Abstract—Larvae of the myctophid *Diaphus* "slender-type" form a dominant component of the late winter larval-fish assemblage in the Kuroshio waters of the East China Sea. However, ecological information on the larvae at the species level is limited due to difficulties with morphological identification. Based on species identification using mitochondrial DNA analysis, we describe the species composition, distribution, and growth of *Diaphus* "slender-type" larvae. Larvae of 6 species were found. *Diaphus fulgens* was the most abundant, accounting for 75.5% of the total catch, followed by *D. kuroshio* (14.0%) and *D. slender* sp. 1 (8.5%). *Diaphus fulgens* occurred over a broad area in the Kuroshio waters. *Diaphus kuroshio* occurred abundantly in the northeastern part of the study area, while the other 4 species were more abundant in the southwestern part. There was no significant interspecific difference in both mean absolute growth rates (AGR) and the weight-specific instantaneous growth coefficients (G_w) of *D. fulgens, D. kuroshio,* and *Diaphus* slender sp. 1 (0.105–0.119 mm/d and 0.094–0.118 d^{-1}, respectively). The AGR of the larvae of the 3 species were markedly lower than previously reported values for other genera of myctophids in subtropical waters, while the G_w were within the range of the other myctophids.

Species composition, distribution, and growth of *Diaphus* "slender-type" larvae (Pisces: Myctophidae) in the Kuroshio waters of the East China Sea

Chiyuki Sassa (contact author)
Motomitsu Takahashi
Youichi Tsukamoto

Email address for contact author: sassa_chiyuki40@fra.go.jp

Nagasaki Field Station
Pelagic Fish Resources Division
Fisheries Stock Assessment Center
Fisheries Resources Institute
Japan Fisheries Research and Education Agency
1551-8 Taira-machi
Nagasaki 851-2213, Japan

Introduction

Myctophids, or lanternfishes, are among the most common and widely distributed mesopelagic fishes in the world's oceans and a key component of oceanic ecosystems (Gjøsæter and Kawaguchi, 1980; Hulley and Paxton, 2016). They have the highest species diversity and greatest biomass of all oceanic fishes (Irigoien et al., 2014; Priede, 2017). Myctophids are an important mid-trophic level that transfers energy from zooplankton to upper trophic levels, linking surface production and the deep sea through diel vertical migrations (Brodeur and Yamamura, 2005; Davison et al., 2013). To understand the mechanisms controlling the population dynamics and biodiversity of myctophids, it is necessary to gather information on their life history (St. John et al., 2016; Hidalgo and Browman, 2019). The larval stage has been considered as an especially critical period of the life history, as the recruitment success of many marine fishes is determined largely by processes affecting larval distribution, dispersal, growth, and survival (Fuiman and Werner, 2002; Houde, 2016). Myctophid larvae have a vast array of morphological and pigment characters that permit larval identification of various species (Moser and Ahlstrom, 1996; Moser and Watson, 2006). Accumulated information on larval morphological characteristics of species has greatly contributed to the understanding of the early life history of this family, as well as systematic and evolutional studies of genera and subfamilies (e.g., Moser and Ahlstrom, 1972, 1974; Moser, 1981; Moser et al., 1984, 1993; Moser and Smith, 1993a).

Myctophid larvae occur in the productive epipelagic layer (upper 200-m depth) during both the day and night where they find enough food to grow and survive (Loeb, 1979; Sassa et al., 2004). They descend to the mesopelagic layer when they begin to metamorphose from the larval stage to the juvenile stage (Sassa et al., 2007; Olivar et al., 2018). After the juvenile stage, most species begin diel vertical migrations to the epipelagic layer at night for feeding, although some species in the genus *Diaphus* undergo diel vertical migrations during the transforming stage, showing earlier adaptation to juvenile–adult behaviors (Clarke, 1973; Sassa et al., 2007).

The dominance of myctophid larvae in oceanic ichthyoplankton has been reported from various parts of the major oceans (Moser and Ahlstrom, 1996; Moser and Watson, 2006). Many studies have been con-

ducted on species composition and spatiotemporal distribution of myctophid larvae, providing data on spawning seasons and grounds for various species (e.g., Moser et al., 1993; Olivar and Beckley, 1994; Koslow et al., 2011; Holliday et al., 2012; Sassa and Hirota, 2013; Daudén-Bengoa et al., 2020). Also, the growth, mortality, and feeding of myctophid larvae have been reported for some dominant species in recent decades (e.g., Conley and Gartner, 2009; Bystydzieńska et al., 2010; Namiki et al., 2015; Sassa and Takahashi, 2018; Contreras et al., 2019; Mei et al., 2019).

Diaphus is the most speciose myctophid genus and comprises 78 species (Priede, 2017). Although larvae of various myctophid species can be morphologically identified (Moser and Ahlstrom, 1972, 1996), identification of larval *Diaphus* species has proven to be extremely difficult (Moser and Ahlstrom, 1974). Larvae of *Diaphus* have been separated into slender and stubby-types (Moser and Ahlstrom, 1974; Moser et al., 1984): the *slender-type* has numerous persistent postanal ventral melanophores, and the *stubby-type* has fewer postanal melanophores that coalesce before flexion. *Diaphus* slender-type larvae are associated with species having a suborbital photophore (So) as adults (the so-called species of the So-group) (Moser and Ahlstrom, 1974). Larval differentiation within each of these 2 types still is not clear because it depends on slight morphological and pigmentation differences (Ozawa, 1986; Olivar and Beckley, 1995). This makes it difficult to investigate the early life history at a species level. Mitochondrial DNA (mtDNA) analysis is an effective identification tool for larval fishes (e.g., Aoyama et al., 2007; Hubert et al., 2010; Marancik et al., 2010; Tawa et al., 2012; Ko et al., 2013). In recent years, this method has also been applied to species identification of myctophid larvae (e.g., Bernal et al., 2014; Batta-Lona et al., 2019; Park et al., 2019; Lee et al., 2020).

The Kuroshio originates from the northward extension of the North Equatorial Current off the Philippines and flows northeastward along the continental slope of the East China Sea (ECS) and the Pacific coast of southern Japan, then turns east near 35–36°N off central Japan (Ichikawa and Beardsley, 2002) (Fig. 1). Approximately 32 species of *Diaphus* occur as adults in the Kuroshio waters (Kawaguchi and Shimizu, 1978; Nakabo, 2013), where high abundances of *Diaphus* larvae have been reported throughout the year (Sassa and Hirota, 2013; Sassa and Konishi, 2015). In the Kuroshio waters of the ECS, *Diaphus* slender-type larvae are one of the dominant components in the late winter larval fish assemblage (e.g., Sassa et al., 2004; Moku et al., 2005; Sassa and Konishi, 2015; Sassa and Takahashi, 2018; Mei et al., 2019). However, there is little information on the larval ecology at the species level.

In this study, we initially identified *Diaphus* slender-type larvae to species based on mtDNA sequence analysis to examine species composition in the Kuroshio waters of the ECS during late winter. We then described the distribution and habitat of each species and discussed the locations of spawning grounds. Finally, we examined the larval growth of the 3 dominant species based on otolith increments. The results were compared with the larval growth of 6 other genera of myctophids in subtropical waters to examine the growth characteristics of *Diaphus* slender-type larvae.

Materials and methods

Sample collection

In this study, larval fish were collected at 70 stations in the Kuroshio waters of the ECS during cruises of the RV *Yoko-Maru* (Japan Fisheries Research and Education Agency) between 15 and 28 February 2013 (Fig. 1). For larval sampling, a paired bongo net (60 cm mouth diameter; 0.32 mm mesh) was used with a flowmeter attached to the net for quantitative sampling. A double-oblique tow was conducted at each station from the surface to 150-m depth or 10 m above the bottom at shallow stations. The net was towed regardless of day, night, or twilight. To collect the adults of *Diaphus* species, a Matsuda-Oozeki-Hu trawl (2.24×2.24 m^2 mouth opening; 1.59 mm mesh net) (Oozeki et al., 2004) was obliquely towed from the surface to approximately 500 m (Sassa and Takahashi, 2022). Both larval and adult samples were preserved in 99.5% ethanol immediately after capture.

For zooplankton sampling, a long Norpac net (45 cm mouth diameter, 65 cm+130 cm-long cylindrical-conical net) with 0.1 mm mesh was towed vertically from 50 m to the surface at each station. The volume of water filtered by the net was measured with a flowmeter mounted at the net mouth. The plankton samples were fixed in 5% borax-buffered formalin seawater immediately after collection.

To estimate the Kuroshio mainstream, currents were measured throughout the cruise with an acoustic Doppler current profiler (38 kHz, Teledyne RD Instruments, Poway, CA), being routinely monitored at 60 layers in the upper 1500 m with a 24-m interval and the shallowest layer at 40 m. The position of the Kuroshio during the sampling period was obtained from the Quick Bulletin of Ocean Conditions, of the Japan Coast Guard (available from https://www1.kaiho.mlit.go.jp/KANKYO/KAIYO/qboc/index.html, accessed March 2020). A conductivity-temperature-depth profiler (SBE 9plus CTD, Sea-Bird Electronics Inc., Bellevue, WA) was used at each sampling station to 200-m depth or 10 m above

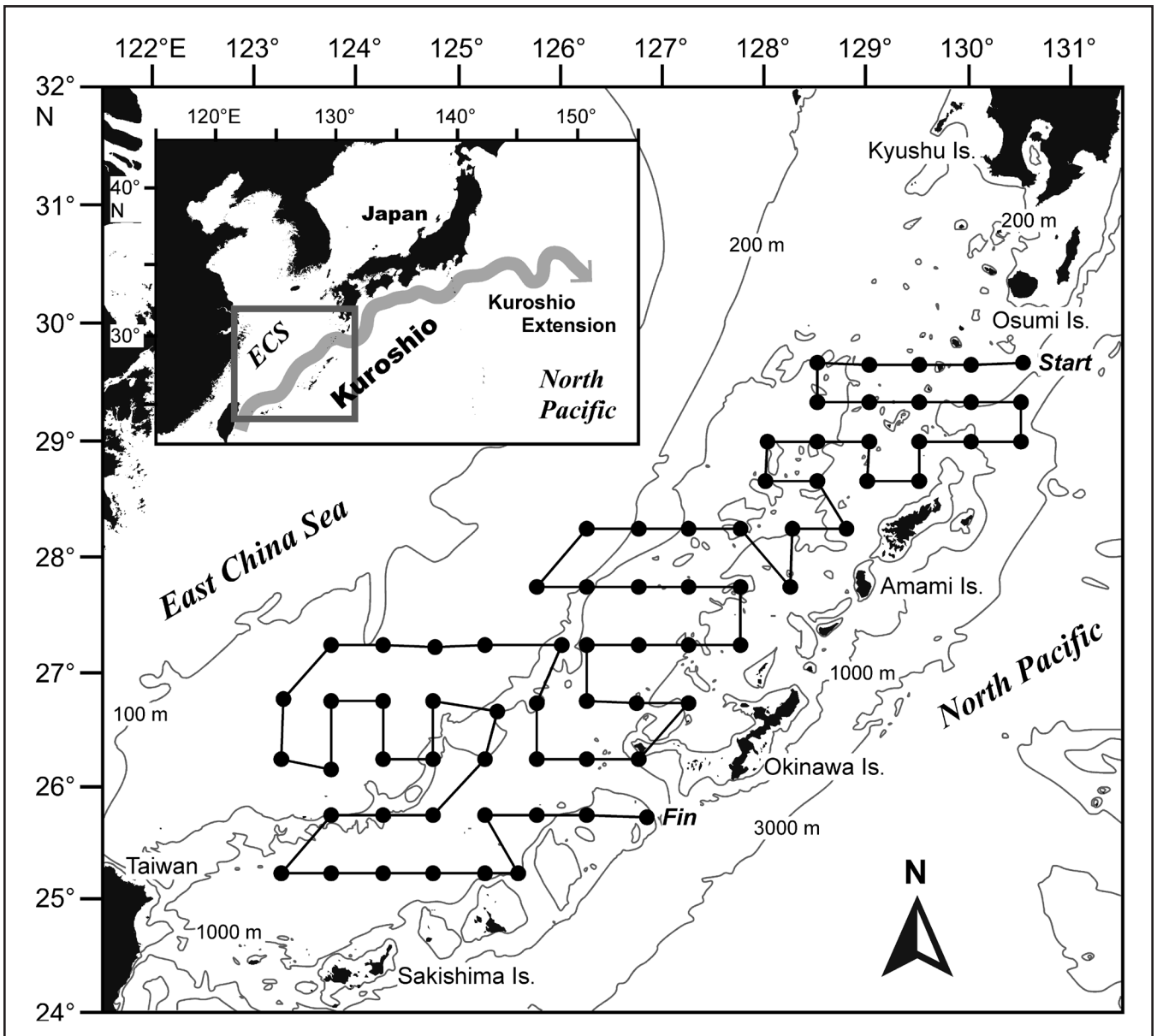


Figure 1

Map of the study area showing the locations of 70 stations (dots) where *Diaphus* slender-type larvae were collected in the Kuroshio waters of the East China Sea (ECS) between 15 and 28 February 2013. The stations are connected in the order that they were visited by the research vessel. The gray lines indicate the 100-, 200-, 1000-, and 3000-m isobaths. The gray arrow in the inset map indicates the position of the Kuroshio and Kuroshio Extension. Is.=island.

the bottom at shallower stations. Chlorophyll *a* fluorescence was also profiled using a submersible fluorometer (ECO-FLD, WET Labs, Philomath, OR) mounted on the conductivity-temperature-depth profiler. The fluorescence values were converted to chlorophyll *a* concentration based on the relationship between chlorophyll *a* concentration and in situ fluorescence value of water during this cruise; $y=1.14x+0.084$ (sample size [n]=42; coefficient of determination [r^2]=0.94), where y is fluorescence (in arbitrary units), and x is chlorophyll *a* concentration (in micrograms per liter) (Hasegawa et al., 2019).

Molecular species identification

The mitochondrial cytochrome *b* gene has been found to be a useful tool for phylogenetic and population studies of myctophids (Gordeeva and Volkov, 2016). In the present study, the cytochrome *b* gene region was used be-

cause there are previous studies on the species identification and phylogenetic analysis of myctophids, including *Diaphus* (e.g., Rodríguez-Graña et al., 2004; Suzuki et al., 2005; Kojima et al., 2009; Zahuranec et al., 2012).

The genetic species identifications were carried out by directly comparing the mitochondrial cytochrome *b* gene sequences of *Diaphus* slender-type larvae and morphologically clearly identifiable adults. A portion of the mitochondrial cytochrome *b* gene (511 base pairs) was amplified by polymerase chain reaction using the universal primer pair GLUDG-L (5′-TGACTTGAARAACCAYCGTTG-3′) and CB3-H (5′-GGCAAATAGGAARTATCATTC-3′) (Palumbi et al., 2002). For the samples that failed to amplify with this pair, we used a new set of primers of H_Iwashi_CBL (5′-ACCAGCCTACGAAAAACGCA-3′) and H_Iwashi_CBH (5′-GATCCTGTTTCGTGGAGGAA-3′) (Kitamura[1]). The reaction mixtures were preheated at 98°C for 30 s followed by 30 cycles of amplification (at 98°C for 10 s in denaturation, 55°C for 30 s in annealing, and 72°C for 60 s in extension) with a final polymerization step at 72°C for 120 s. Amplified products were purified with the GFX PCR DNA and gel band purification kit (Amersham Biosciences, Amersham, UK).

Sequencing reactions were analyzed on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA) using the Applied Biosystems BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Waltham, MA). The sequence data obtained from *Diaphus* slender-type larvae were then compared with those of 7 *Diaphus* species of the So-group occurring in the western North Pacific and its marginal seas, for which information on cytochrome *b* is available (Table 1). The sequence data from adult specimens of 3 species (*D. fulgens*, *D. kuroshio*, and *D. parri*) collected by the Matsuda-Oozeki-Hu trawl tows were newly obtained in the present study (Table 1, Suppl. Table 1). The cytochrome *b* sequence data of *D. anderseni*, short-headed lantern fish (*D. brachycephalus*), *D. mollis*, and California headlightfish (*D. theta*) were from the DNA data bank of Japan (available from https://www.ddbj.nig.ac.jp/index-e.html), European Molecular Biology Laboratory nucleotide sequence database (available from https://www.ebi.ac.uk/ena/browser/home), and GenBank database (available from https://www.ncbi.nlm.nih.gov/genbank/) (Table 1). We used prickly lanternfish (*Dasyscopelus asper*) as an outgroup for the phylogenetic analysis (Table 1). The sequences were aligned using Clustal W, vers. 2.1 (Thompson et al., 1994) in the program BioEdit, vers. 7.0.5.3 (Hall, 1999). Neighbor-joining tree (Saitou and Nei, 1987) and distance matrices were generated using MEGA7 (Kumar et al., 2016) on an analysis of Kimura 2-parameter distances (Kimura, 1980). The cytochrome *b* sequences of the larvae obtained in the present study were submitted to the DNA data bank of Japan/European Molecular Biology Laboratory/GenBank nucleotide sequence databases (Suppl. Table 2).

Table 1

Accession numbers for the cytochrome *b* sequence data of adults of 8 myctophid species obtained from the DNA data bank of Japan and used for species identification of *Diaphus* slender-type larvae.

Species	Accession no.
Diaphus anderseni	KU159142
Diaphus brachycephalus	KU159143
Diaphus fulgens	LC647047
Diaphus kuroshio	LC647050
Diaphus mollis	KU159112
Diaphus parri	LC647053
Diaphus theta	AP012240
Dasyscopelus asper	AP012234

Analysis of larval distribution

In the laboratory, all larval fish were sorted from the samples and counted. In all, we collected 12,939 larval fish from 70 sampling stations, and *Diaphus* slender-type larvae accounted for 5.3% of the total catch. For all intact *Diaphus* slender-type larvae, body lengths (BLs) were measured to the nearest 0.1 mm using a measurement system that was composed of a stereomicroscope (AZ100, Nikon Instech Co. Ltd., Tokyo, Japan) and digital camera (Digital Sight DS-Fi1, Nikon Instech Co. Ltd.) equipped with a control unit (Digital Sight DS-L2, Nikon Instech Co. Ltd.). Notochord length was measured for preflexion larvae and standard length (SL) for flexion and postflexion larvae. All larval BLs were standardized as the initial fresh length using the shrinkage (given in percent) reported by Moku et al. (2004) for larval *Diaphus* slender-type (5.1–10.2 mm BL). Shrinkage in 90% ethanol is 4.7% of the BL of fresh specimens; thus, the larval BL was adjusted by multiplying by 1.047 in the present study.

The number of larvae collected in the samples was standardized to larvae per 10 m^2 of sea surface using the volume of water filtered by the nets and the maximum depth to which the net sampled. In our protocol for the mtDNA analysis, all *Diaphus* slender-type larvae in good condition were analyzed in stations with <20 larvae, and approximately 50% of the larvae were randomly selected in stations with >20 larvae. The abundance of *Diaphus* slender-type larvae was multiplied by the ratio of each species identified. Catches of myctophid larvae by bon-

[1]Kitamura, T. 2012. Unpubl. data. JAPAN NUS Co. Ltd., Nishi-Shinjuku Prime Square 5F, 7-5-25 Nishi-Shinjuku, Shinjuku-Ku, Tokyo 160-0023, Japan.

go net towing showed no significant differences among day, night, and twilight values (Sassa et al., 2015), which would be mainly due to limited sensory perception of the net and avoidance reactions. Thus, we pooled these diel periods.

For analysis of larval habitat, we used the 30-m depth temperature, salinity, and chlorophyll *a* concentration. During late winter, (1) the mixed-layer depth is usually deeper than 100 m due to the strong northwest monsoon in the study area (Ichikawa and Beardsley, 2002; Sassa and Takahashi, 2018; observations in this study), and (2) *Diaphus* slender-type larvae are concentrated in the mixed layer with peak densities in the 10–50 m layer (Watanabe et al., 2010), so the environmental values at 30-m depth directly represent the larval habitat.

Copepod nauplii and early-juvenile-stage copepods are important prey items for *Diaphus* slender-type larvae (Sassa and Kawaguchi, 2005; senior author, unpubl. data). To assess spatial variations in the food availability for the larvae, copepod nauplii were counted in the long Norpac net samples from each tow. The number of nauplii were standardized to individuals per liter in the upper 50-m layer where *Diaphus* slender-type larvae mainly occur (Watanabe et al., 2010). The mean BL and width (standard deviation [SD]) of copepod nauplii were 0.26 mm (standard deviation [SD] 0.27) and 0.13 mm (SD 0.04) (n=4321), respectively. The use of the 0.1 mm mesh net implies that a high percentage of the small-sized nauplii are extruded through the net. Therefore, although the abundances estimated in the present study underrepresent the small-sized nauplii, data were used as a proxy for food availability for the larvae.

The weighted mean (WM) of temperature, salinity, chlorophyll *a* concentration, and copepod nauplii density of the larval habitat for each dominant species was calculated using the following equation:

$$WM = \frac{\sum_{i=1}^{N}(a_i \times x_i)}{\sum_{i=1}^{N} a_i}, \quad (1)$$

where a_i = the larval abundance of each species in the i-th sampling station (in larvae per 10 m^2);
x_i = the 30 m-temperature, 30 m-salinity, 30 m-chlorophyll *a* concentration, and copepod nauplii density in the top 50 m at the i-th sampling station; and
N = the total number of sampling stations.

Prior to the analysis, the larval abundance was square root-transformed to reduce any bias caused by sampling stations with extremely large catches.

Otolith analysis and growth rates

In sagittal otoliths of myctophids, growth increments during the larval stage are well-defined, enabling counts using light microscopy, although those during the transformation from the larval to the juvenile stage are difficult to detect due to the drastic change in crystalline structure and the formation of accessory primordia (e.g., Gartner, 1991; Linkowski, 1991; Moku et al., 2001; Takagi et al., 2006). Daily otolith increments of *Diaphus* slender-type larvae have been validated in sagittal otoliths, based on the marginal increment growth of specimens collected over a 24-h period (Moku et al., 2005). In the present study, a total of 265 *Diaphus* slender-type larvae of the three dominant species, *D. fulgens*, *D. kuroshio*, and *Diaphus* slender sp. 1 (see Results) in good condition, were used for otolith analysis. Sagittal otoliths were extracted using a dissecting microscope at 10×–40× magnification and embedded on a glass slide with enamel resin. Otolith radii were measured, and the total number of otolith daily growth increments was counted using an otolith measurement system, consisting of a light microscope at 400×–1000× magnification equipped with charge coupled device (CCD) camera controlled by a PC (Otolith sun wheel/fish scale measurement system ARP/W+RI, RATOC System Engineering Co. Ltd., Tokyo, Japan). Rearing experiments of small pelagic fish in subtropical and temperate waters indicate that the first increment is deposited a few days after hatching,corresponding to the day of first-feeding in various species (Tsuji and Aoyama, 1984; Xie et al., 2005). However, there is no literature on the timing of the first deposition of growth increment for myctophids. In this study, the total number of increments was considered as the age; thus, it is possibly underestimated by several days.

The relationships between BL and otolith radius were fitted using linear and allometric formulae using the least squares method to adopt the best fitted formulae. The relationship between BL and age was fitted using a linear formula, and the slope of the regression line represents the mean absolute growth rate of larvae (AGR; in millimeters per day). To test the suitability of the linear regression, the BL-at-age data were also fitted by allometric and exponential regression. Differences in AGR among the 3 species were evaluated using analysis of covariance (ANCOVA) followed by the Bonferroni post-hoc test for multiple comparisons. Weight-specific instantaneous growth coefficient (G_w) and the relative rate of growth (K) of the larvae were estimated for each species as follows (Yamashita and Bailey, 1989):

$$W_t = W_0 \cdot e^{G_w t}, \quad (2)$$

$$K = e^{G_w} - 1, \quad (3)$$

where W_t = the dry weight (in milligrams) at time t (in days); and
W_0 = the estimated dry weight at hatching.

The daily weight-specific growth rate was defined as K×100%. The dry weight of *Diaphus* slender-type lar-

vae was estimated from the unadjusted BL using the following relationship:

$$W = 0.00008L^{4.4278}, \quad (4)$$

where W = the dry weight (in milligrams); and
L = BL (in millimeters).

The slope is the growth allometric coefficient (Sassa and Takahashi, 2018). The above relationship is based on *Diaphus* slender-type larvae whose species have not been identified by mtDNA analysis. Since the larvae used in the present study and Sassa and Takahashi (2018) were collected in the same season and region, the above relationship can be considered to include the data of multiple species that occurred in the present study. Differences in G_w among the 3 species were evaluated using ANCOVA followed by the Bonferroni post-hoc test for multiple comparisons, which was performed for the linearized exponential models.

Results

Physical oceanographic and biological conditions

Acoustic Doppler current profiler observations identified the strong northeasterly Kuroshio mainstream along the continental slope south of 29°N, with a velocity of 0.75–1.5 m/s (Fig. 2A). Then, it turned sharply eastward near 29°N, passing through Tokara Strait between the Ōsumi and Amami Islands. Our acoustic Doppler current profiler observations closely corresponded with the position of the Kuroshio based on data from the Quick Bulletin of Ocean Conditions of the Japan Coast Guard (Fig. 2B). The position of the Kuroshio corresponded with the temperature fields at 30-m depth of 23–25°C isotherms (Fig. 2A). Between 123° and 125°E, the Kuroshio branch current intrudes onto the shelf (<200 m-depth) to 26°30′N, flowing eastward at approximately 0.75 m/s (Fig. 2A). This was also recognized by the warm Kuroshio waters (23–25°C) in this area. In the area west of the Kuroshio mainstream off the Okinawa and Amami Islands, where the temperature (21–22°C) was lower than that of the Kuroshio mainstream, there was a southwestward countercurrent (0.5–0.75 m/s). Cold shelf waters <21°C were observed in the northwestern stations shallower than 130 m depth. The salinity was high (>34.65) in the area east of 127°E, while it was lower in the western part, with the lowest salinity waters of >34.5 on the shelf (Fig. 2B). The distribution of low salinity water tended to extend northeastward along the Kuroshio in the area west of 127°E.

Chlorophyll *a* concentration at 30-m depth ranged from 0.27 to 1.60 µg/L, with a mean of 0.65 µg/L (SD 0.23) (Fig. 2C). High chlorophyll *a* concentrations (>1 µg/L) were restricted to the southwestern shelf. On the contrary, the concentrations in the Kuroshio waters were markedly lower than those on the shelf, except for the area northwest of the Amami Islands where relatively high concentrations were observed. Nauplii occurred broadly in the study area, and their densities ranged from 0.16 to 1.20 individuals/L, with a mean of 0.59 individuals/L (SD 0.26). Spatial variations in nauplii densities were relatively low, although the densities in the Kuroshio were slightly lower compared to those on the shelf (Fig. 2C). Density of nauplii showed a positive correlation with chlorophyll *a* concentration (Pearson's correlation coefficient test; r=0.486, n=70, P<0.05).

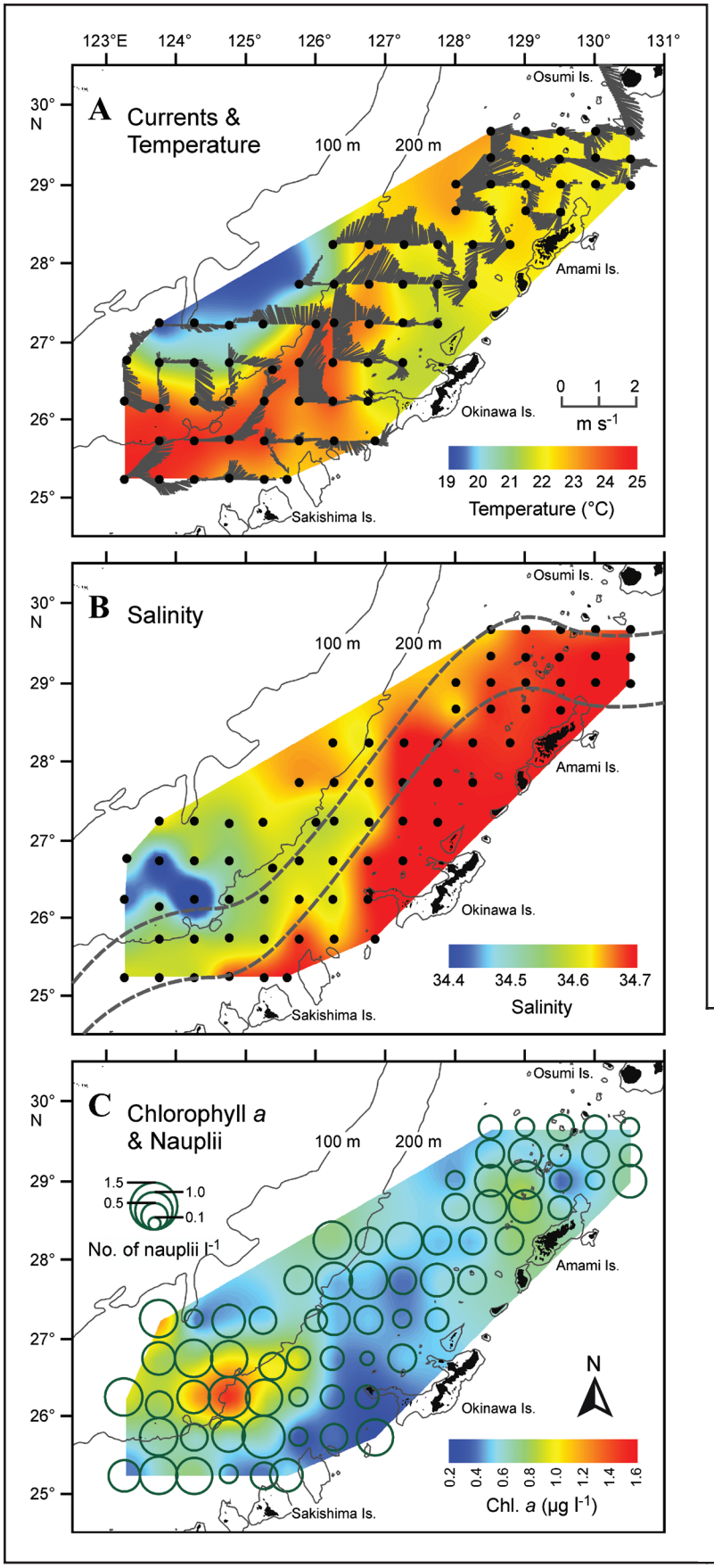
Species identification and composition

A total of 689 *Diaphus* slender-type larvae ranging from 1.9 to 8.4 mm BL were collected during the 70 bongo net tows. Of these, 385 individuals (56% of total catch) were used for the analysis of the mtDNA for species identification. Twenty-four larvae were unidentifiable since the DNA extracted was not sufficient for analysis. A neighbor-joining tree using sequences of *Diaphus* slender-type larvae and 7 species of morphologically well-identified adults is shown in Figure 3. Six separate clades from A to F were recognized. Of these, *Diaphus* slender-type larvae in the clades A, E, and D were identified as *D. fulgens*, *D. kuroshio*, and *D. parri*, respectively, since clearly identifiable adults occurred in the same clades. In clades F, B, and C, however, no adult sequences showing high similarity to the larval sequences were found. We named the larvae belonging to these 3 clades as *Diaphus* slender sp. 1, *Diaphus* slender sp. 2, and *Diaphus* slender sp. 3, respectively, in descending order of number of individuals collected (Table 2).

Diaphus fulgens was the most abundant, with a mean abundance of 31.4 larvae/10 m^2 (standard error [SE] 4.5) (Table 2). This species accounted for 75.5% of the total catch, followed by *D. kuroshio* (14.0%), *Diaphus* slender sp. 1 (8.5%), *D. parri* (0.9%), *Diaphus* slender sp. 2 (0.8%), and *Diaphus* slender sp. 3 (0.4%). The mean BL of the 6 species ranged from 4.2 mm (*Diaphus* slender sp. 1) to 5.4 mm (*D. parri* and *Diaphus* slender sp. 2) (Table 2).

Larval distribution and habitat conditions

Larvae of *D. fulgens* occurred over a broad area in the Kuroshio waters of the ECS, while abundance was low on the shelf (<200-m depth) and in the area just west of the Okinawa and Amami Islands (Fig. 4). They were collected in 85.7% of the sampling stations, with a mean abundance at positive stations of 36.6 larvae/10 m^2. Although larvae of *D. kuroshio* and *Diaphus* slender sp. 1 were also distributed within the Kuroshio, the percentages of positive tows were markedly lower than that of



D. fulgens, i.e., 30.0% and 27.1%, respectively. Relatively high abundances of *D. kuroshio* (>20 larvae/10 m^2) were observed in the area north of the Amami Islands as well as in the area north of the Sakishima Islands (Fig. 4). *Diaphus* slender sp. 1 frequently occurred in low abundance (<10 larvae/10 m^2) in the Kuroshio waters in the southwestern edge of the study area west of 125°E where few *D. kuroshio* larvae were collected. On the other hand, *Diaphus* slender sp. 1 larvae were rare in the area north of the Amami Islands where *D. kuroshio* larvae occurred abundantly. Although the number of specimens collected was limited, occurrences of larval *D. parri*, *Diaphus* slender sp. 2, and *Diaphus* slender sp. 3 were restricted to the Kuroshio waters west of 125°E, with mean abundance at positive stations of 8.2, 7.6, and 3.9 larvae/10 m^2, respectively.

For the 3 dominant species, the weighted mean of temperature of larval habitats ranged from 22.5°C (*D. kuroshio*) to 23.2°C (*Diaphus* slender sp. 1), without any major difference between the species (Table 3). The weighted mean of salinity and chlorophyll *a* concentration of larval habitats also showed similar values among these species, ranging from 34.6 to 34.7 and from 0.60 to 0.64 µg/L, respectively (Table 3). The weighted mean of copepod nauplii of habitats of *Diaphus* slender sp. 1 larvae was higher than that of the other 2 species (0.73 versus 0.54–0.59 individuals/L) (Table 3) because *Diaphus* slen-

Figure 2

Horizontal distributions of (**A**) current velocity and direction (dark gray lines, 40 m depth) and temperature (30 m depth), (**B**) salinity (30 m depth), and (**C**) chlorophyll *a* concentration (30 m depth) and copepod nauplii density (upper 50 m of the water column) in the Kuroshio waters of the East China Sea during 15–28 February 2013. The black dots in panels A and B represent the sampling stations where *Diaphus* slender-type larvae were collected. The dashed gray lines in panel B indicate the position of the Kuroshio current based on data from the Quick Bulletin of Ocean Conditions of the Japan Coast Guard. Circles in panel C represent the density of nauplii as a continuous range of values >0. The 100- and 200-m isobaths are indicated by gray lines in each of the panels. Is.=island.

Table 2

Species composition, abundance (larvae per 10 m^2 of sea surface), and body length of *Diaphus* slender-type larvae in the Kuroshio waters of the East China Sea during 15–28 February 2013. The body length of each larva was standardized as the initial fresh length using the shrinkage (4.7%) reported by Moku et al. (2004). *n*=total number of larvae identified to species based on the sequence analysis of the mitochondrial DNA of the cytochrome *b* gene; SE=standard error; %=percentage of total abundance; SD=standard deviation.

		Abundance			Body length		
Species	*n*	Mean	SE	%	Mean	SD	Range
Diaphus fulgens	279	31.41	4.48	75.46	4.4	0.8	2.4–7.3
Diaphus kuroshio	46	5.81	1.50	13.97	4.7	0.9	3.3–7.2
Diaphus slender sp. 1	26	3.55	1.01	8.54	4.2	0.8	3.5–7.0
Diaphus parri	3	0.35	0.21	0.85	5.4	0.7	5.0–6.3
Diaphus slender sp. 2	4	0.33	0.20	0.78	5.4	2.0	4.1–8.4
Diaphus slender sp. 3	3	0.17	0.10	0.40	5.0	1.2	4.1–6.4

Table 3

Weighted mean temperature (WMT, °C), salinity (WMS), chlorophyll *a* concentration (WMC, micrograms per liter), and copepod nauplii density (WMN, individuals per liter) of the larval habitat of the 3 most abundant *Diaphus* species in the Kuroshio waters of the East China Sea during 15–28 February 2013.

Species	WMT	WMS	WMC	WMN
Diaphus fulgens	22.83	34.63	0.641	0.593
Diaphus kuroshio	22.54	34.66	0.637	0.538
Diaphus slender sp. 1	23.15	34.62	0.603	0.733

der sp. 1 larvae frequently occurred in the southwestern part of the study area where the density of nauplii was comparatively higher.

Larval growth

Otoliths of larval *D. fulgens*, *D. kuroshio*, and *Diaphus* slender sp. 1 displayed a typical disk-like, slightly conical shape, having clear and readable growth increments (Fig. 5). No accessory primordia were observed in the 3 species. The relationship between the otolith radius and BL of larval *D. fulgens* and *D. kuroshio* showed best fits with allometric equations (Fig. 5). Although a linear equation was adopted for *Diaphus* slender sp. 1, our data does not include individuals <3.5 mm BL whose otolith growth would be slower than that in larger-sized larvae. Comparing the otolith radius between species at the same SL, the radius of *Diaphus* slender sp. 1 was markedly larger than that of the other 2 species. For example, the radius of *D. fulgens* and *D. kuroshio* at 5 mm SL estimated by the equations was 41 and 39 µm, respectively, while *Diaphus* slender sp. 1 was 82 µm (Fig. 5).

The linear model fitted the BL and age data of the 3 *Diaphus* species better than the allometric and exponential models (Fig. 6A). Mean AGR were 0.119 mm/d in *D. fulgens*, 0.112 mm/d in *D. kuroshio*, and 0.105 mm/d in *Diaphus* slender sp. 1 (Fig. 6A). No significant difference was observed in the mean AGR among the larvae of the 3 species (ANCOVA and Bonferroni test, $P>0.05$). The G_w was estimated to be 0.118 d^{-1} in *D. fulgens*, 0.107 d^{-1} in *D. kuroshio*, and 0.094 d^{-1} in *Diaphus* slender sp. 1, without a significant interspecific difference (ANCOVA and Bonferroni test, $P>0.05$) (Fig. 6B). These G_w values were equivalent to the *K* of 12.5%, 11.3%, and 9.9% of dry larval body weight per day.

Discussion

Species identification and composition

Diaphus larvae, including both slender and stubby-types, are usually dominant in the assemblage of the myctophid larvae in subtropical-tropical waters of the world's oceans (e.g., Loeb, 1979; Moser et al., 1993; Holliday et al., 2012; Daudén-Bengoa et al., 2020). In the Kuroshio waters off central Japan, *Diaphus* larvae numerically accounted for nearly half of the total larval fish catch during spring to summer (Sassa et al., 2002; Sassa and Hirota, 2013). In the Kuroshio waters of the ECS, *Diaphus* slender-type larvae are reported to comprise 8.6–13.9% of the total larval fish in late winter, ranking as the second or third most abundant myctophid larvae by species or taxa (Sassa et al., 2004; Sassa and Konishi, 2015; Sassa and Takahashi, 2018). In the present study, *Diaphus* slender-type larvae accounted for 5.3% of the total larval fish catch, slightly lower than that in previous studies. However, information on the species composition of

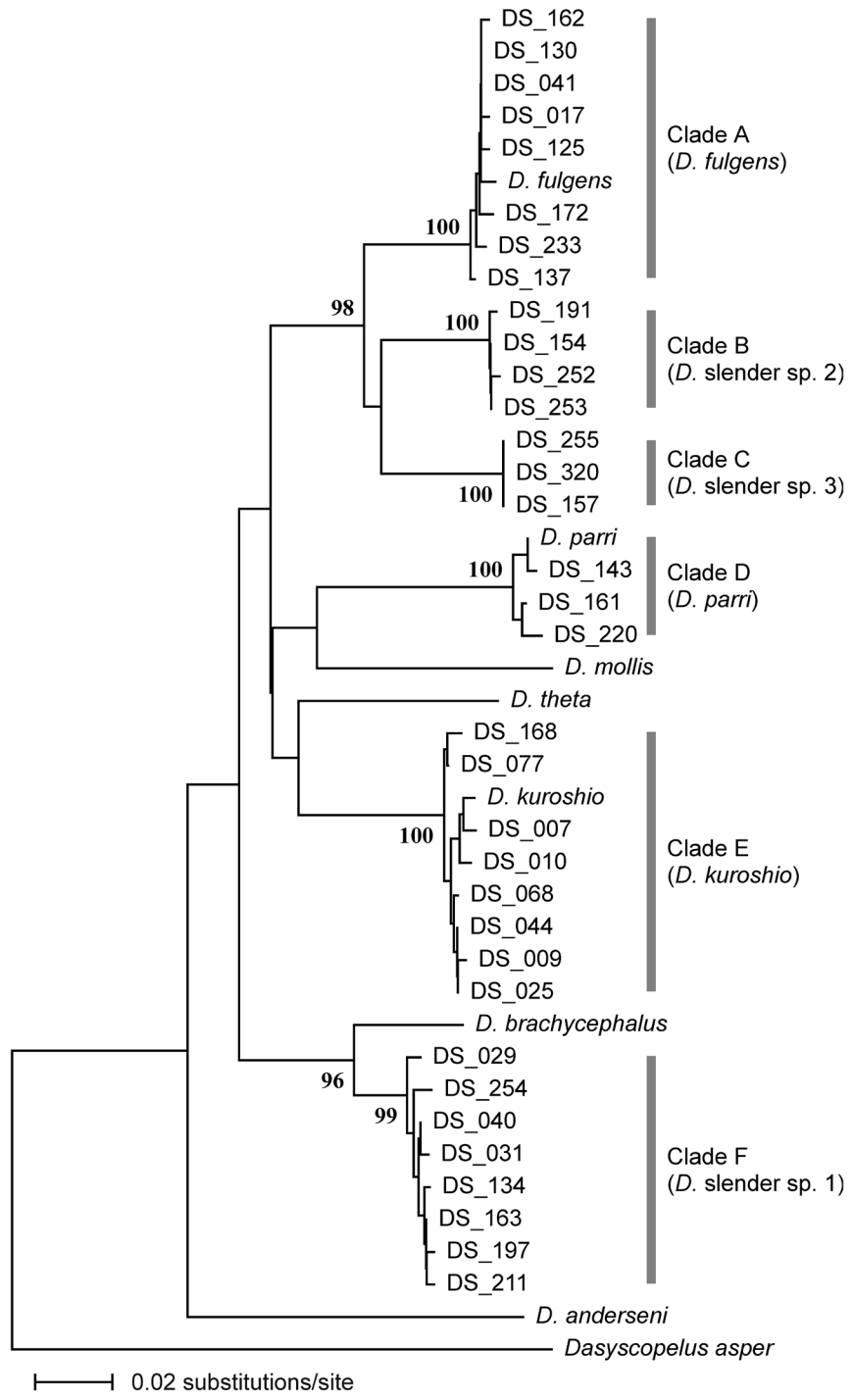


Figure 3

Neighbor-joining tree based on the cytochrome *b* partial region of *Diaphus* slender-type larvae and 7 species of morphologically well-identified adults collected in the Kuroshio waters of the East China Sea between 15 and 28 February 2013. Distance was calculated using the Kimura 2-parameter model of base substitution. Numbers beside internal branches indicate bootstrap probabilities (>90%) based on 1000 pseudoreplicates. Since the larval sequence belonging to clade A (*D. fulgens*), clade E (*D. kuroshio*), and clade F (*Diaphus* slender sp. 1) occurred in large numbers of 279, 46, and 26 individuals, respectively (Table 2), only 10 randomly selected individuals are shown in the tree. All larval sequences data belonging to *D. parri*, *Diaphus* slender sp. 2, and *Diaphus* slender sp. 3 are used in this tree.

Diaphus larvae is limited not only in the Kuroshio waters but also worldwide due to the difficulty of species discrimination based on morphological and pigmentation characters. Despite the occurrence of 78 *Diaphus* species in the world's oceans (Priede, 2017), only 10 species are known at the early stages of development (e.g., Olivar, 1987; Olivar and Beckley, 1995; Moser and Ahlstrom, 1996; Sassa et al., 2003; Moser and Watson, 2006; Evseenko and Bolshakova, 2020; Lee et al., 2020). This study is the first to apply genetic species identification to *Diaphus* larvae collected in the Kuroshio waters to examine species composition, distribution, and growth of the larvae at the species level.

Adults of 9 *Diaphus* species of the So-group, having slender-type larvae, have been recorded in the western North Pacific (Kawaguchi and Shimizu, 1978; Nakabo, 2013). Of these, the genetic data of 7 species were available for species identification of the larvae in the present analysis, although we could not obtain data of *D. aliciae* and *D. richardsoni*. In this study, the nucleotide sequence data of 361 larvae were divided into 6 clades, 3 of which were identified as *D. fulgens*, *D. kuroshio*, and *D. parri*. However, we could not identify the species of the 3 other clades; they tentatively were named *Diaphus* slender sp. 1, sp. 2, and sp. 3, although *Diaphus* slender sp. 1 is considered to be a closely related species to *D. brachycephalus* based on the phylogenic tree (Fig. 3). Genetic information could not be obtained for species that have been described in the eastern Pacific or the Indian Ocean, but not recorded around Japanese waters thus far,

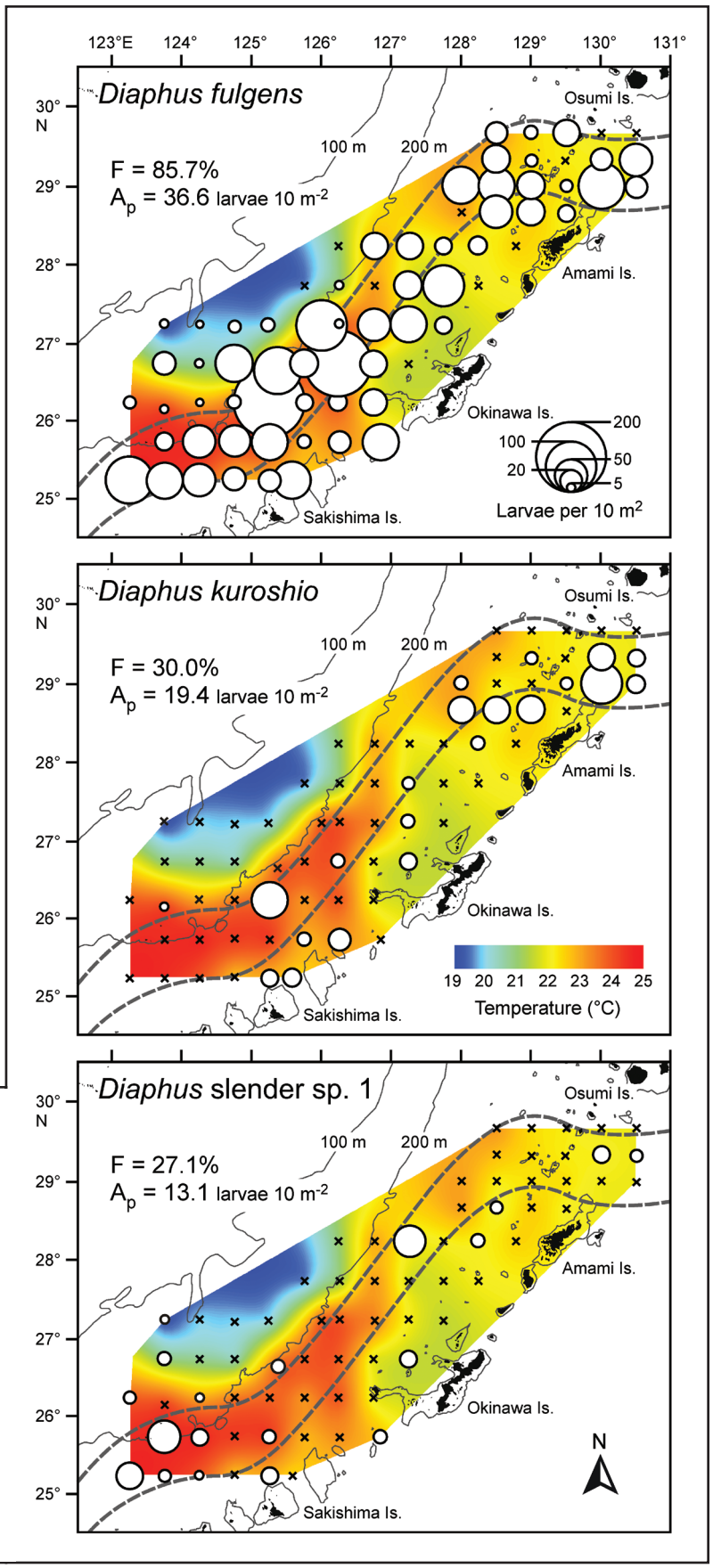


Figure 4

Horizontal distributions of the 3 numerically dominant *Diaphus* slender-type larvae collected in the Kuroshio waters of the East China Sea during 15–28 February 2013. The position of the Kuroshio (dashed gray lines) is overlaid on the map based on data from the Quick Bulletin of Ocean Conditions of the Japan Coast Guard. The color contours indicate the temperature at 30 m depth. Circles represent the larval abundance as a continuous range of values >0. Crosses indicate no catch. The 100- and 200-m isobaths are indicated by gray lines in each of the panels. Is.=island; F=percent frequency of positive stations; Ap=mean abundance at positive stations.

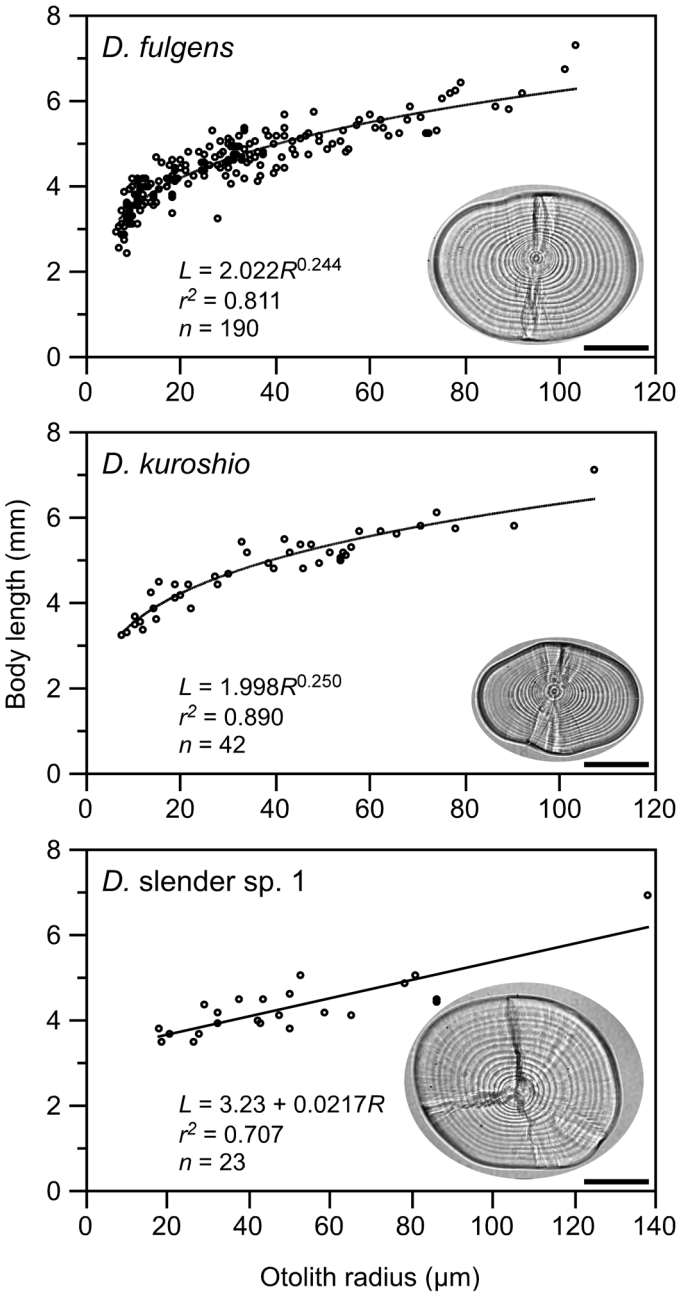


Figure 5

Relationship between otolith radius (*R*) and body length (*L*) of the 3 numerically dominant *Diaphus* slender-type larvae collected in the Kuroshio waters of the East China Sea during 15–28 February 2013. Photos of sagittal otoliths of *D. fulgens* (6.2 mm standard length [SL]), *D. kuroshio* (5.4 mm SL), and *Diaphus* slender sp. 1 (4.3 mm SL) are shown at the bottom right of each graph. Scale bar is 50 μm. r^2=coefficient of determination.

such as *D. impostor*, *D. kora*, *D. lobatus*, *D. megalops*, *D. rafinesquii*, and *D. wisneri* (Kawaguchi and Shimizu, 1978; Nafpaktitis et al., 1995). In the future, it will be necessary to collect genetic information on adult *Diaphus* to identify the 3 unidentified species (Poulsen et al., 2013).

Diaphus fulgens was the most abundant of the *Diaphus* species, accounting for 75.5% of the total catch in this study, followed by *D. kuroshio* (14.0%) and *Diaphus* slender sp. 1 (8.5%). *Diaphus fulgens* is widely distributed in the subtropical–tropical waters of the Indo-Pacific (Wisner, 1976; Nafpaktitis, 1978) and is one of the most dominant *Diaphus* in the Kuroshio waters (e.g., Kawaguchi and Shimizu, 1978; Shinohara and Matsuura, 1997; Senou et al., 2002). It is a small species, with a maximum BL of approximately 45 mm SL. *Diaphus fulgens* has been considered a species complex and is classified into 4 forms, A, B, C, and D, based on slight differences in the number of gill rakers and photophores (Wisner, 1976). Kawaguchi and Shimizu (1978) indicated that form C of *D. fulgens* predominates in the waters around Japan. The phylogenetic tree (Fig. 3) indicates that *Diaphus* slender sp. 2 and sp. 3 are closely related to *D. fulgens* and may correspond to any of the other 3 forms. In the future, investigation of the degree of genetic differentiation among the 4 forms will be necessary for further identification.

Species identification through mtDNA analysis facilitates the re-evaluation of differences in larval morphology among *Diaphus* species. In the present study, the otolith radius of *Diaphus* slender sp. 1 was significantly larger than that of the other 2 species. Linkowski (1991) also suggested the potential importance of otolith microstructure and growth patterns as distinguishing characteristics for myctophid larvae. There might be other small interspecific differences in morphometric characteristics and pigmentation that have not so far been recognized in *Diaphus* slender-type larvae (e.g., Ozawa, 1986; Olivar and Beckley, 1995; Sassa et al., 2003; Evseenko and Bolshakova, 2020). Such information potentially will contribute to efficient species identification of formalin-fixed larvae. *Diaphus fulgens* and *D. kuroshio* are possible species for the re-examination of larval morphology (Fig. 7). In this case, particular attention will need to be paid to the number and shape of (1) melanophores on a lateral surface of the gut between the cleithral and terminal sections and (2) melanophores present along the ventral margin of the postanal region (Ozawa, 1986; Olivar and Beckley, 1995). In *D. fulgens*, both the lateral

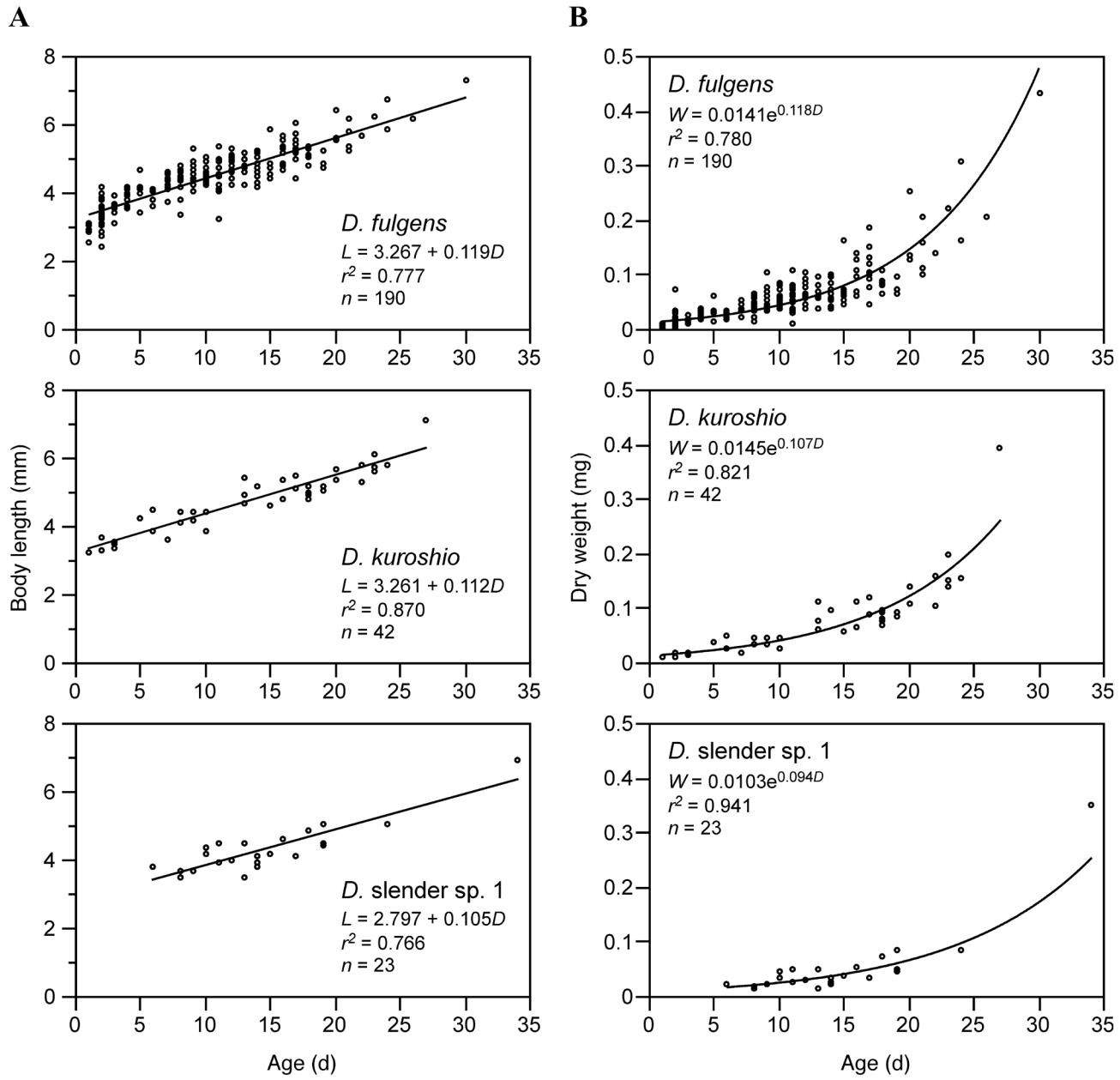


Figure 6

Relationship between (**A**) age (*D*) and body length (*L*) and (**B**) age and dry body weight (*W*) of the 3 numerically dominant *Diaphus* slender-type larvae collected in the Kuroshio waters of the East China Sea during 15–28 February 2013. Age is based on daily increment counts of sagittal otoliths. r^2=coefficient of determination; *n*=total number of larvae analyzed.

and postanal melanophores tend to be more numerous than those in *D. kuroshio* (Fig. 7).

Distribution

Because *Diaphus* slender-type larvae occurred along the Kuroshio mainstream with a velocity of approximately 0.75–1.50 m/s, we cannot ignore the effect of northeastward larval transport by the Kuroshio when discussing the larval distribution. The northeastward linear advection of larvae simply calculated from this current speed could be as much as 65–130 km/d. However, there are usually clockwise and counterclockwise submesoscale eddies (5–20 km in radius) on both sides of the Kuroshio (Liu et al., 2017), suggesting that this northeastward transport of larvae is likely to be more complex and slower than that calculated above.

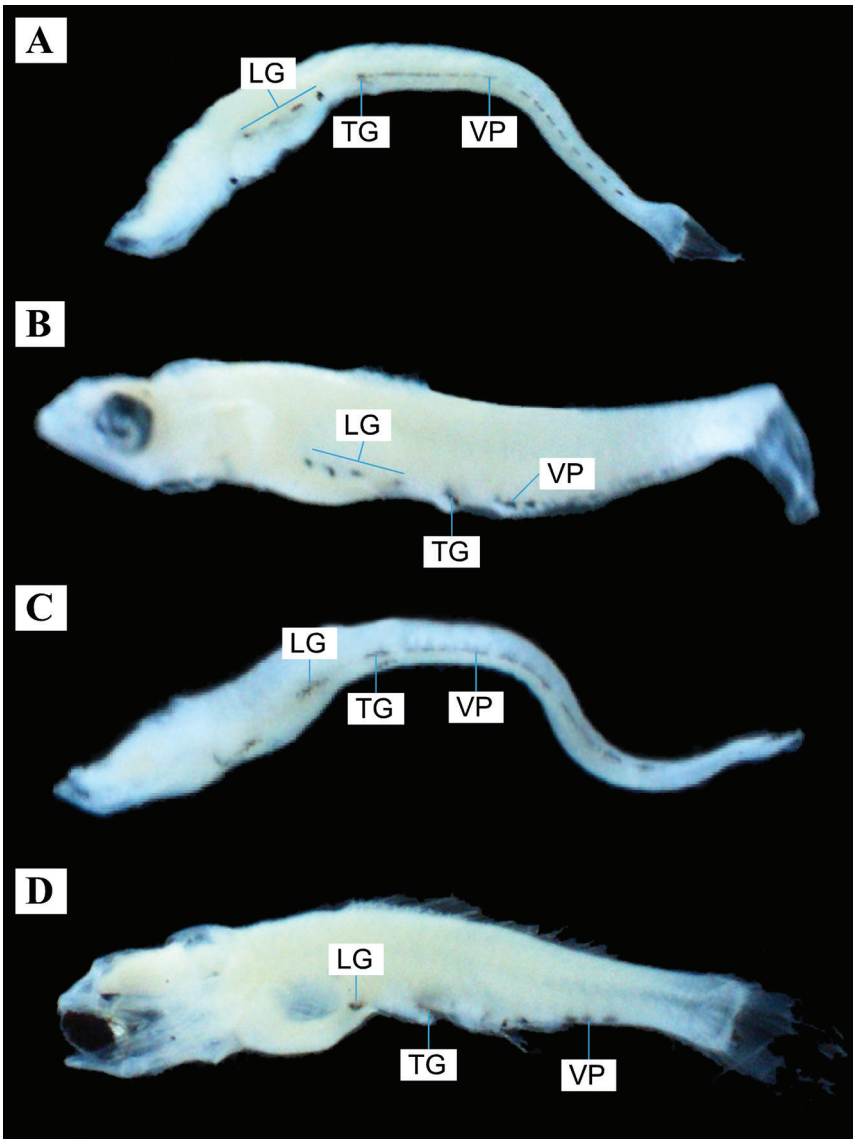


Figure 7

Photographs of *Diaphus* slender-type larvae identified to the species level based on sequence analysis of the mitochondrial DNA of the cytochrome *b* gene: (**A**) *D. fulgens* (5.1 mm standard length [SL]), (**B**) *D. fulgens* (5.9 mm SL), (**C**) *D. kuroshio* (5.0 mm SL), and (**D**) *D. kuroshio* (5.5 mm SL). Larvae were collected in the Kuroshio waters of the East China Sea during 15–28 February 2013. LG=melanophores on a lateral surface of the gut between the cleithral and terminal sections; VP=melanophores along the ventral margin of the postanal region; TG=melanophore on the free terminal section of the gut.

The density of prey items for the larval fish in the Kuroshio waters is generally less than those in the shelf waters of the ECS and western North Pacific, i.e., west of the Kuroshio mainstream, and the variation of prey density is small in the spatial–temporal scale in the Kuroshio waters (e.g., Nakata et al., 1995; Okazaki et al., 2008; Sassa and Konishi, 2015; Kobari et al., 2018). Our results also indicate that there were no remarkable spatial variations in densities of nauplii in the Kuroshio waters, although the results underestimated the densities of nauplii due to the lack of small-sized nauplii <0.1 mm in body width. While the estimated copepod densities in the

Kuroshio waters are lower than those in the shelf waters, the production rate of copepod nauplii in the Kuroshio waters has been estimated to be comparable to or even higher than those in the shelf waters of the ECS during late winter (Okazaki et al., 2008; Kobari et al., 2018). This suggests that the Kuroshio waters form a relatively stable prey environment for *Diaphus* slender-type larvae and that it is possibly favorable for survival.

Larval abundance largely reflects the spawning seasons and grounds of the adult fish populations (Moser and Smith, 1993b; Koslow et al., 2011). Therefore, larval sampling surveys as well as the analysis of the gonadal development of adult fish are an effective method to obtain information on spawning (Sassa and Hirota, 2013; Daudén-Bengoa et al., 2020). This is advantageous for examining the life history of myctophids whose adults are usually challenging to sample seasonally because they live in the mesopelagic layer over extensive offshore areas (Clarke, 1973; Gjøsæter and Kawaguchi, 1980). High abundances of *D. fulgens* larvae with mean SL of 4.4 mm were observed over a broad area of the Kuroshio waters of the ECS during February. Since larvae of this size were approximately 10 d after hatching, the distributional area of the larvae would represent the approximate location of the spawning grounds, even considering the northeastward larval transport by the Kuroshio. Mature females of *D. fulgens* occur over a broad area of the Kuroshio waters of the ECS from February to March (Sassa and Takahashi, 2022), which overlaps with the larval distribution. This confirms that investigations of larval distribution with species identification using mtDNA analysis can be useful in estimating the spawning seasons and grounds of the adult population of *Diaphus* species.

Although the catches of 5 other species of *Diaphus* slender-type larvae were markedly lower than those of *D. fulgens*, the larval distribution pattern possibly reflects adult spawning seasons and grounds. The second most abundant larva in this study was *D. kuroshio*, a middle-sized myctophid, reaching approximately 68 mm SL (Kawaguchi and Nafpaktitis, 1978). This species is endemic to the Kuroshio and Kuroshio Extension off Japan (Kawaguchi and Nafpaktitis, 1978). The center of distribution of *D. kuroshio* is located north of *D. fulgens* and *D. parri* since the distribution of the latter 2 species extends broadly to the tropical waters of the Indo-Pacific (Kawaguchi and Shimizu, 1978). In the present study, a high abundance of *D. kuroshio* larvae was observed frequently in the area north of the Amami Islands. *Diaphus kuroshio* >60 mm SL have occasionally been collected by a midwater trawl in the epipelagic layer at night in the ECS during winter, although there is no record of catches of mature females (senior author, unpubl. data). However, the larval distribution suggested that spawning occurred in the ECS, especially in the northeastern part of the study area. On the contrary, *Diaphus* slender sp. 1 larvae frequently occurred in the Kuroshio waters of the southwestern stations in our study area where *D. kuroshio* did not occur. The larval occurrences of *D. parri* and *Diaphus* slender sp. 2 and sp. 3 were also restricted to the Kuroshio waters in the southwestern part of the study area. This result suggested that the primary spawning grounds of these 4 species extends to the Kuroshio upstream region southwest of the Sakishima Islands.

Growth

Early growth has been suggested to be a key factor determining the survival and recruitment success of various marine fishes (Anderson, 1988; Houde, 2016). However, available information on the larval growth of myctophids is restricted to only 16 species worldwide, of which only one species belongs to *Diaphus* (e.g., Moku et al., 2001; Takagi et al., 2006; Conley and Gartner, 2009; Namiki et al., 2015; Sassa and Takahashi, 2018). In the present study, the AGR of larval *D. fulgens*, *D. kuroshio*, and *Diaphus* slender sp. 1 ranged from 0.11 to 0.12 mm/d. The subarctic species, California headlightfish, also having slender-type larvae, showed an AGR of 0.13 mm/d during the larval stage in the transition region of the western North Pacific in July, just north of the Kuroshio Extension (Moku et al., 2001) (Fig. 1). The AGR of larvae of 10 species of myctophid previously reported in the subtropical-tropical waters ranged from 0.12 to 0.39 mm/d (Table 4), although growth rates of marine fish larvae have been shown to vary depending on habitat temperature and food availability, even in the same species (Yamashita et al., 2001; Houde, 2016). The AGR of the 3 *Diaphus* slender-type larvae estimated in the present study corresponds to the lowest AGR values reported in myctophids.

Myctophid larvae show a high morphological diversity among species (Moser, 1981; Moser and Ahlstrom, 1996). Since different body shapes can be considered to have different growth patterns along the axis of body length, width, and height, the variations in the AGR can be considered to largely reflect the morphological characteristics of each species (Conley and Gartner, 2009; Sassa and Takahashi, 2018). Therefore, information on G_W is also needed to conduct interspecific comparisons of growth to discuss the early life history strategy of myctophid fishes (Sassa et al., 2015). In Table 4, we summarized G_W of the 12 species of subtropical–tropical myctophids. The mean G_W of the previously reported 9 species was calculated to be 0.122 d^{-1} (SD 0.044) (range: 0.045–0.172 d^{-1}). In the present study, the G_W of the 3 dominant *Diaphus* larvae ranged from 0.094 to 0.118 d^{-1}, which were within the range of the 9 other myctophid larvae but slightly lower than the mean.

To discuss whether the slow growth of the 3 *Dia-*

Table 4

Summary of mean absolute growth rate (AGR, millimeters per day) and weight-specific instantaneous growth coefficient (G_w, per day) of the larvae of subtropical–tropical myctophid species from different regions. WMT=weighted mean temperature (°C) of the larval habitat.

Species	AGR	G_w	WMT	Regions
Benthosema pterotum	0.26	0.172	26.1	East China Sea shelf[a]
B. suborbitale	0.17	0.066	–	Gulf of Mexico[b]
Ceratoscopelus townsendi	0.37	0.154	–	Gulf of Mexico[b]
C. warmingii	0.35	0.148	20.8	Kuroshio Extension[c]
Dasyscopelus asper	0.16	0.150	20.9	Kuroshio[d]
Diaphus fulgens	0.12	0.118	22.8	Kuroshio[e]
D. kuroshio	0.11	0.107	22.5	Kuroshio[e]
D. slender sp. 1	0.11	0.094	23.2	Kuroshio[e]
Hygophum taaningi	0.14	0.091	–	Gulf of Mexico[b]
Myctophum affine	0.39	–	–	Off southeastern Brazil[f]
M. selenops	0.22	0.147	–	Gulf of Mexico[b]
Notolychnus valdiviae	0.12	0.045	–	Gulf of Mexico[b]
Notoscopelus japonicus	0.15	0.128	20.1	Kuroshio[d]

a=Sassa et al. (2015); b=Conley and Gartner (2009); c=Takagi et al. (2006); d=Sassa and Takahashi (2018); e=this study; f=Namiki et al. (2015). The G_w of the species in references b and c is estimated from the age–body length (BL) relationship and the dry weight–BL relationship by Conley and Gartner (2009).

phus species with slender-type larvae is associated with low temperature during the winter period, we examined the relationship between larval growth and habitat temperature using data from the 4 other species for which weighted mean temperature of the larval habitat is available (Table 4). Skinnycheek lanternfish (*Benthosema pterotum*) larvae in a high habitat temperature of 26.1°C showed markedly faster growth than the 3 *Diaphus* species with slender-type larvae (Sassa et al., 2015). However, larvae of Warming's lanternfish (*Ceratoscopelus warmingii*), prickly lanternfish, and Japanese lanternfish (*Notoscopelus japonicus*) also showed faster growth than the 3 *Diaphus* species with slender-type larvae even though their respective habitat temperatures were approximately 2–3°C lower (Takagi et al., 2006; Sassa and Takahashi, 2018). The lower growth rate of *Diaphus* slender-type larvae is therefore not likely to be due to lower habitat temperature, though more data on various other species are needed to clarify the relationship between larval growth and habitat temperature in myctophids.

The growth rates of the juveniles and adults of myctophids are reported to be lower than those of epipelagic fishes (Childress et al., 1980; Takagi et al., 2006). In the onshore side of the Kuroshio during winter, the G_w of Japanese sardine (*Sardinops melanostictus*), Japanese jack mackerel (*Trachurus japonicus*), Pacific chub mackerel (*Scomber japonicus*), and spotted chub mackerel (*Scomber australasicus*) are estimated to be 0.206–0.312, 0.160–0.217, 0.227–0.283, and 0.280–0.336 d^{-1}, respectively (Sassa and Takahashi, 2018; and references therein). The G_w of the 3 dominant *Diaphus* larvae was markedly lower, approximately one half to one third of the G_w of small pelagic fish larvae that occurred in more productive waters compared to *Diaphus* larvae. In addition, based on the data set of Houde and Zastrow (1993), mean G_w of the larval fishes of the pelagic and demersal species in the estuary (11 species), shelf (20 species), and upwelling regions (11 species) were 0.195 d^{-1} (SD 0.063), 0.178 d^{-1} (SD 0.076), and 0.178 d^{-1} (SD 0.073), respectively. The mean G_w of myctophid larvae in Table 4, excluding the skinnycheek lanternfish that occurs in the shelf waters, was 0.113 d^{-1} (SD 0.037). This was markedly lower than the mean G_w of the pelagic and demersal species in the other regions (Houde and Zastrow, 1993). Food availability for larval fish in tropical–subtropical oceans would be poorer compared with that in the estuary, shelf, and upwelling regions (Longhurst, 2006), which possibly relates to the lower larval growth in oceanic myctophids. Myctophids are thought to have early life history strategies that allow them to survive in oligotrophic tropical–subtropical oceans despite low larval growth (Sassa and Takahashi, 2018). This might be related to some predatory avoidance behavior, probably relating to the morphological characteristics of each species and swimming ability (Moser, 1981; Sassa et al., 2002). Further research is needed on the early life history strategies of this family in the context of larval growth and survival, as well as behavior in relation to larval morphology.

Conclusions

Diaphus is the most speciose genus in the family Myctophidae (approximately 78 species) and a key component of mesopelagic fish assemblages in various major oceans (Kawaguchi and Shimizu, 1978; Priede, 2017). Although the larvae of various myctophid species can be morphologically identified (Moser and Ahlstrom, 1996), *Diaphus* larvae have only slight morphological and pigmentation differences between species, separated into slender and stubby-types (Moser and Ahlstrom, 1974). Therefore, ecological information on *Diaphus* larvae at the species level remains limited, despite their numerical dominance in oceanic larval fish assemblages (Loeb, 1979; Daudén-Bengoa et al., 2020). In the present study, we identified species of *Diaphus* slender-type larvae in the Kuroshio waters during late winter based on mtDNA analysis and described the species composition, distribution, and growth at the species level. These results provide information on spawning seasons and grounds of adults as well as the early life history strategies of each species. Because survival during the larval stage is closely linked with recruitment success or failure in various marine fish (Houde, 2016), ecological research on the larvae of *Diaphus* species is essential for understanding the mechanisms controlling the population dynamics and biodiversity of myctophids. Further research on *Diaphus* larvae, including both slender and stubby-types, is needed in other areas and seasons based on species identification using mtDNA analysis to accumulate ecological information on the larvae of this speciose genus.

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