Journal of Marine Science and Technology

Volume 27 | Issue 5 Article 8

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We are grateful to the Fisheries Agency, Council of Agriculture, Executive Yuan for providing partial financial support and to the crew of the vessel Ocean Research II of National Taiwan Ocean University for the collecting samples and environment data. We would also like to thank Wallace Academic Editing for editing this manuscript.

DOI: 10.6119/JMST.201910_27(5).0008

COMPOSITION AND DISTRIBUTION OF FISH LARVAE SURROUNDING THE UPWELLING ZONE IN THE WATERS OF NORTHEASTERN TAIWAN IN SUMMER

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Key words: fish larvae, upwelling zone, northeastern Taiwan.

ABSTRACT

We investigated the species composition and distribution of fish larvae surrounding the upwelling zone in the waters of northeastern Taiwan in July 2011. The surface water had higher temperatures (25.7°C-28.3°C) and lower salinity (33.67-34.05 psu) than did lower water columns. A divergent trend was observed between temperature and salinity in the waters above 80 m. Moreover, we identified a cold-core eddy at the upwelling of the Kuroshio subsurface at waters approximately 60 m beneath the surface. In total, 1834 fish larvae were collected from eight stations; 85 taxa contributing to 60 families were identified. The abundance of fish larvae varied among stations. The five predominant larval taxa, which constituted 50% of the total fish larvae, were *Auxis* spp. (30.14%), Sciaenidae spp. (6.73%), *Decapterus* spp. (6.29%), *Champsodon* spp. (5.52%), and Gobiidae spp. (4.83%). Higher diversity and lower evenness index values were recorded in areas of high temperature and low salinity. Two larval fish assemblages, Mixed Coastal Group and Upwelling Group, were identified from a cluster analysis. Mixed Coastal Group exhibited higher density, higher temperature, and lower salinity than Upwelling Group did. Thus, in general, the density, spatial distribution, composition, and diversity of fish larvae differed, and the salinity at the 20-m layer exerted a more substantial effect on larval distribution in this study.

I. INTRODUCTION

Upwelling regions, which constitute a small proportion of the total ocean areas (approximately 0.1%), are among the most productive (Carr and Kearns, 2003; Hamaoka et al., 2014). Fish catches are abundant in these regions because of the high rates of production, supporting up to 50% of global fish catches (Lalli and Parsons, 1993). The waters of northeastern Taiwan are near the continental slope of the southern East China Sea where a topographically induced upwelling water exists. This upwelling zone forms when the Kuroshio Current reaches the southeastern area of the East China Sea and is blocked by the East China Sea shelf, providing year-round supplies of enriched nutrients to fish habitats and spawning grounds (Chern, 1989; Liu et al., 1992). An important commercial fishing ground is formed in this upwelling water (Chiu, 1991).

This upwelling region has seasonal variation (Liu et al., 1992). Cold upwelling water is easily observed and more intense in summer than in winter (Chang et al., 2009). Chao (1991) suggested that the Kuroshio Current is closer to the shelf break when it shifts seaward during the summer than in the winter. Wu et al. (2008) indicated that the upwelling zone strengthens and weakens during the respective seasons as the Kuroshio Current migrates seaward and shoreward, respectively. Gong et al. (1997) and Tang et al. (2000) reported that as the Kuroshio Current shifts shoreward in the winter, the center of the upwelling water also shifts shoreward. Therefore, the migration of the Kuroshio Current path may affect the upwelling area.

Most studies on the upwelling zone in the waters off northeastern Taiwan have investigated economic fish species, such as mackerel, jack mackerel, and hairtail. Wang et al. (2006) and Chen et al. (2010) have reported that larval composition, abundance, and distribution are influenced by the fish spawning season, the Kuroshio Current, and upwelling water in the waters off northeastern Taiwan. Lee et al. (2006) investigated the environmental factors associated with mackerel and scad spawning in the waters off northeastern Taiwan during spring (the spawning season for mackerel and scad) and summer. They reported that the distribution of mackerel and scad was related to the location of the cold eddy. Chen and Chiu (2003) noted that those waters serve as a crucial nursery ground for

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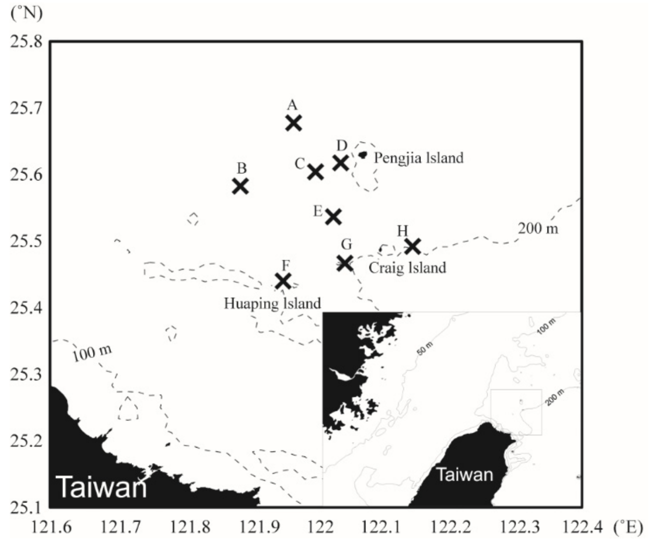

Fig. 1. Location of sampling stations (solid cross) in the upwelling zone off the northeastern coast of Taiwan.

late anchovy larvae. Such high primary productivity has rendered this area one of the most important fishing grounds in Taiwan (Chiu, 1991).

The association of fish to the upwelling zone varies with the progression of seasons, but specific information regarding the effect of upwelling water on fish assemblage is unclear. Adult fish spawning, larval behavior, oceanographic features, and food availability all affect the distribution of fish larvae, which possess weak swimming abilities (Sabates, 1990; Gray and Miskiewicz, 2000; Lo et al., 2010). The survival of fish larvae is a critical factor for fish management (Houde, 2008). Gaining an overall understanding of fish larvae density, assemblage, and diversity is essential. Because summer is the peak season for fish spawning and economic fishing in the northeastern waters of Taiwan, we investigated the fish larval composition and distribution surrounding the upwelling region by using Ocean Research Institute (ORI) nets onboard the R/V Ocean Researcher 2 in July 2011. The results reveal the effects of environmental factors on larval assemblage.

II. MATERIALS AND METHODS

In this study, biological samples were collected using ORI nets, with a mouth diameter of 1.6 m and mesh size of 330 μm, at eight sampling stations from July 11 to 13, 2011 (Fig. 1) in the waters surrounding The Three Northern Islands, Taiwan. At the front center of the net mouth was a flowmeter, which was used to estimate the volume of filtered water. All samples were collected from 5 m above the sea bottom at each station and were fixed onboard in 90% alcohol pending laboratory analysis. At each station, hydrological environmental data, including temperature and salinity data, were obtained using a conductivity–temperature–depth instrument (CTD) from the surface to a depth of 200 m. At the laboratory, all fish were sorted and identified at the level of species or the lowest possible taxon (Okiyama, 1988). Larval fish were named according to different morphological types on the basis of their pigmentation when they were identified as being in a certain genus or family. In our study, most larvae belonging to the same genus (or family) also belonged to the same species because of the shared melanophore pattern, but we still used "spp." to name these species. Larvae were identified for five developmental stages, namely yolk-sac larvae, preflexion larvae, flexion larvae, postflexion larvae, and juvenile stages (Leis and Rennis, 1983; Kendall et al., 1984). Yolk-sac larvae that were unidentifiable in early life stages were classified as unknown. The densities of fish larvae and zooplankton were expressed as the number of individuals per 1000 m^3 (ind./1000 m^3) and per 1 m^3 (ind./ m^3), respectively. Biodiversity was evaluated using the Shannon-Wiener index of species diversity (H') (Shannon and Weaver, 1963) and Pielou's index of evenness (J') (Omori and Ikeda, 1984). Cluster analysis with the Bray-Curtis similarity measure was used to determine similarity among stations and species. The density data were log(x + 1)-transformed for normalization before conducting analyses. The BEST-BIOENV analysis was employed to determine the Spearman's rank correlation (ρ) between the larval fish community (by Bray–Curtis similarity) and environmental factor matrices (by Euclidean distance). The 10 environmental factors were related to temperature (10, 20, 40, and 60 m), salinity (10, 20, 40, and 60 m), mean chlorophyll *a* concentration (from 5 to 10 m), and zooplankton density. All analyses were performed using Primer-E6. For temperature and salinity analysis, the profile of each layer distribution was formed using Surfer 9 (Golden Software Inc., Golden, C.O., USA).

III. RESULTS

1. Water Column Structure

In summer, the surface water (5 m) temperature was high (25.31°C-28.29°C) and salinity was low [33.67-34.05 practical salinity units (psu)] in the study area (Fig. 2). An opposite trend was observed between temperature and salinity in the water above 80 m. The water column had a clear structure, water temperature decreased, and salinity increased southeastward in the water below 100 m. A cold (< 17°C) and salty (> 34.5 psu) eddy formed over the region near stations G and H at the water layer 40-60 m from the surface.

2. Fish Density and Composition

The ORI net collected 1834 fish larvae, of which 60 families and 85 species were identified. Yolk-sac larvae constituted 9.6% of all larval fish collected. The density of larval fish at each station varied from 402.01 to 1544.57 ind./1000 m^3 (Fig. 3(a)). The areas with peak abundances of larval fish did not correspond with the areas with a high abundance of zooplankton (Fig. 3(b)). Fish larval density was the highest at station C and lowest at station F.

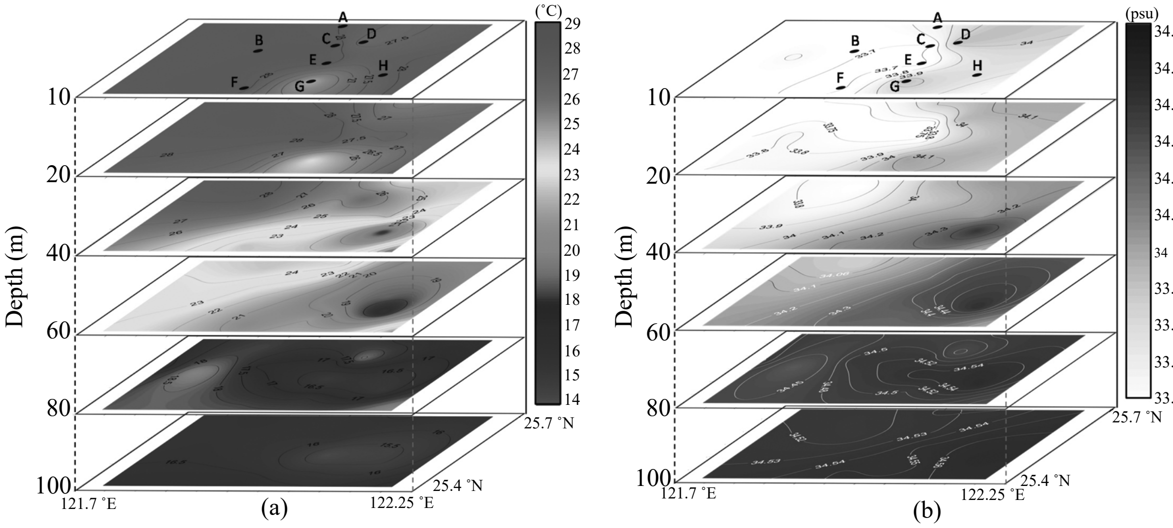

Fig. 2. Three-dimensional structure of temperature (°C) (a) and salinity (psu) (b) between depths of 10 and 100 m in the study area.

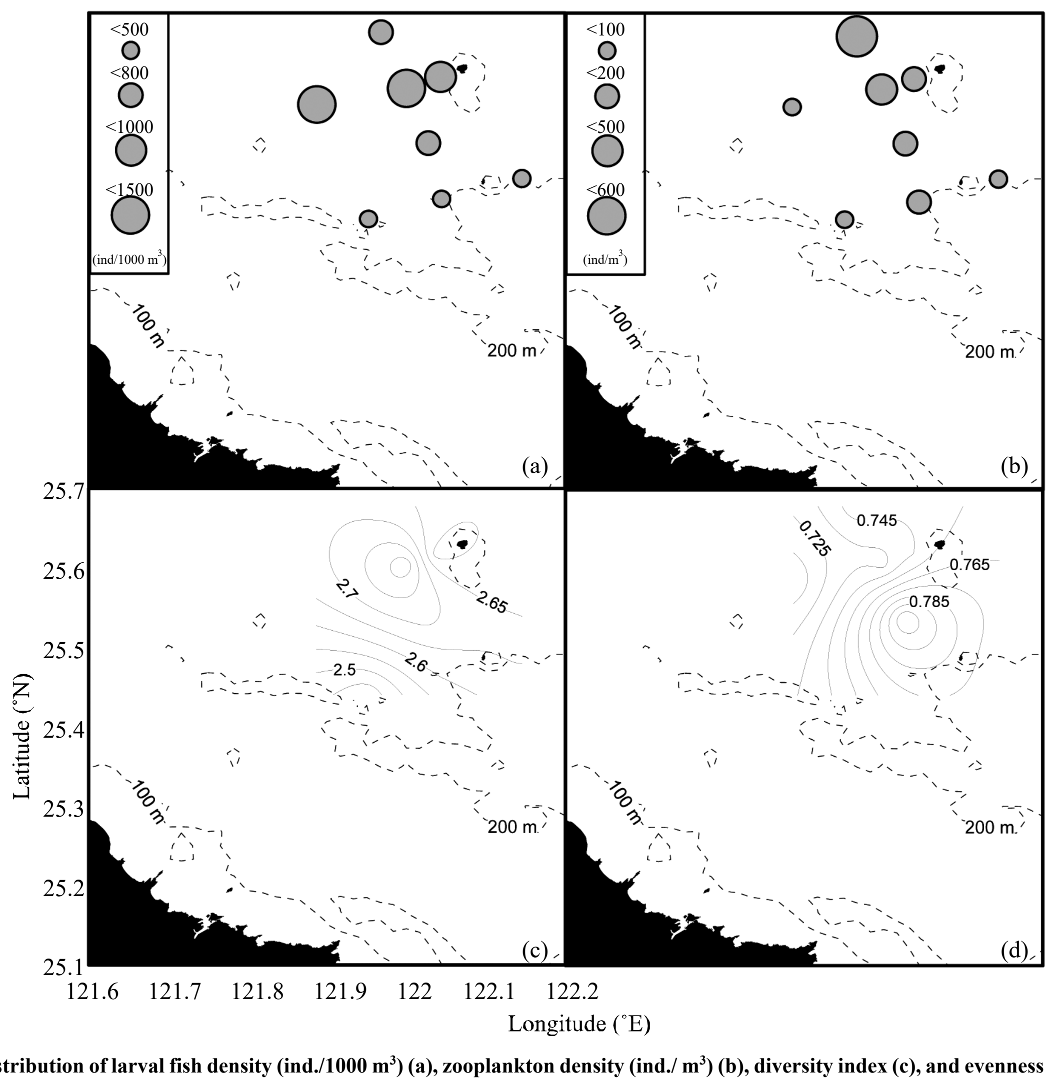

Fig. 3. Spatial distribution of larval fish density (ind./1000 m^3) (a), zooplankton density (ind./ m^3) (b), diversity index (c), and evenness index (d) of larval fish in the study area.

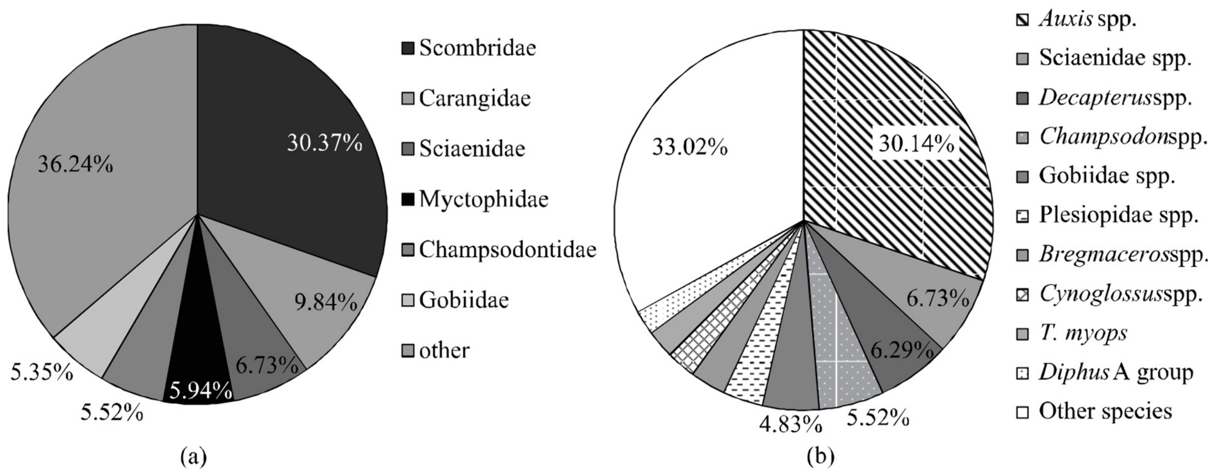

Fig. 4. Composition of larval fishes at family (a) and species (b) levels in this study.

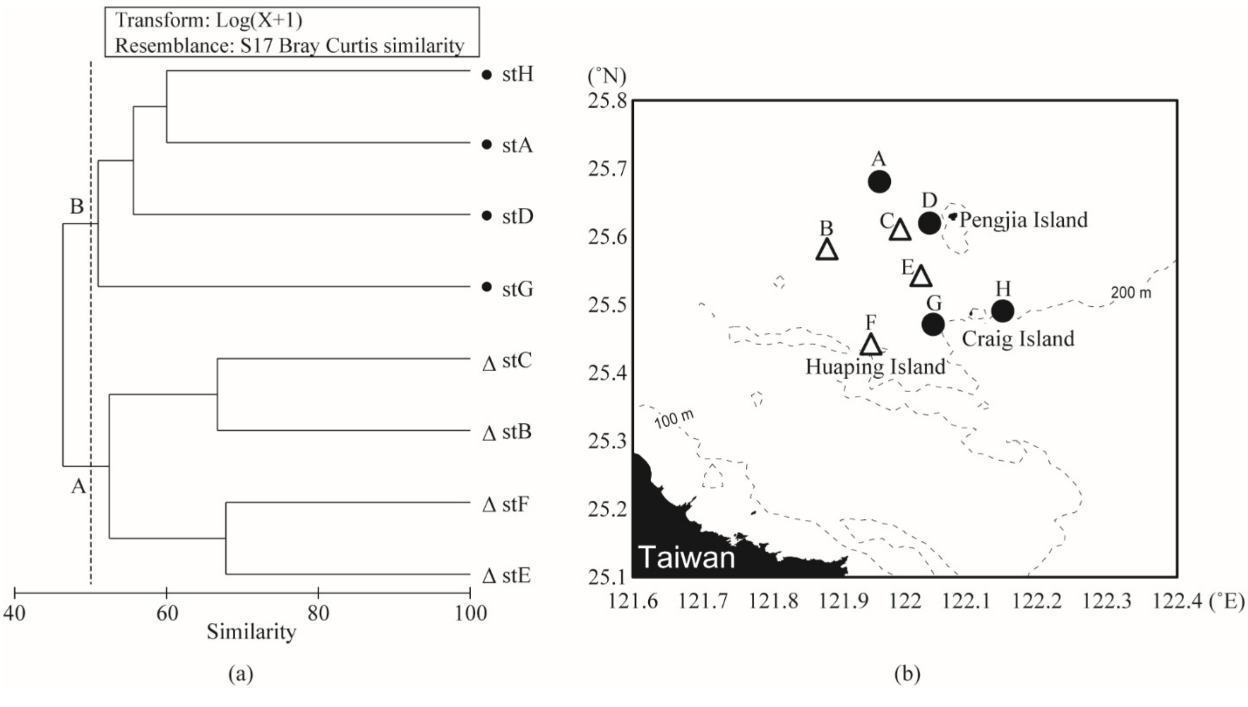

Fig. 5. Summary of the cluster analysis results (a) and the distribution of larval fish assemblages (b) for each station from July 11 to 13, 2011. Hollow triangles and solid circles represent Mixed Coastal Group (A) and Upwelling Group (B), respectively.

In terms of families, Scombridae was the most abundant, constituting 30.37% of all fish larvae from all stations, followed by Carangidae (9.84%), Sciaenidae (6.73%), Myctophidae (5.94%), Champsodontidae (5.52%), and Gobiidae (5.35%; Fig. 4(a). The five predominant taxa of larvae, constituting 50% of the total fish larvae, were *Auxis* spp. (30.14%), Sciaenidae spp. (6.73%), *Decapterus* spp. (6.29%), *Champsodon* spp. (5.52%), and Gobiidae spp. (4.83%; Fig. 4(b)).

The diversity and evenness index of larval fish at sampling stations are featured in Figs. 3(a) and 3(b), respectively. Higher diversities were recorded at stations B and C, which were characterized by high temperature and low salinity. The evenness index exhibited an opposite trend to that of the diversity index. Higher levels of evenness were observed at stations E, G, and H, which had low temperatures and high salinity.

3. Fish Assemblage Structure in Relation to Environmental Factors

The cluster analysis and geographic locations of sampling stations are presented in Fig. 5. All sampling stations were divided into two groups. According to the geolocation of station, the defined two groups are further referred to as the Mixed Coastal Group (A), and Upwelling Group (B). Mixed Coastal Group comprised stations B, C, E, and F, which were

Table 1. Density (ind./1000 m^3) and percentage of dominant larval fish species in Mixed Coastal Group and Upwelling Group according to cluster analysis results

Mixed Coastal Group			Upwelling Group		
Species	Density (ind/1000 m^3)	%	Species	Density (ind/1000 m^3)	%
Auxis spp.	1203.52	32.45	*Auxis* spp.	605.80	26.39
Sciaenidae spp.	384.28	10.36	*Champsodon* spp.	269.73	11.75
Decapterus spp.	342.87	9.25	Plesiopidae spp.	206.12	8.98
Gobiidae spp.	157.88	4.26	Gobiidae spp.	132.12	5.76
Cynoglossus spp.	146.31	3.95	Mullidae spp.	94.71	4.13
Trachinocephalus myops	120.22	3.24	Creediidae spp.	81.32	3.54
Bregmaceros spp.	116.40	3.14	Diodontidae spp.	80.45	3.50
Leiognathidae spp.	88.95	2.40	*Diphus* B group	80.24	3.50
Carangidae spp.	79.78	2.15	*Synagrops* spp.	75.58	3.29
Other species (<1%, 58 species)	1068.09	28.8	*Diphus* A group	70.67	3.08
Total	3708.3	100	*Bregmaceros* spp.	65.11	2.84
			Other species (<1%, 52 species)	533.69	23.25
			Total	2295.55	100

Table 2. Spearman's rank correlations (ρ) between larvae and environmental factor resemblance matrices according to BEST-BIOENV analysis results

Number of variables	Best Variable combinations	Correlation (ρ)
4	S_{10}, S_{20}, S_{60}	0.733
3	S_{10}, S_{20}, S_{40}, S_{60}	0.681
2	S_{10}, S_{20}, S_{40}	0.679
1	S_{20}	0.662

S, salinity; index number, water level.

characterized by high temperature, low salinity, and high larval density (3708.3 ind./1000 m^3). Upwelling Group consisted of stations A, D, G, and H, which were characterized by low temperature, high salinity, and low larval density (2295.55 ind./1000 m^3; Table 1). Mixed Coastal Group contained nine dominant species of larval fish (> 1%): *Auxis* spp., Sciaenidae spp., *Decapterus* spp., Gobiidae spp., *Cynoglossus* spp., *Trachinocephalus myops*, *Bregmaceros* spp., Leiognathidae spp., and Carangidae spp. Next, 11 dominant species of larval fish (> 1%) were found in Upwelling Group: *Auxis* spp., *Champsodon* spp., Plesiopidae spp., Gobiidae spp., Mullidae spp., Creediidae, Diodontidae spp., *Diaphus* B group, *Synagrops* spp., *Diaphus* A group, and *Bregmaceros* spp.

According to the results of a BEST-BIOENV analysis, salinity is a major factor affecting larval distribution (Table 2). A combination of factors associated with S_{10}, S_{20}, and S_{60} best explained the larval distribution, but S_{20} demonstrated the highest ρ value; in other words S_{20} is more influential factor than the other factors in larval distribution.

IV. DISCUSSION AND CONCLUSIONS

This study investigated the hydrographic environment and assemblages of fish larvae surrounding the upwelling zone in the waters of northeastern Taiwan during the summer. This study identified 60 families and 85 taxa of fish larvae. Higher density and diversity and a lower evenness index were noted at locations with high temperatures and low salinity, specifically at the boundary of a cold eddy (Fig. 2.). In general, upwelling areas are richer in nutrients (Franco et al., 2006), but have lower dissolved oxygen levels. Therefore, these areas are unconducive for larval fish survival. However, areas with higher dissolved oxygen due to the upwelling boundary areas provided a more favorable location for survival. Larval fish were more abundant in upwelling boundary areas than in the upwelling center zone. Similar results have been reported by Hsieh and Chiu (2002), Franco et al. (2006), Chen et al. (2010), and Wang et al. (2013). Moreover, lower abundance and species diversity have generally been observed in low-temperature areas (Okazaki and Nakata, 2007; Lo et al., 2010).

According to the cluster analysis results, all stations could be divided into two groups. Stations in Mixed Coastal Group had a higher larval density and temperature and lower salinity than those in Upwelling Group. According to the dominant species list of the two groups (Table 1), the most abundant species in the two groups was *Auxis* spp., but the density was higher in Mixed Coastal Group than in Upwelling Group. Density and distribution in northeastern Taiwan waters have yielded similar results. For instance, Huang and Chiu (1998) observed that *Auxis* spp. is the second most abundant taxon in the Kuroshio edge exchange area off northeastern Taiwan in summer, and Wang et al. (2006) and Chen et al. (2010) indicated that *Auxis* spp. is the most abundant taxon in the waters off northeastern Taiwan during summer. Similarly, we observed the highest density of this species in this study area. In addition, this species mostly inhabits waters with high temperatures and low salinity (Okazaki and Nakata, 2007; Chen et al., 2010; Lee et al., 2013). This is similar to our observation that such species were more abundant in Mixed Coastal Group than in Upwelling Group.

Sciaenidae spp. and *Decapterus* spp. were the second and third most dominant larvae in Mixed Coastal Group, respectively. Using morphological characteristics for identifying sciaenids is difficult because melanophore numbers and types are similar in all species of Sciaenidae. The same problem was also observed for carangids. We could identify only the family or genus of larval fish; nevertheless, this limitation did not affect the accuracy of our results. The abundance of sciaenid larvae during spring and summer was due to it being spawning season (Cowan and Birdsong, 1985; Griffiths, 1996). Moreover, sciaenids prefer to inhabit waters with low salinity. This is why their density was higher in Mixed Coastal Group than in Upwelling Group. *Decapterus* spp. spawning grounds are in the waters of northeastern Taiwan and spawning season is during the summer (Tzeng et al., 1997; Sassa and Konishi, 2006; Wang et al., 2006); therefore, a high density was observed in this study area. The densities of other species, such as *Cynoglossus* spp., *T. myops*, and Leiognathidae spp. have been reported to be positively associated with temperature and negatively associated with salinity (Lai et al., 2013; Lee et al., 2013), suggesting greater abundance in Mixed Coastal Group, which had warm and fresh water, than in Upwelling Group, which had cold and salty water.

Most gobiids were distributed in the estuary and coastal waters with low salinity (Hsieh et al., 2007; Chen et al., 2012; Zhang et al., 2015). Many studies have found *Bregmaceros* spp. larvae in shallow to deeper waters surrounding Taiwan, but more larvae were distributed in shallow waters than in deeper waters (Hsieh et al., 2007; Lo et al., 2010; Chen et al., 2012; Wang et al., 2013). In this study, Gobiidae spp. and *Bregmaceros* spp. were collected in Mixed Coastal Group and Upwelling Group. We speculated that these species were observed in both shallow and deeper waters because of current transport effect. Larger-scale studies that collect samples and evaluate the direction of currents are required to determine the distribution characteristics of these species.

Champsodon spp. was the second most dominant species in Upwelling Group, which were characterized by low temperatures and high salinity. The biological features of various *Champsodon* species are poorly understood because these are caught only in small amounts in nets and not through commercial fishing (Ganga et al., 2014). Shen and Cheng (2008) revealed that *Champsodon snyderi* is an oceanic and deep-sea fish. A relatively low temperature (17°C-23°C) and high salinity (34.3-35.2 psu) area is an optimal habitat for this species according to the GAM model. Chang et al. (2012) reported that *C. snyderi* demonstrated a positive correlation to bottom depth in the East China Sea. This result resembled ours: *Champsodon* spp. was abundant at stations H and G, where the bottom depths were deeper than at other stations in Upwelling Group. In addition, Xu et al. (2019) indicated that *C. snyderi* corresponded to greater salinity and that this species may be an indicator for the intrusion of the Kuroshio Current in the East China Sea. The subsurface Kuroshio water intrusion forming an upwelling affected Upwelling Group more than it did Mixed Coastal Group in this study. This may explain the high density of *Champsodon* spp. observed in this area.

The identified *Diaphus* A and B groups belong to Myctophidae, for which the postanal melanophores and body length are identifying features. More than 10 *Diaphus* species may have been present in our study (Wang and Chen 2001; Hsieh and Chiu 2002). *Diaphus* species were more abundant in the Kuroshio Current waters, and their distribution was affected by the Kuroshio Current (Sassa et al., 2002; Sassa et al., 2004; Lo et al., 2010; Wang et al., 2013). Some species of Myctophidae have been used as indicator species for the Kuroshio Current because they are found primarily in the Kuroshio and adjacent waters (Hsieh et al., 2010). Most *Diaphus* B groups (primarily *D. garmani* and *D. kuroshio*) are transported to the transitional region by the Kuroshio Current (Sassa et al., 2002). Muko et al. (2003) noted that the spawning ground of *D. theta* was related to the transitional waters between the Oyashio and Kuroshio fronts. Ohshimo et al. (2012) reported that *D. garmani*, *D. chrysorhynchus*, and *D. watasei* were widely distributed throughout the continental shelf and slope regions in the East China Sea, and the abundance was affected by the Kuroshio Current (Watanabe and Kawaguchi, 2003; Sassa et al., 2016). Upwelling Group is located at the cold eddy area formed by the subsurface Kuroshio Current water intruding into the southern East China Sea. Therefore, *Diaphus* spp. may have been transported to northeastern Taiwan by the Kuroshio Current.

Synagrops spp. is a small fish that lives between nearshore waters and the shelf break. In our study, *Synagrops* spp. was abundant at stations G and H, at the shelf break of the southern East China Sea. Okazaki and Nakata (2007) observed that the distribution of *Synagrops* spp. was associated with the eddy of Kuroshio. The offshore water intrusion may allow *Synagrops* spp. off-shelf transport, thus suggesting that they may be abundant in the Kuroshio Current. Chen et al. (2016) found the distributions of *Synagrops* spp. to be abundant in the salty waters of the East China Sea shelf and surrounding Taiwan. Xu et al. (2019) also suggested that the abundance of *Synagrops japonicus* in the Kuroshio and is an indicator of the intrusion by the Kuroshio Current. These studies have suggested that the distribution of *Synagrops* spp. is similar to that of mesopelagic fishes (such as myctophids and gonostomatids), which are abundant in the Kuroshio Current, as observed in our results.

Four families, namely Plesiopidae spp., Mullidae spp., Creediidae spp., and Diodontidae spp., were dominant in Upwelling Group. Each family contained more than five fish species, except Creediidae (which contained < 5 species), in the waters surrounding Taiwan. The varying results for the distributions of these fishes may be a result of their species not being identified. In addition, most relevant studies in Taiwan have used relatively small sample sized for these fishes (Hsieh et al., 2007; Chen et al., 2010, 2012). In the future, we could focus on fewer fishes but concentrate on those inhabiting the waters surrounding Taiwan to investigate their distribution, density, spawning season, and other biological parameters.

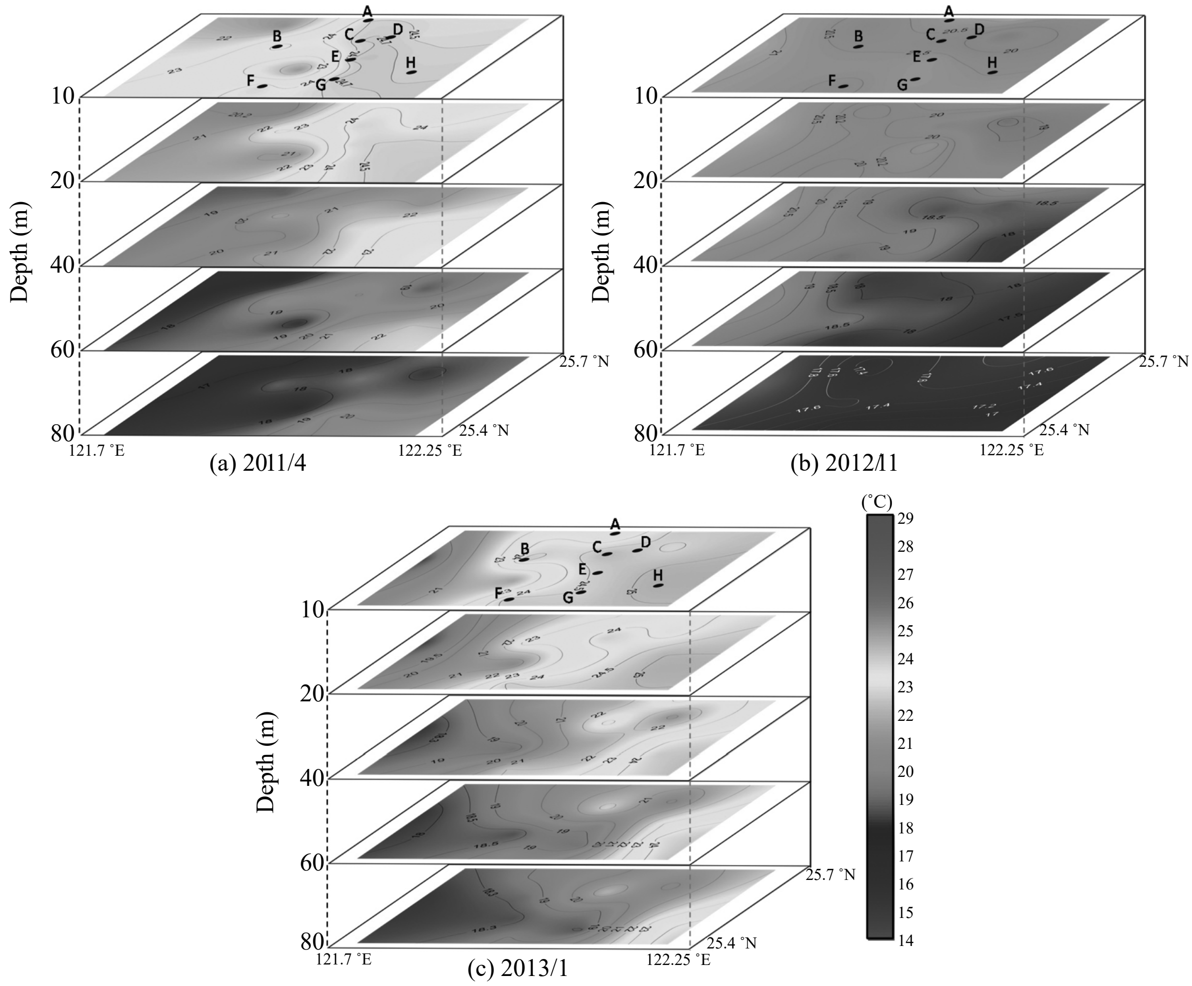

Fig. 6. Three-dimensional structure of temperature (°C) in April 2011 (a), November 2012 (b), and January 2013 (c) between depths of 10 and 80 m in the study area.

In our study, the salinity at the 20-m water layer was a major factor affecting larval distribution according to the BEST-BIOENV analysis. Studies have described salinity as an important influential factor in or indicator of fish larvae assemblage and distribution. Alemany et al. (2006) indicated that in the August survey, the patterns of horizontal distribution of fish larvae off the western Mediterranean were significantly correlated with the surface salinity gradient. Kimura et al. (2001) believed that salinity front displacement in the North Equatorial Current affected the spawning ground and larval transport of Japanese eel. In addition, most fish larvae were observed mainly in the surface mixed layer in the upper part of the thermocline, particularly between 10 and 40 m (Loeb, 1979; Olivar and Sabates, 1997; Smith and Suthers, 1999; Coombs et al., 2001). In addition, Chen (1992) observed that the vertical distribution of chlorophyll *a* was maximum between 0 and 25 m in the upwelling water. Therefore, the environmental variations between the 10-m and 40-m layers were more influential than variations between other layers. A clear salinity front occurred at the 20-m water layer, where the salinity change was more obvious than the temperature change in this study. We speculate that these are the reasons for why surface salinity affected larval distribution and assemblages.

In a comparison of the three-dimensional structure of temperature between depths of 10 and 80 m on the dates of the present study and others within the study area (Fig. 6), the location and depth of the upwelling waters were slightly different. In April and January, upwelling zones formed in the water layer that is 60 to 80 m from the surface. The upwelling zone in April was nearer to the shore than in January. In November, the upwelling formed in a more seaward area in the water layer that is 40 m from the surface. The results were similar to the reports of Chao (1991), Gong et al. (1997), Tang et al. (2000), and Chang et al. (2009). In addition, when the Kuroshio Current intrudes the waters of northeastern Taiwan, the Kuroshio Front occurs and moved into nearshore in winter (Chao, 1991; Wu et al., 2008; Wang et al., 2018). The intensity of upwelling waters changed over the variation of Kuroshio Front (Wu et al., 2008; Wang et al., 2018).The seasonal variation of upwelling is well known, but information regarding the effects of upwelling on fish assemblage remains unclear. The relationship between larval fish assemblages and seasonal variation of upwelling should be further investigated in the future.

In summary, the distribution of species differs among sampling areas; the density, diversity, and composition of fish larvae reflect the environmental features of the waters. The dominant species in summer are *Auxis* spp., Sciaenidae spp., and *Decapterus* spp. in the upwelling zone of northeastern Taiwan. The BEST-BIOENV analysis results also indicated that salinity at the 20 m layer is a major factor affecting larval distribution. This water layer exhibits a great change in salinity and may be the layer where most fish larvae were observed. In this study, the hydrographic environments of two fish assemblages were divergent according to the results of a cluster analysis and the vertical structure of temperature and salinity. Some species were observed in only one group. Some, such as scombrids, carangids, and gobiids, appeared in two groups. In addition, spawning area and season may be factors affecting larval density and distribution. However, more samples and evidence are required to confirm the relationship between fish larval distribution and hydrological environment.

ACKNOWLEDGMENTS

We are grateful to the Fisheries Agency, Council of Agriculture, Executive Yuan for providing partial financial support and to the crew of the vessel Ocean Research II of National Taiwan Ocean University for the collecting samples and environment data. We would also like to thank Wallace Academic Editing for editing this manuscript.

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