

Original Article

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Seasonal occurrence and vertical distribution of larval and juvenile northern smoothtongue, *Leuroglossus schmidti* (Pisces, Bathylagidae), in the western subarctic Pacific

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Abstract

We investigated the seasonal occurrence and vertical distribution/migration of larval and juvenile northern smoothtongue, *Leuroglossus schmidti* (Pisces, Bathylagidae), in oceanic areas of the western subarctic Pacific. This species was the most abundant larval fish and one of the most abundant juvenile/adult fish at the study site. Larval recruitment of this species occurred in early March to mid-October. Larvae were found, however, throughout all seasons, suggesting that some had overwintered. The highest abundance (5.8 individuals m⁻²) of larvae was in summer. During summer and autumn, hatching mainly occurred at 100–150-m depth and larvae migrated toward the surface with growth. Once larvae reached about 20 mm in length, they moved below 100 m, and larger larvae (over 24 mm) exhibited diel vertical migration. The abundance of juveniles integrated through the water column was relatively constant (0.3 individuals m⁻²) throughout the study period. They were collected from below 300 m during the day, and part of the population (13–38%) swam into the epipelagic layer at night. The information on early stages of *L. schmidti* presented here provides a basis for future investigations of mesopelagic fish ecology in oceanic areas of the western subarctic North Pacific Ocean.

Introduction

Mesopelagic fish likely dominate the world's total fish biomass (Gjøsaeter & Kawaguchi, 1980; Irigoien *et al.*, 2014). They are also an important component of the pelagic ecosystem because they serve as the main trophic link between plankton and larger predators. Mesopelagic fish prey upon many taxa of zooplankton with a preference for crustaceans, and are eaten by pinnipeds, cetaceans and seabirds (Kajimura & Loughlin, 1988; Beamish *et al.*, 1999; Springer *et al.*, 1999; Moku *et al.*, 2000). These fish are also expected to have a significant role in vertical active carbon flux in the ocean (e.g. Longhurst *et al.*, 1990; Davison *et al.*, 2013), and are one of the main scatterers in the deep scattering layer, a characteristic feature of the mesopelagic zone (Marshall, 1951). Despite their ecological importance, mesopelagic fish remain one of the least investigated components of the open-ocean ecosystem, with many uncertainties about their biology (Irigoien *et al.*, 2014).

In the western subarctic North Pacific Ocean, 119 mesopelagic fish species have been recorded and their total abundance is higher than that of epi- and bathypelagic fish in the same area (Beamish *et al.*, 1999; Orlov & Tokranov, 2019). Beamish *et al.* (1999) and Willis *et al.* (1988) report that the mesopelagic species *Chauliodus macouni*, *Cyclothone atraria*, *Diaphus theta*, *Leuroglossus schmidti*, *Protomyctophum thompsoni*, *Stenobrachius leucopsarus* and *Stenobrachius nannochir* are abundant in this area. Other than these faunal studies, there are also reports of their horizontal distributions associated with internal waves (Rogachev *et al.*, 1996), feeding habits (e.g. Sobolevskii & Sokolovskaya, 1994; Kosenok *et al.*, 2006), and predation by larger animals (e.g. Sanger & Ainley, 1988; Orlov, 1997a, 1997b; Ohizumi *et al.*, 2003). In spite of these studies, ecological information on mesopelagic fish in the western subarctic Pacific is still limited compared with information for those in the eastern subarctic Pacific or the Bering and Okhotsk seas.

From 2006 to 2012, we conducted seasonal sampling of zooplankton and micronekton at an oceanic site in the western subarctic Pacific to understand their community structure and ecological roles, such as in active carbon flux (Kitamura *et al.*, 2016; Kobari *et al.*, 2016). In this sample series, we also collected many specimens of micronektonic fish, and a mesopelagic Bathylagidae, *L. schmidti*, was the most abundant. *Leuroglossus schmidti* is widely distributed in the subarctic Pacific, including in the Bering and Okhotsk seas (Mason & Phillips, 1985; Willis *et al.*, 1988; Beamish *et al.*, 1999). Larvae of this species are dominant over the continental slope and in coastal waters in the North-east Pacific Ocean and Bering Sea, accounting for up to 5% of the fish larvae collected (Dunn, 1983). On the other hand, in the western subarctic Pacific, the main spawning ground of this species was thought to be in oceanic rather than coastal waters (Sobolevskii & Sokolovskaya, 1994; Sobolevsky & Sokolovskaya, 1996). The spawning season was reported as winter–summer or summer–winter in the eastern



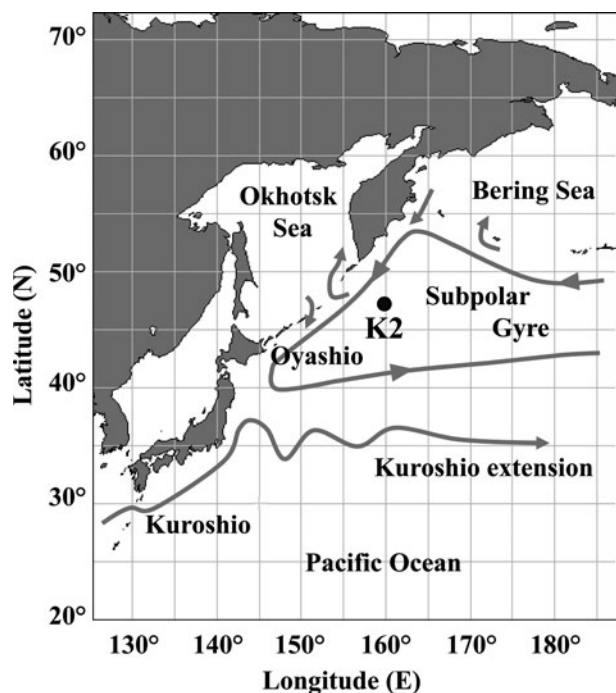


Fig. 1. Map of the western North Pacific Ocean showing the sampling location (station K2; 47°N 160°E) and the surface current system in the area (modified from Qiu, 2008).

Pacific and as late autumn–spring off the Kamchatka Peninsula (Dunn, 1983; Mason & Phillips, 1985; Sobolevsky & Sokolovskaya, 1996). Reproduction, population size, age structure, vertical migration and predator–prey relationships have been previously studied in the Strait of Georgia on the Pacific side of Canada (Mason & Phillips, 1985). This species is known as a diel vertical migrant (e.g. Gorbatenko & Il'Inskii, 1992; Brodeur & Yamamura, 2005). Its main diet has been reported as crustacean zooplankton along with some gelatinous ones (e.g. Gordon *et al.*, 1985; Mason & Phillips, 1985; Gorbatenko & Il'Inskii, 1992; Sobolevsky *et al.*, 1996). Despite these many studies, ecological studies of *L. schmidti* larvae are still limited, especially in oceanic areas and in the western subarctic Pacific. Here we describe the seasonal occurrence, size composition, and vertical distribution and migration of larval and early juvenile stages of *L. schmidti* at an oceanic site in the western subarctic North Pacific.

Materials and methods

This study was conducted at the time-series station K2 in the western subarctic North Pacific Ocean (47°N 160°E; Figure 1) during eight cruises including all four seasons from 2006 to 2012 (Table 1). Station K2 was established in 2001 to understand long-term changes of oceanographic conditions by analysing physical, biological and chemical properties and processes of the ocean.

Mesopelagic fish were collected with a multiple opening/closing net system (IONESS; SEA Corporation, Chiba, Japan) equipped with nine nets of 0.33-mm mesh size and with a mouth area of 1.5 m² when towed at 45°. The net system was towed obliquely at about 2 knots (ship speed; ~1 m s⁻¹) and at discrete depth intervals from 0 to 1000 m. Samples were obtained on the upcast during both day and night. In 2006 and 2007, the sampling depth intervals were 0–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–500, 500–750 and 750–1000 m. During the other six cruises, the sampling intervals 300–400 m and

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

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

400–500 m were combined into a single depth interval of 300–500 m so that fish were collected from eight depth intervals: 0–50, 50–100, 100–150, 150–200, 200–300, 300–500, 500–750 and 750–1000 m. A calibrated mechanical flowmeter was mounted on the net frame, and flow counts were sent to the deck unit and recorded. Frame angles during tows were also recorded. The volume of water filtered by each net was estimated by using the flow count and the frame angle. Larger fish specimens were immediately sorted from the net samples and fixed in 5–10% formalin in seawater, and the remaining subsamples were also fixed in 5% formalin-seawater. Representative vertical profiles of water temperature and salinity were collected by deploying a conductivity-temperature-depth (CTD) instrument cluster (SBE 911 plus; Sea-Bird Scientific, Bellevue, WA, USA) to 1000-m depth during every cruise.

At the laboratory on land, smaller fish specimens were sorted out from the formalin-preserved subsamples. All fish samples were identified to the species level if possible and counted. To follow the abundance of *Leuroglossus schmidti* in the mesopelagic fish community at K2, we determined the species compositions based on numerical abundances for every season. The species compositions were determined separately for larval fish and for juvenile/adult fish. We used vertically integrated abundances of *L. schmidti* (individuals m⁻²) through the water column from 0 to 1000 m, or through discrete sampling depth intervals, to describe their seasonal occurrence and vertical distribution patterns. Mean abundances for each cruise were calculated by using the multiple abundance data from all net samplings in a cruise. Seasonal mean abundances were then estimated by using the data from all cruises in each season.

For this study, meteorological seasons at K2 were defined according to Matsumoto *et al.* (2014): winter (December–February), spring (March–May), summer (June–August) and autumn (September–November). To show any seasonal variability in abundance and vertical distribution, we used estimated seasonal mean abundances. Because we had only one cruise in spring during our study period (cruise MR11-03), we used cruise mean abundances obtained during this cruise as the spring abundances. To determine the size distribution of *L. schmidti*, we measured the standard length (SL) of all collected specimens to the nearest 0.1 mm using a Vernier calliper. For larvae, the length from snout tip to notochord tip was defined as the SL (Dunn, 1983).

Results

Hydrography

During the eight cruises, the sea surface temperature ranged from 1.7 (winter and spring) to 10.2°C (autumn) and sea surface

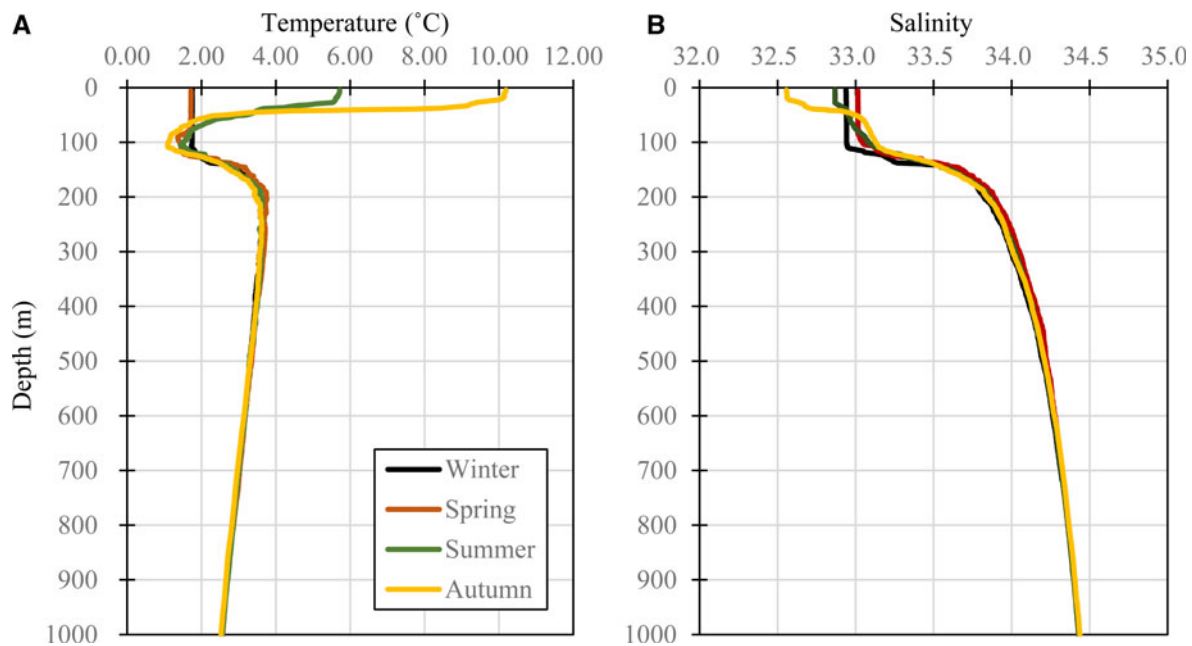


Fig. 2. Vertical profiles of seasonal mean water temperature (A) and salinity (B) at the time-series station K2. Note that summertime profiles are means of data collected during cruises MR11-05 and MR12-02; data from cruise MR06-03 were omitted.

salinity ranged from 32.6 (autumn) to 33.0 (spring). Winter vertical mixing reached about 100 m during winter and spring, whereas a prominent seasonal thermocline was located above 100 m during summer to autumn (Figure 2). Intermediate cold water, which is the remnant of winter mixing (Uda, 1963), was observed at around 100-m depth from summer to autumn. The minimum temperature in this water mass ranged between 1.2 and 1.5°C except in the summer of 2006, as described in the next paragraph. Above 100-m depth, water temperature and salinity varied with the seasons. Vertical profiles of water temperature in winter and spring were very similar. Those in summer and autumn were also similar because of the prominent stratification. Hydrographic conditions at K2 can therefore be divided into two states: the cold, mixing season (winter and spring) and the warm, stratified season (summer and autumn).

We observed permanent thermo- and haloclines, where both temperature and salinity increased with depth, between 100 and 200 m. Just below this we observed intermediate warm water, which is another notable feature in this region (Uda, 1963). The maximum water temperature in this water mass was around 3.6°C at around 250 m in depth, except in summer in 2006. During the summer of 2006, the vertical profile of water temperature was slightly different than those obtained during the other two summer cruises in 2011 and 2012: the minimum water temperature in the intermediate cold water (2.0°C) was about 0.7°C higher than in the other two summers, whereas the water temperature at around 250-m depth (3.1°C) was about 0.5°C lower. We observed no seasonal variability in water properties below the permanent clines.

Seasonal occurrence

In the larval fish community, *L. schmidti* was the most abundant (83–92%) throughout the four seasons, followed by *Coryphaenoides* spp., *Hemilepidotus gilberti* and *Malacocottus* sp. (Figure 3). There was considerable variability in their seasonal occurrence; the highest abundance (5.8 ind. m⁻²) was observed in summer and the lowest (0.9 ind. m⁻²) was in spring (Figure 4). Larvae of this species ranged from 4.2 to 31.6 mm in SL. The size distribution also had seasonal variability (Figure 5). During

spring, two cohorts were clearly recognizable: a group of smaller larvae ranged from 8–12 mm and larger ones were over 18 mm. Because no larvae smaller than 12 mm were collected during winter, the smaller larvae during spring were considered to be newly hatched after the winter samplings. From spring to autumn, larvae smaller than 12 mm were continuously collected. The summertime size distribution also shows two cohorts, with smaller larvae of 4–20 mm and larger ones of 23–31 mm. In summer, the smaller larvae predominated while the larger ones had very low abundance.

From the group of small larvae during spring (8–12 mm) to the winter community, the modal size classes increased sequentially. Furthermore, mean standard lengths increased from the winter population to the group of larger larvae in spring (>18 mm). Larvae were found throughout the cold mixing season, confirming that they overwintered, and their body sizes increased during the overwintering.

In the juvenile/adult fish community, *L. schmidti* was one of the abundant species but not necessarily the most abundant (9.5–31%) (Figure 3). Specifically, it was the most abundant in the community during winter but third or fourth most abundant in the other seasons. Standard lengths of the juvenile/adult specimens collected in this study ranged from 28.0–128.4 mm. All specimens except the largest one were in the early juvenile size class (up to 45.2 mm SL). The largest specimen was collected at night from the depth interval 50–100 m in early summer (cruise MR06-03). The abundances of the juvenile specimens were lower than those of larvae and were relatively constant through the four seasons (0.3 ± 0.1 ind. m⁻², mean ± SD) (Figure 4). Based on the sizes of the largest larva (31.6 mm) and smallest juvenile (28.0 mm), we suggest that *L. schmidti* metamorphoses at about 30 mm SL.

Vertical distribution and migration

Vertical distribution and diel vertical migration (DVM) patterns differed between larvae and juveniles (Figure 6). In the cold mixing season, larvae were collected from only a limited depth range during the day: 200–300 m in winter and 150–200 m in spring. In contrast, vertical distribution ranges during the night were

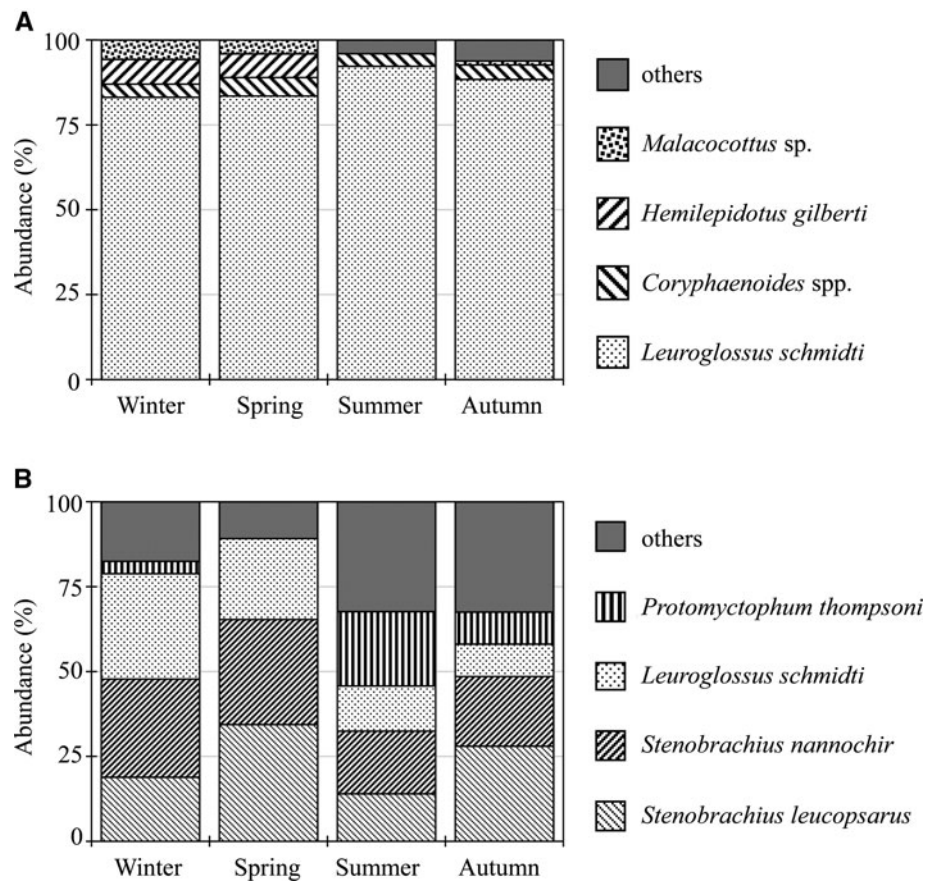


Fig. 3. Seasonal changes in the species composition of the mesopelagic fish community at station K2 in the western subarctic North Pacific. Panels (A) and (B) show the larval and juvenile/adult mesopelagic fish communities, respectively. The community compositions are based on vertically integrated abundances from 0 to 1000 m in the water column during the night to reduce the effect of net avoidance by fish.

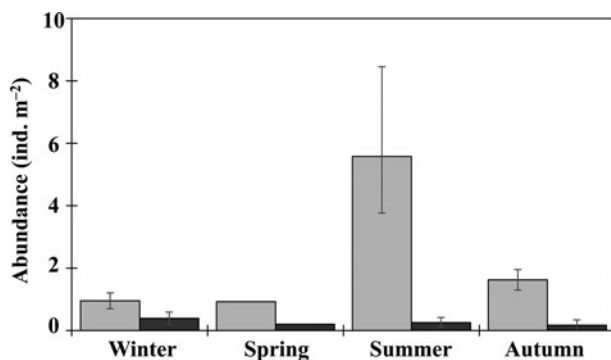


Fig. 4. Seasonal abundances of *Leuroglossus schmidti* larvae (grey) and juveniles (black) at station K2 in the western subarctic North Pacific. Abundances are vertically integrated from 0- to 1000-m depth. Error bars show ranges of the cruise mean abundances. To reduce the effect of net avoidance by fish, night-time abundances are used here.

extended upward. Some, but not all, of the larval population showed DVM, and no migrants were captured above a depth of 100 m. The migratory larvae were a minor portion of the winter population and a major one in the spring.

During the warm stratified season, vertical distribution ranges of larvae were wider than those in the cold mixing season (Figure 6) and we observed ontogenetic changes in their vertical distribution. Most of the small larvae less than 10 mm SL (72%) were collected in the depth interval of 100–150 m, and relative abundances of these small larvae in the depth intervals decreased from 100–150 m (29%) to 0–50 m (4%). Above 150 m, the mode of body size increased from deep to shallow (Figure 7). These patterns show that hatching of larvae from eggs mainly occurred between 100 and 150 m in depth and larvae shifted their vertical

distributions toward surface layers with growth. Larvae between 20 and 24 mm in length were collected between 100 and 500 m in depth (Figures 7 and 8). Specimens over 24 mm also occurred at depths below 100 m during the day, but most swam to the upper 100 m during the night (Figure 8). From this we conclude that larvae that had grown to about 20 mm swam down below 100 m, and larger larvae over 24 mm showed DVM.

In contrast, all juvenile specimens were collected from below 300 m during the day, and part of this population (13–38%) swam into the epipelagic layer at night (Figure 6). There was no clear seasonality in the percentage showing DVM (>30% in summer and winter, 13% in autumn and spring), but night-time distribution depths in the epipelagic layer changed seasonally. Migrating specimens swam up to the shallowest sampling depths (0–50 m) during the warm season, whereas no fish migrated into this depth interval during the cold season. Excluding the specimen of 128.4 mm SL, there was a significant difference in mean SL between migratory (35.4 mm) and non-migratory (32.9 mm) juveniles (Wilcoxon rank sum test, $P=0.03$) (Figure 9). Here, migratory juveniles were defined as juvenile specimens collected from above 200 m in depth at night whereas non-migratory juveniles were those collected below 300 m at night. This difference in SL reveals that smaller juveniles showed lower DVM activity than larger ones.

Discussion

Although underestimation of the population density of fish is inevitable in studies based on trawl sampling because of net avoidance behaviour (Gjøsaeter & Kawaguchi, 1980), the effect of net avoidance is less prominent in larval fish compared with juveniles or adults. In this study, therefore, we focused on seasonal patterns in the early life of *Leuroglossus schmidti*. Larval *L. schmidti* have previously been well studied in the semi-enclosed

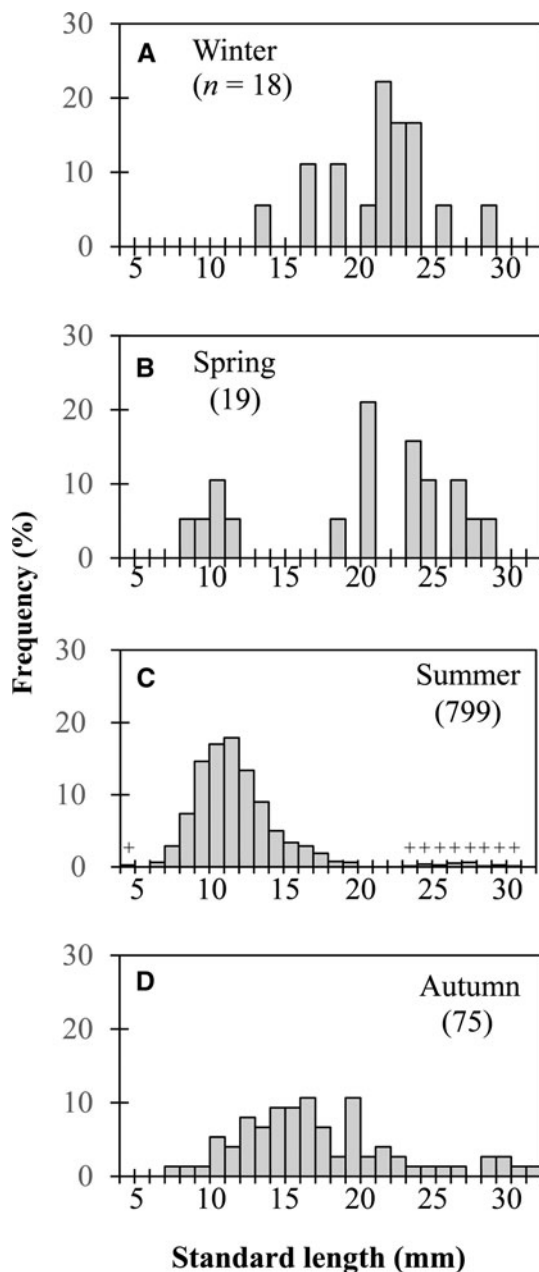


Fig. 5. Size distributions of larval *Leuroglossus schmidti* for (A) winter, (B) spring, (C) summer and (D) autumn, at station K2 in the western subarctic North Pacific. The sample sizes (n) are the total numbers measured.

Strait of Georgia (British Columbia, Canada; Mason & Phillips, 1985), but are still poorly understood in the open ocean. In addition, in the western subarctic Pacific, little is known about *L. schmidti* larval ecology in both coastal and oceanic waters, although there have been several investigations dealing with this species (Gordon *et al.*, 1985; Sobolevskii & Sokolovskaya, 1994; Sobolevsky & Sokolovskaya, 1996; Radchenko *et al.*, 2010; Naydenko & Khoruzhiy, 2014). Our investigation shows that *L. schmidti* is the most abundant larval fish in this region. Our results therefore provide important basic ichthyological data on the oceanic areas of the western subarctic Pacific.

The coastal waters from southern Vancouver Island to the Bering Sea were previously known as spawning and nursery grounds for *L. schmidti* (Dunn, 1983; Mason & Phillips, 1985). We have shown, as did Sobolevsky & Sokolovskaya (1996), that this species also uses oceanic areas in the western subarctic Pacific as nursery grounds. In the larval fish community at station

K2, *L. schmidti* was the most abundant (83–92% of the total larval fish catch) whereas myctophids had low abundance (1.4%). This is a characteristic feature of the larval fish community at K2 as distinct from those in other subarctic areas of the North Pacific. This is because myctophid larvae numerically predominate in the transition region between the Kuroshio and Oyashio currents in the western North Pacific (Sassa *et al.*, 2002, 2004), and larvae of the myctophid *Stenobranchius leucopsarus* were more abundant than those of *L. schmidti* in the Gulf of Alaska (Doyle *et al.*, 2002; Norcross *et al.*, 2003; Lanksbury *et al.*, 2005). Although *L. schmidti* larvae were captured throughout the four seasons at K2, they were more abundant during the warm season than in the cold season. This seasonality was probably associated with the seasonality of primary productivity at K2: high in the warm season but very low in the cold (Matsumoto *et al.*, 2014).

In the juvenile/adult fish community at K2, *L. schmidti* was one of several abundant fish species (9.5–31%), together with *Protomyctophum thompsoni*, *S. leucopsarus* and *Stenobranchius nannochir*. This is consistent with previous reports in the western subarctic Pacific (Willis *et al.*, 1988; Beamish *et al.*, 1999). Among these four abundant species, larvae of *P. thompsoni* and *S. leucopsarus* had very low abundances and larvae of *S. nannochir* were not collected in this study. These three species were therefore probably recruited to the fish community at K2 through horizontal migration of their juvenile/adult populations; *L. schmidti*, which spawned and grew up in this area, is a unique species at the study site.

The highest abundance of *L. schmidti* larvae was during summer, but before that, larvae in the small size classes (<12 mm SL) first appeared in spring. The spring samplings were conducted from 20–23 April 2011. Assuming an initial length after hatching of 5 mm and a maximum daily length increment of 0.16 mm for *L. schmidti* larvae (Mason & Phillips, 1985), the larvae needed 44 days for a growth increment of 7 mm (from 5 to 12 mm). Therefore, specimens 12 mm in length at the spring sampling probably hatched out in early March and might have been spawned in February. Furthermore, the larval recruitment of this species probably continued until at least mid-October, because at the end of October we collected a larval specimen of 7.1 mm SL that might have hatched out half a month earlier. We therefore conclude that around K2 this species spawns almost all year round but has a phase from late autumn to early winter when adult females stop spawning. Although prolonged spawning by this species was already known in several areas of the subarctic North Pacific, its seasonality differs between studies: winter–early summer in the Strait of Georgia (Mason & Phillip, 1985), summer–winter in the Kodiak Island shelf waters of the north-easternmost Pacific (Dunn, 1983), late autumn–spring in the western Pacific off Kamchatka (Sobolevsky & Sokolovskaya, 1996), and late winter–mid autumn at K2 (present study).

Larvae of this species were collected throughout the four seasons. The sequential increase of their modal size through the four seasons and evidence of overwintering suggest two possibilities for their larval development: (1) all larvae metamorphose after overwintering, or (2) most larvae metamorphose by autumn in the year of hatching but some that were spawned around the end of the spawning season overwinter. In the Strait of Georgia, larvae of *L. schmidti* metamorphose some 90 days from hatching (Mason & Phillips, 1985). Assuming the same larval development on the eastern and western sides of the subarctic Pacific, the latter scenario is reasonable for the western subarctic Pacific where K2 is located. Unfortunately, we did not observe the otoliths of specimens collected in this study, which would help determine which scenario is more likely.

Our data showing *L. schmidti* larval hatching in the subsurface layer (mainly 100–150-m depth) and ontogenetic upward

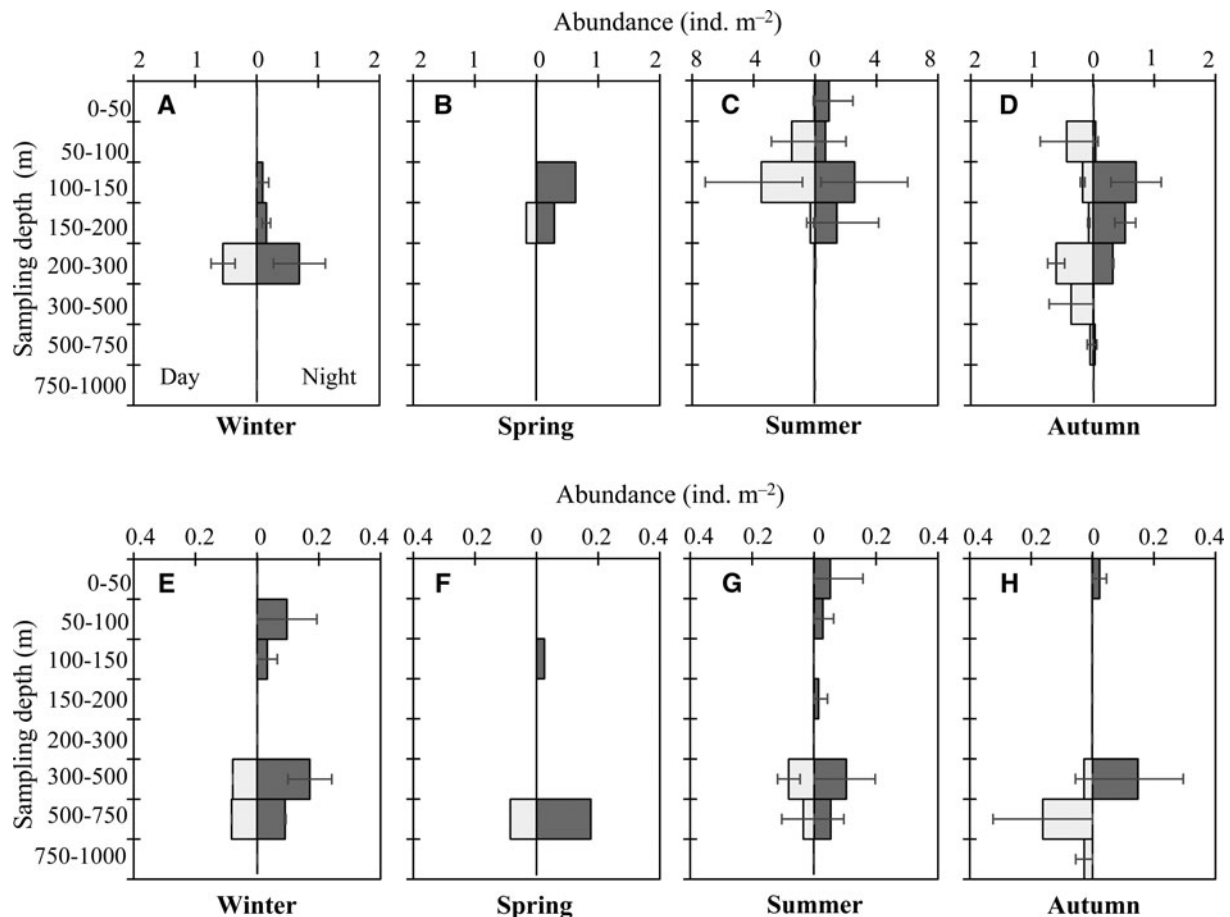


Fig. 6. Diel and seasonal variations in the vertical distribution of larval (A–D) and juvenile (E–H) *Leuroglossus schmidti* at station K2 in the western subarctic North Pacific. Abundances are vertically integrated values through each sampling depth interval.

migration from the hatching depths to the surface are consistent with data from the Strait of Georgia (Mason & Phillips, 1985). Larval *L. schmidti* begin feeding on copepod eggs and shift to a diet of crustacean zooplankton such as copepods as they grow (Adams, 1979; Mason & Phillips, 1985). In the subarctic Pacific, including the area around K2, *Neocalanus* copepods predominate in the zooplankton community (Kobari *et al.*, 2013; Kitamura *et al.*, 2016). These copepods release eggs at mesopelagic depths. Their main spawning season is from autumn to spring, although part of the *N. cristatus* population spawns throughout the year. Hatched nauplii larvae migrate to the surface layer with growth (Miller *et al.*, 1984; Kobari & Ikeda, 1999; Tsuda *et al.*, 2004). In the present study, we found larval recruitment of *L. schmidti* starting in early spring, and hatched larvae migrated to the surface layer with growth. This is advantageous to *L. schmidti* larvae for feeding on copepod eggs and nauplii.

In addition, this study is the first to observe that larvae reaching about 20 mm in length migrate to below 100 m, and larvae >24 mm show DVM during the warm season. Downward migration at the end of the larval stage is widely known for mesopelagic fish species in the western subtropical Pacific and the tropical Atlantic (Sassa *et al.*, 2007; Olivar *et al.*, 2018). However, the depths where we found the late larval stages of *L. schmidti* (100–750 m) are shallower than those of other mesopelagic species in tropical and subtropical oceans (300–900 m; Sassa *et al.*, 2007; Olivar *et al.*, 2018). We suggest two possible reasons for this downward migration of late-staged larvae: (1) energy savings in the deeper layer where water temperature is lower and (2) avoiding predation at depths where predation pressure is expected to be low (Herring, 2002). Because the difference in water

temperatures between the surface and the depths of downward migration was only 2–4°C during summer at K2, the latter scenario might be more reasonable for this species. In the epipelagic water of the western subarctic Pacific, nekton such as Pacific salmon or gonatid squids are thought to be potential predators on early stages of *L. schmidti* because they consume juvenile fish (e.g. Nesis, 1997; Karpenko *et al.*, 2007).

After the ontogenetic downward migration, *L. schmidti* in the late larval stage (>24 mm SL) showed DVM. Similar DVM behaviour has been observed only in *Diaphus* species and *Notolychnus valdiviae* among mesopelagic fish in the western North Pacific Subtropical Gyre, and it is hypothesized that metamorphosis without drastic morphological change allows them to quickly attain juvenile/adult behaviours such as DVM (Sassa *et al.*, 2007). This explanation is reasonable for this species because *L. schmidti* does not show drastic changes in morphology at metamorphosis (Dunn, 1983; Sobolevsky & Sokolovskaya, 1996). Such larval DVM might not necessarily be a behaviour specific to only a few species, but could be more common because it is seen not only in subtropical species but also in subarctic *L. schmidti*.

After metamorphosis, early juvenile *L. schmidti* (up to 45 mm SL) showed opportunistic DVM and smaller juveniles showed less DVM activity. There seemed to be less DVM activity in this species right after metamorphosis. Immature and adult *L. schmidti* are known as opportunistic diel vertical migrators (Brodeur & Yamamura, 2005).

The early life described here of *L. schmidti*, the most abundant fish species in the larval community at station K2, forms a basis for future investigations of its ecological role in oceanic areas of

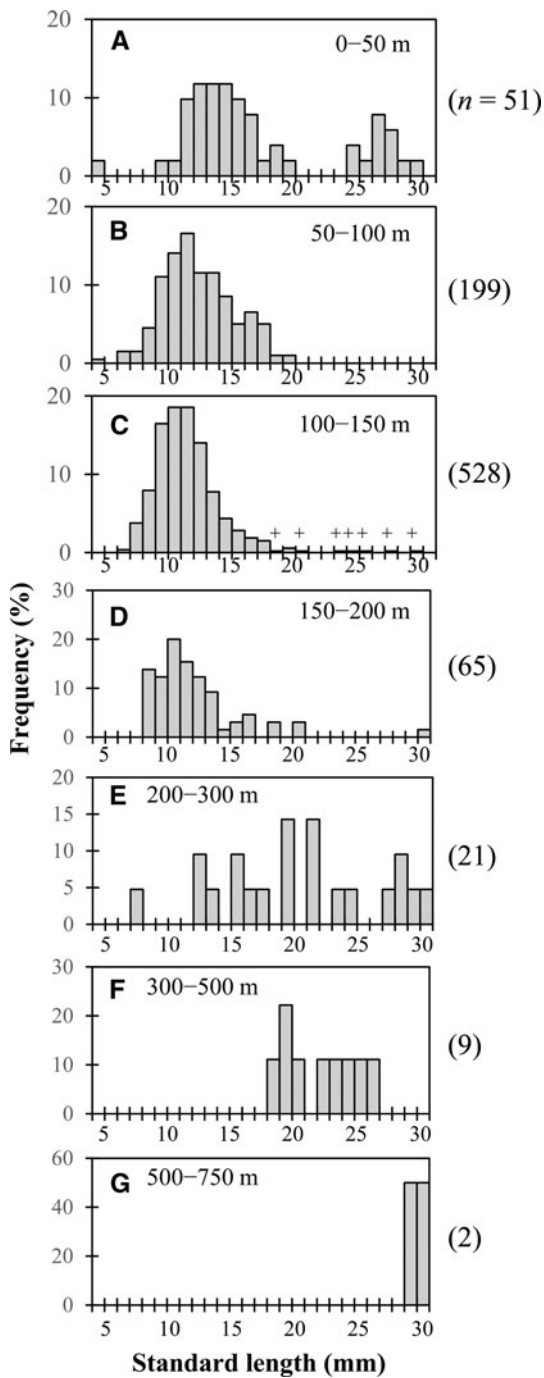


Fig. 7. Vertical size distribution of larval *Leuroglossus schmidti* during the warm season at station K2 in the western subarctic North Pacific. Panels (A–G) show the size distributions in the seven sampling depth intervals. The sample sizes (*n*) are the total numbers measured.

the western subarctic North Pacific. Although its preferred prey have been reported (e.g. Adams, 1979; Gordon *et al.*, 1985; Mason & Phillips, 1985; Sobolevsky *et al.*, 1996), there has been only limited investigation of the predation pressure by *L. schmidti* on the zooplankton community. Even though predation on *L. schmidti* by larger animals in coastal or bottom waters is well known (e.g. Orlov, 1997a, 1997b; Zeppelin & Orr, 2010), predation by epi- and mesopelagic animals is poorly studied in oceanic areas of the subarctic Pacific.

The western subarctic North Pacific is well known as a hot-spot of biological draw-down of atmospheric carbon into the ocean (Takahashi *et al.*, 2002), and recently the vertical transport of carbon from the surface to mesopelagic depths of the ocean by

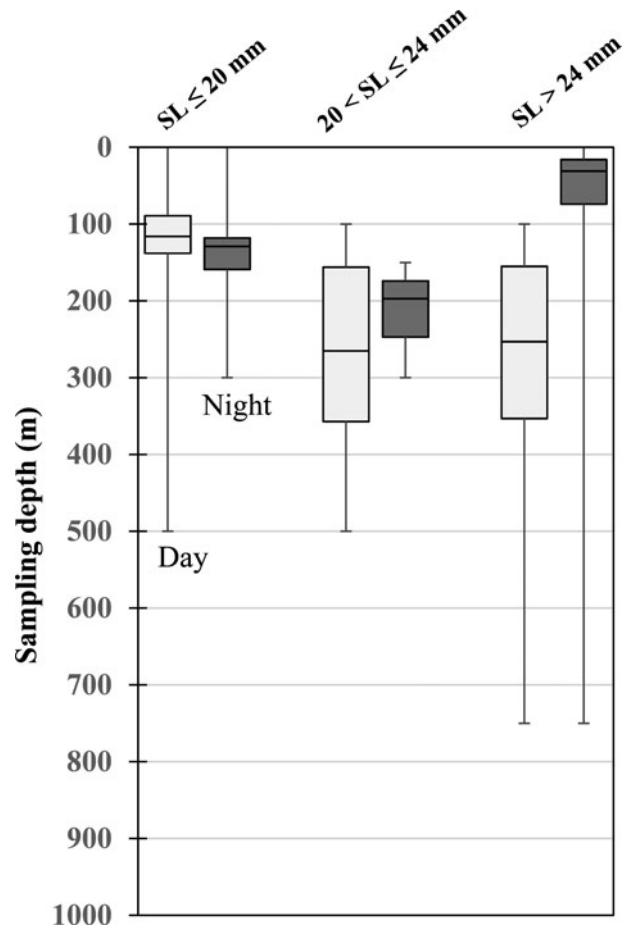


Fig. 8. Ontogenetic changes in the vertical distribution and diel migration of larval *Leuroglossus schmidti* during the warm season at station K2 in the western subarctic North Pacific. Boxes indicate the depth ranges where 50% of the population resided, and horizontal bars in boxes are the mean depths of the vertical distributions. These ranges and depths are calculated using the technique described by Pennak (1943) based on the mean abundances in the warm season. Whiskers show the depth ranges of the larval distributions.

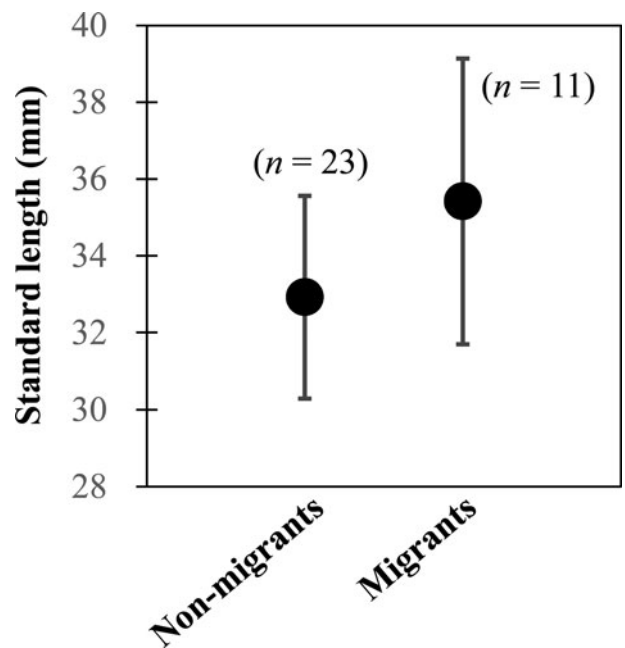


Fig. 9. Comparison between mean standard lengths of vertically migratory and non-migratory juvenile *Leuroglossus schmidti* at station K2. Migratory and non-migratory specimens were defined as juvenile specimens collected above 200-m and below 300-m depth during the night, respectively. Error bars show standard deviations. The sample sizes (*n*) are the total numbers measured.

the mesopelagic migrant pump has attracted attention (e.g. Davison *et al.*, 2013; Boyd *et al.*, 2019). Thus, the roles of mesopelagic vertical migratory fish such as *L. schmidti* in material cycles in the ocean should be evaluated in future studies in the western subarctic North Pacific.

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