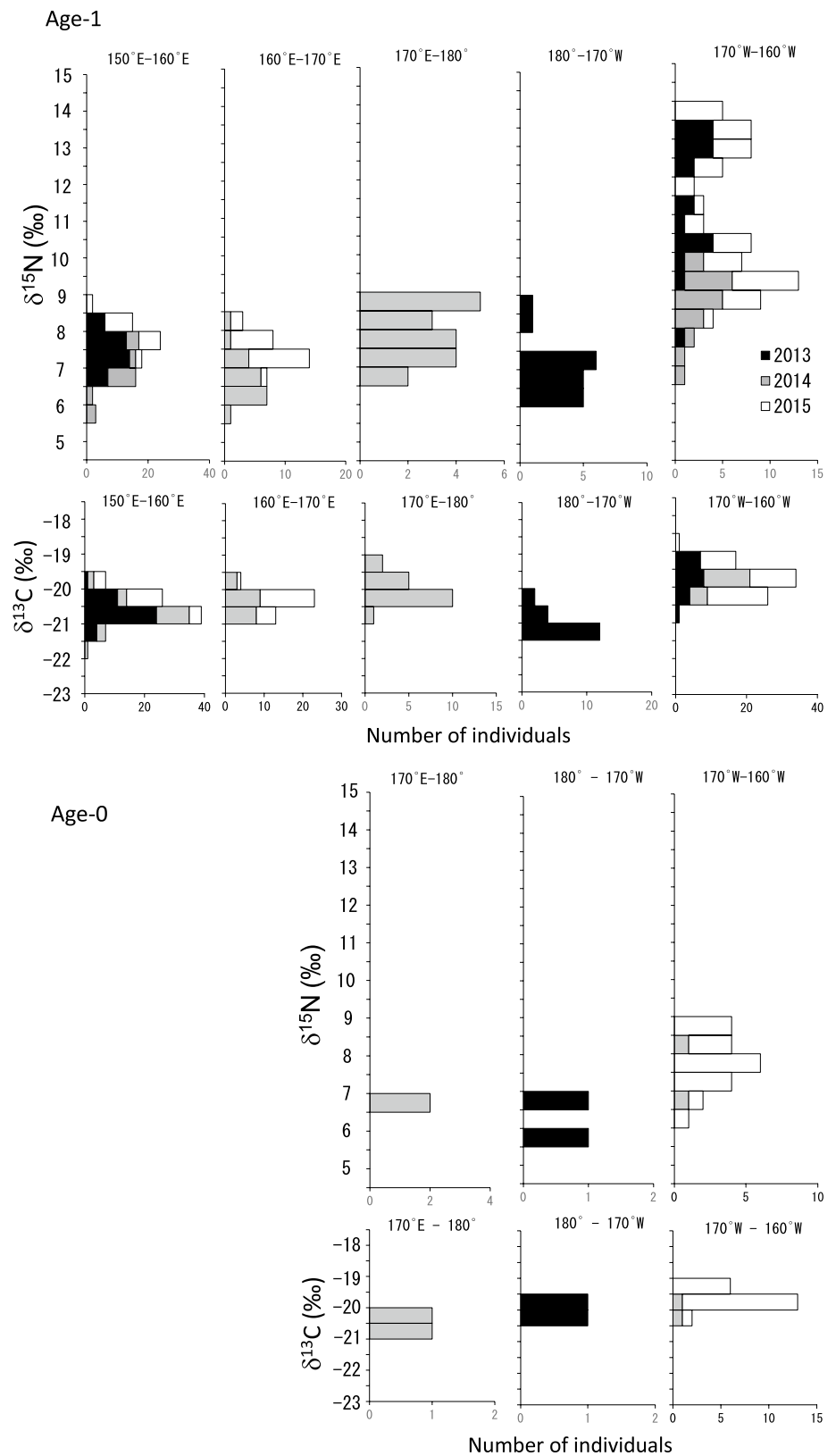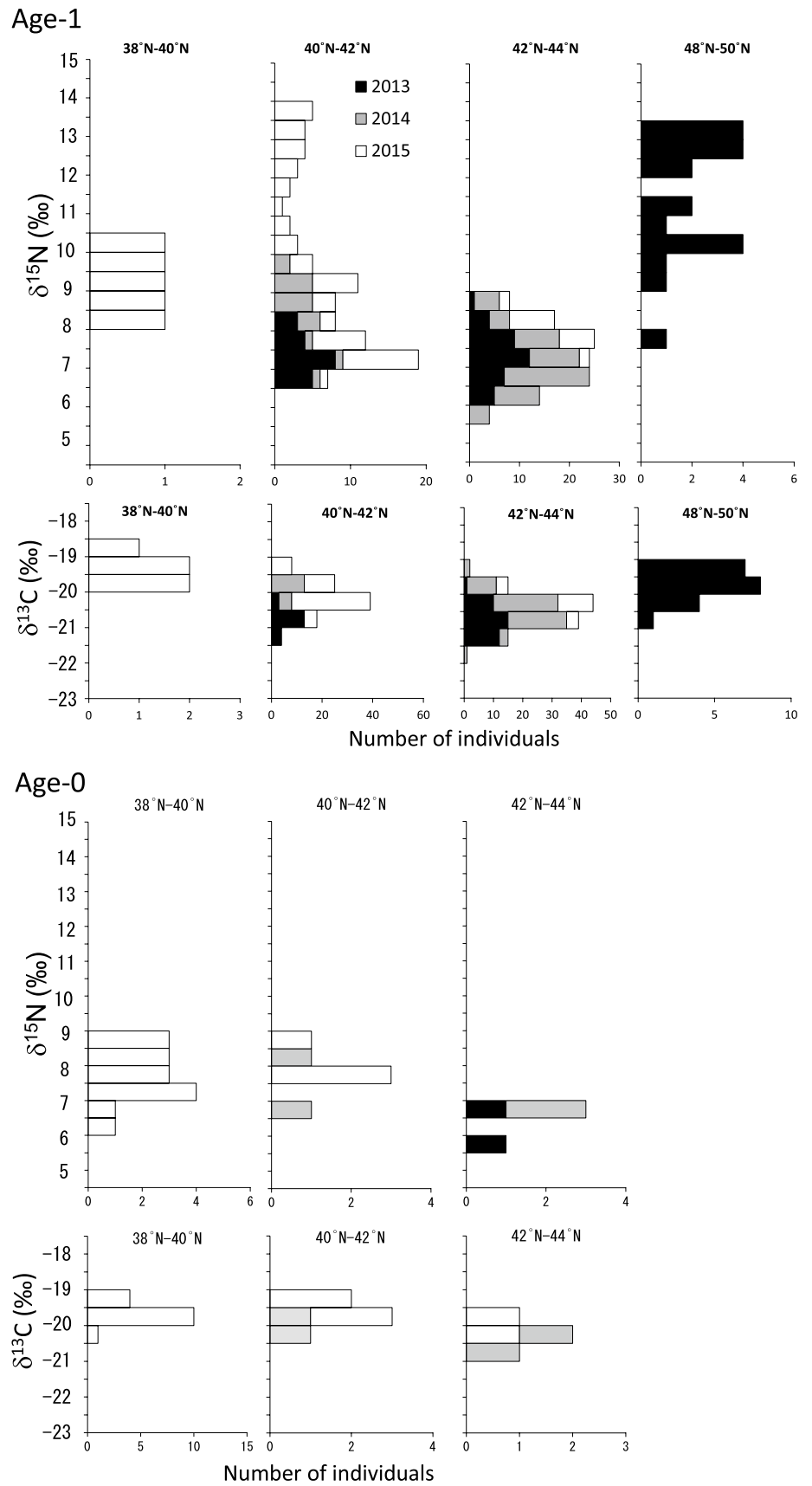**Fig. 3** Histograms of δ^{15}N and δ^{13}C of age-1 (above) and age-0 (below) Pacific saury in each two-degree latitudinal area
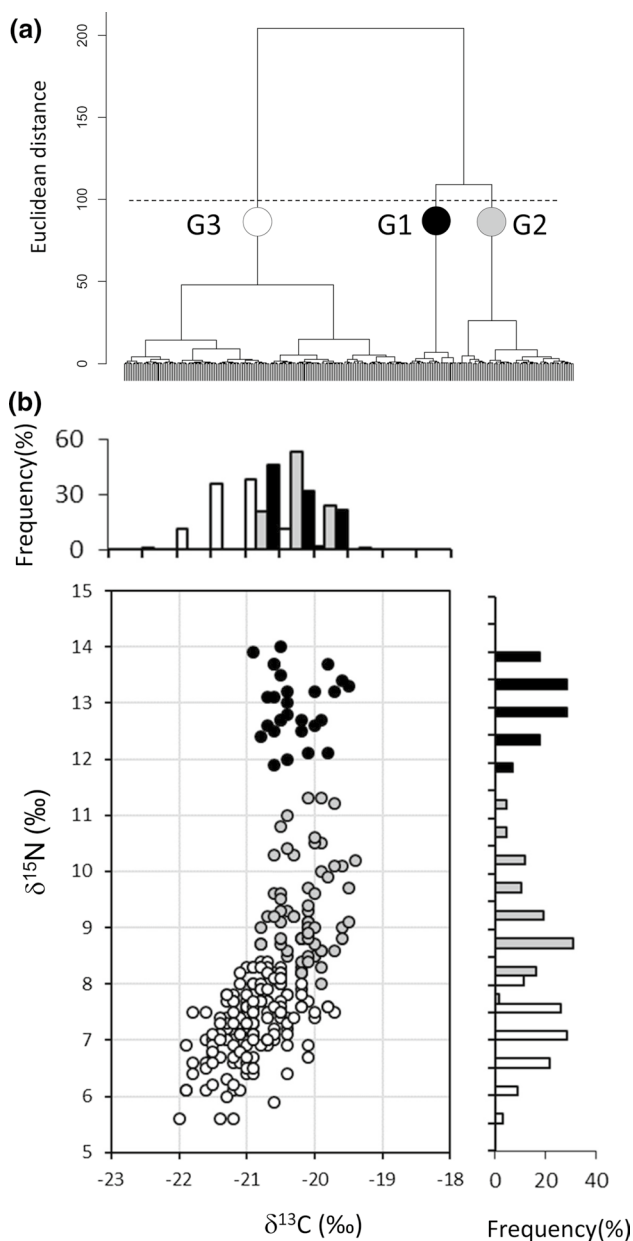
(a)

(b)

Fig. 4 a Cluster analysis dendrogram of Pacific saury created with individual $\delta^{15}N$ and $\delta^{13}C$. Broken line: levels at which the groups are established in the dendrogram. Names and legends of the groups are defined on the sides of the branches. **b** Scatterplots of $\delta^{15}N$ and $\delta^{13}C$ of Pacific saury. Black, gray, and white circles indicate G1, G2, and G3, respectively. Histograms of $\delta^{13}C$ and $\delta^{15}N$ for each group are indicated above and to the right of the scatterplot, respectively

Fig. 5 Relationships between knob length (KnL, mm) and $\delta^{15}N$. Black, gray, and white plots indicate G1, G2, and G3 classified by the cluster analysis, respectively. Triangles and circles indicate age-0 and age-1 Pacific saury, respectively

although it should be noted that this allometry equation does not account for the developmental changes in growth rate that occur as the fish passes from larva to juvenile to adult.

Ontogenetic dietary shifts with increasing trophic levels may cause variations in $\delta^{15}N$, which can differ substantially depending on the trophic level (e.g., Morinville and Rasmussen 2006; Graham et al. 2007). However, it is well
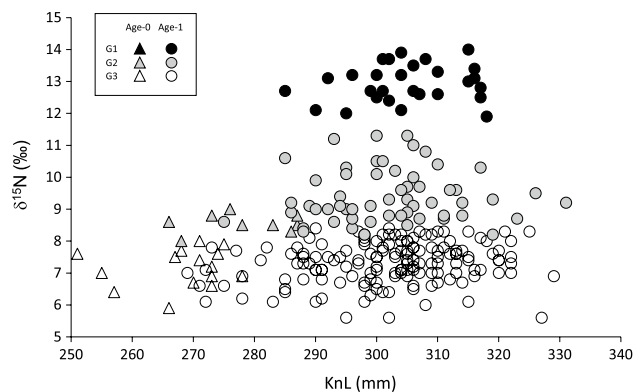
known that Pacific saury feed on zooplankton throughout their life (Odate 1977; Taka et al. 1982; Miyamoto et al. 2020). Feeding habits of Pacific saury change according to the ambient prey environment rather than age/KnL (Miyamoto et al. 2020). This study indicated that the relationship between KnL and $\delta^{15}N$ was not significant for any group (Fig. 5). In addition, $\delta^{15}N$ values for small age-0 individuals previously reported from the west coast of the United States (Table 1) are much higher than those of age-1 individuals in WA in this study, supporting the idea that the sampling location would be more important than size and/or trophic level in determining the $\delta^{15}N$ of Pacific saury. Thus, the observed variations in $\delta^{15}N$ were not caused by increases in the trophic level with growth. The longitudinal difference in stable isotope ratios of Pacific saury would stem from those of prey zooplankton.

The difference in $\delta^{15}N$ between Pacific saury and its prey could be interpreted as a trophic enrichment of Pacific saury. The difference in $\delta^{15}N$ between the dominant group in EA (G2, average 9.3%) and its gut contents (5.0–5.1%) was similar to the general difference between a predator and its diet (3.4 ± 1.1%; Minagawa and Wada 1984). Thus, this value could be assumed to indicate a trophic enrichment of Pacific saury in $\delta^{15}N$. The difference in $\delta^{15}N$ between the dominant group of Pacific saury in WA (G3, 7.3% in average) and *Neocalanus* copepods, which is known as the main prey item (Odate 1977; Taka et al. 1982; Miyamoto et al. 2020), in the same area (~ 3%, Chiba et al. 2012) is also similar (~ 4.3%), supporting this assumption. This result suggests that *Neocalanus* copepods are important prey for the energy supply of Pacific saury during northward migration after spring, as mentioned by previous studies analyzing the gut contents (Odate 1977; Taka et al. 1982; Miyamoto et al. 2020).

The difference in $\delta^{15}N$ between G2 (dominant in EA, 9.3% in average) and G3 (dominant in WA, 7.3% in average)

Fig. 6 Spatial variation in the compositions of Pacific saury groups G1 (black), G2 (gray), and G3 (white). Upper, middle, and lower figures represent the data for samples collected in 2013, 2014, and 2015, respectively. Locations of pie charts indicate sampling stations
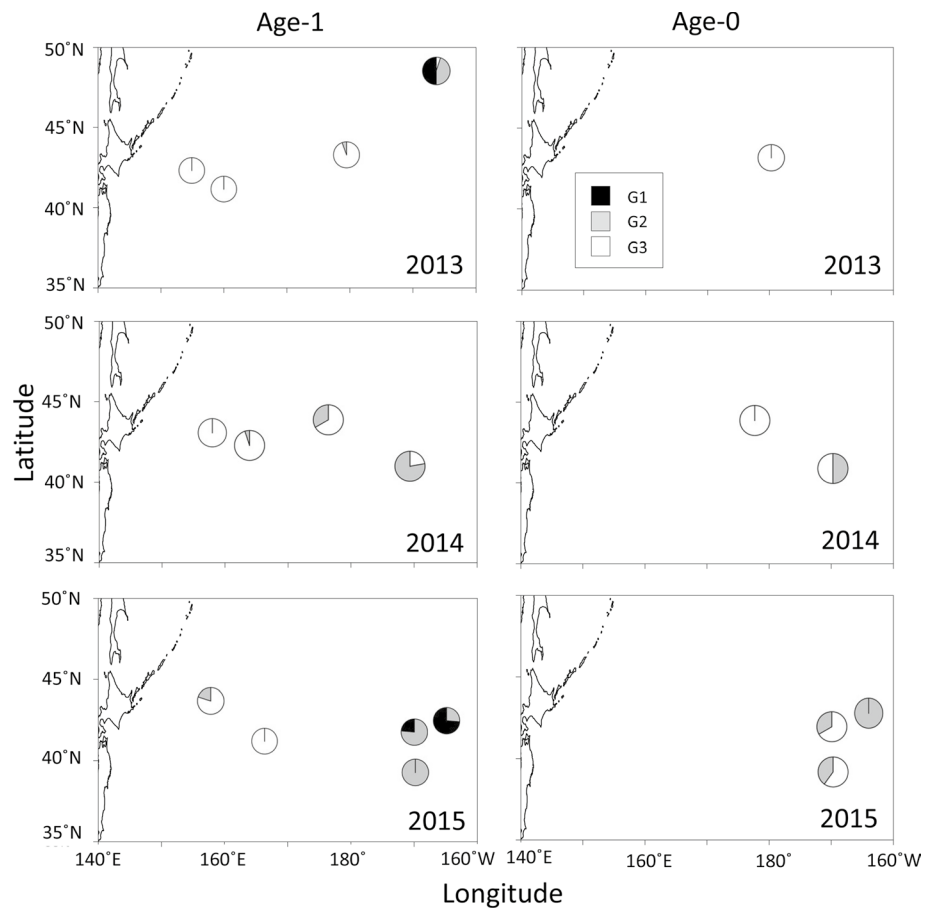
may be explained by the inequalities between EA and WA in terms of the δ^{15}N of their prey. Geographical differences in δ^{15}N of prey items of Pacific saury might be explained by variations in phytoplankton nutrient availability. Previous studies reported that surface nitrate concentration was negatively correlated with δ^{15}N of nitrate and particulate organic matter (POM) in the transition domain (Horii et al. 2018; Yoshikawa et al. 2018) because the degree of isotope fractionation was influenced by phytoplankton nitrate availability (Saino and Hattori, 1987; Minagawa et al. 2001). In fact, several studies showed that the regional δ^{15}N of copepods was lower in the western part (160° E-180°) than the eastern part (180°–145° W) of the transition domain, corresponding to the surface nitrate distribution and its seasonal drawdown (Chiba et al. 2012; Matsubayashi et al. 2020).

However, the substantially enriched δ^{15}N observed in G1 (mean: 12.9%) is not explained by δ^{15}N of local potential prey items in EA and general trophic enrichment. This unexpected δ^{15}N resembles the values measured for fishes and squid at higher trophic levels in the central and eastern North Pacific Ocean (Welch and Parsons 1993; Kaeriyama et al. 2004; Parry 2008; Choy et al. 2015), despite the zooplanktivory of Pacific saury (Miyamoto et al. 2020). Given the estimated half-life of ca. 70 days and its high migratory

ecology, one possible explanation for the substantially enriched δ^{15}N observed in G1 is that it is an immigrant from outside our survey area where prey items with enriched δ^{15}N were distributed. This might be the reason why G1 comprised only age-1 individuals, because age-1 individuals have higher migration ability than age-0 individuals (Yasuda and Kitagawa, 1996). Several studies reported the distribution of enriched δ^{15}N of nitrate in the southeastern part of the transition domain (30° N-42° N, east of 160° W), where the nitrate concentration was low (Somes et al. 2010; Matsubayashi et al. 2020). Previous studies also reported similarly enriched δ^{15}N in Pacific saury off the west coast of the United States (Table 1). Pacific saury with substantially enriched δ^{15}N (G1) might migrate from such an area with low nitrate concentration. Distribution and stable isotope ratios of Pacific saury and its prey items in the southeastern part of the transition domain (30° N-42° N, east of 160° W) should be further examined to estimate the precise origin of G1.

δ^{13}C of POM are determined in part by the growth rate of phytoplankton and concentration of dissolved inorganic carbon (DIC) in seawater (Takahashi et al.1991). The value of ^{13}C/^{12}C ratios is controlled by the ratio of dissolved inorganic carbon in seawater and physiological processes such

as respiration and photosynthesis (Spero et al. 1997), and a negative relationship between δ^{13}C and concentration of DIC has been found. Meanwhile, phytoplankton δ^{13}C is enriched during algal blooms because biological carbon fractionation decreases with increasing growth (Takahashi et al. 1991; Laws et al. 1995). We observed a decreasing tendency of δ^{13}C of Pacific saury from south to north and from east to west (Figs. 2 and 3). Such a tendency is generally observed in the western North Pacific Ocean (Ohshimo et al. 2019). On the other hand, the estimated DIC concentration was higher in the northwest and lower in the southeast part of the North Pacific Ocean (Yasunaka et al. 2013). Given the negative relationship between δ^{13}C and concentration of DIC, the geographical pattern of δ^{13}C of Pacific saury may generally agree with that of DIC concentration. Higher primary production in the western area (Shiomoto and Hashimoto 2000) might lead to higher δ^{13}C in the WA, although our results showed an inverse pattern. DIC concentration may be the dominant factor determining the δ^{13}C of POM in the North Pacific Ocean.

The geographical pattern of stable isotope ratios, especially longitudinal tendency, shown in this study could be related to longitudinal differences in the growth and maturity of this fish (Suyama et al. 2012b and 2019). Higher δ^{15}N of G2 than G3 might be due to lower nitrate concentration in EA than WA, implying the lower productivity in EA (e.g., Shiomoto and Hashimoto 2000; Yasunaka et al. 2013). The higher growth rate and earlier age at maturation in the WA than the EA (Suyama et al. 2012b and 2019) may stem from the higher productivity and better prey environment in the WA than the EA. As the next step, the geographical difference in stable isotope ratios of phytoplankton and/or zooplankton in the west-central North Pacific Ocean should be studied as well as the heterogeneity of ambient prey abundance to understand the geographical variation in the growth and maturity of Pacific saury.

The clear difference in stable isotope ratios between WA and EA also suggests that the population does not mix between these two areas, at least during its northward migration. This idea is supported by the previous hypothesis for the migration route (Fig. 1). Although these results suggest that there are different stocks of Pacific saury in the east and west of the North Pacific Ocean, Chow et al. (2009) indicated that there is no genetic structure of Pacific saury within its distribution. This fish might mix well during extensive southwestward migration after the summer season (Miyamoto et al. 2019).

The stable isotope ratios of Pacific saury and the composition of clusters based on them varied from year to year, even in the same area. For example, in the area west of 160° E, δ^{15}N values were higher in 2015 than in 2013 and 2014, and thus the percentage of G2 was higher in 2015. Such interannual variability might be influenced by the availability of

nitrogen in the area, but this could not be fully verified in the present study. In the future, it is necessary to clarify the spatiotemporal changes in the stable isotope ratios of Pacific saury by using a more extensive multi-year data set covering a broader transition region (especially north–south direction) which can be applied to statistical modelling.

After early summer, Pacific saury migrate southwestward and recruit to fishing ground formed west of 160° E in autumn (Miyamoto et al. 2019). The longitudinal difference in the stable isotope ratios of Pacific saury in early summer suggests that these ratios could be useful natural tags for estimation of the origin of this fish caught by fisheries (e.g., Tawa et al. 2017). Thus, an informative next research step would be the measurement of stable δ^{15}N and δ^{13}C ratios for Pacific saury in their fishing grounds during autumn. In this way, the migration dynamics of this species may be delineated from the central open ocean to the western region of the North Pacific near Japan. This information would contribute to the reasonable and sustainable management of this species.

In conclusion, this study showed that Pacific saury utilize subarctic copepods, such as *Neocalanus* spp., as the main energy resource during their northward migration, and that Pacific saury showed higher δ^{15}N in the EA than in the WA. We also found a group in the EA with a different origin, which experienced another prey environment outside the study area. Such information implies the heterogeneity of the prey environment and would aid in understanding the geographical variation in the growth and maturation of Pacific saury (Suyama et al. 2012b and 2019).

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