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Seasonal changes of community structure and vertical distribution/migration for mesopelagic fish in the western subarctic Pacific

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Abstract

Although mesopelagic fish dominate the oceanic ecosystem, they remain one of the least investigated components. From the vertically stratified sample collections, we investigated community structure, vertical distribution and diel/ontogenetic vertical migration covering four seasons for larval and juvenile/adult mesopelagic fish at the time-series station K2 in the Western Subarctic Gyre of the North Pacific. We collected 10 and 20 species of larval and juvenile/adult fish, respectively. Among the larval fish community, *Leuroglossus schmidti* was the most abundant; total abundances except *L. schmidti* were low throughout the year; species richness of myctophids were low. Among the 20 species of juvenile/adult fish, larvae of only six species were collected; thus, most mesopelagic fish species do not use the Western Subarctic Gyre as their nursery. In the juvenile/adult fish community, *Stenobrachius leucopsarus* and *Stenobrachius nannochir* were abundant. Species diversity and total abundance in the warm seasons (summer and autumn) were higher than in the cold seasons (winter and spring). The decreasing of species diversity and total abundance during the cold seasons was probably affected by horizontal migrations of fish for reproduction toward the southern transition or subarctic slope areas. *Stenobrachius leucopsarus* was distributed at shallow depths with opportunistic diel vertical migration (DVM); in contrast *Stenobrachius nannochir* occurred at greater depths, without DVM. The distribution depths of *S. leucopsarus* during day and those of *S. nannochir* changed seasonally and synchronously; shallowest in autumn, deepest in spring.

Introduction

Among total fish biomass in the world, mesopelagic fish are likely dominant with an estimated biomass of over 1000 million tons (Irigoien *et al*., 2014). From the viewpoint of abundance, the mesopelagic fish genus *Cyclothone* is likely the most abundant vertebrate on earth (Nelson *et al*., 2016). Because of their huge abundance and biomass, mesopelagic fish play key roles in trophic linkage and material cycles in the ocean. These fish prey upon many taxa of zooplankton with a preference for crustaceans such as copepods, amphipods, and euphausiids (Beamish *et al*., 1999; Moku *et al*., 2000). Squids and marine mammals spend a portion of their day feeding in mesopelagic waters, and mesopelagic fish are important prey (Kajimura and Loughlin, 1988; Phillips *et al*., 2001; Watanabe *et al*., 2004). Not only in midwater but also near the sea surface, mesopelagic fish are also important prey for larger predators such as seabirds and salmonid fish because of their DVMs (Koval and Karpenko, 1998; Jacobsen and Hansen, 2001; Watanuki and Thiebot, 2018). Mesopelagic fish also play an important role in carbon transport from the surface euphotic zone to the ocean interior. In the equatorial Pacific, the downward carbon flux due to micronekton (mesopelagic fish are the dominant component) respiration was suggested to be at the same level as that by sinking particles (Hidaka *et al*., 2001). The respiratory carbon flux by micronekton was equivalent 53% of the sinking particulate carbon flux at 150 m, based on their larger migratory ranges, micronekton are expected to be the dominant component exporting carbon to deeper waters in the subtropical Atlantic (Ariza *et al*., 2015). In addition, mesopelagic fish are one of the main scatterers in the deep scattering layer (Marshall, 1951). Despite their ecological importance, mesopelagic fish remain one of the least investigated components of the midwater ecosystem (Irigoien *et al*., 2014).

In the subarctic Pacific, the mesopelagic fish have been relatively well investigated. Beamish *et al*. (1999) summarized the occurrence of a total of 99 mesopelagic fish species in the western and eastern subarctic Pacific gyres. In their report, there were 48 and 13 species unique to the western and eastern gyres, respectively, Myctophidae were the most diverse and abundant, and the Myctophid *Stenobrachius leucopsarus* was considered as the most ecologically important species there. In the Russian waters of the western subarctic Pacific, Orlov and Tokranov (2019) listed 80 mesopelagic fish species that accounted for 33% of the total number of fish species and they also summarized depth ranges of observed fish. Combining the results of Beamish *et al*. (1999) and Orlov and Tokranov (2019), 119 mesopelagic fish species have been recorded from the western subarctic Pacific gyre. Ecologically, mesopelagic fish species

dominated among the fish community on the continental shelf and beyond the shelf break in the Gulf of Alaska (McGowan *et al.*, 2019) and in the western and eastern subarctic gyres (Beamish *et al.*, 1999). There are also reports of feeding habits (Gordon *et al.*, 1985; Moku *et al.*, 2000; Kosenok *et al.*, 2006) and predation by larger predators (e.g., Sanger and Ainley, 1988; Orlov, 1997; Ohizumi *et al.*, 2003). Compared with the studies on trophic linkages, however, vertical distribution and migration of mesopelagic fish have been poorly investigated. For example, Nishikawa *et al.* (2001) reported summertime vertical distributions of bulk biomass for Pisces in the western subarctic Pacific, although no information on species was provided. To understand ecological processes and the roles of mesopelagic fish, knowledge of vertical distribution and migration is crucial baseline information. Vertical distribution patterns are also needed to assess the abundance of these fish because sampling just the upper depths of a species range can lead to substantial underestimates of abundance (Brodeur and Rugen, 1994). In addition, knowledge of larval mesopelagic fish is also quite limited in oceanic areas of the western subarctic Pacific, although these have been well reported from the eastern Pacific from Alaska to Hawaii (Norcross *et al.*, 2003), the Sea of Okhotsk (Davydova *et al.*, 2007; Andreeva and Shebanova, 2010; Mukhametva and Mukhametov, 2022), and the transition region south of the western subarctic Pacific (Sassa *et al.*, 2004b, 2007). Previously, most of studies on oceanic fish in the western subarctic Pacific were carried out along the Kamchatka Peninsula, off the Kuril Islands and in Japanese waters off Hokkaido but ecological study inside the Western Subarctic Gyre (WSG) has been limited.

In this study, we investigated seasonal changes of community structure, abundance, vertical distribution, and diel/ontogenetic migrations for both larval and juvenile/adult mesopelagic fish in the WSG of the North Pacific. To understand these topics, sample collections for fish were carried out from eight or nine discrete depths between 1000 m and sea surface by using the opening/closing net system, covering all four seasons. In our collected fish samples, quite a few specimens of non-mesopelagic fish species were also included. Although this study focused on mesopelagic fish, simple descriptions of the non-mesopelagic fish species were also added in this paper.

Methods

The present study was carried out at the time-series station K2 in the western subarctic Pacific (47°N, 160°E, Figure 1) from 2006 to 2012 including all four seasons (Table 1). In this study, the meteorological seasons at K2 are defined in accordance with Matsumoto *et al.* (2014): winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). K2 is a time-series station established in 2001 to evaluate long-term changes of the environment of the western subarctic Pacific (Honda *et al.*, 2017). In addition to the long-term environmental monitoring, many kinds of biological studies have been carried out (e.g., Kobari *et al.*, 2022; Taniguchi *et al.*, 2023). As regards mesopelagic fish at K2, Kitamura and Murata (2020) reported the vertical distribution and migration of the predominant mesopelagic fish, *Leuroglossus schmidti*. However, mesopelagic fish other than *L. schmidti* have not been investigated.

All fish specimens used in this study were obtained from the same cruises and net samples reported by Kitamura and Murata (2020). To collect fish samples, we operated a multiple opening/closing net system (IONESS; SEA Corporation, Chiba, Japan) which was equipped with nine nets of 0.33-mm mesh and 1.5-m² mouth area each. The net system was towed obliquely at about 2 knots and fish samples were collected during the upcast of the system at discrete depth intervals from 0 to 1000 m during
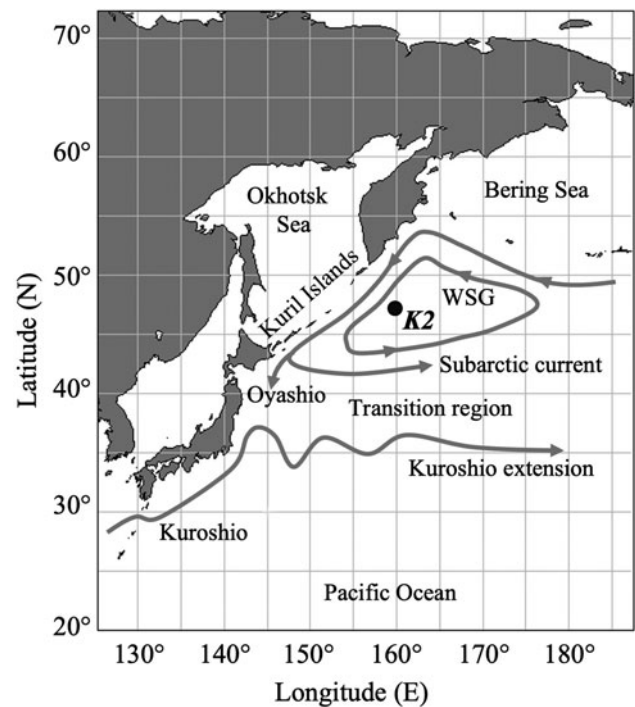
Figure 1. Map of the western North Pacific Ocean showing the study site, time-series station K2 (47°N, 160°E), with the surface current system (modified from Qiu, 2023). WSG is the Western Subarctic Gyre.

both the day and night. The discrete depth intervals were changed from the 2006 and 2007 cruises (nine layers: 1000–750, 750–500, 500–400, 400–300, 300–200, 200–150, 150–100, 100–50, and 50–0 m) to cruises during and after 2010 (eight layers: 1000–750, 750–500, 500–300, 300–200, 200–150, 150–100, 100–50, and 50–0 m). In the data analysis, fish abundances in the two sampling layers 300–400 and 400–500 m of 2006 and 2007 cruises were combined into a 300–500-m abundance to compare with data collected from cruises during and after 2010. The volume of water filtered by each net was estimated by using a calibrated flowmeter mounted on the net frame. Larger fish were immediately sorted from the net samples and fixed in 5–10% formalin-seawater; the remaining subsamples were also fixed and preserved in 5% formalin-seawater. To obtain typical vertical profiles of water temperature, salinity, and dissolved oxygen (DO), a conductivity–temperature–depth (CTD) instrument cluster (SBE 911plus; Sea-Bird Scientific, Bellevue, WA, USA) with a DO sensor (SBE43; Sea-Bird Scientific) was deployed during every cruise.

Table 1. Sampling of mesopelagic fish at time-series station K2 in the western subarctic Pacific

Cruise	Season	Year	Date
MR06-03	Summer	2006	13, 15, 23–25 June, 10–12 July
MR07-05	Autumn	2007	13–15, 25–26 September
MR10-01	Winter	2010	15–16 February
MR10-06	Autumn	2010	29 October, 1 November
MR11-02	Winter	2011	26 February
MR11-03	Spring	2011	20, 22–23 April
MR11-05	Summer	2011	2–3 July
MR12-02	Summer	2012	12–14 July

After our return to the laboratory on land, smaller fish were sorted out from the formalin-preserved subsamples. All fish samples were morphologically identified and enumerated. To understand body sizes of all fish species, we measured the standard length (SL) of the collected specimens to the nearest 0.1 mm using a Vernier caliper. For larvae, the length from snout tip to notochord tip was defined as the SL (Dunn, 1983). We also measured wet weight of juvenile and adult specimens to the nearest 0.001 g using an electronic balance (GR-202; A & D Company, Limited, Tokyo, Japan). Vertically integrated abundances (ind. m^{-2}) within each sampling layer and through the 0–1000-m water column were calculated, respectively. Mean abundance for each cruise was calculated (cruise mean). Then, seasonal mean abundances were obtained by averaging the cruise means in each season. In this study, larvae and juvenile/adult stages for each species were separately enumerated. Among the collected species, standard lengths of some specimens for *Cyclothone pallida* and *Stenobrachius leucopsarus* exceeded lengths at maturity which reported by a website of FishBase (Froese and Pauly, 2024) and Smoker (1970), respectively. Unfortunately, length of maturity seems to be not reported for other species collected in this study, some of our specimens of *Stenobrachius nannochir*, *Cyclothone atraria* and *Melamphaes lugubris* were over 90% of their maximum lengths reported by the FishBase. Although we didn't observe maturation of specimens anatomically, we considered that adult specimens were also included in our materials. We dealt with specimens after metamorphosis as 'juvenile and adult' in this study.

To quantify species diversity of the mesopelagic fish community, we counted species richness (number of species collected) and calculated Simpson's index of diversity (SID) based on the seasonal means of vertically integrated abundances through the 0–1000-m water column. SID is expressed as

$$\text{SID} = 1 - \sum (b/B)^2,$$

where b is the abundance of a particular taxon and B is the total abundance of the mesopelagic fish community. Both abundances are vertically integrated through the 0–1000-m water column. The value of this diversity index ranges between 0 and 1 and higher values indicate greater sample diversity.

To understand seasonal changes in the fish community, cluster analyses were performed independently for larval and juvenile/adult fish communities throughout the 0–1000-m water column. Abundance data were normalized via square root transformation, and the Bray–Curtis similarity matrix (Bray and Curtis, 1957) between seasons was obtained. Based on the similarity matrix, significant groups within the hierarchical clustering using group average linkage were established with the SIMPROF test (Clarke *et al.*, 2008) at 5% significance level. To minimize the effect of net avoidance by fish, only nighttime abundances were used for each species in this similarity analysis. This analysis was carried out using PRIMERv6 software (PRIMER-E, Ltd., Auckland, New Zealand).

To evaluate the presence/absence and extent of DVM, we calculated weighted mean depth (WMD, m) for each species:

$$\text{WMD} = \sum (n_i \times z_i \times d_i) / \sum (n_i \times z_i),$$

where d_i is the depth of sample i (centre of the depth interval, m), n_i is the population density of each species in the depth interval (ind. m^{-3}), and z_i is the thickness of the depth interval (m) (Andersen *et al.*, 2004). The amplitude of the migration (ΔWMD) was calculated as day WMD minus night WMD. In this study, juvenile/adult fish of three species (*Leuroglossus schmidti*, *Lipolagus ochotensis*, and *Stenobrachius leucopsarus*)

undertook opportunistic DVM, in which only a part of the population swam up to the surface layer, but others stayed at mesopelagic depths at night. For these three species, nighttime WMDs were calculated separately for both the migratory and nonmigratory populations. Furthermore, ΔWMD of only the migratory population was obtained as day WMD minus night WMD in the surface layer.

Results

Hydrography

Seasonal changes in water temperature and salinity were detected shallower than about 100 m (Figure 2). In this layer, two phases of the vertical profiles of temperature and salinity were apparent: vertical mixing during the cold seasons from winter to spring and stratification during warm seasons from summer to autumn. During the cold seasons, water temperature and salinity in this mixed layer were recorded as 1.7°C and 32.9–33.0, respectively. During the warm seasons when stratification was observed, the maximum water temperature (10.2°C) and the minimum salinity (32.6) were detected at the sea surface in an autumn cruise. In the warm stratified seasons, intermediate cold water was observed at around 100 m depth. The minimum water temperature in this water mass ranged from 1.2 to 1.5°C. Seasonal variability of DO was also detected in the surface layer (Figure 2). During the cold seasons, DOs between 0 and 100 m were homogenized as 325 μmol kg^{-1} which was the highest value through the annual DO variability. In the warm seasons, DOs above 30 and 40 m were homogenized in summer (312 μmol kg^{-1}) and autumn (286 μmol kg^{-1}), respectively, and both were lower than those in the cold seasons.

Below 100 m depth, no seasonal variability in water temperature, salinity, and DO was observed. Between 100 and 200 m depth, there were permanent thermo- and haloclines, where both temperature and salinity increased with depth. On the other hand, DOs were decreasing in this depth layer. Intermediate warm water was detected just below the permanent thermocline: the maximum water temperature in this water mass was around 3.6°C at around 250 m depth. Below the intermediate warm water, temperature gradually decreased to 2.5°C at 1000 m depth. Salinity gradually increased below the permanent halocline: the maximum observed salinity of 34.4 was recorded at 1000 m depth. And quite low DOs were observed below the permanent halocline: the minimum DO (ca 13–14 μmol kg^{-1}) was recorded between 595 and 620 m depth.

During summer in 2006, vertical profiles of water temperature, salinity, and DO were slightly differed from those obtained during the summers of 2011 and 2012.

Seasonality for occurrence and community structure

Larval fish

Ten species of fish larvae belonging to six families were collected (Table 2): among them, seven species (*Bathylagus pacificus*, *L. schmidti*, *Macropinna microstoma*, *Protomyctophum thompsoni*, *Pseudobathylagus milleri*, *S. leucopsarus*, and *Tarletonbeania* sp.) were larvae of mesopelagic fish whereas three (*Coryphaenoides* sp., *Hemilepidotus gilberti* and *Malacocottus* sp.) were demersal, as defined by Orlov and Tokranov (2019). The most and second-most abundant *L. schmidti* and *Coryphaenoides* sp. were collected throughout the four seasons with the highest abundance in summer (Figure 3A, B). Larvae of *H. gilberti* were detected only in the cold seasons (Figure 3C) whereas those of *P. milleri* (Figure 3D) and the other five species (*B. pacificus*, *M. microstoma*, *S. leucopsarus*, *P. thompsoni*, and *Tarletonbeania* sp.) were restricted to the
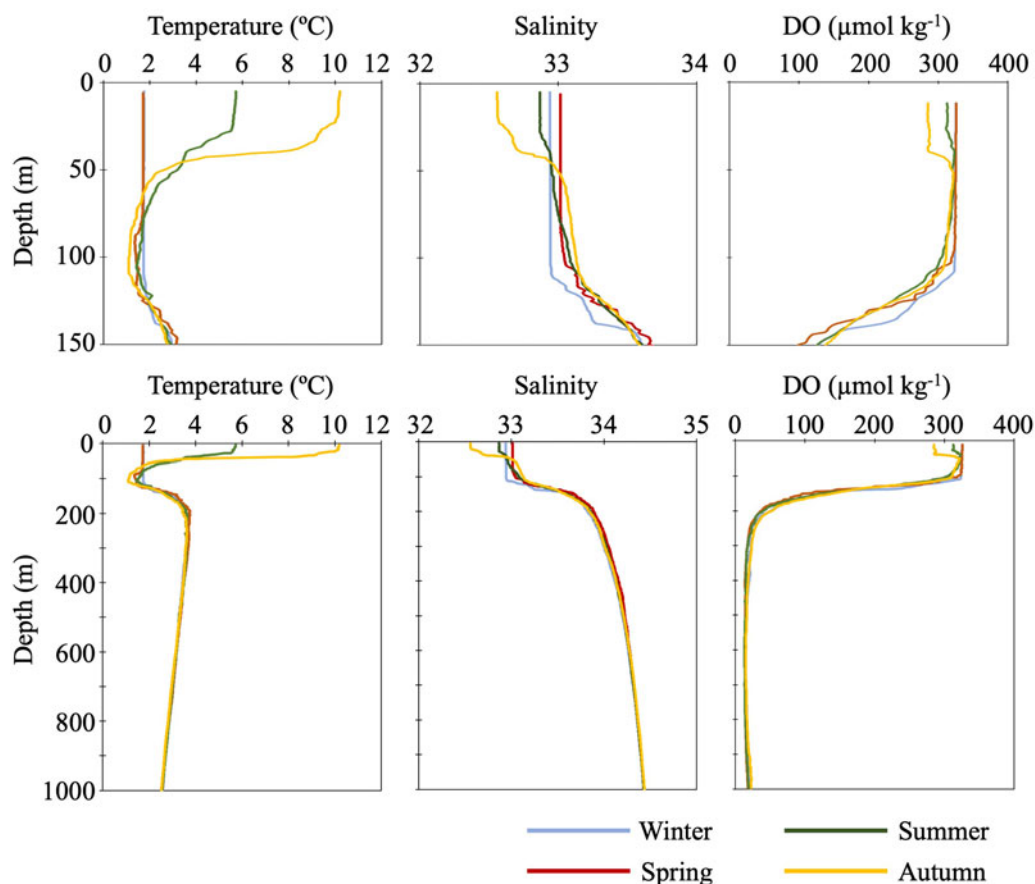
Figure 2. Vertical profiles of seasonal mean water temperature (˚C), salinity and dissolved oxygen (μmol kg^{-1}) at the time-series station K2. Top three panels are enlarged drawings of the profiles in surface layer (0–150 m) and bottom three panels indicate profiles between 0 and 1000 m in depth. Note that summertime profiles are means of data collected during cruises MR11-05 and MR12-02, data obtained from cruise MR06-03 are omitted.

warm seasons (Table 2); among these five species, three mycto-phid larvae (*P. thompsoni*, *S. leucopsarus* and *Tarletonbeania* sp.) were collected. Although we collected seven species of juvenile/adult myctophids (see Result section 'Juvenile/adult fish' in 'Seasonality for occurrence and community structure'), species richness and abundances of their larvae were quite limited. *Malacocottus* sp. occurred in all seasons except summer with rela-tively high abundance in the cold seasons (Figure 3E). Standard

Table 2. Seasonal and annual mean abundances of larval fish through the 0–1000-m water column (ind. m^{-2}) at time-series station K2 in the western subarctic Pacific, with standard length (mm) for each species and seasonal variability of diversity indexes

Species	Abundance (ind. m^{-2})					Standard length (mm)		
	Winter	Spring	Summer	Autumn	Annual mean	Mean	Range	*n*
Leuroglossus schmidti[#] (1)	0.95	0.93	5.58	1.62	2.27 (89.5)	12.6	4.2–31.6	907
Coryphaenoides sp.[#] (2)	0.04	0.06	0.22	0.08	0.10 (3.9)	22.2	10.8–62.2	30
Pseudobathylagus milleri[#] (1)			0.11	0.07	0.05 (1.8)	11.5	7.3–16.7	29
Hemilepidotus gilberti (3)	0.08	0.08			0.04 (1.6)	13.5	9.8–15.6	7
Malacocottus sp. (4)	0.07	0.04		0.02	0.03 (1.3)	14.9	10.2–20.1	5
Macropinna microstoma (5)			0.04	0.04	0.02 (0.8)	13.1	10.7–15.5	2
Bathylagus pacificus[#] (1)			0.02	0.04*	0.02 (0.6)	7.9	5.6–16.3	16
Stenobrachius leucopsarus[#] (6)			0.03		<0.01 (0.3)	4.8	3.5–5.9	15
Protomyctophum thompsoni[#] (6)			0.01		<0.01 (0.1)	4.5	3.6–5.3	2
Tarletonbeania sp. (6)			0.01*		<0.01 (0.1)	17.0	-	1
Species richness	4	4	8	6				
Simpson's D	0.30	0.29	0.15	0.21				

As for species with hashtags, both larval and juvenile/adult specimens were collected in this study. Numbers within parentheses in the column of species indicate family for each species: (1) Bathylagidae, (2) Macrouridae, (3) Cottidae, (4) Psychrolutidae, (5) Opisthoproctidae and (6) Myctophidae. Although abundances were primarily calculated based on the nighttime samples, data with asterisks were collected during day because of no sample collected during night. A column of annual mean contains annual mean abundance with its percentage in parentheses for each species
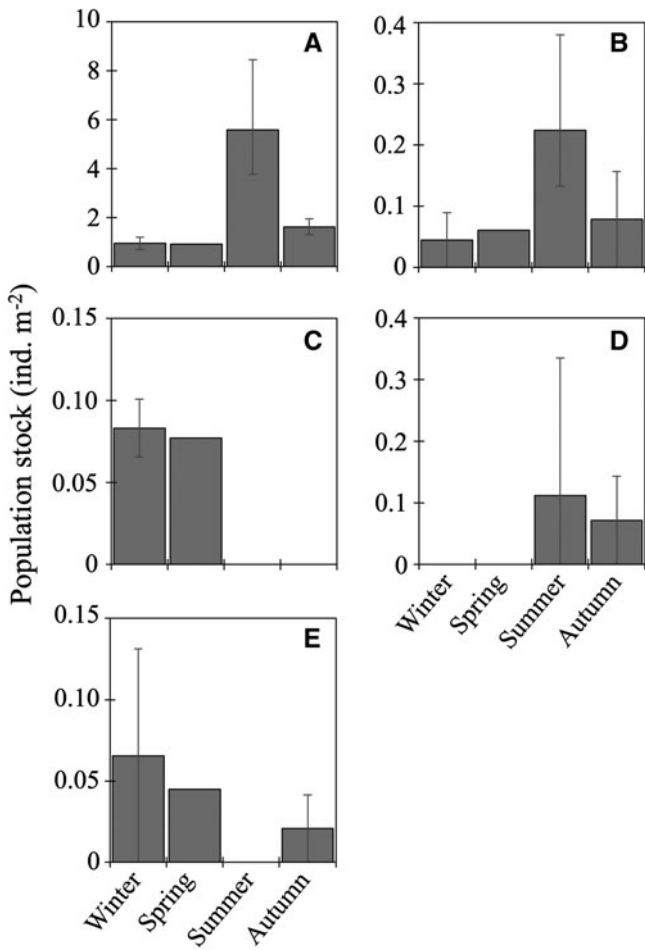
Figure 3. Seasonal vertically integrated abundance through the 0–1000-m water column (ind. m^{-2}) for five dominant fish larvae at time-series station K2: *Leuroglossus schmidti* (A), *Coryphaenoides* sp. (B), *Hemilepidotus gilberti* (C), *Pseudobathylagus milleri* (D) and *Malacocottus* sp. (E). Abundances are based on the nighttime data to reduce the influence of net avoidance by fish. Whiskers show range of the cruise mean abundances (*n* = 2 for winter and autumn, *n* = 3 for summer). Data for *L. schmidti* are from Kitamura and Murata (2020).

lengths of the collected *Malacocottus* larvae increased from autumn to spring: 10.2 mm in autumn (*n* = 1), 14.8 ± 2.0 mm in winter (mean ± standard deviation, *n* = 3), and 20.1 mm in spring (*n* = 1). We categorized seasonal occurrences of larvae into four types: (1) in all four seasons with summer peak (*L. schmidti*,

Coryphaenoides sp.), (2) in the cold seasons only (*H. gilberti*), (3) in the warm seasons only (*B. pacificus*, *M. microstoma*, *P. milleri*, *P. thompsoni*, *S. leucopsarus*, *Tarletonbeania* sp.), and (4) from autumn to spring with relatively high abundance during the cold seasons (*Malacocottus* sp.).

Total abundance of larvae in the 0–1000-m water column was high in summer but low in other seasons (Figure 4). From the cluster analysis based on Bray–Curtis similarity, larval fish were seasonally classified into three communities: summer, autumn, and the cold seasons (Figure 5). *Leuroglossus schmidti* was the most abundant larva detected among the three communities, whereas abundances of the other species were relatively low (Figure 5). The summer community was characterized by high species richness (eight species) and total abundance. The larval community in the cold seasons had low species richness (four species) and total abundance, and relatively high percentages of abundance for *H. gilberti* and *Malacocottus* sp. The autumn community had moderate species richness and total abundance. Although a pie chart showing species composition in autumn is similar to that in summer (Figure 5), presence of *Malacocottus* sp. and composition of rare species shown by bar chart are different from the summer community. Species diversities based on SID were low (0.15–0.30) throughout the four seasons (Table 2).

Juvenile/adult fish

The 20 species of juvenile/adult fish belonging to seven families were collected (Table 3). The most abundant three species (*Stenobrachius nannochir*, *S. leucopsarus*, and *L. schmidti*) along with *Chauliodus macouni* occurred throughout the four seasons (Figure 6A–C). The fourth through sixth most abundant species (*P. thompsoni*, *Cyclothone atraria*, and *Sigmops gracilis*) along with *P. milleri* and *Lampanyctus jordani* occurred in both the cold and warm seasons, but not in all four seasons (Figure 6D–F). The other 11 species were collected only during the warm seasons; there was no species collected during only the cold seasons. Only for *S. leucopsarus* in the warm seasons, standard lengths of the collected specimens during day were significantly shorter than nighttime ones (Student's *t* test, $P < 0.05$) (Figure 7), that probably affected net avoidance by larger fish. In the warm seasons, the largest specimen collected during day was 56.6 mm SL whereas specimens larger than 57 mm SL occupied 31% of the nighttime community of *S. leucopsarus*. On the other hand, the large specimens of this species (>57 mm, SL) were collected both during day and night in the cold seasons.
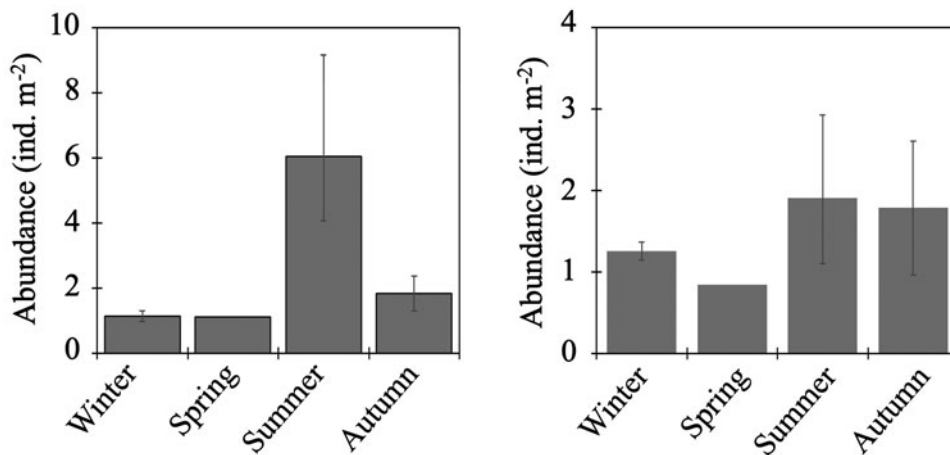
Figure 4. Seasonal vertically integrated total abundance through the 0–1000-m water column (ind. m^{-2}) for fish larvae (left) and juvenile/adult fish (right) at time-series station K2. Whiskers show range of the cruise mean abundances (*n* = 2 for winter and autumn, *n* = 3 for summer).
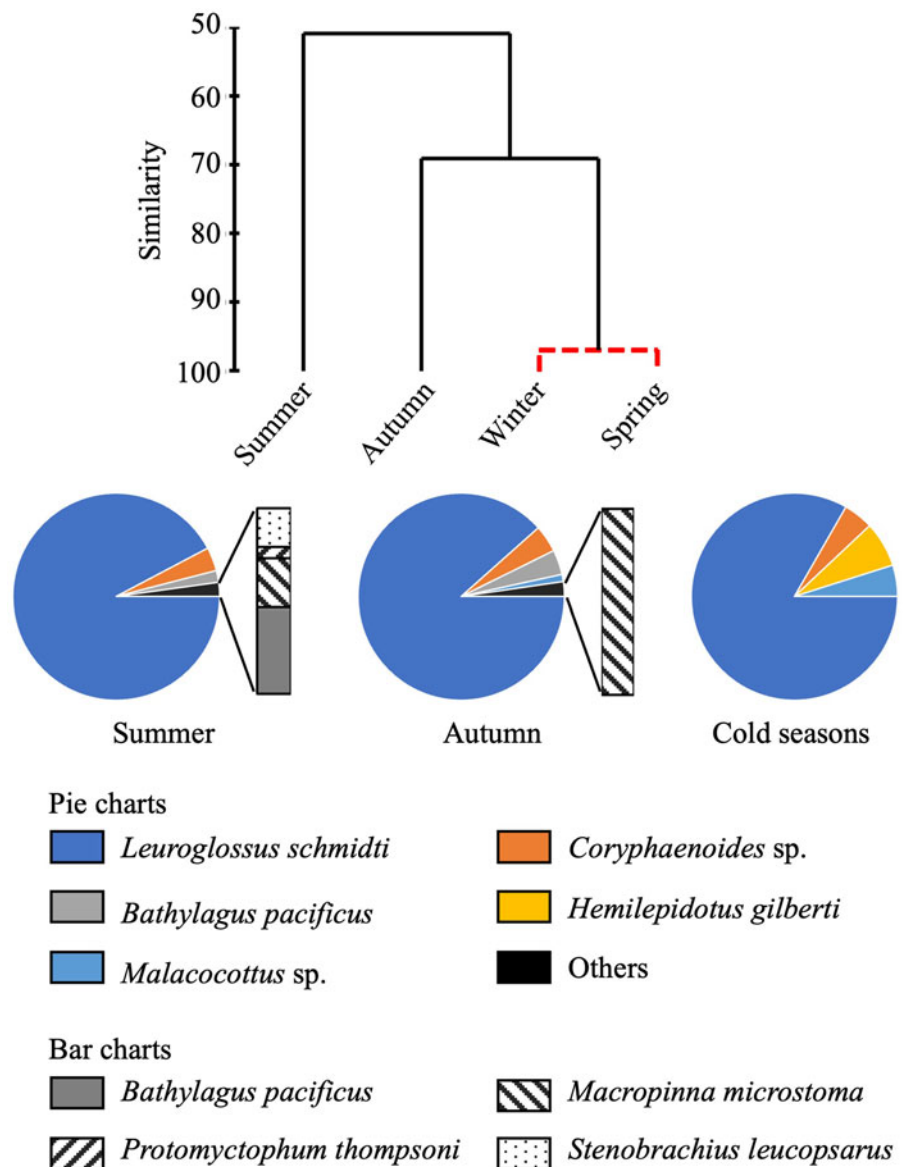
Figure 5. Seasonal change of larval fish communities. Similarity of larval fish communities in different seasons at time-series station K2 derived from hierarchical clustering with the SIMPROF test (top). Solid lines of the dendrogram indicate significantly different communities and groups of communities ($P < 0.05$) and the red dashed line indicates groups of communities for which the null hypothesis could not be rejected ($P > 0.05$). Species composition in each group of communities (bottom); composition of the cold season community is based on mean abundances between winter and spring.

Total abundance of juvenile/adult fish through the 0–1000-m water column varied seasonally, with high abundance in the warm seasons and low in the cold seasons (Figure 4). The seasonal variability of abundance of juvenile/adult fish, however, was lower than that of larvae. We classified the juvenile/adult fish based on the Bray–Curtis cluster analysis into cold- and warm-season communities (Figure 8). In the cold season community, the most abundant three species (*L. schmidti*, *S. leucopsarus*, and *S. nannochir*) accounted for 83% of the juvenile/adult fish abundance (Figure 8). In contrast in the warm season community, the proportion of the three species decreased to 52% whereas the abundance of *P. thompsoni* increased to 16% of total abundance. Species richness was high (16–18 species) and low (5–7 species) during the warm and cold seasons, respectively; species diversities revealed by SID were also high in the warm seasons (0.85–0.86) whereas those in the cold seasons were slightly lower (0.72–0.76) (Table 3).

Vertical distribution and migration

Larval fish

Although vertical distributions of fish larvae varied diurnally and seasonally, *L. schmidti* was the most abundant in almost all depth strata during both day and night throughout the four seasons

(Figure 9). In the cold seasons, vertical distributions of fish larvae below 300 m were quite limited. Larval distributions were vertically elongated during the warm seasons, especially in autumn. Peaks in abundance were observed at 100–150 or 200–300 m depth. Although the euphotic layer at K2 was restricted to the upper 50 m (Kitamura *et al.*, 2016), the total abundance of fish larvae in this layer was quite low throughout the four seasons.

Vertical distribution and migration of the most abundant fish, *L. schmidti*, and their seasonal changes are here cited briefly from Kitamura and Murata (2020). From summer to autumn, *L. schmidti* is distributed widely from the surface to 750 m. Hatched larvae at the subsurface (mainly 100–150 m) migrated towards the surface as they grew. Once larvae reached 20 mm in length, they migrated down to midwater, and some of the larger larvae (>24 mm) exhibited DVM. On the other hand, some of the larval population overwintered at depths between 100 and 300 m.

The second most abundant, *Coryphaenoides* sp., was widely collected from 50 to 1000 m, and their vertical distribution changed not diurnally but ontogenetically (Figure 10). During summer, *Coryphaenoides* larvae, which were 10–27 mm SL, were distributed from 50 to 500 m with no relationship between depths and standard lengths. After that, they seemed to migrate down with growth (up to 62 mm SL) to below 750 m until winter (Figure 10A, B). In addition, small larvae (<20 mm SL) were

Table 3. Seasonal and annual mean abundance of juvenile/adult fish through the 0–1000-m water column (ind. m^{-2}) at time-series station K2 in the western subarctic Pacific, with standard lengths (mm), wet weights (g) and seasonal variability of diversity indexes

Species	Abundance (ind. m^{-2})					Standard length (mm)		Wet weight (g)		n
	Winter	Spring	Summer	Autumn	Annual mean	Mean	Range	Mean	Range	n
Stenobrachius nannochir (1)	0.36	0.26	0.35	0.37	0.34 (22.2)	66.1	32.8–106.9	3.03	0.28–11.57	75
Stenobrachius leucopsarus# (1)	0.24	0.29	0.27	0.50	0.33 (21.6)	52.2	20.6–124.5	2.02	0.05–9.99	88
Leuroglossus schmidti# (2)	0.39	0.20	0.12	0.22	0.23 (15.4)	36.4	27.95–128.4	0.66	0.10–16.12	59
Protomyctophum thompsoni# (1)	0.05		0.42	0.17	0.16 (10.6)	26.4	19.6–41.9	0.29	0.08–1.18	77
Cyclothone atraria (3)		0.04*	0.19	0.15	0.10 (6.3)	26.5	12.6–56.4	0.12	0.01–1.12	26
Sigmops gracilis (3)	0.17		0.1	0.05*	0.08 (5.3)	75.6	64.6–94.2	1.04	0.54–2.16	20
Chauliodus macouni (4)	0.09*	0.09	0.04	0.05	0.07 (4.5)	118.0	58.6–150.8	6.24	0.53–12.68	10
Bathylagus pacificus# (2)			0.05	0.09	0.04 (2.3)	69.5	23.7–137.7	4.23	0.09–19.79	9
Pseudobathylagus milleri# (2)	0.08*		0.03*		0.03 (1.9)	42.7	24.7–72.2	1.27	0.09–3.48	3
Diaphus theta (1)			0.03	0.06	0.02 (1.5)	64.6	48.9–77.6	4.7	1.81–7.76	10
Melamphaes lugubris (5)			0.04	0.05	0.02 (1.5)	80.7	76.0–83.6	13.8	11.9–16.0	5
Lipolagus ochotensis (2)			0.04	0.03	0.02 (1.2)	44.1	35.4–52.9	0.71	0.3–1.0	7
Lampanyctus jordani (1)	0.05			0.02*	0.02 (1.2)	108.6	100.3–116.9	15.28	13.10–17.45	2
Cyclothone pallida (3)			0.03	0.03	0.02 (1.0)	31.2	11.9–45.1	0.16	0.01–0.30	5
Cyclothone alba (3)			0.01	0.05	0.02 (1.0)	20.2	16.7–24.2	0.02	0.01–0.06	9
Cyclothone pseudopallida (3)			0.01	0.05	0.02 (1.0)	30.0	23.0–36.3	0.08	0.04–0.13	4
Coryphaenoides sp.# (6)			0.05		0.01 (0.8)	119.0	59.9–174.9	2.96	0.27–7.43	3
Tarletonbeania tylori (1)				0.02	<0.01 (0.3)	55.7	51.6–59.9	1.82	1.40–2.25	2
Lampanyctus regalis (1)			0.01		<0.01 (0.2)	185.3		64.59		1
Careproctus sp. (7)			0.01*		<0.01 (0.2)	24.2		0.07		1
Species richness	7	5	18	16						
Simpson's D	0.76	0.72	0.86	0.85						

As for species with hashtags, both larval and juvenile/adult specimens were collected in this study. Numbers within parentheses in the species column indicate family for each species: (1) Myctophidae, (2) Bathylagidae, (3) Gonostomatidae, (4) Stomiidae, (5) Melamphaidae, (6) Macrouridae and (7) Liparidae. Although abundances were primarily calculated based on the nighttime samples, data with asterisks were collected during day because of no sample collected during night. A column of annual mean contains annual mean abundance with its percentages within parentheses for each species.
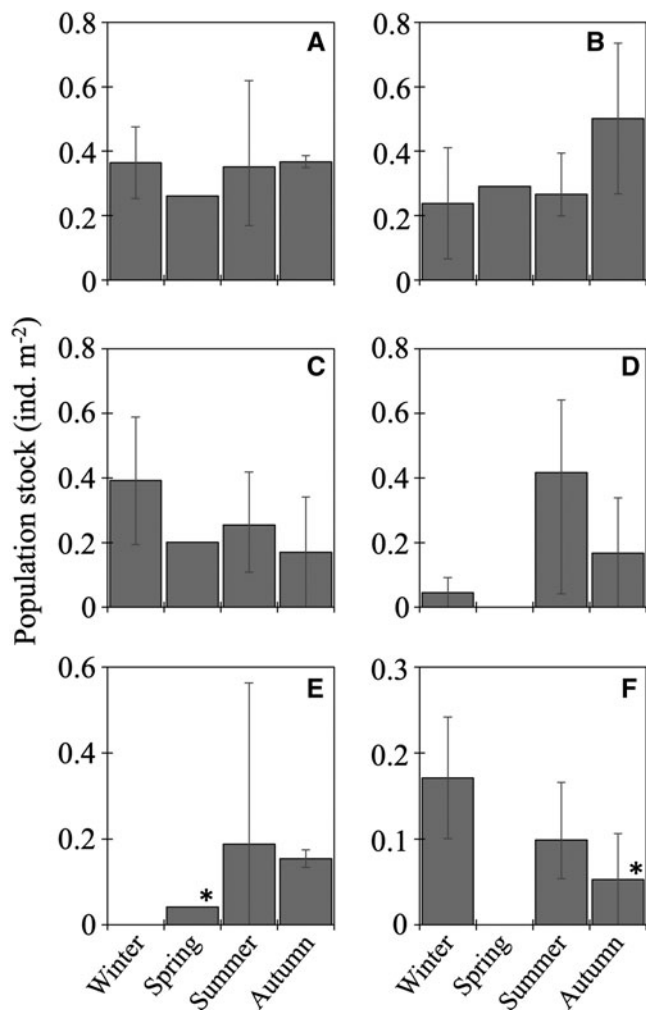
Figure 6. Seasonal vertically integrated abundance through the 0–1000-m water column (ind. m^{-2}) for six dominant juvenile/adult fish at time-series station K2: *Stenobrachius nannochir* (A), *Stenobrachius leucopsarus* (B), *Leuroglossus schmidti* (C), *Protomyctophum thompsoni* (D), *Cyclothone atraria* (E), and *Sigmops gracilis* (F). Abundance is based on nighttime data to reduce the influence of net avoidance by fish except for two data marked with asterisks that were collected in the daytime because no specimen were collected during night. Whiskers show range of the cruise mean abundances. Data for *L. schmidti* are from Kitamura and Murata (2020).

also collected at 200–300 m from autumn to spring. We found no evidence of larvae of this species exhibiting DVM. The third most abundant larvae, *P. milleri,* were primarily distributed at 150–300 m (Table S1); only one specimen was collected from 500 to 750 m. In this species, ontogenetic migration was also recognized: larger larvae were distributed deeper (10.7 ± 2.5 mm SL at 150–200 m, 13.3 ± 2.3 mm SL at 200–300 m, and 35.5 mm SL at 500–750 m, $n = 32$). This species did not show DVM during summer (daytime and nighttime WMDs were 209 and 198 m, respectively) although DVM during autumn was unclear because none were collected during the day.

Among rare species, *H. gilberti*, which occurred in the cold seasons only, was distributed above 150 m (Table S1); diel or ontogenetic migration was not recognized due to low abundance. *Malacocottus* sp., which occurred in all seasons except summer, was collected at 50–200 m (Table S1). Although seasonal increase in their standard lengths was detected (see Result section 'Larval fish' in 'Seasonality for occurrence and community structure'), presence or absence of ontogenetic migration was not clear because of the low number of specimens collected. DVM of this species also was not recognized. *Bathylagus pacificus* and *M. microstoma* were distributed at 100–200 m and 200–300 m, respectively, without DVM (Table S1). The depths at which three myctophids (*P. thompsoni*, *S. leucopsarus*, and *Tarletonbeania* sp.) were collected differed slightly from each other: 0–50 m for *S. leucopsarus*, 0–100 m for *P. thompsoni*, and 100–150 m for *Tarletonbeania* sp. (Table S1).
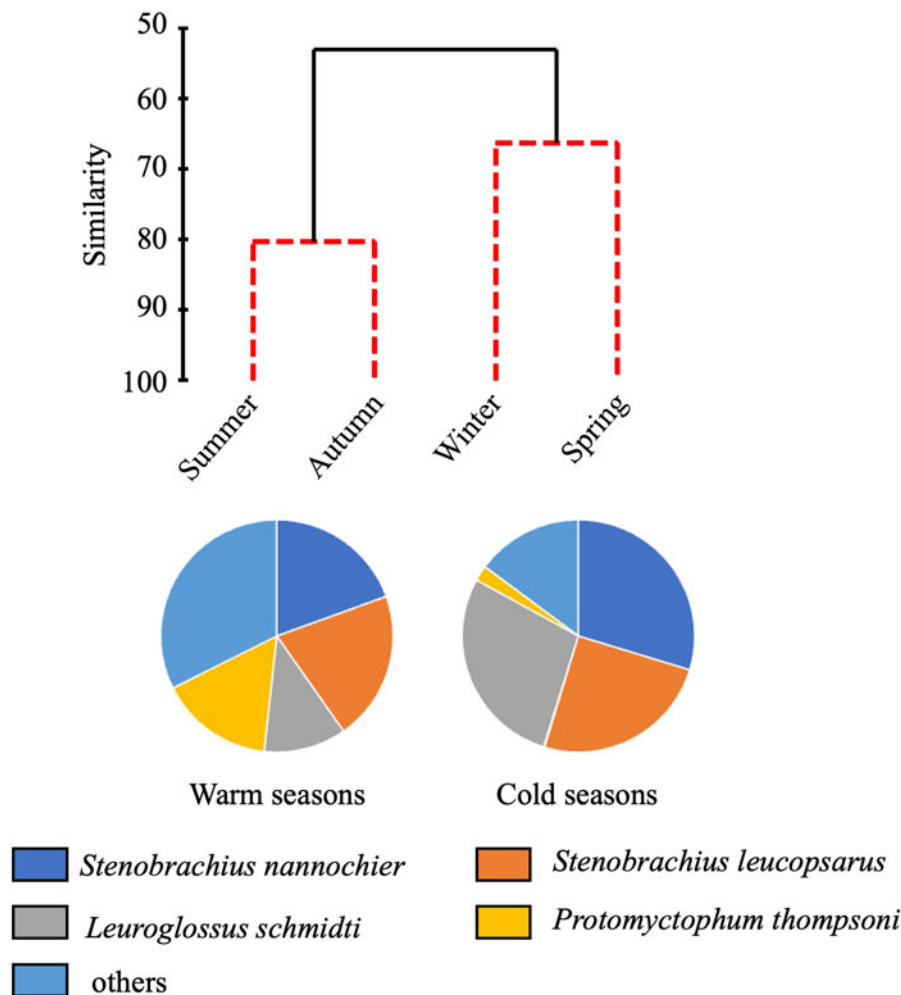
Juvenile/adult fish
Unlike larval fish, no juvenile/adult fish was collected from surface layers during daylight (above 300 m in the cold seasons or above 150 or 200 m in the warm seasons); a few species migrated up into epipelagic depths during the night (Figure 11). In the cold seasons, only *S. leucopsarus* and *L. schmidti* showed DVM; in the warm seasons, the two species together with *Diaphus theta*, *Tarletonbeania taylori*, and *Lipolagus ochotensis* showed DVMs (Table 4). Note that, results of *D. theta*, *T. taylori*, and *L. ochotensis* were based on the small numbers of materials (Table S3). Among these, the DVMs of *S. leucopsarus* and *L. schmidti* were opportunistic; that of *L. ochotensis* seemed to be opportunistic although collected materials were quite few ($n = 7$). Total abundances of diel vertical migrants swimming up above 200 m were
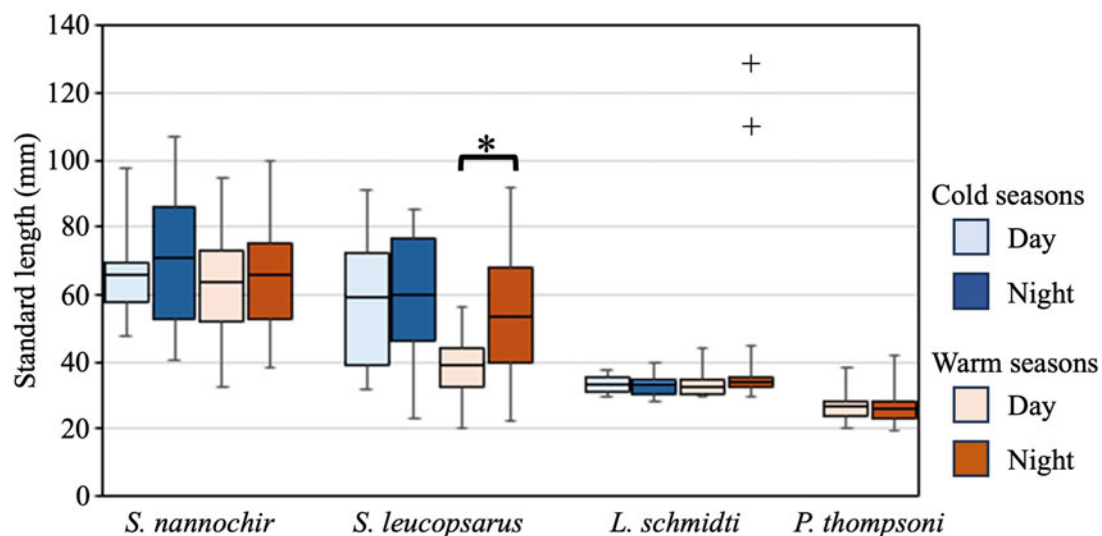
Figure 7. Diel changes of standard lengths of the collected juvenile/adult specimens for four abundant species, *Stenobrachius nannochir*, *Stenobrachius leucopsarus*, *Leuroglossus schmidti*, and *Protomyctophum thompsoni* at K2. Boxes indicate ranges of the standard lengths where 50% of the population are included in, and horizontal bars in the boxes are the mean standard lengths. Whiskers show the ranges of the standard lengths. Cold seasons include winter and spring whereas warm seasons have summer and autumn. Although two specimens of *L. schmidti* larger than 100 mm were collected in the warm seasons (shown by plus marks), these were excluded from the comparison as outliers. A significant diel difference is detected in *S. leucopsarus* during the warm seasons (as shown by asterisk).

Figure 8. Seasonal change of juvenile/adult fish communities. Similarity of fish communities in different seasons at time-series station K2 derived from hierarchical clustering with the SIMPROF test (top). Solid lines of the dendrogram indicate significantly different groups of communities ($P < 0.05$) and red dashed lines indicate groups of communities for which the null hypothesis could not be rejected ($P > 0.05$). Species composition of the warm season community is based on mean abundances between summer and autumn and the cold season community based on mean abundances between winter and spring.

low ($0.14–0.27$ ind. m^{-2}) and high ($0.38–0.54$ ind. m^{-2}) in the cold and warm seasons, respectively. The diel vertical migrants correspond to 17–30% of juvenile/adult mesopelagic fish communities through the 0–1000-m water column.

Two abundant *Stenobrachius* species, *S. leucopsarus* and *S. nannochir*, had different distribution/migration patterns (Figure 12). During the day, *S. leucopsarus* was collected from 200 to 750 m in the warm seasons whereas their vertical distribution ranges went down to 300–750 m in winter and 500–1000 m in spring. Dynamic seasonal change of their daytime vertical distribution was also clearly shown by WMDs in the four seasons: 400 (summer), 299 (autumn), 458 (winter), and 712 m (spring). Note that daytime vertical distributions of larger specimens (>57 mm SL) of this species were still not clear during the warm seasons because they were not collected as previously noted (see Result section 'Juvenile/adult fish' in 'Seasonality for occurrence and community structure' and Figure 7). This species showed opportunistic DVM through the four seasons. But percentages of migratory individuals among their population varied seasonally: 84–94% in the warm seasons and 40–58% in the cold seasons. The nighttime distribution of diel vertical migrants was reached to the shallowest sampling layer (0–50 m) in the warm seasons but they did not swim above 50 m depth in the cold seasons. This seasonal difference seemed to have relation to body sizes: smaller specimens were observed in the shallower depths (Figure 13). In 0–50 m layer, only specimens up to 44 mm SL distributed there during night of the warm seasons. In the cold seasons, however, abundance of such small specimens was quite low, no specimen of this species was collected from the shallowest sampling layer. Distances of DVM varied

seasonally from 204 m (autumn) to 579 m (spring). *Stenobrachius nannochir*, whose mean body size was larger than that of *S. leucopsarus* (Table 3), was distributed deeper than *S. leucopsarus* without DVM throughout the year (Figure 12). Its vertical distribution also shifted seasonally: averages of day- and nighttime WMDs of this species were 658 (summer), 638 (autumn), 715 (winter) and 851 m (spring). Similar to *S. leucopsarus*, *S. nannochir* was distributed in its shallowest depths during autumn, whereas it shifted to its deepest layer during spring. Although the vertical distributions of the two *Stenobrachius* species only partially overlapped, the seasonal changes of their WMDs were synchronous.

The third most abundant fish, *L. schmidti*, was distributed below 300 m during daylight and a part of this population (13–38%) showed DVM (Figure 11). ΔWMD changed from 405 m in summer to 603 m in autumn. Details of the DVM of this species were reported by Kitamura and Murata (2020). During their DVM, nighttime distribution depths in the epipelagic layer changed seasonally. Migrating specimens swam up to the shallowest sampling depths (0–50 m) during the warm seasons, whereas no fish migrated into this layer during the cold seasons. Smaller juveniles tended to have lower DVM activity than larger ones.

Among three other diel vertical migrants, *D. theta* and *T. taylori* migrated between the upper part of the mesopelagic and surface layers: from 200–500 to 50–200 m for the former species and from 300–500 to 0–50 m for the latter species (Table S2). For these two species, no specimen was collected from the mesopelagic layer at night. In contrast, *L. ochotensis* seasonally changed its DVM manner (Table S2). In summer,
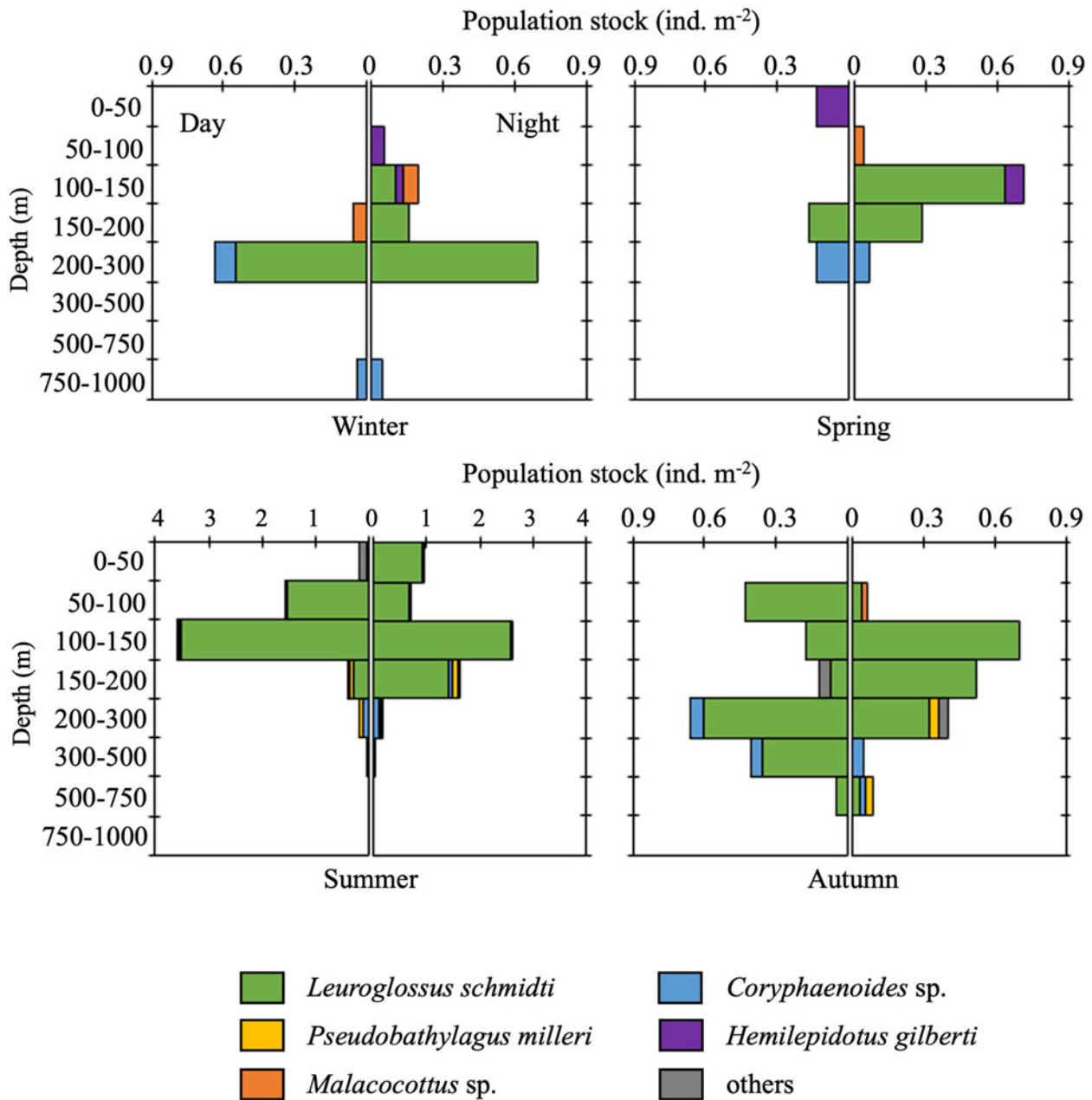
Figure 9. Diel and seasonal vertical distributions of fish larvae at time-series station K2. Note that the scale of the horizontal axes for summer is larger than that in other seasons.

it was distributed at 500–750 m during the day, whereas most of the population (94%) migrated up to above 100 m during the night. Although this species was also collected in autumn, then it was distributed from 500 to 750 m during both the day and night.

The fourth most abundant fish, *P. thompsoni*, was distributed between 150 and 500 m without DVM. During the warm seasons, a peak in its abundance was recognized at 200–300 m (Figure 11) and it accounted for 60–87% of the total fish abundance in this layer. In the cold seasons, however, this species was collected only from 150 to 200 m with quite low abundance during winter. For *Cyclothone*, four species were collected mainly in the warm seasons and their vertical distributions fell into two patterns. *Cyclothone alba* and *C. pseudopallida* were distributed above 500 m without DVM, and their vertical distributions mostly overlapped each other during both the day and night (Table S2). The other two *Cyclothone* species were distributed in deeper layers. *Cyclothone atraria* was distributed below 500 and 300 m during

the day and night, respectively (Table S2). Although the vertical range of its distribution was elongated upward at night, ΔWMDs did not support the presence of upward migration for *C. atraria*. *Cyclothone pallida* was collected at 500–750 and 300–1000 m during the day and night, respectively, but DVM was not clear because the numbers of specimens collected at night were quite low.

Vertical distributions of *S. gracilis* and *P. milleri* were limited to within 300–500 m and 500–750 m, respectively, whereas those of *Bathylagus pacificus* (500–1000 m), *Chauliodus macouni* (300–1000 m), *Coryphaenoides* sp. (200–1000 m) and *Melamphaes lugubris* (300–500 and 750–1000 m) were wide (Table S2). Among them, *Coryphaenoides* sp. and *M. lugubris* were collected only at night. One of the *P. milleri* specimens (24.7 mm SL) collected during winter was just metamorphosing, although a larval *P. milleri* specimen of 35.5 mm was also collected between 500 and 750 m (see Result section 'Larval fish' in 'Vertical distribution and migration').
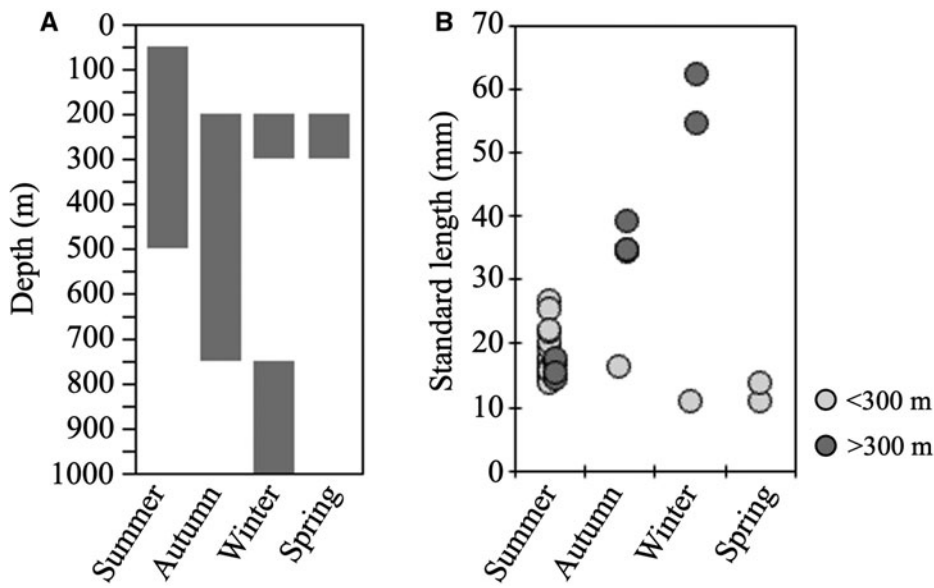
Figure 10. Seasonal vertical distribution ranges (A) and standard lengths (B) for larvae of *Coryphaenoides* sp. at time-series station K2.
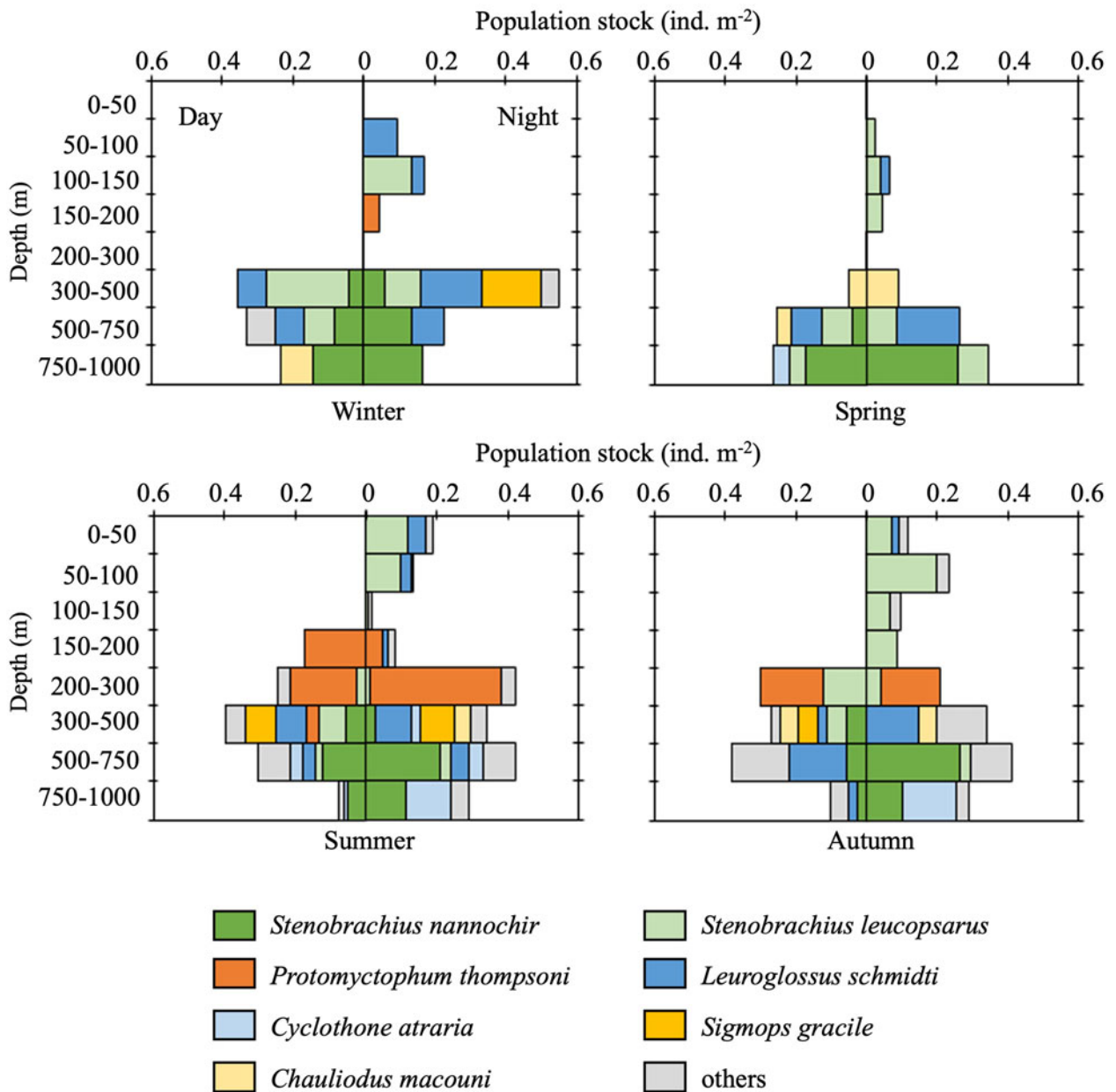

Figure 11. Diel and seasonal vertical distributions of juvenile/adult mesopelagic fish at time-series station K2.

Table 4. Vertical distribution and diel vertical migration of juvenile/adult of five mesopelagic fish species at time-series station K2

| Species | Season | Ranges of vertical distributions (m) | | WMD (m) | | |
		Day	Night	Day	night	Distance of DVM (m)
*Stenobrachius leucopsarus**	Winter	300–750	300–500, 100–150	458	400, 125	333
	Spring	500–1000	500–1000, 50–200	712	749, 133	579
	Summer	200–750	200–750, 0–150	400	491, 50	350
	Autumn	200–500	200–750, 0–200	299	403, 95	204
*Leuroglossus schmidti**	Winter	300–750	300–750, 50–150	515	478, 88	427
	Spring	500–750	500–750, 100–150	625	625, 125	500
	Summer	300–750	300–750, 0–200	467	477, 62	405
	Autumn	300–1000	300–500, 50–0	628	400, 25	603
*Liporagus ochotensis**	Summer	500–750	500–750, 0–100	625	625, 38	587
Diaphus theta	Summer	200–500	100–200	356	161	195
Tarletonbeania tylori	Autumn	300–500	0–50	400	25	375

Three species marked with asterisks had opportunistic diel vertical migration (only a part of the population swam up to the surface layer, but others stayed at mesopelagic depths at night). For the three species, nighttime weighted mean depths (WMDs) were calculated separately for both the migratory and non-migratory populations.

Discussion

Limitations and advantages of this study

We used a relatively smaller net system (1.5-m^2 mouth area) compared with other sampling gear for fish, such as the Issacs–Kidd midwater trawl with up to 7.5-m^2 mouth area (Issacs and Kidd, 1953). Although underestimation due to net avoidance by fish is inevitable in abundance estimation based on trawl sampling (Gjøsaeter and Kawaguchi, 1980), it is probably more substantial in the present study. The total number of mesopelagic fish species
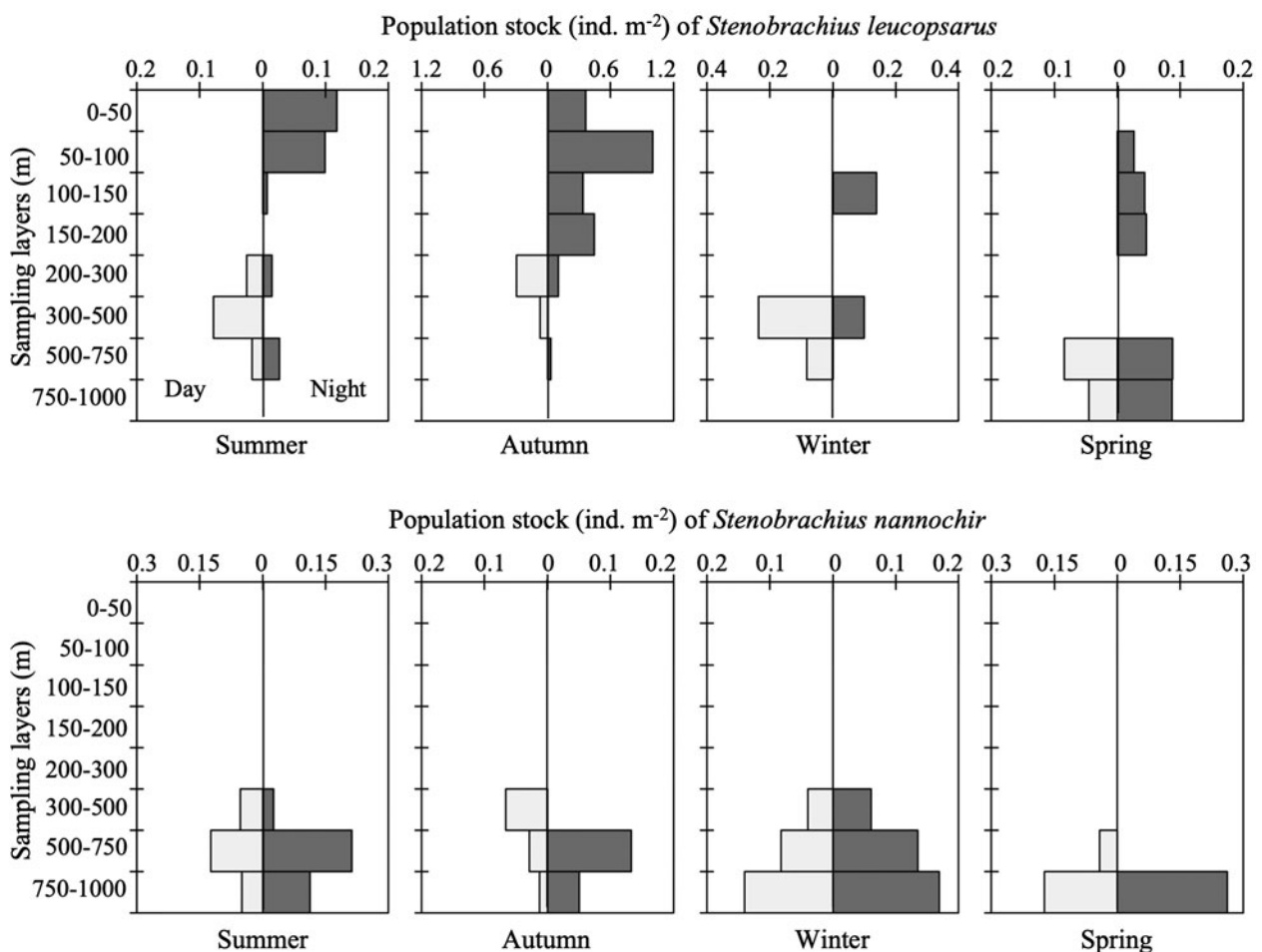
Figure 12. Diel and seasonal vertical distributions for juvenile/adult *Stenobrachius leucopsarus* (top row) and *Stenobrachius nannochir* (bottom row) at time-series station K2. Bars show seasonal mean abundances (ind. m^{-2}) which are vertically integrated through each sampling layer.
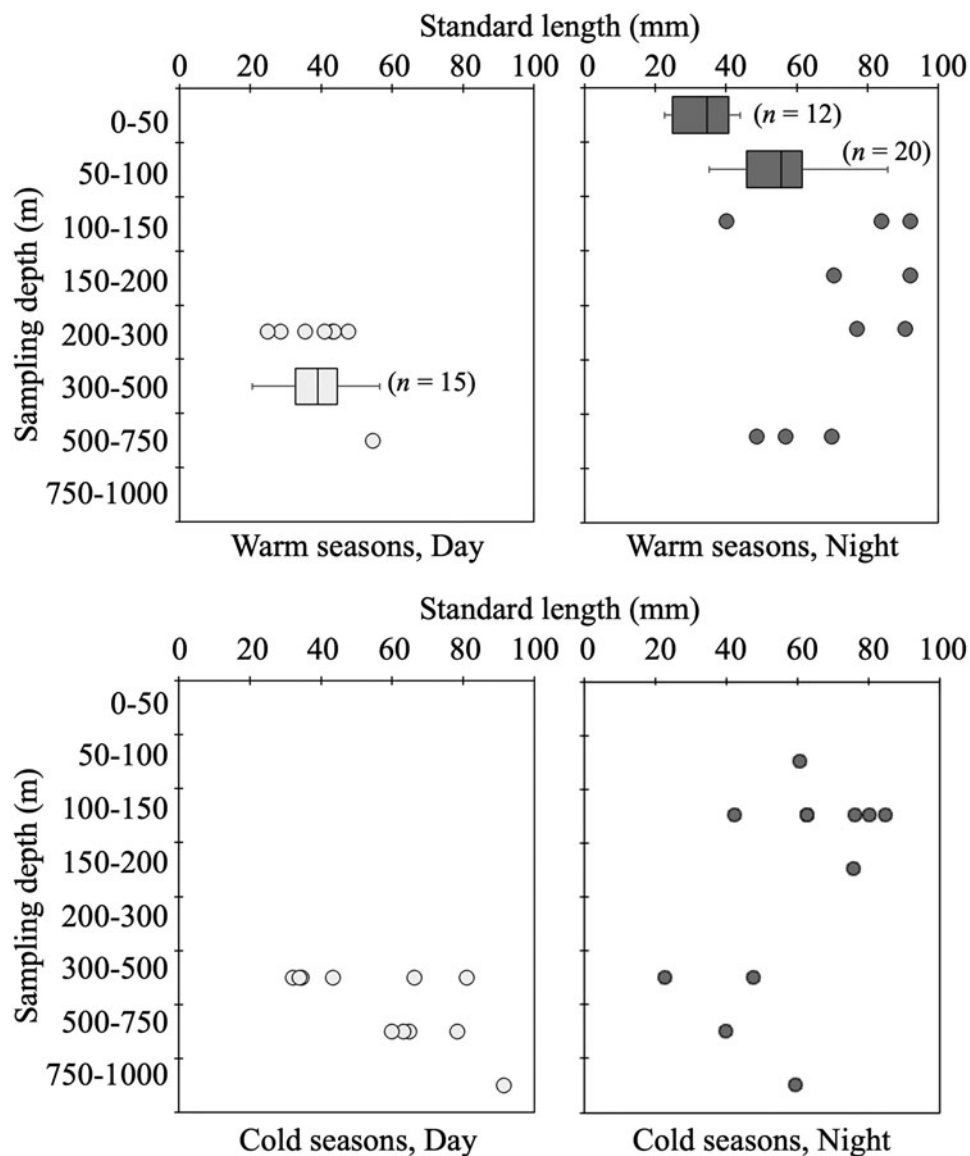
Figure 13. Diel and vertical changes of standard lengths (mm) for *Stenobrachius leucopsarus* collected from K2 during the warm (top panels, summer and autumn) and cold seasons (bottom panels, winter and spring). Boxes indicate ranges of the standard lengths where 50% of the population are include in, and vertical bars in the boxes are the mean standard lengths. Whiskers show the ranges of the standard lengths. In the sampling depths where total numbers of the collected materials are less than 10 individuals, all data are plotted. The sample sizes (*n*) are the total numbers measured.

obtained in this study (27 species) was lower than those in previous records in the western part of the subarctic Pacific (86 species by Beamish *et al.*, 1999). This was probably due to higher net avoidance by fish, a restricted research area (only at K2) in the present study, or both. However, Willis *et al.* (1988) reported that only seven species (*C. macouni*, *C. atraria*, *D. theta*, *L. schmidti*, *P. thompsoni*, *S. leucopsarus*, and *S. nannochir*) accounted for 91.8% of the individuals captured from the western subarctic Pacific. These seven species were also abundant in the juvenile/adult community observed by the present study that accounted for 82.1%. We considered that basic structure of mesopelagic fish community was successfully described in this study.

In the present study, vertical distributions and migrations of all the abundant species as well as other species are shown. Due to use of smaller sampling gear, numbers of collected materials for the latter species were relatively small (Table S3). Although we obtained species-specific vertical distribution and migration patterns for them, further study based on much more materials collected by using larger net system is needed. On the other hand, the vertical resolution of the distributions we observed (eight layers through the 0–1000-m water column) was finer than

those in previous studies, such as Beamish *et al.* (1999; three layers between 0 and 1000 m). And our field samplings successfully covered in all four seasons that revealed seasonal changes in fauna and in vertical distribution of and migration by mesopelagic fish. In addition, we investigated not only juvenile/adult fish but also larval fish. Research on fish larvae has been limited in oceanic areas of the western subarctic Pacific, unlike in the Okhotsk Sea (Davydova *et al.*, 2007; Andreeva and Shebanova, 2010) or the transition region (Kubota *et al.*, 2001; Tsukamoto *et al.*, 2001; Sassa *et al.*, 2004b). Thus, this study also provides useful baseline information for larval fish ecology there.

Community

Larvae

In the Okhotsk Sea and the Pacific waters along the Kurils/Kamchatka, 64 taxa of fish larvae have been recorded, and coastal and demersal species were numerically abundant (Davydova *et al.*, 2007; Andreeva and Shebanova, 2010; Mukhametva and Mukhametov, 2022). In comparison, the larval fish community at K2 had lower species richness (10 species) and a higher

percentage of mesopelagic species (93%). Only *H. gilberti* was common to both K2 and the Okhotsk/Kuril/Kamchatka waters. In addition, the larval fish community at K2 also differed from those at the transition region located south of our study site. In the transition region, 37 species of larval mesopelagic fish were recorded, myctophid larvae dominated, and the myctophid community was more diverse (28 species) (Sassa *et al.*, 2004b; 2007). Furthermore, Kubota *et al.* (2001) reported 80 species of larval and early stage juvenile fish in the transition region: myctophids (11–45%) as well as Japanese anchovy (41–79%) were dominant in the community. Compared to the larval fish community in the transition region, the K2 community had lower species diversity and lower myctophid abundance; the absence at K2 of epipelagic fish larvae such as Japanese anchovy was also a big difference. Between the transition region and K2, larvae of four mesopelagic fish (*B. pacificus*, *L. schmidti*, *P. milleri*, and *P. thompsoni*) occurred in common.

On the eastern side of the subarctic Pacific, mesopelagic bathylagids and myctophids together with walleye pollock and deep-sea pleuronectids formed the larval fish community in the continental slope area, where abundances of these mesopelagic fish larvae tended to be high (Doyle *et al.*, 2002; Lanksbury *et al.*, 2005). However, the oceanic community in the eastern subarctic Pacific contained larvae of only mesopelagic fish, such as Myctophidae and Chauliodonitidae, with low diversity and their abundances were lower than those in the shelf break areas (Norcross *et al.*, 2003). Unfortunately, Norcross *et al.* (2003) showed a species list not in the oceanic area of the eastern subarctic Pacific but in the subarctic domain including the shelf break area. Between the subarctic domain and K2, however, four larvae (*L. schmidti*, *P. milleri*, *P. thompsoni*, and *S. leucopsarus*) occurred in common. Characteristics of the larval fish community at K2 (dominance of the mesopelagic fish species, low species diversity and low abundance) were relatively similar to those in the oceanic area of the eastern subarctic Pacific.

Although 20 species of juvenile/adult fish were collected in this study, larvae of 14 of the 20 species were not found at K2. Among these 14 species, four myctophids (*D. theta*, *Lampanyctus jordani*, *S. nannochir*, *T. taylori*) and a bathylagid (*L. ochotensis*) are known to migrate southward across the subarctic front for reproduction, and the hatched larvae grow in the Kuroshio or transition regions (Moku *et al.*, 2003; Sassa *et al.*, 2004b; Sassa, 2019). Larvae of *Lampanyctus regalis* and *S. gracilis* were abundant in the transition region (Sassa *et al.*, 2004b, 2007) and those of *M. lugubris* were observed only in the subarctic front in the eastern subarctic Pacific (Norcross *et al.*, 2003). Thus, these species also probably migrate horizontally between southern spawning/nursery areas and subarctic feeding grounds. These horizontal migrations may decrease the species richness of the larval fish community at K2. In addition, the abundance of all of the mesopelagic fish larvae collected at K2 was very low except for *L. schmidti*. In the Gulf of Alaska, larvae of *P. thompsoni* and *S. leucopsarus* were abundant over the slope area (Lanksbury *et al.*, 2005) and mesopelagic fish larvae were more abundant in the shelf break stations compared to the oceanic area (Norcross *et al.*, 2003). For many mesopelagic fish species that spawn in the subarctic oceans, the main nursery grounds may be distributed in slope areas rather than oceanic areas. Perhaps prey resources in the slope area are more appropriate for these larvae. Primary productivity in the WSG, including K2, is low compared with the Kamchatka/Kuril area, especially during spring (Kitamura *et al.*, 2016). Also, the copepods that dominate the epipelagic layer in the WSG are large oceanic *Neocalanus* and *Eucalanus* (Yamaguchi *et al.*, 2002; Kitamura *et al.*, 2016). Furthermore, the nauplius larvae of the dominant *Neocalanus* do not occur in the epipelagic layer because they hatch in the meso-

or bathypelagic layers (Miller *et al.*, 1984). In slope waters, in contrast, small copepods such as *Pseudocalanus* spp. were dominant together with large copepods (Coyle and Pinchuk, 2005).

Unlike in the Okhotsk or transition region waters, only limited fish species use the interior area of the WSG around K2 as their nursery ground. In contrast, spawning and larval growth of *L. schmidti* has been widely observed not only in coastal waters, but also in oceanic areas all over the subarctic Pacific (Dunn, 1983; Mason and Philips, 1985; Sobolevsky and Sokolovskaya, 1996). Low abundance of competitors may allow *L. schmidti* to dominate the larval fish community at K2. Larvae of *L. schmidti* are distributed mainly from subsurface to upper mesopelagic layers (Kitamura and Murata, 2020). Although they show ontogenetic upward migration to the sea surface, larvae larger than 20 mm sink down to the mesopelagic layer again. Thus, they are distributed near the sea surface only during a limited span of their larval stage. At K2, the second most abundant larvae, *Coryphaenoides* sp., also were not collected near the sea surface. Dominance by larvae that are not strongly associated with the surface layer is a characteristic feature of the larval fish community at K2.

Juvenile/adult fish

In the present study, 18 of 20 collected species were identified to the species level and all of them were previously reported from the WSG, Russian waters along the Kamchatka/Kuril area, or both (Beamish *et al.*, 1999; Ivanov and Sukhanov, 2015; Orlov and Tokranov, 2019). Numerically, *L. schmidti*, *P. thompsoni*, *S. leucopsarus*, and *S. nannochir* were the most abundant members of the juvenile/adult fish community at K2, which is consistent with previous research in the western subarctic Pacific (Willis *et al.*, 1988; Beamish *et al.*, 1999). In addition, other dominants (*C. macouni*, *C. atraria*, and *D. theta*) listed by Willis *et al.* (1988) were also abundant at K2.

As noted in Discussion section 'Larvae' in 'Community', only limited fish species use the WSG area as their nursery ground. Thus, the juvenile/adult fish community at K2 is thought to be formed by overlapping of three types of species: species hatched and grown in the WSG (*Coryphaenoides* sp. and *L. schmidti*), horizontal migratory species from the southern area (*D. theta*, *L. jordani*, *L. ochotensis*, *L. regalis*, *M. lugubris*, *S. gracilis*, *S. nannochir*, and *T. tylori*), and those from the slope area in the subarctic Pacific (*P. thompsoni* and *S. leucopsarus*). But the types of other eight species collected at K2 (*C. macouni*, *B. pacificus*, *P. milleri*, *C. alba*, *C. atraria*, *C. pallida*, *C. pseudopallida*, and *Careproctus* sp.) are still not clear.

Insights into the fish fauna during the cold seasons is one of the important results of this study. In the mesopelagic layer below the permanent thermocline at K2, physical conditions did not change seasonally. The zooplankton community at K2 had a mesopelagic biomass peak where dormant copepods such as *Neocalanus* and diel vertical migratory *Metridia pacifica* dominated; the peak was maintained through the year (Kitamura *et al.*, 2016). So, from warm to cold seasons, physical and trophic conditions in the mesopelagic layer at K2 are thought to be largely static, especially for species without DVM, but both the species richness and total abundance are low. One of the possible reasons for the low species richness and total abundance is the previously mentioned horizontal migration for reproduction. In fact, *S. nannochir*, *L. jordani*, and *T. taylori*, are thought to migrate southward from autumn to winter (Sassa *et al.*, 2004b). Moku *et al.* (2003) suggested that *D. theta* matures and migrates for spawning one year after hatching. At K2, this species occurred in the warm seasons only. The suggestion by Moku *et al.* (2003) could explain the absence of this species at K2 during the cold seasons. In contrast, the most abundant *S. nannochir*, which is also a southward migratory species, occurred at K2 throughout the four seasons.

Although maturation size and age of this species are not known, the closely related *S. leucopsarus* becomes reproductively mature when it reaches about 65 mm in length, which corresponds to four years of age (Smoker, 1970). Immature population of *S. nannochir* probably stay at K2 throughout the year if the age of their maturation is similar to that of *S. leucopsarus*. The presence or absence of southward migratory fish at K2 during the cold seasons is partially explained by their maturation strategies.

Vertical distribution, migration, and their seasonality

Larval fish

In the world's oceans, many larval fish, including mesopelagic species, are distributed in the epipelagic layer during both day and night (e.g., Sabates, 2004; Sassa, 2019; Nagaiwa *et al.*, 2023). At K2, however, abundances of larval fish were low, especially in the most productive euphotic layer shallower than 50 m. This low abundance was a characteristic feature of the larval fish community there; consequently, grazing and feeding pressures by the larval fish community on primary producers and zooplankton seems to be low. The low abundances of mesopelagic fish larvae in the epipelagic layer at K2 are probably caused by multiple factors. Survival and growth of fish larvae are influenced by water temperature and food resources (e.g., Houde, 1989; Cushing, 1990; McCormick and Molony, 1995). Mesopelagic fish species whose larvae cannot thrive in the water temperatures of the subarctic ocean probably migrate southward before spawning; even for fish species whose larvae are well adapted to subarctic water temperatures, the prey resources in the epipelagic layer at K2 are probably unsuitable for larval fish (see Discussion section 'Larvae' in 'Community'). In addition, competition with large zooplankton such as *Neocalanus* or *Eucalanus* for prey resources may influence the abundance of larval fish. Because euphausiids are the major invertebrate predators on pollock larvae (Bailey *et al.*, 1993), they may predate other larvae at night (Brodeur and Rugen, 1994).

In the mesopelagic layer, ontogenetic vertical migration of *Coryphaenoides* sp. larvae was clearly detected. Seven species of *Coryphaenoides* were previously reported from the western subarctic Pacific and all of them were demersal fish from bathyal to abyssal depths (Orlov and Tokranov, 2019); so, this species probably uses the mesopelagic layer as its nursery and the larvae change their distribution from shallower to deeper waters with growth. Ontogenetic downward migration was already reported off Oregon for *Coryphaenoides acrolepis* (Stein, 1980). At K2, the abundance of *Coryphaenoides* sp. larvae was the highest during summer and their greatest abundance was observed at 200–300 m. These results suggest that the hatching of larvae mainly occurs at this depth during summer. In addition to the larval population sinking down to greater depths, small larvae were also collected at 200–300 m from autumn to spring, although population densities at the 200–300 m were low. This occurrence pattern suggests two possibilities: (1) spawning of this species occurs throughout the year, or (2) some of the larval population (probably hatched later in the reproduction season) overwinter. Unfortunately, because of the small numbers of collected specimens, the reason for this continuous occurrence of *Coryphaenoides* sp. larvae remains unclear; further investigations are needed. In addition, because the total length of the largest larva was 62.2 mm whereas that of the smallest juvenile was 59.9 mm, this species probably metamorphoses at around 60 mm.

At K2, DVM by larval fish was recognized for larger larvae of *L. schmidti* (>24 mm SL) between the upper mesopelagic and surface layers (Kitamura and Murata, 2020) but we could not detect it in other species. Previously, many researchers suggested no DVM for mesopelagic fish larvae (e.g., Sassa *et al.*, 2004a; Watanabe *et al.*, 2010), but Sabates (2004) described reverse DVM. Larval fish have limited capacity to migrate vertically (Sassa, 2019) and the vertical distances of DVM seem to be several dozens of metres as in the larvae described by Sabates (2004). To detect DVM for larval fish, the stratified sampling in the present study (an interval of 50 m in the upper 200 m of the water column) was likely too coarse.

Juvenile/adult fish

The vertical distributions and migrations of the two abundant myctophids, *S. leucopsarus* and *S. nannochir*, differed. The former species was distributed at shallower depths with opportunistic DVM and the latter at greater depths without DVM, although their vertical distributions partially overlapped. These same differences in vertical distributions and DVMs among these two species were also recognized in the transition region (Watanabe *et al.*, 1999) and the Bering Sea (Furuhashi and Shimazaki, 1989) and were interpreted as niche partitioning (Moku *et al.*, 2000). In addition, we found that daytime WMDs of *S. leucopsarus* and day–night means of WMDs for *S. nannochir* changed in synchrony through the seasons: shallowest in autumn and deepest in spring. In reality, it was possible that daytime WMDs of *S. leucopsarus* during the warm seasons were somewhat different from those estimated in this study because our sample collections in these seasons were affected by net avoidance by larger fish. However, the larger specimens of *S. leucousarus* only occupied 31% of their population in the warm seasons. In addition, most of the larger specimens likely distributed above 750 m (same as the smaller ones) in the warm seasons because their vertical distribution was not extended below the 750 m even in winter. So, we consider that estimated daytime distributions for *S. leucopsarus* during the warm seasons were probably reasonable and there are synchronous migrations by the two *Stenobrachius* species. The vertical distributions of these two species rarely overlap and they distributed each other in different niches in any season. For *S. leucopsarus* and *S. nannochir*, the presence of high levels of wax esters in their body was well known (Butler and Pearcy, 1972; Saito and Murata, 1996). Although wax esters may play an important role in buoyancy (Phleger, 1998), Butler and Pearcy (1972) suggested another role: a long-term energy reserve. And Vollenweider *et al.* (2011) revealed a seasonal change of lipid content, peaked in autumn and declined to a minimum in spring, in more than half of mesopelagic fish species which they observed in the eastern North Pacific. The seasonal change in lipid content probably resulted from metabolic consumption during the cold seasons, and we speculate that specific gravities of the mesopelagic fish are also changed seasonally. In addition, swimming with pectoral fins spreading provides lifting force (Tsukamoto, 1993). During the cold seasons, however, the swimming activity seems to be decreased down at least for *S. leucopsarus* as shown by their lower DVM activity. The lower lipid content and the lower swimming activity may affect deepening of vertical distributions for *S. leucopsarus* and *S. nannochir* synchronously during the cold seasons observed in the present study. Or the deepening distribution of *S. leucopsarus* may depress down the *S. nannochir* distribution. This hypothesis still lacks quantitative proof, further research is needed.

We detected DVM by *S. leucopsarus* throughout the four seasons at K2, but it stopped during winter in the Bering Sea (Brodeur and Yamamura, 2005). Another geographical difference in DVM possibly exists in *D. theta* although number of our collected specimens is quite low ($n = 10$, Table S3): it swam up into the upper 50 m in the Gulf of Alaska (Frost and McCrone, 1979) but did not migrate into the surface layer in the western Pacific (Watanabe *et al.*, 1999; present study). One possible explanation could be geographical differences in predation pressures. That is, several piscivorous sea birds such as the northern

fulmar and Laysan albatross are much more abundant in the western subarctic Pacific compared with the eastern side (Sydeman et al., 2010). In this study, DVM was also recognized in *L. ochotensis*, and its DVM seems to be opportunistic. Although opportunistic DVM has been known only from *S. leucopsarus* and *L. schmidti* (Brodeur and Yamamura, 2005; Kitamura and Murata, 2020), this type of DVM seems to be more common in mesopelagic fish than previously thought. During the cold seasons at K2, DVMs were detected in only two species: *S. leucopsarus* and *L. schmidti*, but compared to the warm seasons, smaller portion of populations showed DVM. Activities of DVMs seem to be decreased down in the cold seasons.

Among non-diel migratory species, *P. thompsoni* was distributed between 150 and 500 m at K2, which is similar to the vertical distribution reported from the transition region of the western Pacific (Watanabe et al., 1999), off Oregon (Frost and McCrone, 1979), and in the Alaskan Gyre (Pearcy et al., 1977). *Sigmops gracilis* at K2 was collected only from 300 to 500 m depth without seasonal variability. Although this species is widely distributed in the subarctic and subtropical Pacific, mainly on the western side, detailed vertical distribution with its seasonal change seems to not have been investigated before the present study. Previously, the vertical range of its distribution was simply reported as 100–500 m around Japan (Nakabo, 2013) or 300–800 m in the western Pacific and its marginal seas (Orlov and Tokranov, 2019). *Chauliodus macouni* was widely collected from 300 to 1000 m at K2 and WMDs of this species were observed as 400–500 m except during winter. Although the depth range of its distribution was previously reported as 25–4231 m (Allen and Smith, 1988), the peak in its abundance was observed above 500 m off Oregon (Pearcy et al., 1977; Willis and Pearcy, 1982). The vertical distribution of *C. macouni* at K2 was similar to that off Oregon.

At K2, the vertical distributions of four *Cyclothone* species had two patterns: *C. alba* and *C. pseudopallida* were distributed in the shallower layer (above 500 m) whereas *C. atraria* and *C. pallida* were observed at greater depths (below 500 and 300 m during day and night, respectively), which is consistent with the vertical distributions of these species off Japan (Nakabo, 2013). The vertical distributions of *Cyclothone* at K2 are also similar to those off Oregon (Willis and Pearcy, 1982): peaks in abundance of *C. atraria* were observed at 600–1000 m at K2 and at 600–800 m off Oregon, and WMDs of *C. pseudopallida* were at 400 m at K2, whereas it was most abundant at 500 m off Oregon. For DVM in *Cyclothone* species, although many investigations showed an absence of DVM (e.g., Miya and Nemoto, 1987; Brodeur and Yamamura, 2005), Willis and Pearcy (1982) reported DVM. The suggestion by Willis & Pearcy was based on horizontal net sampling during both day and night: the abundance of *Cyclothone* species at a particular depth during night was significantly higher than that at the same depth during day (at 500 m for *C. pseudopallida*, at 800 m for *C. atraria*). The authors concluded that the increasing abundance during night corresponded to populations that swam up to those depths from deeper layers. At K2, WMDs without diel variability suggest the absence of DVM, but depth ranges of the two species (*C. atraria* and *C. pallida*) elongated upward during night. We categorize the two species as non-migratory species at this time, but the diel variabilities of depth ranges could suggest the presence of DVM. Further investigation is needed to understand the biology and ecology of the most abundant vertebrate on the earth.

Recently, vertical transport of carbon from the epipelagic into mesopelagic layers by vertical migrants has attracted attention as the mesopelagic migrant pump (Boyd et al., 2019). Although the western subarctic Pacific is known as a hot spot of biological draw-down of atmospheric carbon into the ocean (Takahashi et al., 2002), the roles of mesopelagic fish in the mesopelagic migrant pump there have not been evaluated. Consistent with global warming, sea surface temperatures at K2 show decadal increase (Kitamura & Sasaoka, unpublished data). Furthermore, a marine heat wave was observed in the western subarctic Pacific, including the K2 area (Pak et al., 2022). However, the biological response to ocean warming has not been studied in this region. In the future, investigations to understand these issues are required. We believe that the present study showing community structure, seasonal occurrences, and the vertical distribution and migration of mesopelagic fish provides important baseline information for future studies.

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