

Late winter vertical distribution of mesopelagic fish larvae in the Kuroshio Current region of the western North Pacific

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Vertical distribution patterns of five abundant mesopelagic fish larvae (*Diaphus* slender type, *Notoscopelus japonicus*, *Myctophum asperum*, *Lipolagus ochotensis* and *Sigmops gracilis*) were firstly described in the western North Pacific Kuroshio Current region; samples were taken at discrete depths (0–150 m) during both day and night on 28 and 29 February 1996. Habitat depths of all larvae collected did not differ between day and night. *Diaphus* slender type, *N. japonicus* and *M. asperum* occurred mainly in the 25–80-m, 30–75-m and 35–80-m depth layers, respectively, all of which were within the mixed layer above the thermocline at a depth of 80 m. The distributions of *L. ochotensis* and *S. gracilis* were centered in the 30–100-m and 55–100-m layers, respectively, depths that were between the mixed layer and the thermocline. Habitat depths of all species or types overlapped primarily in the 55–75-m layer; overlapping distributions were likely related to the vertical mixing of the Kuroshio waters in winter because previous report indicated that larvae of mesopelagic fish were generally habitat-segregated by depth in the stable water column that develops during the summer thermal stratification. The fish species had ontogenetic vertical migrations, with smaller individuals distributed primarily in the mixed layer and larger larvae in the thermocline.

Key words: Kuroshio Current region, mesopelagic fish larvae, vertical distribution, mixed layer, ontogenetic migration, winter

Introduction

Mesopelagic fish larvae are a dominant component of oceanic ichthyoplankton in various regions of the world oceans, with most of the larvae distributed in the productive upper 150-m layer during both day and night (Loeb, 1979; Moser and Smith, 1993; Sassa et al., 2002). Because mesopelagic fish larvae may compete for food resources with larvae of commercially important fishes such as Japanese anchovy (*Engraulis japonicus*), Japanese sardine (*Sardinops melanostictus*) and Pacific saury (*Cololabis saira*) (Sassa et al., 2004b; Sassa and Kawaguchi, 2005), information on the vertical distributions of mesopelagic fish larvae is important, especially in winter and early spring when the Kuroshio waters off southern Japan are the primary spawning and nursery grounds for anchovy, sardine and saury (Odate and Hayashi, 1977; Konishi, 1980; Funakoshi, 1984; Kuroda, 1991). The aim of the present study was to examine the vertical distributions of the five most abundant species in the larval mesopelagic fish assemblage during the winter, i.e. three species or types of myctophidae

(*Myctophum asperum*, *Notoscopelus japonicus* and *Diaphus* slender type), one species of Bathylagidae (*Lipolagus ochotensis*), and one species of Gonostomatidae (*Sigmops gracilis*) (Sassa et al., 2004b). The size-depth distributions of the five chosen species or types were also studied to elucidate ontogenetic vertical migrations. Our study provides the first record of vertical distributions of *N. japonicus* larvae and small larvae (<15 mm) of *L. ochotensis* and *S. gracilis*.

Materials and Methods

Four series of samples were taken during daytime and nighttime, respectively, in the Kuroshio Current region off Shikoku (>2000 m depth), Japan, from the Research Vessel ‘Shunyo-Maru’ (National Research Institute of Far Seas Fisheries) during 28–29 February 1996 (Table 1, Fig. 1). Tows conducted between 1 h after sunrise and 1 h before sunset, and between 1 h after sunset and 1 h before sunrise, were considered daytime and nighttime samples, respectively. During sampling, the ship drifted with the current in an attempt to stay within the same water mass. A multilayer depth sampler (MTD net; Motoda, 1971) was towed horizontally at 1.0 m s⁻¹ at each of six target depths (0, 10, 30, 60, 100 and 150 m) for 30 min. The net had a mouth diameter of 56 cm and a mesh size of 0.33×0.33 mm (Motoda, 1971). The volume of water filtered by each net tow was measured with a flowmeter mounted at the net mouth. The mean±standard deviation (*S.D.*) of water volume fil-

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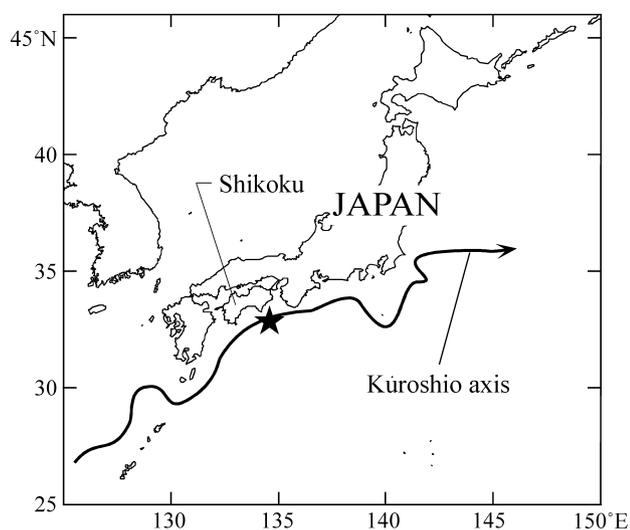
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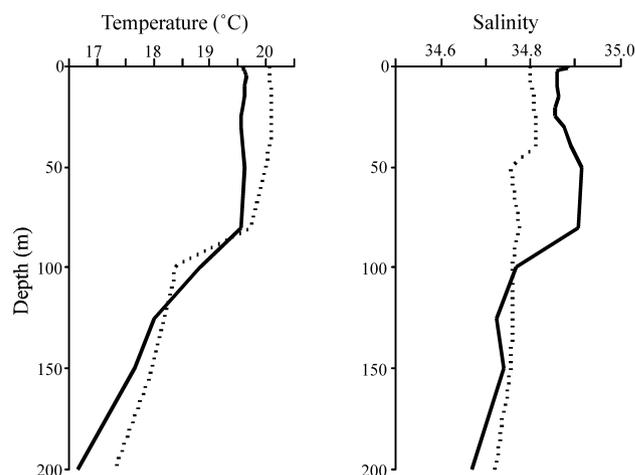
Table 1. Sampling data in the Kuroshio Current region.

Date, 1996	Time (horizontal tow)	Day/ Night	Sampling locality	
			Latitude (N)	Longitude (E)
28 Feb	13:01–13:31	Day	32°49.4'	134°13.6'
28 Feb	15:01–15:31	Day	32°50.8'	134°19.9'
28 Feb	17:08–17:38	Day	32°49.2'	134°14.8'
28 Feb	19:06–19:36	Night	32°51.9'	134°19.9'
28 Feb	21:00–21:30	Night	32°51.7'	134°19.7'
28 Feb	22:59–23:29	Night	32°51.9'	134°19.9'
29 Feb	01:01–01:31	Night	32°53.5'	134°19.6'
29 Feb	08:00–08:30	Day	32°49.2'	134°12.8'

**Figure 1.** Sampling location (solid star; 32°49'–32°54'N, 134°13'–134°20'E) off Shikoku, Japan, from 28 to 29 February 1996. The solid grey line denotes the Kuroshio Current axis (Japan Coast Guard, 1996).

tered was $360.0 \pm 205.9 \text{ m}^3$ (range: 158.6–1638.2 m^3). A Conductivity–Temperature–Depth (CTD) profiler cast was made down to 1000 m at the start and end of sampling. Samples were fixed in 10% buffered formaldehyde seawater whilst at sea.

All fish larvae collected were sorted and counted. Body lengths were measured to the nearest 0.1 mm on individuals of the five most abundant mesopelagic species; notochord length was measured on preflexion larvae, and standard length was measured on flection and postflexion larvae. Larval 'concentration' (indiv. 1000 m^{-3} filtered seawater in each depth layer) was used to describe and compare larval distributions by depth. To obtain the average features of day-night vertical distribution patterns, the vertical distributions were depicted as average values during the

**Figure 2.** Vertical profiles of water temperature (°C) and salinity at the sampling station in the Kuroshio Current region. Solid line: 28 Feb, Dashed line: 29 Feb.

day and night, respectively. For a quantitative comparison of day and night depth distributions, we calculated abundance (indiv. m^{-2}) of the five chosen larvae at 0–10, 10–30, 30–60, 60–100 and 100–150-m layers during daylight and nighttime, respectively, using trapezium rule. Then the depths (D) at which 25, 50 and 75% of the population occurred (beginning at the shallowest depth where the species was found) were calculated ($D_{25\%}$, $D_{50\%}$ and $D_{75\%}$; Pennak, 1943). A larval distribution center for each species or type was defined as the depth of $D_{50\%}$, and also as the depth at which 50% of the total catch occurred (i.e., between $D_{25\%}$ and $D_{75\%}$).

Results

Oceanographic features

Vertical temperature and salinity profiles down to 200 m depth were similar on 28 and 29 February 1996, suggesting that all sampling was conducted in the same water mass (Fig. 2). CTD data indicated a mixed layer in the upper 80 m, where temperature was 19.5–20.0°C and salinity was 34.8–34.9, conditions typical of winter vertical profiles in the Kuroshio region (Kawai, 1972). Temperature and salinity gradually decreased to 16.7–17.3°C and 34.7, respectively, in the transition from 80 to 200 m depth (Fig. 2).

Vertical distribution

The five mesopelagic fish larvae accounted for 53.2% of the total abundance of fish larvae in the 0–150-m layer. Although the mean night catches of each larval species in each depth layer were sometimes significantly higher than during the day (Mann–Whitney U -test, $p < 0.05$), their vertical distribution patterns were not significantly different between day and night for both $D_{50\%}$ and $D_{25-75\%}$. Furthermore, the shape of the vertical distributions for each species

between day and night was almost similar to each other, suggesting an absence of diel vertical migration (Table 2, Fig. 3). Over 50% of *Diaphus* slender type, *N. japonicus*, *M. asperum* and *L. ochotensis* larvae were collected in the 25–80-m (18.7–20.1°C), 30–75-m (18.8–20.1°C), 35–80-m (18.7–20.1°C) and 30–100-m (18.4–20.1°C) layers, respectively, indicating considerable overlap in species depth distributions within the mixed layer above 80 m (Table 2, Fig. 3). The peak abundance of *S. gracilis* larvae was in the 55–100-m layer (18.4–19.5°C), spanning the bottom of the mixed layer to the top of the thermocline. This indicates that vertical distribution of this species also partly overlapped with other four larvae in the mixed layer.

The shallowest depth distributions of the five species were 10 m or 30 m in the day, but moved up to 0 m at night. This suggests that the upper limits of the depth distributions do slightly shift to shallower waters at night, or net avoidance rate in the shallower waters decreased at night (Fig. 3). However, these shifts were very small scale and did not affect the overall vertical distribution patterns of abundance.

Size distribution

Body length of *Diaphus* slender type, *N. japonicus*, *M. asperum*, *L. ochotensis* and *S. gracilis* larvae were 3.1–9.6 (5.3±1.3, mean±S.D.), 2.1–8.9 (4.3±1.2), 1.8–7.9 (3.2±1.1), 2.8–16.0 (6.5±2.9) and 4.7–14.9 (7.7±2.3) mm, respectively. Of these, the mean body lengths of *M. asperum*, *S. gracilis* and *L. ochotensis* were significantly larger in the 100–150-m layer than in the 0–60-m layer in both day and night samples (Mann–Whitney *U*-test, $p < 0.05$, Fig. 4). A similar result was also observed for *Diaphus* slender-type larvae at night (Mann–Whitney *U*-test, $p < 0.05$) although they were not present in the samples taken at 150-m depth in the daytime. For *N. japonicus* larvae, the mean body lengths were also significantly larger for individuals in the 100–150-m layer than in the 0–60-m layer at night (Mann–Whitney *U*-test, $p < 0.05$, Fig. 4). Day samples of *N. japonicus* larvae were very small and restricted to the 0–60-m layer (Fig. 3). There was no significant size difference between day and night in the 0-, 10-, 30- and 60-m layers in any species or type (Mann–Whitney *U*-test, $p > 0.05$). For *M. asperum*, *S. gracilis* and *L. ochotensis* larvae, the mean body lengths in the 100- and 150-m layers were also similar between day and night (Mann–Whitney *U*-test, $p > 0.05$).

Discussion

The day–night differences in abundance of each species probably indicate diel changes in net avoidance and/or patchiness because the swimming ability of larvae is generally reduced at night by swim bladder inflation (Uotani, 1973; Hunter and Sanchez, 1976), possibly resulting in reduced patchiness at night. Since all of these larval species or types within size range collected in this study are rarely

Table 2. The depth at which 50% of the total catch occurred ($D_{25\%}$ – $D_{75\%}$) and 50% of the population resided ($D_{50\%}$) for the five mesopelagic fish larvae in the Kuroshio Current region.

Species or types	Day		Night	
	$D_{25\%}$ – $D_{75\%}$	$D_{50\%}$	$D_{25\%}$ – $D_{75\%}$	$D_{50\%}$
<i>Diaphus</i> slender type	25–53	41	26–79	46
<i>Notoscopelus japonicus</i>	32–68	48	28–73	48
<i>Myctophum asperum</i>	35–80	55	40–79	59
<i>Lipolagus ochotensis</i>	39–97	61	30–90	57
<i>Sigmops gracile</i>	59–99	79	56–100	79

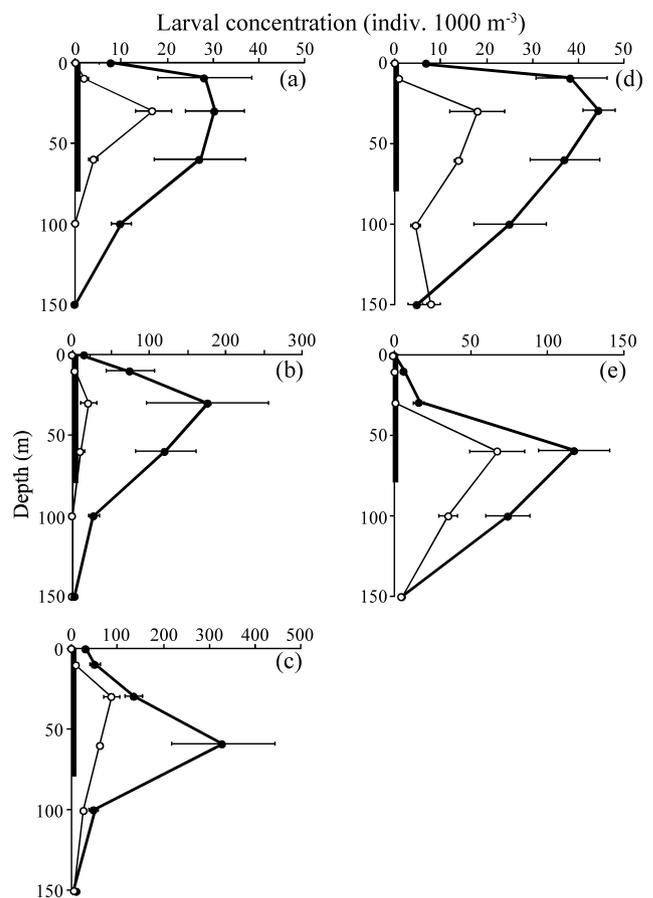


Figure 3. Vertical distributions of larval concentrations in the Kuroshio Current region, 28–29 February, 1996. (a) *Diaphus* slender type, (b) *Notoscopelus japonicus*, (c) *Myctophum asperum*, (d) *Lipolagus ochotensis*, and (e) *Sigmops gracilis*. Horizontal bars indicate ± standard errors ($n=4$). Open circles with thin lines are for daytime; solid circles with thick lines are for nighttime. Vertical thick bars indicate the depth range of mixed layer (0–80 m depth).

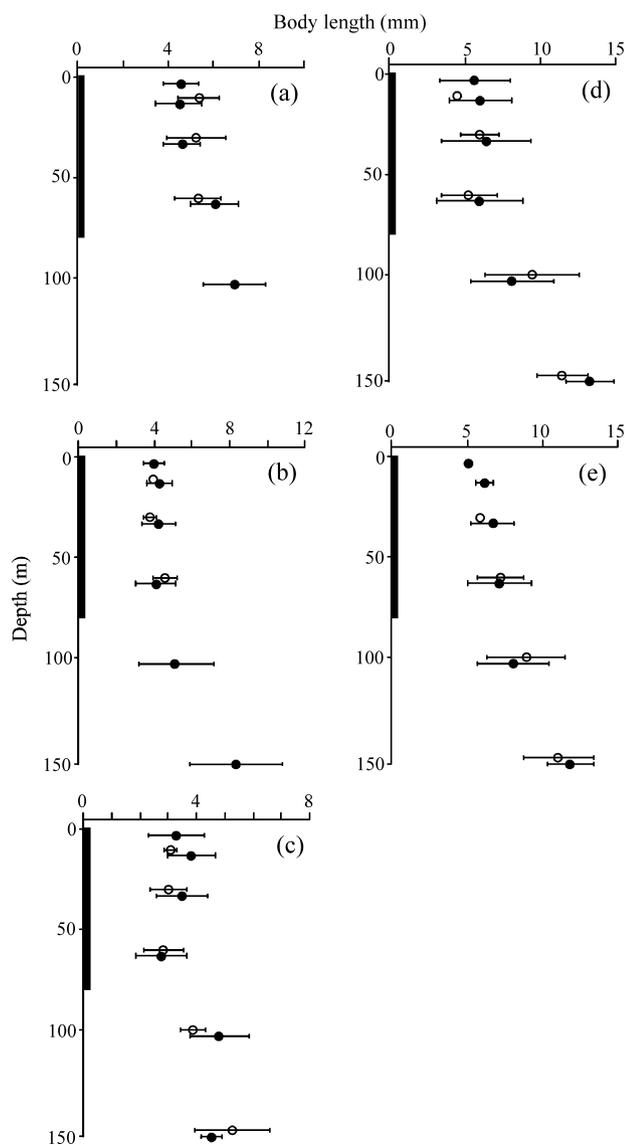


Figure 4. Mean body lengths of larvae by habitat depth in the Kuroshio Current region. (a) *Diaphus* slender type ($n=137$), (b) *Notoscopelus japonicus* ($n=454$), (c) *Myctophum asperum* ($n=963$), (d) *Lipolagus ochotensis* ($n=254$), and (e) *Sigmops gracilis* ($n=445$). Horizontal bars indicate \pm standard deviations. Vertical thick bars indicate the depth range of mixed layer (0–80 m depth). Open circles are for daytime, solid circles are for nighttime.

distributed below 150 m depth except for *N. japonicus* (Loeb, 1979; Miya, 1995; Sassa et al., 2004a; Sassa and Kawaguchi, 2006), increase in their abundance in the 0–150-m layer at night may not be due to their diel vertical migration between meso- and epipelagic zone. The Lampanyctinae myctophid *N. japonicus* is endemic to the western North Pacific and its larvae mostly occur in the Kuroshio region off southern Japan during the winter (Willis et al., 1988; Sassa et al., 2004b). Vertical distributions of the ba-

thylaguid *L. ochotensis* and the gonostomatid *S. gracilis* were reported for large larvae larger than 15 mm (Miya, 1995; Sassa and Kawaguchi, 2006). Large larvae of these species (>15 mm) are mainly distributed in the 200–1000-m layers, and small larvae of these species (<15 mm) are not captured below 200 m depth (Miya, 1995; Sassa and Kawaguchi, 2006), suggesting ontogenetic vertical migrations from epipelagic to mesopelagic zone.

Amongst the myctophids, larvae of the subfamily Myctophinae were generally distributed deeper than those of the Lampanyctinae in areas where thermal stratification occurred at depths shallower than 100 m (Loeb, 1979; Moser and Smith, 1993; Sassa et al., 2002, 2004a). In summer, Kuroshio waters are stratified in the epipelagic zone, and the larvae of Myctophinae, including *M. asperum*, were distributed primarily in the 50–100-m layer (21–25°C); larvae of Lampanyctinae, including *Diaphus* slender type, were in the 20–30-m layer (25–26°C), showing clear vertical segregation of habitats (Sassa et al., 2002). In contrast, the present result showed that the winter vertical distributions of Myctophinae and Lampanyctinae larvae largely overlapped in the 35–75-m layer in daytime and nighttime. In the Kuroshio region in winter, vertical kinematic viscosity in the mixed layer above ca. 80-m depth is estimated to be 10–1000 $\text{cm}^2 \text{s}^{-1}$ (Tanaka, 1992; Tanaka and Franks, 2008). This likely indicates that co-occurrence of Myctophinae and Lampanyctinae larvae in this study resulted from vertical mixing. However, the main distribution depths of Myctophinae and Lampanyctinae larvae exceed 20 m in both winter and summer (Sassa et al., 2002, present study). Considering that vertical visibility below the sea surface is generally 20–30 m year-round in the Kuroshio waters (Hakodate Marine Observatory, <http://www.hakodate-jma.go.jp/>), light conditions may affect the upper limit of main distribution depths of these larvae. This suggests that vertical distributions of these larvae are not simply the result of passive transport in turbulent water, but rather a partially active choice of depth by species.

The present result showed that body sizes of all mesopelagic fish larvae were significantly larger in the thermocline than in the mixed layer. Similar vertical distribution patterns of mesopelagic fish larvae also occur in various regions of major oceans (Clarke, 1973; Badcock and Marrett, 1976; Loeb, 1979; Badcock and Araujo, 1988; Miya, 1995). Such migrations would be adaptive for the vulnerable larval stage because densities of their potential predators (e.g., small epipelagic fishes) generally decrease with depth, and physical conditions below the mixed layer are stable. This form of ontogenetic vertical migration may be also closely related to vertical difference in prey environments between the mixed layer and thermocline. Knowledge on vertical distribution of prey species and prey size

spectrum, and relationship between size of consumed prey and larval size is badly needed to estimate adaptive meaning of their ontogenetic migration.

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冬季の黒潮流域における中層性魚類仔魚の鉛直分布

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冬季の黒潮流域で優占する中層性魚類仔魚5種の鉛直分布を明らかにした。各種とも鉛直分布パターンに昼夜差はみられなかった。*Diaphus slender type*は25–80 m層、オオクチイワシは30–75 m層、アラハダカは35–80 m層を中心に分布しており、これらの仔魚の分布は表層混合層内(0–80 m層)で大きく重なっていた。ソコイワシとヨコエソはそれぞれ表層混合層から水温躍層にかけての30–100 m層、55–100 m層に分布中心があり、混合層内で他の3種と

分布が重複していた。表層が成層している夏季には中層性魚類仔魚の分布水深が種間で異なるという既存の知見を考慮すれば、冬季におけるこれらの仔魚の鉛直分布の重複は、80 m以浅の表層水温の成層構造の崩壊と密接に関連していると考えられる。また各種の仔魚の水温躍層内の体長は混合層内のそれに比べて有意に大きく、成長に伴う中層への移動が示唆された。

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