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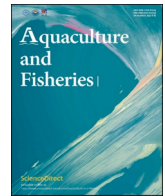


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Geographical and species differences of fatty acid components of small pelagic fishes, micronekton, and squids in the northwestern pacific

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ABSTRACT

Geographical and species differences in fatty acid composition were evaluated among 546 specimens of small pelagic fish, micronekton, and squid in the Northwestern Pacific. For all species except for four micronekton species, the dominant fatty acid was docosahexaenoic acid (DHA). The ratios of ω 3 to ω 6 fatty acids and DHA to eicosapentaenoic acid (EPA) differed among species and organisms. ω 3: ω 6 and DHA:EPA were generally lower in micronekton than in squids and small pelagic fishes. The ω 3: ω 6 values in the northeastern area was higher than that in the southwestern area, meanwhile the DHA:EPA values in the northeastern area was lower than that in the southwestern area. Geographical differences in fatty acid components, DHA:EPA, and ω 3: ω 6 could have been caused by environmental factors as well as by regional differences in the quality and quantity of phytoplankton-produced organic matter. Non-metric multidimensional scaling of the main fatty acid components showed clear species and geographical differences. A permutational multivariate analysis of variance revealed significant differences among small pelagic fishes, micronekton, and squids. These results indicate that fatty acid analysis can be used to understand the ecology and ecosystem roles of various species.

1. Introduction

The Northwestern Pacific (NWP) is the largest marine ecosystem on Earth (Brodeur et al., 1999). Two major ocean currents (the Kuroshio and Oyashio) converge in this region, and the convergence zone is associated with abundant fish production (Benson & Trites, 2002; Pauly et al., 2014). Part of the western margin of the NWP is occupied by the East China Sea and Sea of Japan. The temperate waters of the Tsushima Warm Current, a branch of the Kuroshio Current, flow from south to north through both of these marginal seas (Yanagi et al., 1996). The East China Sea has a large continental shelf and is highly productive (e.g., Liu et al., 2010). The pelagic food web of this area supports numerous commercially important fish species, including Japanese sardine (*Sardinops melanostictus*), Japanese anchovy (*Engraulis japonicus*), jack mackerel (*Trachurus japonicus*), chub mackerel (*Scomber japonicus*), and common squid (*Todarodes pacificus*) (Yatsu, 2019). Effective management of these species requires the implementation of ecosystem-based fisheries management (Pikitch et al., 2004).

The complexity of the food web in the NWP poses a challenge for effective management. The region is characterized by a large biomass of

micronekton taxa such as Myctophidae (Ohshimo et al., 2012), and these micronekton together with small pelagic fish and squid are the main prey items for sharks (Fujinami et al., 2018), tunas (Hiraoka, Fujioka, et al., 2019; Ohshimo et al., 2018), and dolphins (Mitsui et al., 2014). In addition to pelagic forage species, the NWP is also inhabited by a range of medium and large apex predators (Kai et al., 2015; Ohshimo et al., 2016a, 2021; Shiraishi et al., 2010; Tanaka et al., 2020). Evaluating the effects of fisheries on marine food webs requires understanding the properties of these systems through comparison with other food webs.

Primary producers make up the base of marine pelagic food webs, and they consist of unicellular phytoplankton that fix inorganic carbon (CO_2) with the aid of sunlight (photosynthesis). The carbon fixed in the form of glucose by the phytoplankton is directed into various types of molecular components. The carbon, some of which is combined with phosphorus and/or nitrogen, makes up the building blocks of the phytoplankton cell (Jónasdóttir, 2019). These building blocks include proteins, lipids, and carbohydrates, and they are the nutritional foundation for the upper trophic levels in the marine environment, starting with secondary producers such as copepods and krill. These building

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Table 1

Species abbreviations, number of samples, body lengths, stable isotope ratios, and sampling ranges for the species examined in this study.

Scientific Name	Common Name	Abbreviation	Sample Number (FA)	Mean Body Length (mm)	Range (degree)		Sampling Month
					South-North	West-East	
Small Pelagic Fish							
<i>Cololabis saira</i>	Saury	Cs	10	284.0	40–41	145–156	Oct.
<i>Decapterus macarellus</i>	Mackerel scad	Dm	5	184.3	28–28	129–129	Jul.
<i>Engraulis japonicus</i>	Japanese anchovy	Ej	133	71.2	32–42	127–153	All Months
<i>Etrumeus teres</i>	Round herring	Et	8	240.6	37–37	137–137	May
<i>Sardinops melanostictus</i>	Japanese sardine	Sm	22	157.8	31–42	131–153	Jan. Mar. Jul. Sep. Oct.
<i>Scomber australasicus</i>	Spotted mackerel	Sa	11	247.5	31–38	131–138	Mar. Jul.
<i>Scomber japonicus</i>	Chub mackerel	Sj	154	139.5	28–42	126–153	All Months
<i>Trachurus japonicus</i>	Jack mackerel	Tj	8	72.7	34–37	130–138	Sep.
Micronekton							
<i>Ceratoscopelus townsendi</i>	Dogtooth lampfish	Ct	9	56.0	20–31	132–140	Feb. Jul.
<i>Diaphus chrysorhynchus</i>	Golden-nosed lantern fish	Dc	5	86.5	31–31	129–129	Sep.
<i>Diaphus garmani</i>	Garman's lanternfish	Dg	10	57.9	31–31	128–128	Sep.
<i>Diaphus theta</i>	California headlightfish	Dt	5	74.5	40–40	142–142	Apr.
<i>Diaphus watasei</i>	Watases lanternfish	Dw	5	103.1	38–38	141–141	Apr.
<i>Lampanyctus jordani</i>	Brokenline lanternfish	Lj	5	116.6	40–40	142–142	Apr.
<i>Maurolicus japonicus</i>	North Pacific lightfish	Mj	5	39.7	38–38	138–138	Sep.
<i>Myctophum asperum</i>	Prickly lanternfish	Ma	18	71.0	29–36	130–142	Jul.
<i>Notoscopelus japonicus</i>	Japanese lanternfish	Nj	4	129.3	40–40	142–142	Apr.
<i>Stenobrachius nannochir</i>	Garnet lanternfish	Sn	4	110.1	40–40	142–142	Apr.
<i>Symbolophorus evermanni</i>	Everman's lanternfish	Se	27	78.7	20–35	126–132	Feb. Jul. Aug.
Squid							
<i>Abralia similis</i>		As	5	19.0	31–31	132–132	Jul.
<i>Enoploteuthis chunii</i>		Ec	8	42.1	31–39	132–138	Jul.Sep.
<i>Eucleoteuthis luminosa</i>	Striped flying squid	El	20	145.1	30–37	129–142	Jul. Aug.
<i>Stenoteuthis oualaniensis</i>	Flying squid	So	29	104.0	19–31	126–132	Jun. Jul. Dec.
<i>Todarodes pacificus</i>	Common squid	Tp	31	187.1	35–40	134–138	Jan. Mar. May Aug. Oct.

blocks control the growth, reproduction, fitness, and survival of marine organisms (Jónasdóttir, 2019). Fatty acids represent a large group of molecules that comprise the majority of lipids found in all organisms. Their great diversity, biochemical restrictions and, in some cases, unique origins among plants and animals have fostered scientific studies ranging from assessment of animal nutrition and metabolism to investigation of trophic interactions and ecosystem structure (Budge et al., 2006).

One way to evaluate food-web structure is to use chemical biomarkers. Fatty acids (FAs) are particularly effective as trophic biomarkers (Dalsgaard et al., 2003), as reviewed in marine systems by Budge et al. (2006). Ecosystem activities or functions can be defined in terms of the physical, chemical, and biological processes that transform and translocate energy or materials in an ecosystem (Naeem, 1998), and FA signatures are one way to track this transformation and translocation. To date, however, there have been no evaluations of ecosystem activities or functions based on FA signatures in the waters around Japan. Therefore, detailed FA signatures should be obtained from this region.

FA analysis has previously been used successfully to examine pelagic species in other regions. For example, Pacific bluefin tuna (*Thunnus orientalis*) has been shown to acquire different FA signatures in its two spawning grounds (Hiraoka, Okochi, et al., 2019; Hiraoka et al., 2022; Matsumoto et al., 2018), with the percentage of the FA eicosapentaenoic acid (EPA) being higher in individuals caught in the Sea of Japan than in the Pacific. Additionally, Yasuda et al. (2021) reported that concentrations of long-chain polyunsaturated fatty acids (LC-PUFAs) in the muscle of Japanese sardine decrease during the spawning period in this species. Similarly, the composition of LC-PUFAs in chub mackerel varies by body size and geographical area (Ohshimo et al., 2022). These results show the promise of FA analysis for constructing pelagic food webs and evaluating the ecology of pelagic species.

Although several previous studies have examined the FAs of pelagic fish, most to date have only been conducted on a single species. In the present study, we collected many species of pelagic fish and squid in the NWP and compared their FA compositions. The objectives of this study were to analyze the FA compositions of pelagic forage species to identify any geographical and species differences in FA signatures. To understand the ecology and ecosystem roles of various species, we used analysis of variance (ANOVA) to determine whether there were differences between species in terms of their main FAs, $\omega 3:\omega 6$ ratios, and DHA:EPA ratios as described in a previous study (Ohshimo et al., 2022).

2. Materials and Methods

2.1. Sample collection

Forage fish and squid were collected by using mid-water trawls in scientific surveys, as well as with purse seines and set nets. Sampling occurred mainly in three areas: the East China Sea, Sea of Japan, and Pacific Ocean (Table 1; Fig. 1). Samples were measured for fork length to the nearest millimeter and body weight to the nearest gram. The dorsal muscle (for fish) or mantle (for squid) was excised and immediately frozen. The Samples of Animal Statement as follows: All experimental animal protocols in this study were reviewed and approved by Fisheries Research and Educational Agency guideline (No. 284, dated 03/31/2021), and all experimental animal protocols were carried out by following the guidelines of Guidelines for animal experiments at Fisheries Resources Institute, Japan, Japan Fisheries Research and Education Agency.

2.2. Fatty-acid analysis

Total lipids were extracted from samples following the method

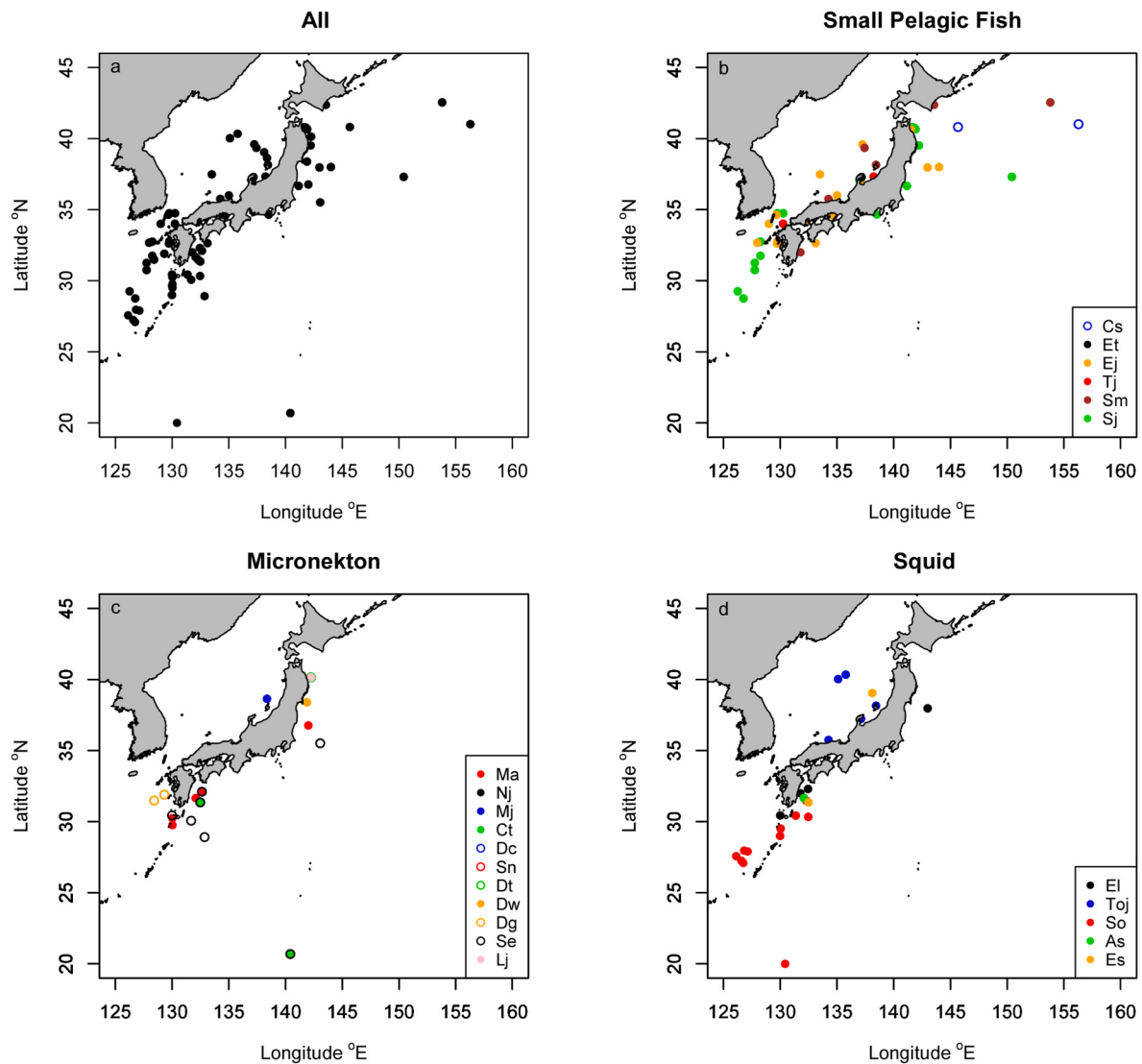


Fig. 1. Sampling sites for all specimens (a), small pelagic fish (b), micronekton (c), and squid (d). Species abbreviations in the legends are as shown in Table 1.

described by Bligh and Dyer (1959). A portion of the total lipids (1–10 mg) was converted to FA methyl esters by heating in 7% BF_3 (v/v) in methanol solution (2 mL) at 100 °C for 1 h in the presence of toluene (0.5 mL) and methyl tricosanoate (0.2–1.0 mg) as an internal standard. Methyl esters were purified by column chromatography on silica gel 60 (Merck) using a mixture of hexane/diethyl ether (90:10, v/v) for elution.

Methyl esters were analyzed using a Shimadzu GC-14 A gas chromatograph (Shimadzu, Kyoto, Japan) equipped with a Restek FAME-WAX column (30 m $\times$ 0.32 mm i. d., 0.25- μm film thickness; Restek, Bellefonte, PA, USA) and a flame ionization detector. The oven temperature was programmed to increase from 170 °C (0 min) to 240 °C at a rate of 4 °C/min and was then held at 240 °C for 24 min. Injector and detector temperatures were both 240 °C. The carrier gas was helium at a linear velocity of 33.5 cm/s at 170 °C (90 kPa). The split ratio was 20:1. Peak areas were measured with a Shimadzu C-R6A integrator.

2.3. Statistical analysis

For FA analysis, we used ANOVA to determine which factors (categories) significantly influenced ω 3: ω 6 and DHA:EPA. We used a Bray–Curtis similarity matrix and permutational multivariate ANOVA (PERMANOVA) (Anderson, 2001; McArdle & Anderson, 2001) to

investigate how FA profiles varied among species categories. Non-metric multidimensional scaling (nMDS) analysis was performed to visualize differences among categories, genera, and region of capture after the proportions of the FA components were arcsine-square-root transformed. For statistical analysis, we used R version 4.1.2 (R Core Team, 2021) with the “vegan” package (Oksanen et al., 2020). A pair-wise test was applied using the “pairwiseAdonis” package (Arbizu, 2020).

3. Results

3.1. Fatty acid components

Fatty acid analysis was carried out on a total of 546 individual fish (Tables 2–4). Chub mackerel accounted for the largest number of specimens ($n = 154$), followed by Japanese anchovy ($n = 133$). The numbers of specimens of small pelagic fish, micronekton, and squid were 356, 97, and 93, respectively.

In most of the species in the present study, 22:6 (n-3) (DHA) was the dominant FA in all species examined (Fig. 2f; Tables 2–4) except for four micronekton species California headlightfish (*Diaphus theta*), Wataes lanternfish (*D. watasei*), Japanese lanternfish (*Notoscopelus japonicus*), and Garnet lanternfish (*Stenobrachius nannochir*). The variances of DHA

Table 2Fatty acid components of small pelagic fishes (Average $\pm$ SD).

Scientific Name	<i>Cololabis saira</i>	<i>Decapterus macarellus</i>	<i>Engraulis japonicus</i>	<i>Etrumeus teres</i>	<i>Sardinops melanostictus</i>	<i>Scomber australasicus</i>	<i>Scomber japonicus</i>	<i>Trachurus japonicus</i>
n	10	5	133	8	22	11	154	8
14:0	4.83 $\pm$ 2.79	0.58 $\pm$ 0.26	1.92 $\pm$ 0.83	1.94 $\pm$ 0.71	3.66 $\pm$ 2.06	0.96 $\pm$ 1.78	1.93 $\pm$ 1.50	2.27 $\pm$ 0.52
15:0	0.40 $\pm$ 0.09	0.33 $\pm$ 0.06	0.53 $\pm$ 0.19	0.28 $\pm$ 0.06	0.41 $\pm$ 0.19	0.31 $\pm$ 0.10	0.46 $\pm$ 0.20	0.55 $\pm$ 0.10
16:0	15.40 $\pm$ 2.63	16.37 $\pm$ 1.58	21.37 $\pm$ 2.37	22.48 $\pm$ 1.10	22.78 $\pm$ 2.21	17.19 $\pm$ 1.84	18.20 $\pm$ 3.23	21.75 $\pm$ 1.24
17:0	0.31 $\pm$ 0.06	1.24 $\pm$ 0.09	0.88 $\pm$ 0.22	0.47 $\pm$ 0.08	0.61 $\pm$ 0.31	0.58 $\pm$ 0.21	0.82 $\pm$ 0.29	0.85 $\pm$ 0.13
18:0	3.12 $\pm$ 1.37	9.50 $\pm$ 0.53	4.18 $\pm$ 0.56	4.05 $\pm$ 0.22	3.83 $\pm$ 1.55	6.57 $\pm$ 1.43	6.03 $\pm$ 1.63	7.70 $\pm$ 1.33
20:0	0.14 $\pm$ 0.04	0.23 $\pm$ 0.03	0.17 $\pm$ 0.12	0.14 $\pm$ 0.04	0.24 $\pm$ 0.29	0.12 $\pm$ 0.02	0.26 $\pm$ 0.17	0.26 $\pm$ 0.12
Other saturated	1.17 $\pm$ 0.22	1.41 $\pm$ 0.32	1.16 $\pm$ 0.33	0.49 $\pm$ 0.15	0.96 $\pm$ 0.25	0.91 $\pm$ 0.16	1.41 $\pm$ 0.46	1.18 $\pm$ 0.14
16:1	3.11 $\pm$ 1.17	1.21 $\pm$ 0.14	2.68 $\pm$ 1.00	2.32 $\pm$ 0.67	4.57 $\pm$ 2.13	1.47 $\pm$ 0.65	2.69 $\pm$ 1.36	3.57 $\pm$ 0.71
17:1	0.17 $\pm$ 0.05	0.23 $\pm$ 0.08	0.24 $\pm$ 0.10	0.16 $\pm$ 0.05	0.22 $\pm$ 0.10	0.24 $\pm$ 0.09	0.27 $\pm$ 0.11	0.20 $\pm$ 0.07
18:1	6.72 $\pm$ 5.84	6.73 $\pm$ 0.60	6.07 $\pm$ 1.39	5.69 $\pm$ 1.30	10.03 $\pm$ 3.49	6.08 $\pm$ 0.50	12.04 $\pm$ 6.10	12.83 $\pm$ 3.30
20:1	9.89 $\pm$ 5.38	0.34 $\pm$ 0.04	0.42 $\pm$ 0.55	2.02 $\pm$ 0.63	3.22 $\pm$ 2.42	1.70 $\pm$ 4.06	2.78 $\pm$ 3.49	1.29 $\pm$ 0.90
22:1	10.67 $\pm$ 5.85	0.21 $\pm$ 0.03	0.33 $\pm$ 0.49	2.30 $\pm$ 0.79	2.33 $\pm$ 1.86	1.63 $\pm$ 4.38	2.30 $\pm$ 3.55	1.47 $\pm$ 1.20
24:1	1.37 $\pm$ 0.61	1.41 $\pm$ 0.18	0.97 $\pm$ 0.36	1.32 $\pm$ 0.23	1.16 $\pm$ 0.47	1.45 $\pm$ 0.30	1.22 $\pm$ 0.42	1.62 $\pm$ 0.31
Other Monoenes	0.31 $\pm$ 0.07	0.38 $\pm$ 0.07	0.40 $\pm$ 0.36	0.15 $\pm$ 0.05	0.17 $\pm$ 0.14	0.24 $\pm$ 0.11	0.29 $\pm$ 0.14	0.23 $\pm$ 0.18
18:2 (n-6)	1.10 $\pm$ 0.29	0.72 $\pm$ 0.04	0.97 $\pm$ 0.58	0.58 $\pm$ 0.15	0.96 $\pm$ 0.19	0.62 $\pm$ 0.25	1.08 $\pm$ 0.30	0.78 $\pm$ 0.23
18:3 (n-3)	0.84 $\pm$ 0.34	0.19 $\pm$ 0.02	0.53 $\pm$ 0.27	0.44 $\pm$ 0.16	0.42 $\pm$ 0.22	0.33 $\pm$ 0.24	0.61 $\pm$ 0.28	0.22 $\pm$ 0.12
18:4 (n-3)	2.49 $\pm$ 1.53	0.16 $\pm$ 0.05	0.76 $\pm$ 0.56	0.80 $\pm$ 0.39	0.96 $\pm$ 0.67	0.43 $\pm$ 0.99	0.87 $\pm$ 1.19	0.34 $\pm$ 0.08
20:2 (n-6)	0.21 $\pm$ 0.04	0.23 $\pm$ 0.03	0.19 $\pm$ 0.06	0.13 $\pm$ 0.02	0.12 $\pm$ 0.04	0.18 $\pm$ 0.04	0.22 $\pm$ 0.11	0.35 $\pm$ 0.10
20:3 (n-3)	0.16 $\pm$ 0.08	0.10 $\pm$ 0.02	0.08 $\pm$ 0.03	0.15 $\pm$ 0.05	0.08 $\pm$ 0.03	0.11 $\pm$ 0.03	0.12 $\pm$ 0.04	0.11 $\pm$ 0.02
20:3 (n-6)	0.08 $\pm$ 0.02	0.07 $\pm$ 0.02	0.07 $\pm$ 0.03	0.04 $\pm$ 0.03	0.11 $\pm$ 0.05	0.09 $\pm$ 0.02	0.11 $\pm$ 0.03	0.11 $\pm$ 0.05
20:4 (n-3)	0.64 $\pm$ 0.19	0.18 $\pm$ 0.02	0.28 $\pm$ 0.16	0.31 $\pm$ 0.07	0.49 $\pm$ 0.26	0.26 $\pm$ 0.16	0.40 $\pm$ 0.24	0.28 $\pm$ 0.10
20:4 (n-6)	0.68 $\pm$ 0.44	2.44 $\pm$ 0.37	1.48 $\pm$ 0.57	2.00 $\pm$ 0.42	1.39 $\pm$ 0.80	4.29 $\pm$ 1.31	2.28 $\pm$ 0.93	1.88 $\pm$ 0.28
20:5 (n-3)	6.18 $\pm$ 1.21	6.02 $\pm$ 0.41	9.00 $\pm$ 2.38	7.25 $\pm$ 1.19	10.72 $\pm$ 3.15	8.53 $\pm$ 1.58	8.23 $\pm$ 1.93	5.72 $\pm$ 0.79
21:5 (n-3)	0.25 $\pm$ 0.05	0.08 $\pm$ 0.01	0.19 $\pm$ 0.12	0.18 $\pm$ 0.04	0.28 $\pm$ 0.14	0.17 $\pm$ 0.05	0.19 $\pm$ 0.09	0.19 $\pm$ 0.04
22:4 (n-6)	0.14 $\pm$ 0.12	0.27 $\pm$ 0.07	0.28 $\pm$ 0.28	0.12 $\pm$ 0.07	0.23 $\pm$ 0.15	0.44 $\pm$ 0.14	0.27 $\pm$ 0.15	0.44 $\pm$ 0.16
22:5 (n-3)	1.40 $\pm$ 0.16	0.86 $\pm$ 0.06	0.80 $\pm$ 0.24	0.95 $\pm$ 0.13	1.91 $\pm$ 0.63	1.48 $\pm$ 0.22	1.47 $\pm$ 0.37	1.85 $\pm$ 0.37
22:5 (n-6)	0.41 $\pm$ 0.21	2.73 $\pm$ 0.14	0.93 $\pm$ 0.35	0.57 $\pm$ 0.05	0.71 $\pm$ 0.51	1.93 $\pm$ 0.58	1.21 $\pm$ 0.64	0.94 $\pm$ 0.43
22:6 (n-3)	26.72 $\pm$ 12.85	45.44 $\pm$ 2.57	42.44 $\pm$ 6.84	42.25 $\pm$ 5.77	25.35 $\pm$ 12.14	40.99 $\pm$ 7.18	31.49 $\pm$ 11.35	29.11 $\pm$ 4.88
Other Polyenes	1.04 $\pm$ 0.40	0.32 $\pm$ 0.07	0.60 $\pm$ 0.48	0.36 $\pm$ 0.26	1.92 $\pm$ 0.80	0.70 $\pm$ 0.32	0.71 $\pm$ 0.47	1.66 $\pm$ 0.36
Unknown	0.03 $\pm$ 0.01	0.00 $\pm$ 0.00	0.06 $\pm$ 0.06	0.07 $\pm$ 0.03	0.18 $\pm$ 0.16	0.01 $\pm$ 0.03	0.06 $\pm$ 0.07	0.25 $\pm$ 0.20

fraction in Saury (*Cololabis seira*) and chub mackerel were large (Fig. 2f). Palmitic acid (16:0) was the second-most prevalent FA in all species (Fig. 2a) except Garnet lanternfish.

The dominant FA in the four micronekton species (California headlightfish, Watases lanternfish, Japanese lanternfish and Garnet lanternfish) was oleic acid (18:1) (Fig. 2c and Table 3). The mean percentage of 18:1 in the FAs of the four micronekton species ranged from 11% to 41% (Fig. 2c). The percentages of 20:1 and 22:1 FAs were greater in Garnet lanternfish than in the other species (Table 3). The mean percentage of EPA (20:5 (n-3)) in the FAs of squid and Japanese sardine exceeded 10% (Fig. 2e; Tables 2 and 4). The percentage of 20:4 (n-6) (ARA) in the FAs of small pelagic fishes was higher than that in micronekton (Fig. 2d), with the exception of two species Prickly lanternfish (*Myctophum asperum*) and Japanese lanternfish.

3.2. ω 3: ω 6

The ω 3: ω 6 ratio is the sum of the fractions of n-3 FAs (ω 3) divided by the sum of the fractions of n-6 FAs (ω 6). ω 3: ω 6 was lower in micronekton species than in small pelagic fishes and squids (Fig. 3a). In particular, ω 3: ω 6 was highest in Japanese flying squid (*Todarodes pacificus*), although with considerable variation (Fig. 3a). The mean $\pm$ standard deviation for Japanese flying squid was 29.6 $\pm$ 4.1 (Table 5). The mean ω 3: ω 6 of small pelagic fishes ranged from 8.2 to 15.7, and that of micronekton ranged from 4.8 to 15.7 (Table 5). ω 3: ω 6 differed significantly among small pelagic fish, micronekton, and squid (Table 6), and pairwise tests showed that values differed significantly between all pairs (Table 7).

There were positive correlations between ω 3: ω 6 and both latitude

and longitude among all organisms (Fig. 4), although with considerable scatter. Japanese anchovy from the coastal Seto Inland Sea had especially high ω 3: ω 6. For small pelagic fishes and squids, ω 3: ω 6 strongly increased with increasing latitude (Fig. 4a and c) and longitude (Fig. 4d and f).

3.3. DHA:EPA

The DHA:EPA of five micronekton species (California headlightfish, Watases lanternfish, Japanese lanternfish and Garnet lanternfish) was lower than that of the other species including small pelagic fishes and squids (Fig. 3b; Table 5). The values of the other micronekton species were similar or higher Golden-nosed lanternfish (*Diaphus chrysorhynchus*) than those of small pelagic fishes (Fig. 3b). DHA:EPA ranged from 2.8 to 7.6 in small pelagic fishes, and from 2.5 to 4.8 in squids (Table 5).

DHA:EPA was negatively correlated with latitude in small pelagic fishes, micronekton, and squids (Fig. 5 a–c), but there was a great deal of scatter in DHA:EPA among small pelagic fishes (Fig. 5a). DHA:EPA was significantly lower in squids (Fig. 5c and f) than in small pelagic fishes and micronekton, and differed significantly among the three groups (ANOVA, $p < 0.001$; Table 6). Pairwise comparisons between the three species groups showed significant differences for all pairs except small pelagic fishes and squids (Tukey's HSD test; Table 7).

3.4. Total LC-PUFA fraction

Total LC-PUFA fraction was calculated by summing the fractions of all LC-PUFAs. Four micronekton species (California headlightfish,

Table 3
Fatty acid components of micronekton (Average ± SD).

Scientific Name	<i>Ceratoscopelus townsendi</i>	<i>Diaphus chrysorhynchus</i>	<i>Diaphus garmani</i>	<i>Diaphus theta</i>	<i>Diaphus watasei</i>	<i>Lampanyctus jordani</i>	<i>Maurollicus japonicus</i>	<i>Myctophum asperum</i>	<i>Notoscopelus japonicus</i>	<i>Stenobranchius nannochir</i>	<i>Symbolophorus evermanni</i>
n	9	5	10	5	5	5	5	18	4	4	27
14:0	1.41 ± 0.44	0.62 ± 0.29	0.86 ± 0.50	3.26 ± 0.55	1.91 ± 0.14	2.46 ± 0.69	3.24 ± 1.06	1.59 ± 0.82	1.20 ± 0.07	2.10 ± 0.65	0.82 ± 0.32
15:0	0.80 ± 0.22	0.17 ± 0.09	0.43 ± 0.05	0.21 ± 0.02	0.15 ± 0.02	0.17 ± 0.03	0.26 ± 0.02	0.70 ± 0.15	0.11 ± 0.01	0.07 ± 0.01	0.35 ± 0.07
16:0	19.76 ± 0.85	17.01 ± 1.12	17.93 ± 1.21	20.57 ± 0.87	20.93 ± 1.02	17.48 ± 1.30	15.76 ± 1.43	21.73 ± 3.52	16.12 ± 1.37	2.36 ± 0.65	20.39 ± 2.49
17:0	1.25 ± 0.29	0.82 ± 0.10	0.85 ± 0.07	0.70 ± 0.07	0.77 ± 0.07	0.68 ± 0.06	0.44 ± 0.03	0.84 ± 0.23	0.93 ± 0.10	1.88 ± 0.88	0.69 ± 0.12
18:0	6.19 ± 1.48	5.93 ± 0.50	4.96 ± 0.46	5.45 ± 0.58	5.85 ± 0.37	2.66 ± 0.31	2.81 ± 0.49	5.68 ± 1.45	4.46 ± 0.30	0.35 ± 0.23	4.80 ± 0.56
20:0	0.20 ± 0.03	0.19 ± 0.08	0.17 ± 0.08	0.13 ± 0.00	0.15 ± 0.01	0.10 ± 0.01	0.17 ± 0.03	0.19 ± 0.09	0.20 ± 0.02	0.04 ± 0.02	0.11 ± 0.03
Other saturated	2.67 ± 0.44	1.59 ± 0.20	1.68 ± 0.15	1.10 ± 0.03	0.68 ± 0.08	0.76 ± 0.04	1.04 ± 0.25	1.91 ± 0.36	0.88 ± 0.42	4.14 ± 2.86	1.30 ± 0.41
16:1	3.61 ± 1.43	1.23 ± 0.40	1.80 ± 0.59	6.71 ± 0.62	3.39 ± 0.25	4.78 ± 1.05	2.37 ± 0.59	3.09 ± 1.45	3.47 ± 0.34	12.99 ± 1.37	2.14 ± 1.03
17:1	0.62 ± 0.09	0.35 ± 0.07	0.38 ± 0.05	0.26 ± 0.02	0.36 ± 0.03	0.21 ± 0.02	0.26 ± 0.03	0.50 ± 0.11	0.18 ± 0.01	0.35 ± 0.04	0.46 ± 0.09
18:1	10.66 ± 0.87	13.96 ± 4.35	11.38 ± 5.27	30.17 ± 1.58	40.91 ± 3.15	18.73 ± 2.14	11.40 ± 1.73	11.92 ± 4.16	29.91 ± 1.46	25.54 ± 4.86	11.51 ± 2.90
20:1	0.84 ± 0.31	1.59 ± 0.82	1.28 ± 0.82	5.62 ± 0.97	2.96 ± 0.57	7.51 ± 0.91	6.20 ± 1.87	0.97 ± 0.51	11.51 ± 1.76	20.30 ± 1.63	0.56 ± 0.24
22:1	0.36 ± 0.20	1.17 ± 0.80	0.74 ± 0.49	4.27 ± 1.10	1.58 ± 0.51	6.76 ± 1.33	9.27 ± 2.57	0.58 ± 0.39	7.31 ± 1.90	14.73 ± 2.50	0.26 ± 0.14
24:1	1.40 ± 0.23	1.76 ± 0.23	1.40 ± 0.21	1.18 ± 0.15	0.66 ± 0.10	1.73 ± 0.28	2.14 ± 0.12	1.12 ± 0.39	0.74 ± 0.09	0.98 ± 0.11	1.39 ± 0.28
Other Monoenes	0.56 ± 0.13	0.25 ± 0.03	0.29 ± 0.04	0.28 ± 0.04	0.09 ± 0.02	0.16 ± 0.05	0.25 ± 0.05	0.54 ± 0.17	0.06 ± 0.01	0.81 ± 0.15	0.23 ± 0.09
18:2 (n-6)	1.16 ± 0.21	0.73 ± 0.07	0.98 ± 0.08	0.68 ± 0.04	0.65 ± 0.06	0.79 ± 0.09	1.03 ± 0.15	1.00 ± 0.44	0.52 ± 0.22	1.37 ± 0.06	0.77 ± 0.10
18:3 (n-3)	0.38 ± 0.14	0.20 ± 0.03	0.40 ± 0.13	0.34 ± 0.03	0.30 ± 0.05	0.30 ± 0.08	0.52 ± 0.11	0.58 ± 0.88	0.29 ± 0.02	0.46 ± 0.04	0.25 ± 0.08
18:4 (n-3)	0.22 ± 0.15	0.09 ± 0.02	0.27 ± 0.09	0.52 ± 0.06	0.24 ± 0.04	0.66 ± 0.22	0.54 ± 0.21	0.23 ± 0.15	0.49 ± 0.06	0.68 ± 0.16	0.08 ± 0.06
20:2 (n-6)	0.21 ± 0.13	0.28 ± 0.02	0.32 ± 0.04	0.15 ± 0.01	0.21 ± 0.02	0.12 ± 0.01	0.15 ± 0.01	0.31 ± 0.10	0.22 ± 0.03	0.14 ± 0.01	0.17 ± 0.04
20:3 (n-3)	0.07 ± 0.06	0.15 ± 0.01	0.20 ± 0.05	0.08 ± 0.01	0.16 ± 0.02	0.06 ± 0.01	0.11 ± 0.01	0.12 ± 0.03	0.17 ± 0.03	0.02 ± 0.03	0.09 ± 0.05
20:3 (n-6)	0.08 ± 0.07	0.10 ± 0.01	0.13 ± 0.02	0.03 ± 0.03	0.04 ± 0.01	0.05 ± 0.03	0.09 ± 0.01	0.10 ± 0.03	0.07 ± 0.01	0.03 ± 0.03	0.07 ± 0.03
20:4 (n-3)	0.28 ± 0.09	0.33 ± 0.01	0.59 ± 0.23	0.71 ± 0.12	0.58 ± 0.10	0.49 ± 0.09	0.38 ± 0.04	0.27 ± 0.16	1.05 ± 0.10	0.26 ± 0.06	0.23 ± 0.06
20:4 (n-6)	3.03 ± 0.31	2.40 ± 0.51	3.02 ± 0.61	0.36 ± 0.06	0.77 ± 0.07	0.90 ± 0.32	1.11 ± 0.22	3.32 ± 0.54	0.66 ± 0.07	0.19 ± 0.02	2.55 ± 0.45
20:5 (n-3)	4.87 ± 1.03	3.73 ± 0.76	5.78 ± 0.61	5.89 ± 1.12	5.99 ± 0.89	9.84 ± 0.95	4.08 ± 0.80	5.09 ± 0.96	8.91 ± 1.31	2.02 ± 0.53	4.66 ± 0.79
21:5 (n-3)	0.08 ± 0.07	0.08 ± 0.01	0.12 ± 0.05	0.28 ± 0.05	0.24 ± 0.03	0.30 ± 0.04	0.11 ± 0.02	0.12 ± 0.07	0.40 ± 0.05	0.20 ± 0.03	0.07 ± 0.04
22:4 (n-6)	0.20 ± 0.18	0.27 ± 0.04	0.35 ± 0.03	0.08 ± 0.06	0.19 ± 0.03	0.01 ± 0.02	0.16 ± 0.11	0.42 ± 0.08	0.25 ± 0.09	0.00 ± 0.00	0.29 ± 0.12
22:5 (n-3)	0.90 ± 0.22	1.24 ± 0.12	1.42 ± 0.11	0.96 ± 0.13	1.12 ± 0.12	0.98 ± 0.31	1.05 ± 0.19	1.33 ± 0.43	1.66 ± 0.22	0.41 ± 0.12	1.10 ± 0.20
22:5 (n-6)	3.81 ± 1.02	1.81 ± 0.30	2.42 ± 0.53	0.13 ± 0.02	0.15 ± 0.02	0.24 ± 0.04	0.55 ± 0.10	2.49 ± 0.70	0.11 ± 0.01	0.05 ± 0.03	2.26 ± 0.80
22:6 (n-3)	34.06 ± 2.65	41.41 ± 6.31	39.01 ± 7.71	8.51 ± 1.23	8.18 ± 1.23	20.07 ± 3.91	33.76 ± 5.46	32.88 ± 7.71	6.29 ± 0.34	5.31 ± 1.27	42.16 ± 5.47
Other Polyenes	0.29 ± 0.22	0.52 ± 0.23	0.82 ± 0.20	1.24 ± 0.19	0.69 ± 0.11	0.87 ± 0.20	0.63 ± 0.19	0.38 ± 0.23	1.75 ± 0.28	1.69 ± 0.38	0.24 ± 0.13
Unknown	0.04 ± 0.04	0.02 ± 0.02	0.01 ± 0.02	0.13 ± 0.04	0.08 ± 0.01	0.12 ± 0.05	0.15 ± 0.06	0.01 ± 0.03	0.11 ± 0.01	0.52 ± 0.10	0.01 ± 0.02

Table 4Fatty acid components of squids (Average $\pm$ SD).

Scientific Name	<i>Abralia similis</i>			<i>Enoploteuthis chunii</i>			<i>Eucleoteuthis luminosa</i>			<i>Sthenoteuthis oualaniensis</i>			<i>Todarodes pacificus</i>		
n	5			8			20			29			31		
14:0	1.06	$\pm$	0.21	1.62	$\pm$	0.85	0.66	$\pm$	0.15	0.84	$\pm$	0.35	1.11	$\pm$	0.29
15:0	0.43	$\pm$	0.02	0.39	$\pm$	0.18	0.36	$\pm$	0.06	0.44	$\pm$	0.12	0.35	$\pm$	0.10
16:0	24.60	$\pm$	1.40	20.77	$\pm$	2.79	20.51	$\pm$	1.89	25.70	$\pm$	2.72	26.78	$\pm$	3.24
17:0	0.99	$\pm$	0.06	0.81	$\pm$	0.06	0.84	$\pm$	0.09	0.92	$\pm$	0.20	0.54	$\pm$	0.25
18:0	6.56	$\pm$	1.69	4.87	$\pm$	0.74	5.33	$\pm$	0.76	4.84	$\pm$	0.62	3.52	$\pm$	0.80
20:0	0.11	$\pm$	0.03	0.13	$\pm$	0.02	0.10	$\pm$	0.03	0.11	$\pm$	0.01	0.07	$\pm$	0.03
Other saturated	0.53	$\pm$	0.11	0.62	$\pm$	0.13	0.56	$\pm$	0.09	0.63	$\pm$	0.20	0.43	$\pm$	0.21
16:1	0.95	$\pm$	0.57	0.82	$\pm$	0.56	0.34	$\pm$	0.10	0.61	$\pm$	0.31	0.55	$\pm$	0.30
17:1	0.18	$\pm$	0.05	0.17	$\pm$	0.12	0.06	$\pm$	0.03	0.12	$\pm$	0.14	0.07	$\pm$	0.05
18:1	4.27	$\pm$	1.45	4.92	$\pm$	1.22	2.40	$\pm$	0.35	2.50	$\pm$	0.57	2.79	$\pm$	1.04
20:1	3.30	$\pm$	0.26	4.98	$\pm$	1.40	4.53	$\pm$	0.95	3.03	$\pm$	0.51	2.89	$\pm$	0.72
22:1	0.25	$\pm$	0.23	1.04	$\pm$	1.16	0.82	$\pm$	0.17	0.68	$\pm$	0.16	0.75	$\pm$	0.18
24:1	1.05	$\pm$	0.12	0.83	$\pm$	0.24	0.80	$\pm$	0.43	0.73	$\pm$	0.43	1.06	$\pm$	0.46
Other Monoenes	0.03	$\pm$	0.04	0.06	$\pm$	0.06	0.00	$\pm$	0.01	0.01	$\pm$	0.03	0.01	$\pm$	0.01
18:2(n-6)	0.26	$\pm$	0.22	0.42	$\pm$	0.69	0.09	$\pm$	0.07	0.09	$\pm$	0.04	0.09	$\pm$	0.11
18:3(n-3)	0.22	$\pm$	0.10	0.82	$\pm$	1.84	0.08	$\pm$	0.22	0.08	$\pm$	0.13	0.07	$\pm$	0.10
18:4(n-3)	0.09	$\pm$	0.04	0.24	$\pm$	0.43	0.02	$\pm$	0.02	0.05	$\pm$	0.04	0.05	$\pm$	0.05
20:2(n-6)	0.14	$\pm$	0.02	0.24	$\pm$	0.05	0.25	$\pm$	0.04	0.24	$\pm$	0.05	0.11	$\pm$	0.03
20:3(n-3)	0.29	$\pm$	0.03	0.25	$\pm$	0.02	0.44	$\pm$	0.12	0.24	$\pm$	0.07	0.13	$\pm$	0.02
20:3(n-6)	0.01	$\pm$	0.01	0.01	$\pm$	0.02	0.00	$\pm$	0.01	0.00	$\pm$	0.01	0.00	$\pm$	0.02
20:4(n-3)	0.06	$\pm$	0.03	0.14	$\pm$	0.10	0.07	$\pm$	0.03	0.08	$\pm$	0.03	0.07	$\pm$	0.04
20:4(n-6)	1.86	$\pm$	0.26	1.50	$\pm$	0.29	1.61	$\pm$	0.38	1.72	$\pm$	0.37	1.44	$\pm$	0.63
20:5(n-3)	14.58	$\pm$	1.31	13.00	$\pm$	2.32	11.83	$\pm$	0.92	9.33	$\pm$	0.93	11.02	$\pm$	1.18
21:5(n-3)	0.09	$\pm$	0.02	0.15	$\pm$	0.04	0.08	$\pm$	0.02	0.08	$\pm$	0.03	0.18	$\pm$	0.07
22:4(n-6)	0.01	$\pm$	0.03	0.07	$\pm$	0.04	0.12	$\pm$	0.09	0.13	$\pm$	0.08	0.09	$\pm$	0.10
22:5(n-3)	0.26	$\pm$	0.11	0.47	$\pm$	0.13	0.34	$\pm$	0.08	0.34	$\pm$	0.06	0.40	$\pm$	0.19
22:5(n-6)	0.65	$\pm$	0.07	0.92	$\pm$	0.48	0.90	$\pm$	0.16	1.20	$\pm$	0.30	0.46	$\pm$	0.30
22:6(n-3)	37.05	$\pm$	3.14	39.53	$\pm$	5.51	46.30	$\pm$	2.75	44.56	$\pm$	2.53	44.54	$\pm$	3.81
Other Polyenes	0.11	$\pm$	0.07	0.23	$\pm$	0.14	0.56	$\pm$	0.47	0.71	$\pm$	0.66	0.38	$\pm$	0.43
Unknown	0.00	$\pm$	0.00	0.00	$\pm$	0.00	0.00	$\pm$	0.01	0.00	$\pm$	0.00	0.06	$\pm$	0.15

Watases lanternfish, Japanese lanternfish and Garnet lanternfish) had especially low total LC-PUFA fraction in comparison to the other collected species (Fig. 3c). The mean total LC-PUFA fraction of the other species was over 40% (Fig. 3c; Table 5). The highest mean total LC-PUFA was observed in the species Striped flying squid (*Eucleoteuthis luminosa*) (62.7%).

Total LC-PUFA fraction was negatively correlated with latitude and longitude for micronekton, but no analogous correlations were identified for small pelagic fishes and squids (Fig. 6).

3.5. Non-metric multidimensional scaling (nMDS)

nMDS analysis showed significant differences in the fraction of the six main FAs (16:0, 18:0, 18:1, 20:4 (n-6), EPA, and DHA), ω 3: ω 6, and DHA:EPA (Fig. 7a, Table 8; PERMANOVA, $p = 0.001$) among small pelagic fishes, micronekton, and squids. For small pelagic fishes, the nMDS results revealed clear segregation between planktivores (Japanese anchovy, Japanese sardine, and Round herring (*Etrumeus teres*)) and omnivores (chub mackerel and Jack mackerel (*T. japonicus*)) (Ohshimo et al., 2016a,b). For micronekton, there was clear separation between northern species (California headlightfish, Watases lanternfish, Japanese lanternfish and Garnet lanternfish) and southern species Dogtooth lampfish (*Ceratoscopelus townsendi*), Golden-nosed lanternfish, Garman's lanternfish (*Diaphus garmani*), North Pacific lightfish (*Maurolucius japonicus*), Prickly lanternfish, and Everman's lanternfish (*Symbolophorus evermanni*), with Brokenline lanternfish (*Lampanyctus jordani*) occupying an intermediate zone between the northern and southern species (Fig. 7c). The range of the results was smaller for squids than for small pelagic fishes and micronekton, with especially large differences observed between striped flying squid and Flying squid (*Sthenoteuthis oualaniensis*).

PERMANOVA of FA components revealed significant differences among micronekton, small pelagic fishes, and squids. All combinations

(micronekton vs. small pelagic fishes, micronekton vs. squids, and small pelagic fishes vs. squids) differed significantly based on pairwise PERMANOVA (Table 9).

4. Discussion

In the present study, we analyzed the FAs of small pelagic fishes, micronekton, and squids in the NWP. We identified the FA signatures of the sampled species and evaluated the presence of any geographical differences in these signatures. The species we analyzed are the main prey of large, apex predators in the pelagic NWP (Fujinami et al., 2018; Hiraoka, Fujioka, et al., 2019; Mitsui et al., 2014; Ohshimo et al., 2018), and the FA signatures of these species are likely to provide insights into their ecology. Our study is the first to report on the FA profiles of a large number of pelagic species in the NWP.

4.1. Fatty acid components

Overall, the identity of the main FA components differed among the three species groups we examined (small pelagic fishes, micronekton and squids). In addition, the ratios of ω 3: ω 6 and DHA:EPA differed significantly among these categories (Table 6); the reasons for these differences are discussed later.

4.2. Small pelagic fishes

Several previous studies have reported the FA components of the forage fish examined in our study. The major FAs in the lipids of Japanese sardine along the Pacific coast are 14:0, 16:0, 18:0, 16:1 (n-7), 18:1 (n-9), EPA, and DHA (Shirai et al., 2002), and the characteristics of the FAs isolated from Japanese sardine in July are similar to those isolated from plankton in the same season. The most abundant FAs in the oils of Pacific sardine (*Sardinops sagax*) are 16:0, 18:1 (n-9), EPA, and DHA

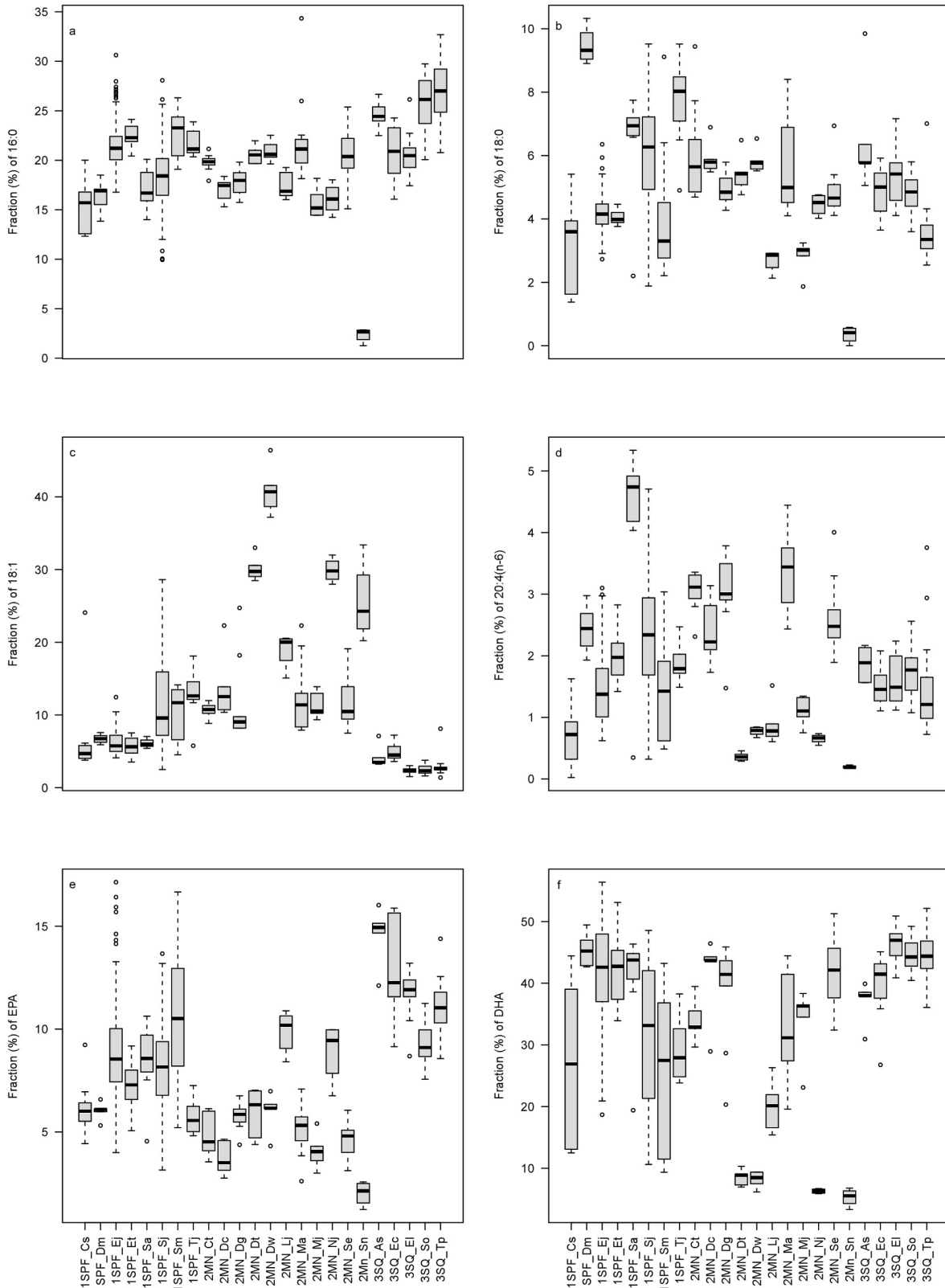


Fig. 2. Box plots of the six major fatty acids identified in our samples. Box plots show medians (solid horizontal lines), interquartile ranges (box outlines), and 5–95 percentile ranges (whiskers); open circles indicate outliers. Species abbreviations are as defined in Table 1. SPF, small pelagic fish; MN, micronekton; SQ, squid.

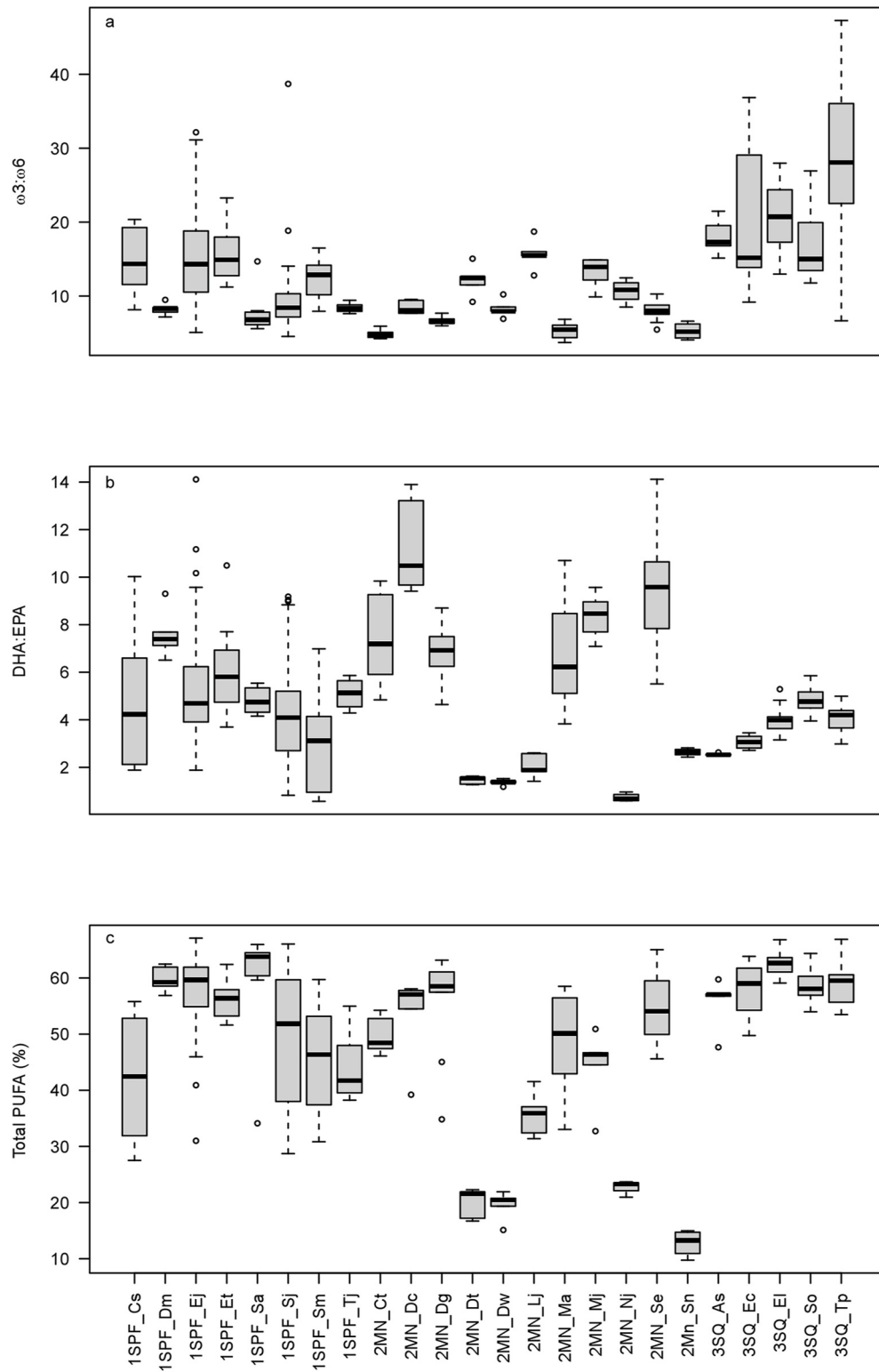


Fig. 3. Box plots of $\omega 3:\omega 6$, DHA:EPA, and LC-PUFA. Box plots show medians (solid horizontal lines), interquartile ranges (box outlines) and 5–95 percentile ranges (whiskers); open circles indicate outliers. Species abbreviations are as defined in Table 1. SPF, small pelagic fish; MN, micronekton; SQ, squid.

Table 5

Average and standard deviations of ω 3: ω 6, DHA:EPA, and LC-PUFA contents (%) for each species.

Organisms	Scientific name	Abbrev.	ω 3: ω 6	DHA:EPA	LC-PUFA
SPF	<i>Cololabis saira</i>	Cs	14.9 $\pm$ 4.0	4.7 $\pm$ 2.7	42.4 $\pm$ 10.6
SPF	<i>Decapterus macarellus</i>	Dm	8.3 $\pm$ 0.8	7.6 $\pm$ 0.9	59.8 $\pm$ 2.1
SPF	<i>Engraulis japonicus</i>	Ej	15.5 $\pm$ 6.1	5.1 $\pm$ 1.9	58.5 $\pm$ 5.3
SPF	<i>Etrumeus teres</i>	Et	15.7 $\pm$ 3.7	6.1 $\pm$ 2.0	56.1 $\pm$ 3.3
SPF	<i>Sardinops melanostictus</i>	Sm	12.2 $\pm$ 2.6	2.9 $\pm$ 1.9	45.6 $\pm$ 8.9
SPF	<i>Scomber australasicus</i>	Sa	7.5 $\pm$ 2.4	4.8 $\pm$ 0.5	60.5 $\pm$ 8.6
SPF	<i>Scomber japonicus</i>	Sj	8.9 $\pm$ 3.2	4.1 $\pm$ 1.8	49.2 $\pm$ 11.0
SPF	<i>Trachurus japonicus</i>	Tj	8.4 $\pm$ 0.6	5.1 $\pm$ 0.6	44.0 $\pm$ 5.5
MN	<i>Ceratoscopelus townsendi</i>	Ct	4.8 $\pm$ 0.5	7.3 $\pm$ 1.7	49.6 $\pm$ 2.8
MN	<i>Diaphus chrysorhynchus</i>	Dc	8.5 $\pm$ 0.8	11.3 $\pm$ 1.9	53.3 $\pm$ 7.2
MN	<i>Diaphus garmani</i>	Dg	6.6 $\pm$ 0.5	6.7 $\pm$ 1.2	55.8 $\pm$ 8.4
MN	<i>Diaphus theta</i>	Dt	12.2 $\pm$ 1.9	1.5 $\pm$ 0.2	20.0 $\pm$ 2.5
MN	<i>Diaphus watasei</i>	Dw	8.3 $\pm$ 1.1	1.4 $\pm$ 0.1	19.5 $\pm$ 2.4
MN	<i>Lampanyctus jordani</i>	Lj	15.7 $\pm$ 1.9	2.1 $\pm$ 0.5	35.7 $\pm$ 3.6
MN	<i>Maurollicus japonicus</i>	Mj	13.2 $\pm$ 1.9	8.4 $\pm$ 0.9	44.2 $\pm$ 6.1
MN	<i>Myctophum asperum</i>	Ma	5.4 $\pm$ 0.9	6.7 $\pm$ 1.9	48.6 $\pm$ 8.0
MN	<i>Notoscopelus japonicus</i>	Nj	10.7 $\pm$ 1.4	0.7 $\pm$ 0.1	22.8 $\pm$ 1.1
MN	<i>Stenobrachius nannochir</i>	Sn	5.3 $\pm$ 1.0	2.6 $\pm$ 0.1	12.8 $\pm$ 2.1
MN	<i>Symbolophorus evermanni</i>	Se	8.1 $\pm$ 1.1	9.4 $\pm$ 2.2	55.0 $\pm$ 5.7
SQ	<i>Abralia similis</i>	As	18.1 $\pm$ 2.2	2.5 $\pm$ 0.0	55.7 $\pm$ 4.2
SQ	<i>Enoplateuthis chunii</i>	Ec	20.3 $\pm$ 9.3	3.1 $\pm$ 0.3	58.0 $\pm$ 4.6
SQ	<i>Eucleoteuthis luminosa</i>	El	20.8 $\pm$ 4.4	3.9 $\pm$ 0.5	62.7 $\pm$ 1.9
SQ	<i>Sthenoteuthis oualaniensis</i>	So	17.1 $\pm$ 4.4	4.8 $\pm$ 0.5	58.8 $\pm$ 2.8
SQ	<i>Todarodes pacificus</i>	Tp	29.6 $\pm$ 9.4	4.1 $\pm$ 0.5	59.0 $\pm$ 3.5

MN, SPF, and SQ indicate micronekton, small pelagic fish, and squid.

Table 6

One-way ANOVA results for ω 3: ω 6 and DHA:EPA.

Response variable		Df	Sum of Sq	Mean Sq	F value	Pr (>F)
ω 3: ω 6	Organisms	2	11,021	5510.5	158.74	<0.001
	Residuals	538	18,676	34.7		
DHA:EPA	Organisms	2	391.55	195.774	40.174	<0.001
	Residuals	538	2621.77	4.873		

(Gámez-Meza et al., 1999). The lipid fraction of chub mackerel and Atlantic horse mackerel (*Trachurus trachurus*) in the Mediterranean Sea is lower in winter than in autumn and spring, and the major FAs in Japanese sardine and Jack mackerel are 16:0, 18:0, 18:1 (n-9), EPA, and DHA (Celik, 2008). The major FAs in Japanese anchovy in the Yellow Sea are 14:0, 16:0, 16:1 (n-7), 18:0, 18:1 (n-7), 18:1 (n-9), EPA, and DHA; these FAs make up 60%–80% of the total FA fraction (Wan et al., 2010).

Table 7

Pair-wise tests (Tukey-HSD) for ω 3: ω 6 and DHA:EPA.

Response variable	Combinations	Differences	Lower	Upper	Adjusted p-value
ω 3: ω 6	SPF-MN	3.861516	2.273114	5.449917	<0.001
	SQ-MN	14.35638	12.34678	16.36598	0
	SQ-SPF	10.49487	8.879923	12.10981	0
DHA:EPA	SPF-MN	-2.08574	-2.68088	-1.49061	0
	SQ-MN	-2.52364	-3.27659	-1.77069	0
	SQ-SPF	-0.4379	-1.04297	0.16718	0.205783

MN, SPF, and SQ represent micronekton, small pelagic fish, and squid.

The results of our FA analysis were largely consistent with those of previous studies. The dominant FA in small pelagic fishes was DHA in the present study. The fractions of 16:0 and EPA were also higher than the other FAs. There was less variability in the main FAs of small pelagic fishes in comparison to micronekton. Ohshimo et al. (2022) reported that the variability of FA components in chub mackerel was mainly determined by body size. This indicates that FA components can be influenced by growth, and that changes in FA components could reflect ontogenetic shifts in prey species.

4.3. Micronekton

Micronekton are important prey for tunas (Duffy et al., 2017; Ohshimo et al., 2018). Duffy et al. (2017) highlighted the importance of global-scale analyses to improve understanding of predator–prey interactions in pelagic ecosystems. In addition, the biomass of micronekton in the East China Sea was dominant (Ohshimo et al., 2012). These indicate the micronekton play an important role in the pelagic ecosystem.

Several previous studies have reported the FA components of the micronekton species examined in our study. Saito and Murata (1996) analyzed the lipids and FAs of 11 species of micronekton (Myctophidae) that were collected in the Oyashio–Kuroshio transition area in the North Pacific, and found that the dominant FAs are monoenes, such as 18:1 (n-9), 20:1 (n-11), and 22:1 (n-11) (Saito & Murata, 1996). In the present study, although Garnet lanternfish had a high component of monoene FAs, the dominant FAs of other micronekton species were 16:0 and 18:1 (Table 3). The percentage of DHA in the FAs of southern micronekton species was as high as 20%. Koizumi et al. (2014) analyzed the FA compositions of the total lipids of three edible deep-sea fishes—Watases lanternfish, *Diaphus suborbitalis*, and skinnycheek lanternfish (*Benthosema pterotum*)—as well as three myctophids, and reported medium levels of EPA and DHA. Sebastine et al. (2011) reported that monounsaturated FAs (predominantly 18:1) are the most abundant FAs of Watases lanternfish. Seo et al. (1996) has reported that 16:0 acid and DHA are the major FAs in tropical myctophids, whereas 18:1 (n-9) and 16:0 are the predominant FAs in temperate species. These previous studies are largely consistent with our results, and indicate that differences of FA profiles among micronekton could largely be caused by differences in ambient water temperature.

In the present study, the dominant FA of four micronekton species (California headlightfish, Watases lanternfish, Japanese lanternfish and Garnet lanternfish) was 18:1, and the mean percentage of 18:1 for these species ranged from 26% to 41%. The percentages of the 20:1 and 22:1 FAs were larger for Garnet lanternfish than for the other three species. Though the mean percentage of EPA in squids and Japanese sardine exceeded 10%, and the mean percentage of 16:0 was high in all micronekton species except Garnet lanternfish. The FA compositions of the four micronekton species (California headlightfish, Watases lanternfish, Japanese lanternfish and Garnet lanternfish) distributed in the northern part of the study area differed from those of other micronekton and from those of small pelagic fishes and squids. Farkas et al. (2001) suggested that the cell membranes of cold-adapted fish are more fluid than those of warm-adapted fish. Because cell-membrane fluidity can be

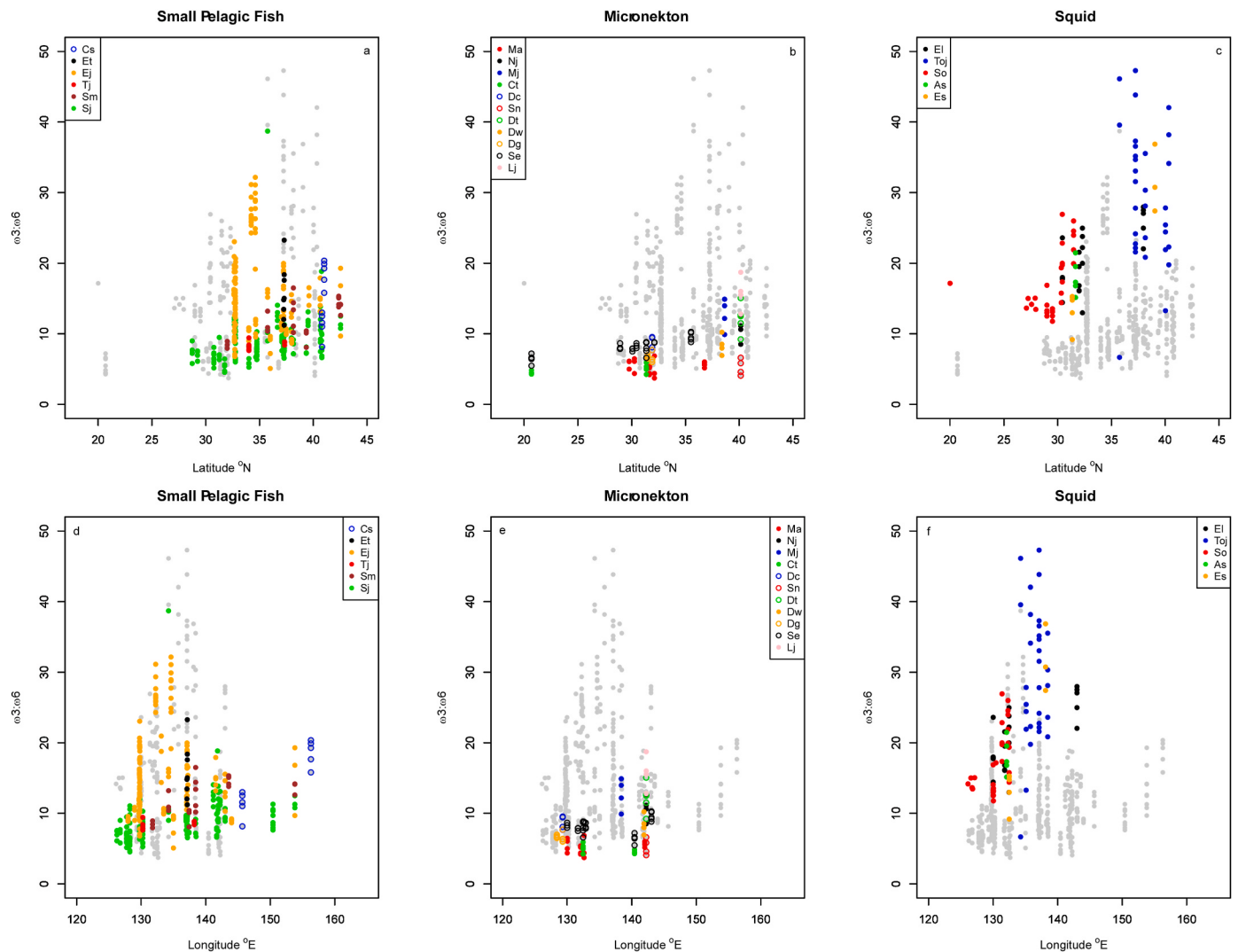


Fig. 4. Scatter plots of latitude and $\omega 3:\omega 6$ for small pelagic fishes (a), micronekton (b), and squids (c), and scatter plots of longitude and $\omega 3:\omega 6$ for small pelagic fishes (d), micronekton (e), and squids (f). Gray circles indicate other species groups. Species abbreviations in the figure legends are as shown in Table 1.

affected by the characteristics of the predominant FAs, the cold ambient temperatures experienced by the four northern micronekton could explain the unique FA profiles of these species.

4.4. Squid

Previous studies have reported consistently high DHA fractions across a range of squid species. DHA is the most abundant FA in Japanese flying squid (*Todarodes pacificus*) (Kim et al., 2006) and in four sympatric loliginid squids (*Uroteuthis duvaucelii*, *Uroteuthis edulis*, *Uroteuthis chinensis*, and *Loliolus uyii*) in the northern South China Sea (Lin et al., 2020). Similarly, high DHA fractions have been reported for neon flying squid (*Ommastrephes bartramii*) (Saito & Ishikawa, 2012).

Our results are consistent with these previous findings, as DHA was also the dominant FA among the squid sampled in our study. In comparison to small pelagic fishes and micronekton, squid had lower fractions of 18:1 FAs and higher fractions of EPA. The high EPA fractions in squid could reflect the greater reliance of the squid in our study on marine food webs supported primarily by diatoms (Parrish, 2013).

4.5. Geographical variability in FA fraction

Both marine and freshwater fishes show latitudinal gradients in FA composition (Parzanini et al., 2020), with high-latitude habitats being associated with higher fractions of unsaturated FAs. This suggests that ambient water temperature could be an underlying factor that affects the lipid composition of fish cell membranes (Parzanini et al., 2020).

In the present study, $\omega 3:\omega 6$ was positively correlated with both latitude and longitude, which suggests that it is negatively correlated with water temperature in our study region. Because water temperature often covaries with other variables, correlations with water temperature could reflect the effect of other environmental factors. For example, $\omega 3:\omega 6$ in southern-hemisphere albacore is positively correlated with sea surface temperature, but is also negatively correlated with chlorophyll-*a* concentration (Dhurmea et al., 2020); in this case, it is possible that primary productivity, which is associated with water temperature, is the causal factor. Hixon and Arts (2016) suggested that increasing water temperature is strongly correlated with a lower proportion of $\omega 3$ LC-PUFAs and a higher proportion of both $\omega 6$ LC-PUFAs and saturated FAs. Although additional evaluation is needed, this could mean that $\omega 3:\omega 6$ is a useful metric for identifying geographical differences in FA profiles overall.

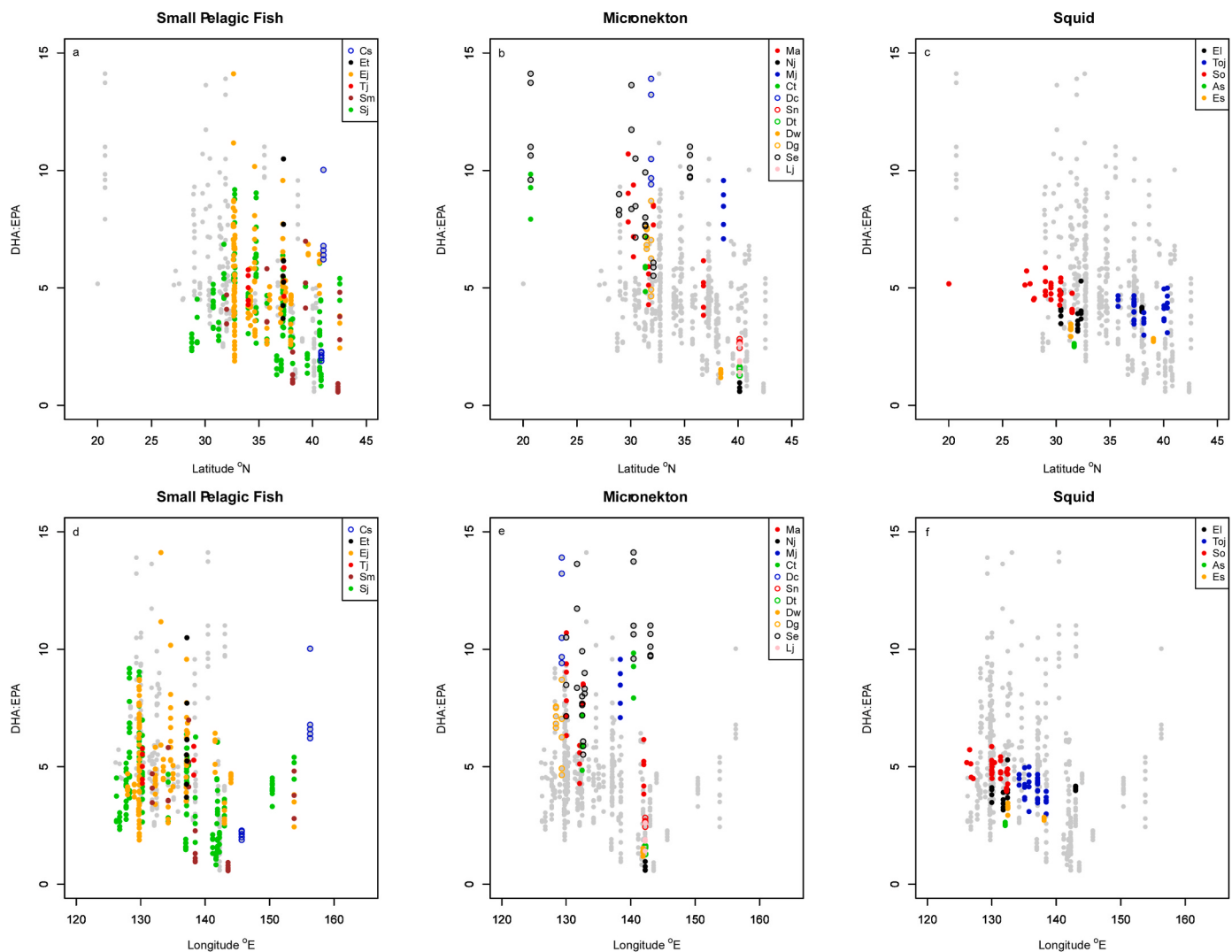


Fig. 5. Scatter plots of latitude and DHA:EPA for small pelagic fishes (a), micronekton (b), and squids (c), and scatter plots of longitude and DHA:EPA for small pelagic fishes (d), micronekton (e), and squids (f). Gray circles indicate other species groups. Species abbreviations in the figure legends are as shown in Table 1.

DHA:EPA was negatively correlated with both latitude and longitude (Fig. 5), which suggests it is positively correlated with temperature in our study area. This is the opposite of the relationship reported for cultured *Phaeodactylum tricornutum*, for which DHA:EPA is significantly higher at 15 °C than at 20 or 25 °C (Qiao et al., 2016). However, DHA:EPA in the calanoid copepods *Temora longicornis* and *Acartia clausi* in the North Sea are lower in winter than in other seasons (Deschutter et al., 2019). Hiltunen et al. (2022) analyzed the FAs of various zooplankton species in Puget Sound, USA, and suggested that high DHA:EPA in copepods could reflect high rates of consumption of flagellates (including dinoflagellates). These observations collectively indicate that the DHA:EPA ratio might be affected by a combination of environmental factors (such as temperature) as well as by the physiological condition of phytoplankton and the characteristics of primary production.

In our study, the total LC-PUFA of micronekton decreased with increasing latitude and longitude (Fig. 6), which is consistent with the effect of water temperature reported by Parzanini et al. (2020). However, similar correlations were not observed for small pelagic fishes and squids. Further study of latitudinal gradients in LC-PUFA should be conducted in the future.

4.6. Non-metric multidimensional scaling (nMDS)

The nMDS analysis showed clear differences among small pelagic fishes, micronekton and squids (Fig. 7), and these three groups were significantly different based on PERMANOVA. Among small pelagic fishes, planktivores (Japanese anchovy) and omnivores (chub mackerel) (Ohshimo et al., 2016b) were strongly differentiated in the nMDS results. For micronekton, there was strong differentiation between northern species (California headlightfish, Wataes lanternfish, Japanese lanternfish and Garnet lanternfish) and southern species (Dogtooth lampfish, Golden-nosed lanternfish, Garman's lanternfish, North Pacific lightfish, Prickly lanternfish and Everman's lanternfish). Squids as a group were strongly differentiated from small pelagic fishes and micronekton. These results demonstrate that nMDS analysis of FA signatures can be used to detect differences in the feeding habits and distributions of pelagic species, and can be used to understand the roles of these species in the ecosystem such as feeding habits.

5. Conclusions

Lipids and their constituent FAs are, along with proteins, the major organic constituents of fish, and they play major roles as sources of

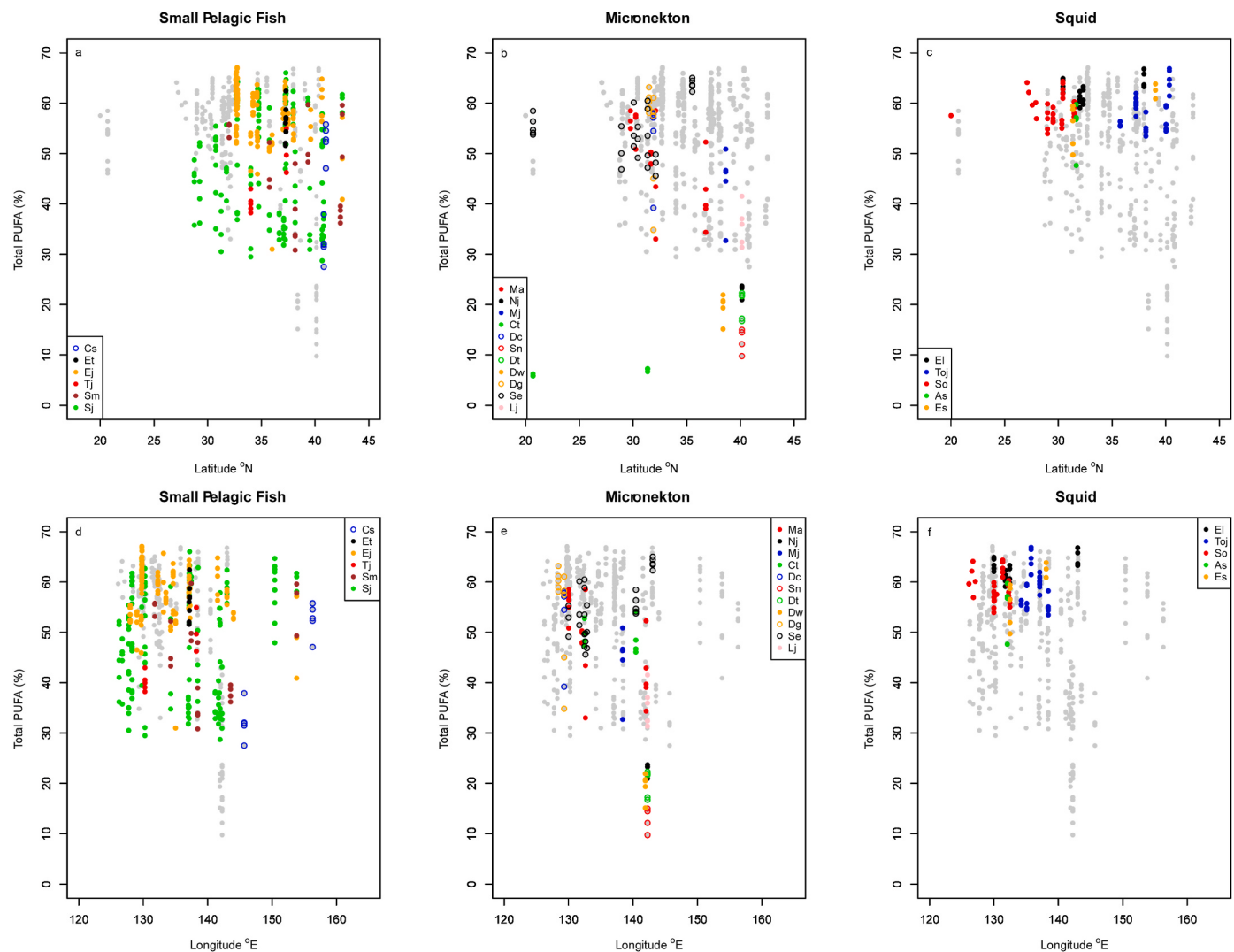


Fig. 6. Scatter plots of latitude and total polyunsaturated fatty acid (PUFA) for small pelagic fishes (a), micronekton (b), and squids (c), and scatter plots of longitude and total PUFA for small pelagic fishes (d), micronekton (e) and squids (f). Gray circles indicate other species groups. Species abbreviations in the figure legends are as shown in Table 1.

metabolic energy for growth, reproduction, and movement (Tocher, 2003). In addition to metabolic energy, recent studies have indicated a critical role of DHA in the functioning of neural tissue (brain and eyes) in fish, and have also demonstrated the importance of dietary DHA in marine fish. The composition of FAs, especially that of LC-PUFAs, is an important determinant of cell membrane fluidity (Bell et al., 1986). Because FA profiles are affected by prey resources, FA analysis can be used to evaluate trophic positions and food-web structuring (Hebert et al., 2006; Kainz et al., 2004). One of our main objectives in this study was to identify the roles and ecologies of fish and squid in the NWP ecosystem.

In the present study, we analyzed FA composition. We successfully detected all FA components in a range of small pelagic fish, micronekton, and squid species. Our nMDS analysis of FA profiles clearly differentiated among small pelagic fish, micronekton, and squid. These species groups also differed significantly based on PERMANOVA. In addition, pair-wise tests show that genus-level differences in small pelagic fish, micronekton, and squid could be detected from our analysis, and could be reflected by feeding habits and geographical differences. This indicates that FA profiles could be used to detect predator-prey interactions (Choy et al., 2019; Iversen et al., 2007;

Kurasawa et al., 2012; Ridoux et al., 2007; Rohner et al., 2013), and that FA compositions can reflect differences in the quality of primary production.

Compliance with ethical standards

This study was carried out in accordance with the Fisheries Resources Institute's guidelines on animal welfare (https://www.fra.affrc.go.jp/kseika/experiment_on_animals/regulation.pdf). All specimens were collected within the exclusive economic zone of Japan or in the international waters, and all research cruises were approved by the Japanese Government.

CRediT authorship contribution statement

Seiji Ohshimo: Conceptualization, Data curation, Formal analysis, Funding acquisition, Validation, Visualization, Writing – original draft. **Yuko Hiraoka:** Conceptualization, Writing – review & editing. **Yasuhiro Ando:** Investigation, Methodology, Writing – review & editing.

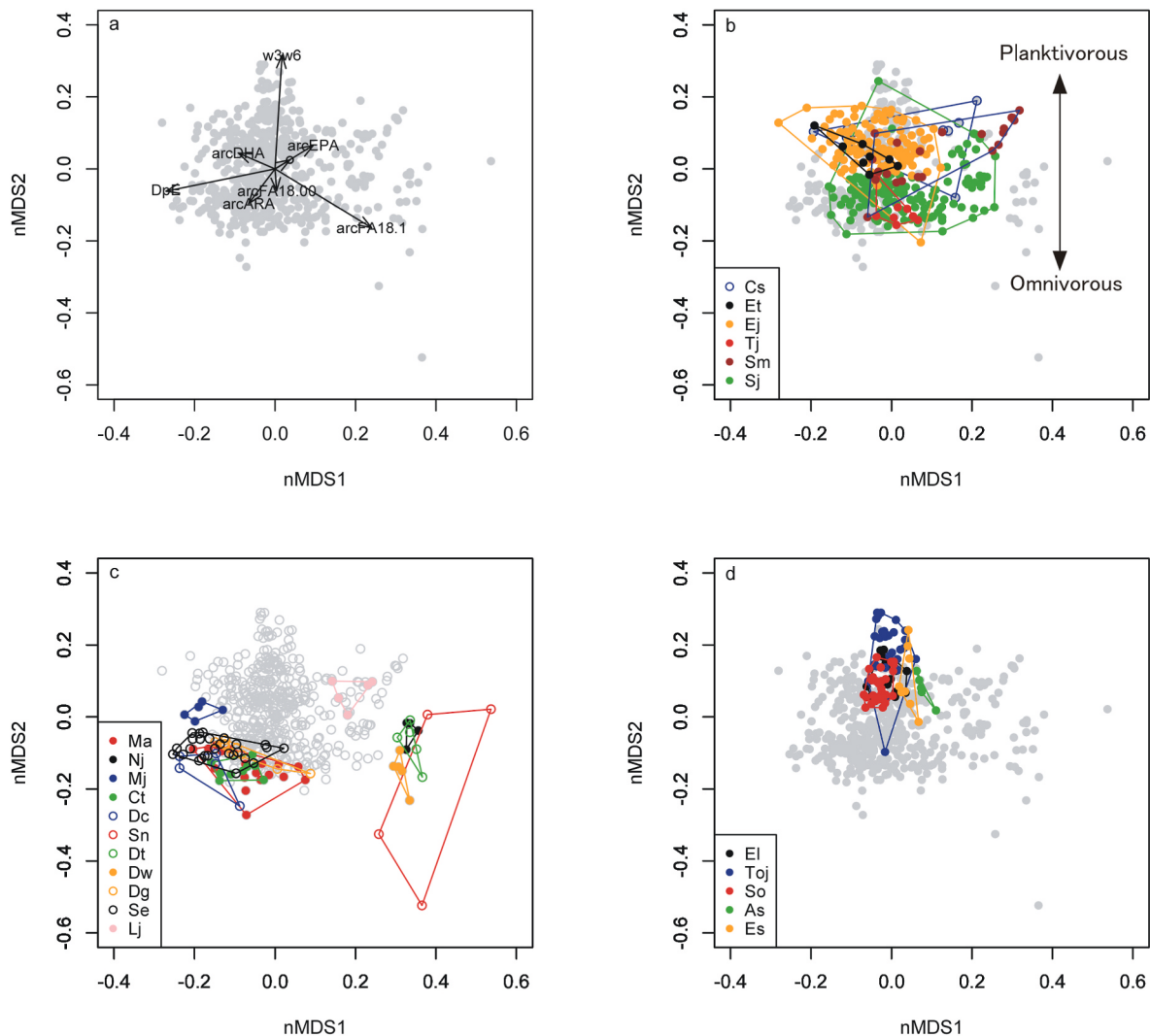


Fig. 7. Scatter plots of non-metric multidimensional scaling (nMDS) results for all specimens (a), small pelagic fishes (b), micronekton (c), and squids (d). Gray circles indicate other species groups. Species abbreviations in the figure legends are as shown in Table 1.

Table 8

One-way PERMANOVA results for fatty acid components.

	Df	SumsOfSqs	MeanSqs	F.Model	R ²	Pr (>F)
Organisms	2	6.1446	3.07228	103.2	0.27727	0.001
Residuals	538	16.0165	0.02977		0.72273	
Total	540	22.1611			1	

Table 9

Pair-wise tests among the three species categories (micronekton, small pelagic fish, and squid).

pairs	Df	Sums of Sqs	F.Model	R ²	p.value	p.adjusted
SPF-MN	1	1.30333	41.93839	0.08595	0.001	0.003
SQ-MN	1	5.655639	184.0379	0.494675	0.001	0.003
SQ-SPF	1	3.751683	133.7814	0.232348	0.001	0.003

MN, SPF, and SQ represent micronekton, small pelagic fish, and squid.

Declaration of competing interest

The authors declare that they have no conflicts of interest.

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