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RESEARCH ARTICLE

Diel Vertical Distribution Patterns of Pelagic Fish Larvae in Yilan Bay, Taiwan

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Abstract

To study the diel migration distribution of larval fish in an area adjacent to the Kuroshio Current, samples were collected from six depths by using a Motoda horizontal net at a fixed station in Yilan Bay on July 30 and 31, 2007. A total of 591 larval fish were collected and assigned to at least 34 families and 57 species. The first five dominant species were *Benthosama pterotum* (40.95%), *Diaphus* B type (12.18%), Callionymidae spp. (8.46%), Gobiidae spp. (6.60%), and Apogonidae spp. (4.0%). The density of larval fish varied across time. The maximum larval density was 1220.34 individuals/1000 m^3 at 19:00, and the minimum larval density was 81.84 ind./1000 m^3 at 14:00. The vertical distribution of species accounting for more than 10% of all fish caught was determined by the diurnal and nocturnal migration of the dominant species *B. pterotum*, which migrated from a depth of 50 m at night to 200 m in the afternoon. The distribution models for other species (e.g., *Diaphus* B type) were also analyzed in this study.

Keywords: Vertical distribution, Diel migration, *Benthosema pterotum*

1. Introduction

"Larval fish" is a general term for fish stages between the hatching and free-swimming stages [1]. Fish in this stage cannot sufficiently move by themselves [2]. Because their fins and inner structures are not yet developed, they cannot respond to environmental changes and avoid enemies [2,3]. Therefore, the distribution of fish larvae can be easily affected by environmental factors such as fronts [4,5], tides and currents [6], winds [8,9], water depth [2,10], bottom features [11,12], the amount of aquatic plants [13], spawning area and time [11], and differences between species and life stages [2].

Some fish species have diel migration patterns in estuaries [14]. Diel migratory behavior of fish can be caused by the stratified structure of water or can be spontaneous [15−17]. Vertical distribution and migration model variation have been observed among individuals [18−20]. Fish larvae lack the ability to swim [3]; thus, they live among planktonic organisms. Therefore, the discovery of diel vertical migration among larval fish is particularly meaningful for understanding fish behavior and ecology [21,22]. Furthermore, information on the vertical distribution of larval fish is crucial for studying the relationship among biology, transportation in current systems, and species survival rates [23]. According to [23]; fish larvae species in the subfamilies of Lampanyctinae and Myctophinae (family of Myctophidae) inhabit different water depths to avoid cannibalism. Moreover, the depth where fish larvae live determines the current routes and distances they are carried over [24,25], which affect resource recruitment in fisheries. Therefore, understanding diel distribution for fish larvae studies

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is important. However, the diel distribution of larval fish in the Kuroshio Current area has not been widely studied. Thus, this study focused on the diel density, species composition, and growth stage differences of larval fish and oceanographic environmental factors (temperature and salinity) to understand their relationships.

2. Materials and methods

This study was conducted from July 30 to 31, 2007, at one fixed station (121°57′E, 24°48′N) in Yilan Bay, Taiwan (Fig. 1) on the research vessel *Ocean Researcher II*. To analyze the diel vertical distribution of larval fish across time, the Motoda horizontal net (MTD net; mouth diameter of 0.6 m and mesh size of 330 μm [26]; was used to collect fish larvae from six depths (multilayered simultaneous tows): 5, 50, 100, 150, 200, and 250 m. Tows began at 19:00 (July 30), followed by towing at 01:00 (July 31), 07:00 (July 31), 14:00 (July 31), and 19:00 (July 31). A flowmeter (model 438 115, HYDRO-BIOS, Kiel-Holtenau, Germany) was attached to the center of each net mouth to calculate the volume of filtered water. The volume of filtered water (V) was calculated using the following formula:

$$L = N \times RC$$

$$V = \frac{\pi \times D^2 \times L}{4}$$

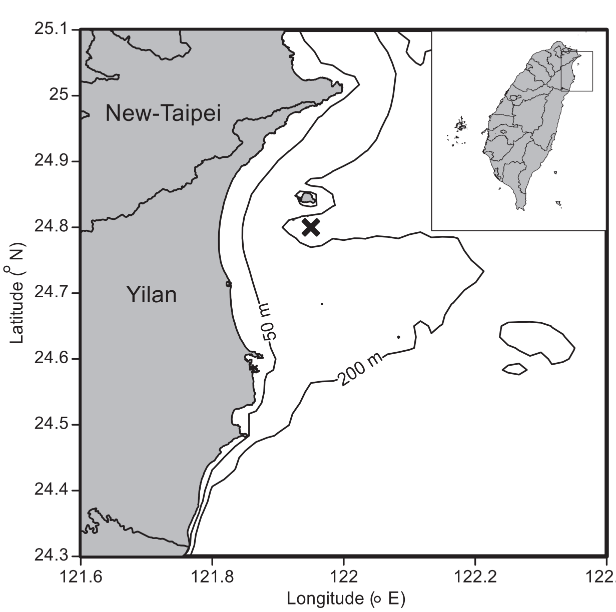

Fig. 1. Location of the study area and sampling site (X) in Yilan Bay, Taiwan.

where *L* is the net towing distance (m), *N* is the number of revolutions, *RC* is the pitch of the impeller at 0.3, π is the ratio of the circumference of a circle to its diameter, and *D* is the diameter of the net mouth.

The MTD net is a type of vertical multiple closing plankton sampler [26]. It can sample at a desired depth, and the net mouth can be closed using a plumb to prevent contaminated materials from upper zones from entering into the net. However, the MTD net still had a slight contamination problem during sampling in the first few minutes of towing; thus, we attempted to maintain an oblique wire angle (close to 45°) to reduce the depth error [23]. After towing horizontally for 30 min at a speed of 1 kn, a signal hammer was dispatched to close the net mouth to avoid catching fish in other layers while retrieving the net. An advantage of the MTD net is simultaneous multilayer sampling, which can help us analyze the diel vertical movement of fish larvae simultaneously. Specimens were immediately stored in 5% formalin and brought to the laboratory for identification. Larval fish were selected from the total samples and identified to the species level or lowest possible taxonomic level in the laboratory in accordance with [27] descriptions. *Diaphus* of the slender and stubby type belonged to *Diaphus* A and B types in this study, respectably. Postanal melanophores and body length were identifying features. More than two fish in a family or genus were identified as many species (spp.). Damaged fish that were difficult to identify were treated as unknown species and were not included in the analysis. Four larval developmental stages were identified: preflexion larvae (pr), flexion larvae (fl), postflexion larvae (po), and juvenile (Ju; [3]. The body lengths of larval fish were measured to the nearest 0.01 mm by using the CCD Vision Image Hunter System. Notochord length was measured for preflexion-stage larvae, and the standard length was measured for flexion- and postflexion-stage larvae.

A conductivity–temperature–depth profiler (SBE 9/11, Sea-Bird Electronics Inc., Bellevue, WA, USA) was cast from the *Ocean Researcher II* during each sampling period to collect temperature and salinity information from the surface to a depth of approximately 250 m. All collected data were transformed into figures based on time, temperature, and depth by using SBE Data Processing (v7.22.1, Sea-Bird Electronics Inc.). These environmental data were displayed using Surfer 9 (Golden Software Inc., Golden, CO, USA).

The collected data were used to calculate the density of larval fish, Shannon–Wiener diversity index (H′; [28], and Pielou's evenness index (J′; [29].

Fish larval density is expressed as the number of individuals per 1000 m^3 (ind./1000 m^3). The Shannon–Wiener diversity index was used to understand the population variation of larval fish at different time points and water depths. Pielou's evenness index was used to calculate the similarity in the number of fish between species.

3. Results

3.1. Oceanographic condition

Oceanographic condition sampling was conducted five times during the research period. From the surface to a depth of 250 m, temperature and salinity ranged from 12.95 °C to 29.63 °C and from 33.75 to 34.62 psu, respectively (Fig. 2). Thermocline and halocline locations varied over time. The thermocline location ranged between 50 and 100 m and was observed in shallower areas at dawn and in the morning and in deeper areas at night. The halocline location ranged from 30 to 100 m, and salinity approached stability at a depth of 100 m. In addition, temperature and salinity differences among the sampling time points were minor.

3.2. Larval density and composition

A total of 591 larvae representing 34 families and 57 species were collected over five sampling time points. The density of larval fish varied over time. The maximum density was 1,220.34 ind./1000 m^3

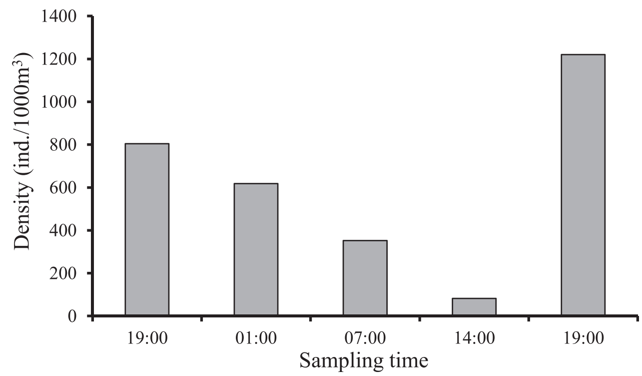

Fig. 3. Total density of fish larva at each sampling time.

(collected at 19:00 on July 31), and the minimum density was 81.84 ind./1000 m^3 (collected at 14:00 on July 31; Fig. 3). Moreover, larval density did not change with variations in thermocline and halocline locations (Fig. 4). Larval fish assembled above the thermocline and halocline locations (50 m) at night but moved below them (100 m) in the morning. In the afternoon, the abundance of larval fish formed two peaks (50 m and 200 m).

In this study, the first five dominant species/families were *Benthosema pterotum*, *Diaphus* B type, Callionymidae spp., Gobiidae spp., and Apogonidae spp., which accounted for 40.95%, 12.18%, 8.46%, 6.60%, and 4.0% of the total catch, respectively. The diversity index ranged from 1.79 to 2.52. The most diverse sample was collected at 19:00 on July 30, and the least diverse sample was collected at 14:00 on

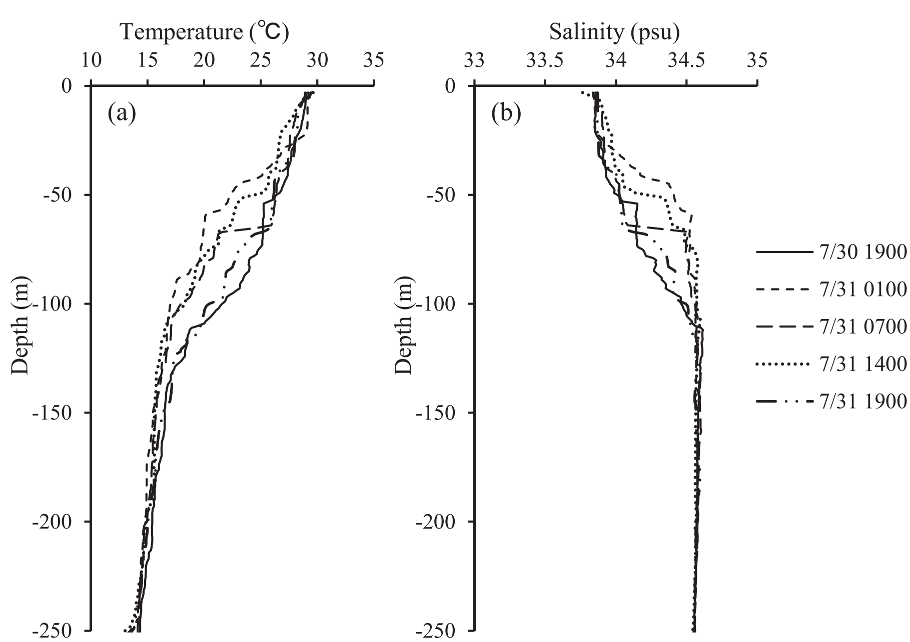

Fig. 2. Vertical structure of (a) temperature (°C) and (b) salinity (psu) at each sampling time.

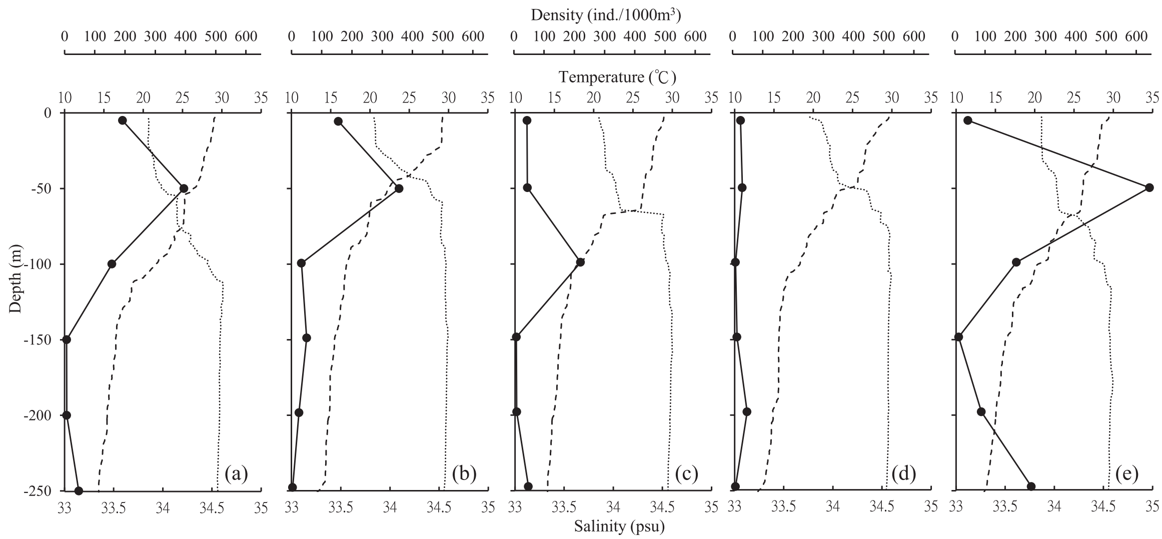

Fig. 4. Vertical distribution and density of larval fish (solid lines) in relation to vertical temperature (°C, dotted lines) and salinity (psu, dashed lines) profiles in Yilan Bay: (a) 19:00 on July 30, (b) 01:00 on July 31, (c) 07:00 on July 31, (d) 14:00 on July 31, and (e) 19:00 on July 31.

July 31. Moreover, the evenness index was between 1.44 and 1.90 and was the highest at 07:00 on July 31. It was lowest at 01:00 on July 31.

3.3. Vertical distribution of fish

Regarding vertical distribution (Fig. 4), most larval fish inhabited water depths between the surface and 100 m. At night, the following high fish density was observed at a depth of 50 m: 394.78 ind./1000 m^3 at 19:00 on July 30, 354.96 ind./1000 m^3 at 01:00 on July 31, and 640.00 ind./1000 m^3 at 19:00 on July 31. At 07:00, larval fish moved to depths between 50 and 150 m, and the maximum density observed at 100 m was 216.89 ind./1000 m^3 (July 31). At 14:00 on July 31, the density of larval fish at a depth of 50 m decreased rapidly to <40 ind./1000 m^3. As illustrated in Fig. 4, another density peak formed at 200 m and was greater than that at 50 m at the same time. Furthermore, the characteristics of the vertical distribution of larval fish at 19:00 on July 31 were identical to those at 19:00 on July 30.

The vertical distribution of species accounting for more than 10% of all fish caught was analyzed. Two distribution models were developed for assessing the vertical distribution of larval fish: a vertical migration model (e.g., *B. pterotum*) and a stable model (e.g., *Diaphus* B type). As detailed in Fig. 5a, a high density of *B. pterotum* individuals moved from a depth of 50 m at night (19:00 and 01:00) to a depth of 100 m in the morning (07:00) and 200 m in the afternoon (14:00). This phenomenon comprised the vertical migration model. Regarding temperature and salinity, *B. pterotum* could cross the thermocline. As detailed in Fig. 5b, *Diaphus* B type individuals were distributed at depths of 50–100 m regardless of time. Therefore, their distribution may be nonmigration. The body lengths of *B. pterotum* were measured at each sampling time (Fig. 6). The most common length was <4 mm; however, fish longer than 8 mm accounted for more than 60% of the sample and became the most abundant at 14:00.

4. Discussion and conclusions

4.1. Oceanographic condition

According to the vertical distribution model by [30]; the temperature of the Kuroshio Current in Taiwan's eastern region is the highest at the surface and decreases with depth to 500 m, after which the temperature remains stable. Maximum salinity and minimum salinity were observed at depths of approximately 200 and 500 m, respectively. Because the sampling station for this study was in Yilan Bay, which is near the Kuroshio Current, the oceanographic structure should be similar to that of the Kuroshio Current. However, because of the effects of fresh water, the oceanographic properties in Yilan Bay differed slightly from those in the Kuroshio Current. Nevertheless, this study revealed that temperature and salinity were stable at the study site, and the effect of fresh water was negligible. Differences were observed in the depths and slope of the thermocline and halocline.

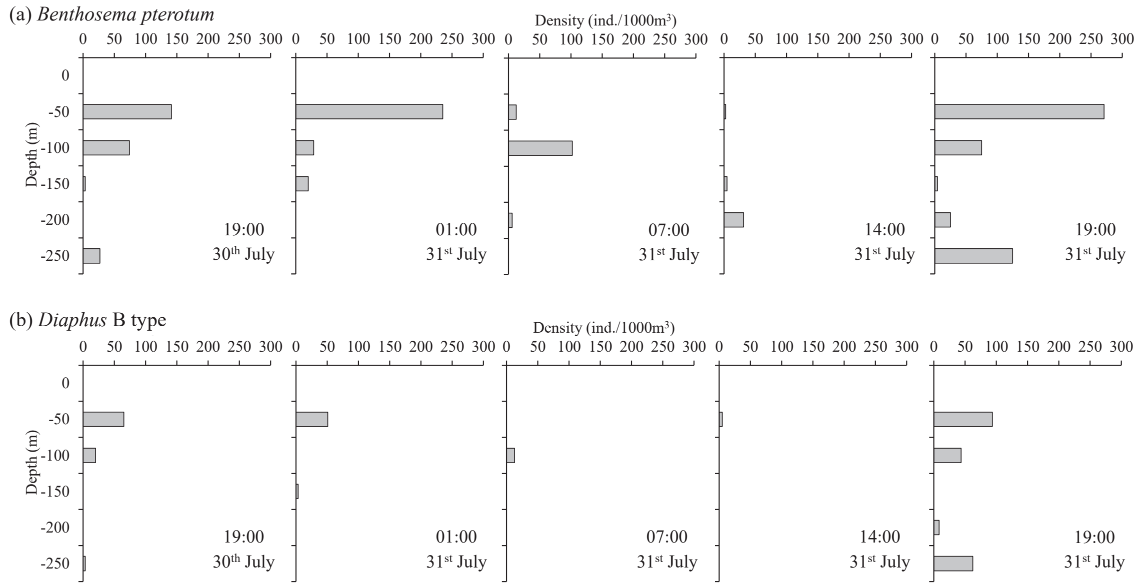

Fig. 5. Vertical distribution and density (individuals/1000 m^3) of (a) Benthosema pterotum and (b) Diaphus B type at each sampling time.

4.2. Species composition and diel vertical distribution

The species composition in the Kuroshio Current is simpler than that in coastal areas [15]. Myctophidae, Gonostomatidae, and Phosichthyidae are the most dominant families, and other species are less prevalent [15,23,31−34]. In this study, *B. pterotum* and *Diaphus* B type of the Myctophidae family accounted for 53.13% of all specimens. The remaining 46.87% was represented by 33 other families and 55 taxa. Therefore, the study site was considerably affected by the Kuroshio Current.

Regarding variation in larval fish abundance, a general cycle of high density at night, declining density at dawn and in the morning, and low density in the afternoon was observed. This was similar

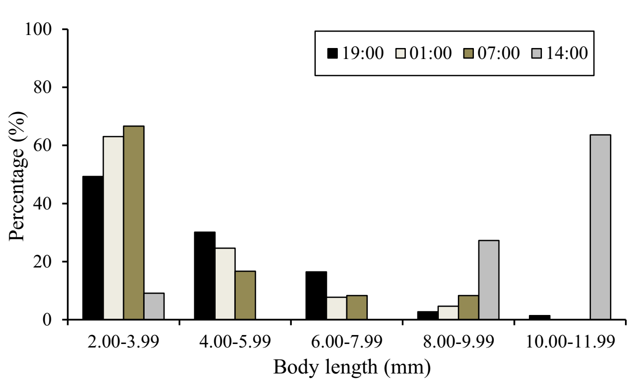

Fig. 6. Body length of Benthosema pterotum at each sampling time.

to previous findings in which larval fish were more numerous at night than during the day [15]. Therefore [15], conjectured that this phenomenon is related to the diel migration of pelagic ichthyoplankton. The density of larval fish is affected by water movement [35]. However, the present study suggested that the density variation of larval fish in Yilan Bay was caused by the diel vertical migration of *B. pterotum* [36]. used the hydroacoustic method (38-kHz scientific echo sounding system) to observe the movement of the deep scattering layer (DSL) in Yilan Bay (the bottom depth was approximately 350 m). The results indicated that the DSL descended before sunrise (stayed at 180 to 280-m depth in the daytime) and ascended before sunset (stayed at 10 to 150-m depth in the nighttime). Lee et al. [37] reported on the diel variations of the sound scattering layer by using a scientific echo sounder in northeastern Taiwan (the bottom depth was approximately 800 m). The DSL was observed at 10−120-m depth at nighttime and remained in the deep layer (400−500-m and 600−700-m depths) during the daytime. Kao et al. [38] found two DSLs during the daytime at depths of 80−130 and 130−230 m, and the DSLs remained at a depth of 10−80 m at nighttime in Yilan Bay (the average bottom depth was approximately 300 m). Furthermore, the depth of both DSLs may be influenced by changes in water temperature. *Benthosema pterotum* is a part of the DSL and migration, along with other fauna [39]. DSL movement may be in response to the diel vertical migration of *B. pterotum* given the high density at night in the surface water and in the daytime in deep water.

We discovered a variation of density between two samplings at 19:00 on July 30 and 31, but no significant difference was found in the species composition. After further analysis, the major density variated were from *B. pterotum*, *Diaphus* B type, and some coastal species (such as Callionymidae spp., Engraulidae spp., and Scombridae spp.) between the two samplings. The density of *B. pterotum* and *Diaphus* B type was higher on July 31 than on July 30, particularly at depths of 50 m and 200–250 m. The density of other species was higher on July 31 than on July 30 at a depth of 50-100 m. Smith and Suthers [40] reported that the highest larval density was associated with the interface between the mixed layer and the thermocline. The interface between the mixed layer and the thermocline may represent a region of optimum growth and feed for larval fish, with maximum chlorophyll concentrations. Furthermore, the location of the thermocline or halocline appears to regulate the vertical distribution of ichthyoplankton in coastal and oceanic waters [41,42]. In our study, the locations of the thermocline and halocline were slightly shallower on July 31 than on July 30. This indicated that shallower locations of the thermocline and halocline may concentrate larvae in the surface water for easy collection. Therefore, we sampled more on July 31 than on July 30. However, we still require additional information for further investigation of the distribution of the deepwater layer (more than 300 m or more samplings layers between 0 and 100 m) in larvae and the possible influence of hydrographic conditions in Yilan Bay to explain this phenomenon.

Auth and Brodeur [43] reported that most larval fish inhabit water shallower than 100 m, and their maximum density is at 50 m of depth [44]. In this study, most larval fish resided in water shallower than 100 m, and the highest density was observed at 50 m. These findings are consistent with those of [43]. Because MTD nets are difficult to operate when sampling in the ocean, few studies on the vertical distribution of larval fish have been conducted. Sassa and Konishi [45] investigated a vertical distribution model for *Trachurus japonicus* larvae in the southern part of the East China Sea by using the MTD net. There was no evidence of either diel vertical migration for the fish larvae of *T. japonicus*. However, many other species exhibit diel vertical migration behavior in the larval stage [45]. Such behavior may be exhibited by larvae by themselves or caused by natural conditions such as lighting, temperature, and food sources [14,45].

Most lanternfish migrate extensively from mesoplagic depths to shallower waters at night, and some even reach the surface [17,46]. The reported habitat depth of *B. pterotum* adults is 130–500 m during the day, and it ranges from the surface to a depth of approximately 300 m at night [47–49]. However, these results are for fish in the juvenile to adult stage and not for larval fish. Wang and Lee [50] indicated that salinity, temperature, zooplankton biomass, and chlorophyll concentration affect *B. pterotum* larval horizontal distribution on the continental shelf of the southern East China Sea in the summer. This species moves to water with low temperature and salinity as it gradually grows up. However, in this study, the density of larval fish varied for the dominant species, *B. pterotum*, and this study found that *B. pterotum* can move across the thermocline and halocline. Therefore, we suggested that the vertical migration of *B. pterotum* was the outcome of ontogenetic movement and was not related to temperature or salinity. Differences in distribution affected by the temperature and salinity may result from horizontal distribution and not vertical distribution. In addition, *B. pterotum* in all samples had a length of 2.18–11.56 mm in our study. Most myctophid species become adults at a length of 12–19 mm [51], which indicates that all samples were in the larval to juvenile stage in our study. Wang and Lee [50] suggested that the density of *B. pterotum* in juveniles does not significantly differ according to different sampling depths and between daytime and nighttime. This result suggested that the diel vertical migration of *B. pterotum* should commence in the juvenile stage. Willis and Pearcy [52] indicated that lanternfish larvae with a length of 30–40 mm can migrate 30 m upward at night. Our study results are similar to those of these studies, and lanternfish larvae with a length of 8 mm can migrate 200 m downward during the day.

Diaphus larvae belong to the Myctophidae family and may have diel vertical migration in the ocean. In previous studies, various vertical distribution patterns have been shown for *Diaphus* larvae, such as *D. theta* and *D. gigas*, which are migrants and show clear day–night habitat separation [53]. The habitat depths of the slender type of *Diaphus* do not differ between day and night, which indicates no vertical migration [17,54]. The day–night differences in the catches of *D. garmani* do not significantly indicate the possibility of diel vertical migration [17]. However, in our study, we perceived *Diaphus* B type individuals to be non-migrants distributed at depths of 50–100 m regardless of time. Similar results stating that this species is abundant in the upper layer (between 0 and 100 m) were reported by [17,23]. However, more than 10 *Diaphus* species may have belonged to *Diaphus* B type in this study because identifying this genus is difficult due to the presence of various postanal melanophores [55,56]. This may be a reason why *Diaphus* B type did not show clear day–night habitat separation. If we can identify more species in this genus in the future, a clear diel vertical distribution pattern may appear.

In summary, the results indicated that the environment in Yilan Bay was considerably affected by the Kuroshio Current. *Benthosema pterotum* and *Diaphus* B type in the Myctophidae family were determined to be dominant species. The density temporal variation of larval fish in Yilan Bay was caused by the diel vertical migration of *B. pterotum*. We suggested that the diel vertical migration of *B. pterotum* was the outcome of ontogenetic movement and was not related to temperature or salinity.

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