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Larval Fish Assemblages and Hydrographic Characteristics in the Coastal Waters of Southwestern Taiwan during Non- and Post-typhoon Summers

Hung-Yen Hsieh[1,2], Wen-Tseng Lo[3], Hsiao-Hao Chen[3], and Pei-Jie Meng[1,2,*]

[1]*Graduate Institute of Marine Biology, National Dong Hwa University, Pingtung 94450, Taiwan*
[2]*National Museum of Marine Biology and Aquarium, Pingtung 94450, Taiwan*
[3]*Institute of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung 80424, Taiwan*

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Hung-Yen Hsieh, Wen-Tseng Lo, Hsiao-Hao Chen, and Pei-Jie Meng (2016) Although research on the larval fish assemblages in the Taiwan Strait has progressively developed in the last two decades, it is difficult to study typhoons' impacts on larval fish assemblages due to (1) the occurrence and path of a cyclone cannot be predicted accurately and (2) the severe weather condition makes shipboard measurements extremely difficult. Larval fish and zooplankton were sampled and hydrographic variables and chlorophyll *a* were measured in the waters of southwestern Taiwan during September 2009 (non-typhoon) and September 2012 (post-typhoon Tembin). Data from these collections were used to elucidate the effects of hydrographic dynamics after the typhoon event on species assemblage and abundance. The results showed that after the typhoon Tembin, the surface temperature and salinity decreased slightly, but the values of the measured chemical and biological parameters were much greater than those derived from the non-typhoon period due to enriched nutrients from entrainment of river runoff of the Kaoping River. Meanwhile, the abundance of larval fish also increased significantly, but the species composition became less diverse. Multivariate statistical analyses revealed two distinct larval fish assemblages that were closely correlated to sampling cruise. The dominant taxa of larval fish changed from *Encrasicholina heteroloba*, *Nuchequula nuchalis*, unidentified Sparidae, *Equulites rivulatus*, and *Cyclothone* spp. during the non-typhoon period to *Engraulis japonicus*, unidentified Engraulidae, *Sillago sihama*, *Pennahia argentata*, and *E. rivulatus* during the post-typhoon period. Canonical correspondence analysis revealed that, in the waters of southwestern Taiwan, the horizontal distribution of larval fish in late summer may be explained by the food availability. The magnitude of the enhancement of measured variables changed with sampling periods, suggesting the study area was at an unsteady status after the passage of the typhoon Tembin. The coastal ecosystem became more productive after the typhoon event.

Key words: Community structure, Engraulidae, Impact of typhoon Tembin, Taiwan Strait, Horizontal distribution.

BACKROUND

Larval fish assemblages result from adult spawning strategies and environmental influences (Sabatés et al. 2007; Franco-Gordo et al. 2008). In tropical and temperate continental shelf waters, the distribution patterns of larval fish assemblages are quite complex (Young et al. 1986; Doyle et al. 1993; Olivar et al. 2010). Because of early ontogenetic stages of fish developed in the planktonic environment, they are subject to the effect of physical (*e.g.* temperature, salinity, fronts, and currents) and biological (*e.g.* food availability and predator stocks) processes (Bakun 2006; Keane and Neira 2008; Olivar et al. 2010). The variability of these processes influences the distribution and survival of larval fish directly or indirectly, leading to great variations in the annual recruitment of species (Govoni 2005). Thus, the relationship between larval fish assemblages

*Correspondence: Pei-Jie Meng contributed equally with Hung-Yen Hsieh to this work.
E-mail: pjmeng@nmmba.gov.tw; hyhsieh@mail.ndhu.edu.tw

and physical-biological processes are becoming increasingly important to ecosystem-based fishery management and fishery-independent stock assessments (Bakun 2006; Olivar et al. 2010).

Coastal waters of southwestern Taiwan are one of the most important fishing grounds around Taiwan (Lee et al. 1995; Tsai et al. 1997; Hsieh et al. 2009). It was a dynamic area where marked seasonal changes occurred in hydrographic and biological features. Two main currents, South China Sea Surface Current (SCSSC) and Kuroshio Branch Current (KBC), dominate the waters of southwestern Taiwan (Jan et al. 2002, 2006). During the southwesterly monsoon from spring (May) to early autumn (September), the warm and low-salinity SCSSC flows northeastward, synchronizing with the southwesterly monsoon, intruding into the southern Taiwan Strait (TS) and dominating in this region. At the end of autumn (November) in the beginning of the northeasterly monsoon, the KBC, a branch of the warm and highly saline Kuroshio Current, passes through the Luzon Strait and intrudes into the waters of southwestern Taiwan. Except for the above-mentioned succession of currents, the continental runoff also plays an important role in the species composition of larval fish (Tzeng et al. 2002).

With the global warming, typhoon activity has been strengthening in both intensity and spatial coverage in the past several decades. For example, hurricane activity in the North Atlantic between 1995 and 2000 doubled compared with that between 1971 and 1994 (Stanley et al. 2001); similarly, in subtropical East Asia typhoon activity also progressively increased (Wu et al. 2005). Unfortunately, Taiwan is on a path frequently traveled by the typhoons. According to the statistical information of the Central Weather Bureau, on Taiwan's part, on average, at least 24 typhoons occur at the northwestern Pacific and the South China Sea every year. Recent studies have evidenced that significant biogeochemical changes occur in the upper ocean waters as a typhoon passes with its intensified winds and precipitation (Lin et al. 2003; Zhao et al. 2008; Chen et al. 2009). In the surface water affected by the typhoon, nutrient concentrations and phytoplankton biomass often significantly increase as winds induce vertical mixing, upwelling, or both (Lin et al. 2003; Babin et al. 2004). In addition, in the coastal waters where river discharge is significant, nutrient concentrations and phytoplankton biomass are increased by entrainment of waters from river runoff from typhoon-related floods (Zheng and Tang 2007; Chen and Chen 2006).

Although research on the larval fish assemblages in the TS has progressively developed in the last two decades, it is difficult to study typhoons' impacts on larval fish assemblages for two major reasons as mentioned by Chang et al. (1996) and Shiah et al. (2000). The first is that the occurrence and path of a cyclone cannot be predicted accurately. In addition, the severe weather condition (even several days after the passage of typhoon) makes shipboard measurements extremely difficult, particularly at more offshore areas. Take the shipboard measurements during the late August of 2012 for example. One strong typhoon (Tembin) swept through the Southern Taiwan. A cruise (3-4 September) was designed originally to examine the correlation between hydrographic variables and larval fish assemblages in the waters of southwestern Taiwan, but it also took an opportunity for us to observe the variations of hydrographic and biological variables and composition of larval fish after the passage of typhoon Tembin. The present study attempts to summarize and compare the differences of hydrographic conditions and larval fish assemblage after the passage of typhoon in the waters of southwestern Taiwan.

MATERIALS AND METHODS

Field sampling

Samplings of larval fish of a non-typhoon cruise (R/V *Hai-Fu*) during 21-23 September 2009 and a post-typhoon cruise (CR1636, R/V *Ocean Researcher III*) during 3-4 September 2012 in the waters of southwestern Taiwan were compared. Zooplankton samples were respectively collected at 10 different stations during two cruises (Fig. 1) in the daytime using an Ocean Research Institute (ORI) net (6 m-long with a 1.6 m mouth diameter and a 330 μm mesh size). After retrieval from the ocean, the zooplankton samples were immediately preserved in 5% seawater-buffered formalin for further identification and enumeration. The net was towed obliquely at approximately 1 m s^{-1} from 100 m (or 10 m above the bottom at stations with a depth of < 100 m) to the surface and a Hydro-Bios mechanical flowmeter (Hydro-Bios, Kiel, Schleswing-Holstein, Germany) was placed in the mouth of the net to calculate the water volume filtered. At each station, prior to zooplankton collection, a General Oceanics

SeaBird conductivity-temperature-depth instrument (SEB-911 Plus, Sea-Bird Electronics, Inc., Bellevue, WA, USA) was used to obtain vertical profiles of temperature and salinity. Water samples for measurements of chlorophyll *a* and nutrients (nitrite-nitrate combined, phosphate, and silicate) concentrations were collected at 5, 25, 50, and 75 m depths by using Go-Flo bottles (General Oceanics, Miami, Florida, USA).

Identification and enumeration

In the laboratory, larval fish were sorted from the zooplankton samples and preserved in 70% alcohol after sorting. Larval fish were identified to the lowest possible taxonomic level based on their morphological characteristics according to Leis and Rennis (1983), Okiyama (1988), Leis and Trnski (1989), Neira et al. (1998), and Chiu (1999). In addition, each sample was repeatedly subdivided until the number of individual zooplankton in the last subsample was estimated to be 1000-2000 or fewer, and organisms in the entire subsample were counted to calculate the abundance of zooplankton at that station. Larval fish and zooplankton abundances were standardized to the number of individuals (ind.) per 1000 m^3 and 100 m^3, respectively.

Statistical analyses

Contours of temperature and salinity were diagramed using SURFER 8.01 software (Golden Software, Inc., Golden, Colorado, USA). The community structure of larval fish from the samples was described with the Shannon-Wiener diversity index (H'; Shannon and Wiener 1949), Pielou's index of evenness (J'; Pielou 1966), and Margalef richness index (d; Margalef 1958). The two-way ANOVA was selected to test for the differences of sampling times and locations in hydrographic and biological variables (Dunn and Clark 1974).

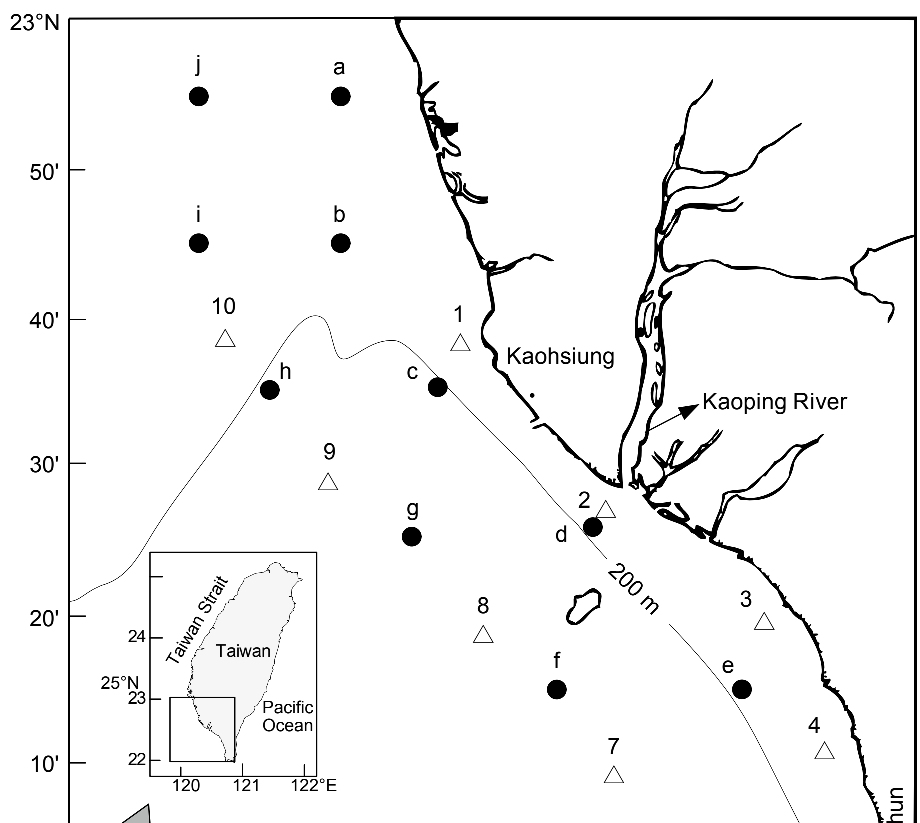


Fig. 1. Map of the study area with sampling stations. Solid circles and triangles represent 2009 and 2012 cruises, respectively.

The Sørensen similarity index (SI) of larval fish between cruises was also calculated by analyzing the similarity of pairs of sites in terms of the presence and absence of species (Sørensen 1948). In order to examine spatial differences in the assemblage, a cluster analysis was performed with the PRIMER-6 statistical software (PRIMER-E Ltd., West Hoe, Plymouth, UK). Data on species abundances were log(x+1)-transformed prior to the assemblage analysis to reduce the weighting of dominant species (Clarke and Warwick 2001). Assemblages were determined from cluster dendograms of the Bray-Curtis similarity matrix using standardized data of station averages (Bray and Curtis 1957). Meanwhile, non-metric multi-dimensional scaling (MDS) was used to provide a 2-D visual representation of assemblage structure (Kruskal and Wish 1978). The similarity percentage (SIMPER) routine showed the percentage contribution of each taxon to the average similarities within the different larval fish assemblages (Clarke 1993). In addition, the relationships among the distribution and abundance of larval fish and environmental variables (temperature, salinity, chlorophyll *a*, zooplankton, nitrite-nitrate combined, phosphate, and silicate) were explored through canonical correspondence analysis (CCA; Ter Braak 1986), which was calculated with PCORD 6.0 software (MjM Software, Gleneden Beach, Oregon, USA).

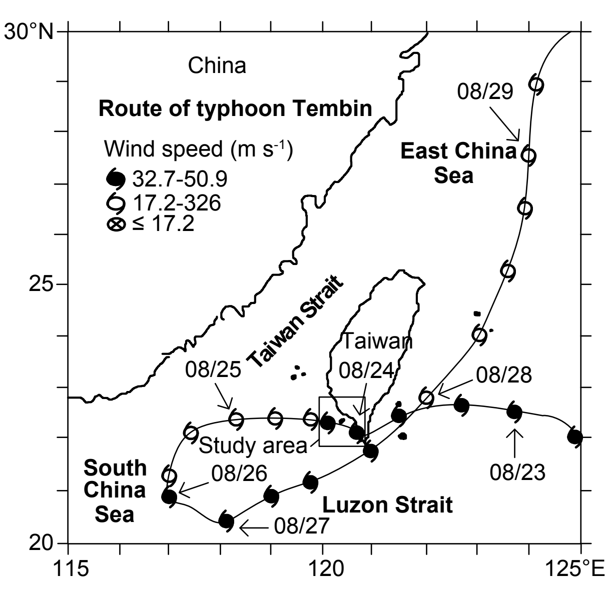


Fig. 2. Track of typhoon Tembin in the waters around Taiwan during 23-29 August 2012.

RESULTS

Hydrographic and biological information

Before five days of the 2012 cruise, a typhoon, Tembin, swept through the Southern Taiwan and our study area (Fig. 2). Typhoon Tembin is a moderate typhoon with a moving speed of 3.33 m s^{-1} and a wind speed of 45 m s^{-1}, which carried the large amount of rainfall for the Southern Taiwan. Counting the daily rainfall before two weeks of the two sampling cruises in Kaohsiung City and Hengchun Township of the Southern Taiwan (data from Kaohsiung and Hengchun weather stations of Central Weather Bureau, Taiwan) (Fig. 3), the precipitation was significantly lower in 2009 than that in 2012. In 2009 the precipitation was 37 mm for Kaohsiung and 79 mm for Hengchun Township; in constant, they were 222 and 788 mm, respectively, in 2012.

Mean values of seawater temperature, salinity, and phosphate concentration at

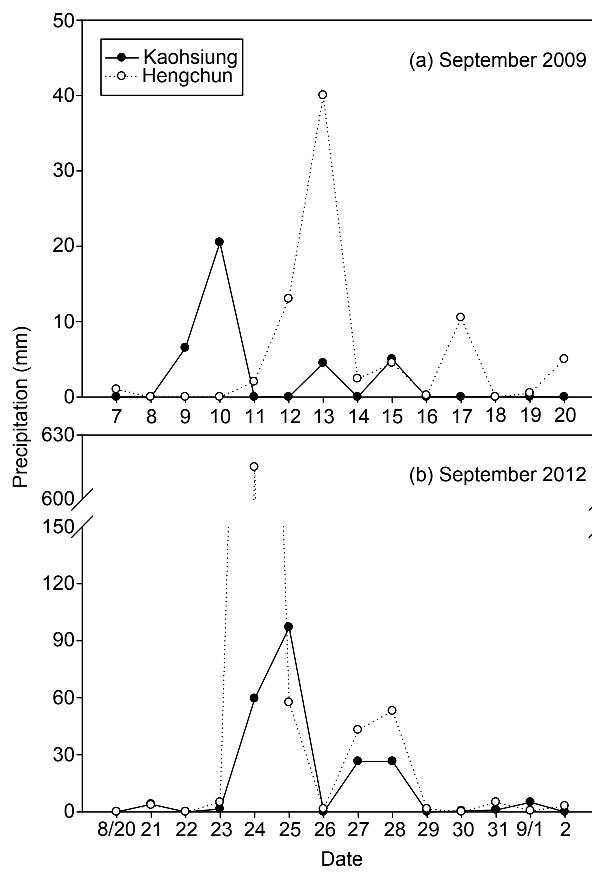


Fig. 3. Precipitation (mm) of each day in Kaohsiung City and Hengchun Township of the Southern Taiwan. Data of precipitation obtained from Central Weather Bureau, Taiwan.

10 m in depth showed clear changes at different sampling times (Table 1). Higher mean values of temperature and salinity were observed in 2009 (temperature: ANOVA, $F_{1,20} = 47.498$, $p < 0.001$; salinity: ANOVA, $F_{1,20} = 187.636$, $p < 0.001$), and the opposite was found for phosphate concentration (ANOVA, $F_{1,20} = 22.177$, $p < 0.001$) (Table 2). Except for salinity (ANOVA, $F_{1,20} = 17.082$, $p < 0.01$), no significant spatial differences were observed between inshore and offshore stations for hydrographic variables in the study (Tables 1 and 2). In 2009 the temperature and

Table 1. Mean values of hydrographic and biological variables at different sampling times and locations

	Inshore 2009 (Stns: a-e)	Offshore 2009 (Stns: f-j)	Inshore 2012 (Stns: 1-5)	Offshore 2012 (Stns: 6-10)
Environmental variables				
Temperature (°C)	29.45 ± 0.15	29.70 ± 0.12	28.36 ± 0.19	28.45 ± 0.21
Salinity	33.53 ± 0.02	33.49 ± 0.03	32.71 ± 0.06	33.11 ± 0.05
Chlorophyll *a* (mg m^{-3})	0.32 ± 0.08	0.19 ± 0.01	0.36 ± 0.09	0.30 ± 0.05
NO_2+NO_3 (μM)	1.22 ± 0.46	0.70 ± 0.14	3.67 ± 2.56	1.96 ± 0.51
PO_4 (μM)	0.13 ± 0.01	0.09 ± 0.01	0.86 ± 0.22	0.44 ± 0.08
SiO_2 (μM)	3.14 ± 0.43	2.36 ± 0.46	4.63 ± 2.35	3.77 ± 0.81
Zooplankton (ind. 100 m^{-3})	2292.31 ± 429.06	1489.95 ± 296.60	25218.84 ± 3314.38	19595.16 ± 4294.31
Larval fish				
Abundance (ind. 1000 m^{-3})	32.46 ± 13.61	11.38 ± 2.67	1764.08 ± 750.51	207.25 ± 57.83
Species number	13 ± 2	11 ± 1	13 ± 3	14 ± 2
Species diversity (H’)	3.22 ± 0.18	3.15 ± 0.11	2.88 ± 0.26	3.39 ± 0.11
Species evenness (J’)	0.89 ± 0.02	0.93 ± 0.02	0.80 ± 0.05	0.90 ± 0.03
Species richness (d)	3.99 ± 0.31	4.23 ± 0.23	1.86 ± 0.41	2.61 ± 0.31

Table 2. Two-way ANOVA (Time (T, 2009 vs. 2012) × Location (L, inshore vs. offshore)) of hydrographic and biological variables

Source	*d.f.*	*F* value	*p* > *F*	Source	*d.f.*	*F* value	*p* > *F*
Temperature				Zooplankton			
Time	1	47.498	< 0.001	Time	1	56.690	< 0.001
Location	1	1.021	0.327	Location	1	1.391	0.256
T × L	1	0.203	0.658	T × L	1	0.783	0.389
Salinity				Larval fish abundance			
Time	1	187.636	< 0.001	Time	1	6.556	< 0.05
Location	1	17.082	< 0.01	Location	1	4.396	0.052
T × L	1	24.998	< 0.001	T × L	1	4.161	0.058
Chlorophyll *a*				Species number			
Time	1	1.283	0.274	Time	1	1.045	0.322
Location	1	2.344	0.145	Location	1	0.116	0.738
T × L	1	0.271	0.610	T × L	1	0.685	0.420
NO_2+NO_3				Species diversity			
Time	1	1.944	0.182	Time	1	0.084	0.776
Location	1	0.705	0.414	Location	1	1.522	0.235
T × L	1	0.199	0.661	T × L	1	2.662	0.122
PO_4				Species evenness			
Time	1	22.177	< 0.001	Time	1	3.410	0.083
Location	1	3.987	0.063	Location	1	4.069	0.061
T × L	1	2.811	0.113	T × L	1	0.588	0.454
SiO_2				Species richness			
Time	1	1.273	0.276	Time	1	34.161	< 0.001
Location	1	0.405	0.533	Location	1	2.396	0.141
T × L	1	0.001	0.976	T × L	1	0.656	0.430

salinity ranged from 29.07°C to 29.97°C and 33.43 to 33.58, respectively, compared to 2012 when they ranged from 27.74°C to 28.99°C and 32.47 to 33.22. Analysis of vertical profiles of temperature and salinity showed that the waters in the study area in the two summers were clearly stratified (Fig. 4). Apparently lower salinity was observed at the upper 10 m layer of water between inshore stations 2 and 4 in 2012. In addition, an upwelling site occurred between inshore stations b and d in 2009 with relatively high salinities. Concentrations of nitrite-nitrate combined, phosphate, and silicate were higher at inshore stations than at offshore stations, especially at Stations d and 2 adjacent to the estuary of the Kaoping River (Fig. 5). They fluctuated from 0.38 μM to 5.59 μM (nitrite-nitrate combined), 0.25 μM to 0.53 μM (phosphate), and 4.63 μM to 18.42 μM (silicate) in 2009, and changed from 0.10 μM to 30.73 μM, 0.50 μM to 4.53 μM, and 6.02 μM to 65.45 μM in 2012, respectively.

Chlorophyll *a* concentration (average concentration in the upper 75 m) showed no apparent temporal (ANOVA, $F_{1,20} = 1.283$, $p = 0.274$) and spatial (ANOVA, $F_{1,20} = 2.344$, $p = 0.145$) differences (Tables 1 and 2). In the study, chlorophyll *a* concentration ranged from 0.16 mg m^{-3} to 0.65 mg m^{-3} in 2009 and 0.14 mg m^{-3} to 0.59 mg m^{-3} in 2012. Slightly higher mean concentration was observed during the 2012 cruise. Meanwhile, higher concentrations were usually found at inshore stations, with the highest values recorded at Stations d and 1 for both cruises, respectively (Fig. 5). Zooplankton abundance varied from 640 ind. 100 m^{-3} to 3339 ind. 100 m^{-3} in 2009 and 6874 ind. 100 m^{-3} to 34695 ind. 100 m^{-3} in 2012, with the mean of 1891 ± 280 (SE) ind. 100 m^{-3} and 22407 ± 2724 ind. 100 m^{-3}, respectively. Significant difference was observed between cruises (ANOVA, $F_{1,20} = 56.690$, $p < 0.001$, Table 2), where the mean abundance during the post-typhoon period was 12 times huger than that during the non-typhoon period. Conversely, no significant difference was noted among sampling locations, although higher zooplankton abundance were generally found at inshore stations (Fig. 5).

Changes of abundance and composition of larval fish

One hundred and twenty-four taxa of larval fish belonging to 72 genera and 52 families were identified in the study. The abundance of larval fish was significantly higher during the post-typhoon period than during the non-typhoon period (ANOVA, $F_{1,20} = 6.556$, $p < 0.001$, Tables 1 and 2). The mean abundances of larval fish were 22 ±

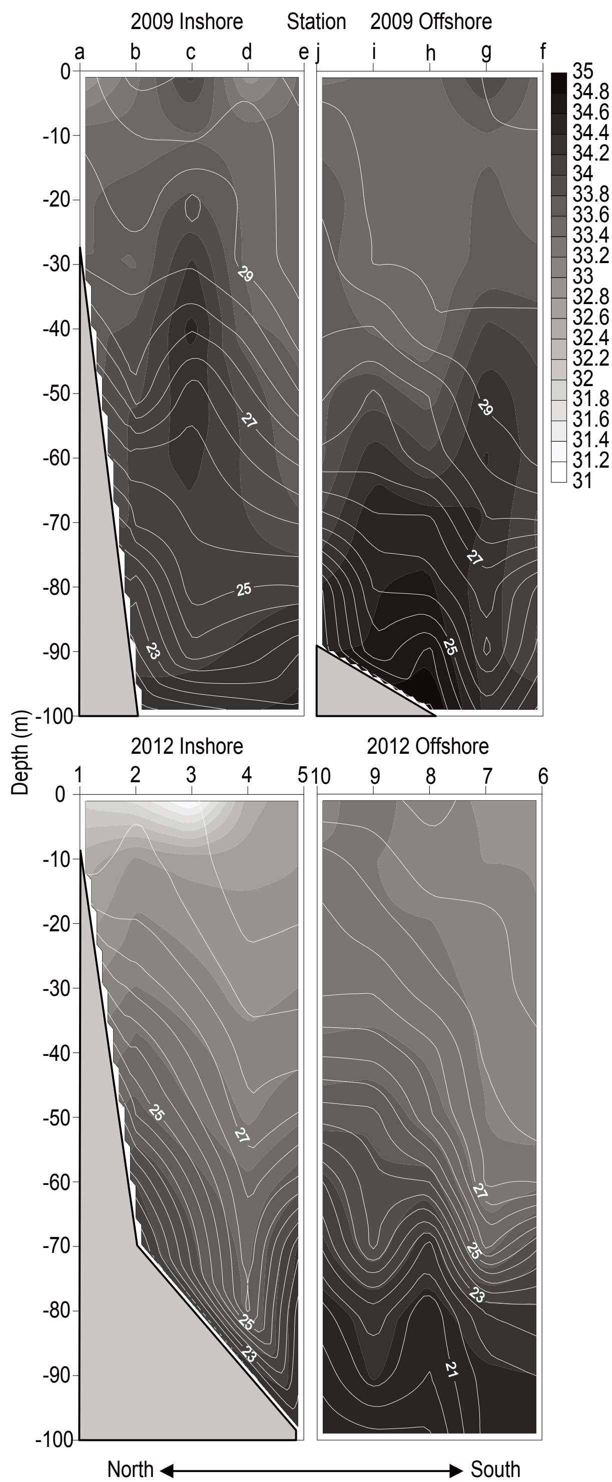


Fig. 4. Vertical profiles of temperature (white lines) and salinity (gray shading) at the upper 100 m.

7 (SE) ind. 1000 m^{-3} in 2009, ranging from 5 ind. 1000 m^{-3} (Station g) to 80 ind. 1000 m^{-3} (Station d), and 986 ± 440 ind. 1000 m^{-3} in 2012, varying from 77 ind. 1000 m^{-3} (Station 10) to 4360 ind. 1000 m^{-3} (Station 3) (Figs. 6a and 6b). Although the mean abundance did not significantly differ between sampling locations (ANOVA, $F_{1,20} = 4.396$, $p = 0.052$, Table 2), in general, comparatively higher abundances of larval fish were found at inshore stations across both cruises, particularly stations (*e.g.* Stations d, 2, and 3) adjacent to the estuary of the Kaoping River.

Larval fish in 49 genera and 72 taxa were found in 2009. The species number and indices of diversity, evenness, and richness varied among stations, from 8 (Stations b and g) to 21 (Station d), 2.82 (Station b) to 3.75 (Station d), 0.82 (Station e) to 0.99 (Station h), and 3.19 (Station a) to

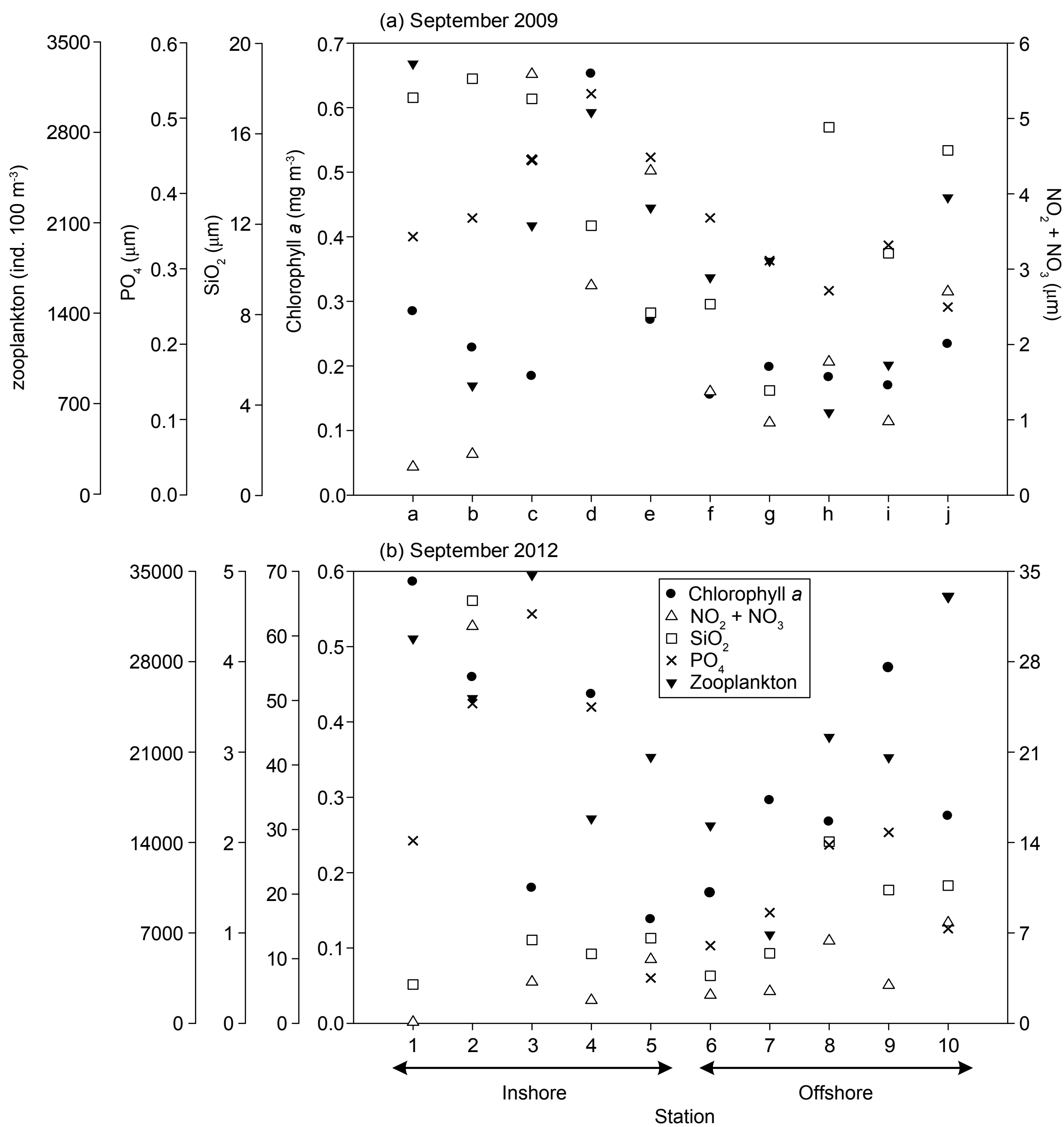


Fig. 5. Concentrations of nutrients and chlorophyll *a* and zooplankton abundance at each sampling station. Nutrients (including nitrite-nitrate combined, phosphate, and silicate) and chlorophyll *a* were shown using the average concentration in the upper 75 m.

4.85 (Station h), respectively (Fig. 6). In 2012, 43 genera and 78 taxa were recorded, with the species number and indices of diversity, evenness, and richness ranging from 8 (Stations 1 and 3) to 23 (Station 5), 2.34 (Station 2) to 3.73 (Station 5), 0.61 (Station 2) to 1.00 (Station 8), and 0.91 (Station 3) to 3.58 (Station 9), respectively. The trend opposite to that of abundance between cruises was found for species richness (ANOVA, $F_{1,20}$ = 34.161, p < 0.001), with apparently higher mean value in 2009; however, no significant differences were observed in number (ANOVA, $F_{1,20}$ = 1.045, p = 0.322), diversity (ANOVA, $F_{1,20}$ = 0.084, p = 0.766), and evenness (ANOVA, $F_{1,20}$ = 3.410, p = 0.083) of species (Tables 1 and 2). In a comparison of spatial differences in sampling locations, the number (ANOVA, $F_{1,20}$ = 0.116, p = 0.738), diversity (ANOVA, $F_{1,20}$ = 1.522, p = 0.235), evenness (ANOVA, $F_{1,20}$ = 4.069, p = 0.061), and richness of larval fish (ANOVA, $F_{1,20}$ = 2.396, p = 0.141) did not significantly differ between inshore and offshore stations (Tables 1 and 2). Nevertheless, the indices of diversity, evenness, and richness showed relatively lower values at several inshore stations, such as Stations d, 2, and 3.

Of all the samples, larvae of the families Engraulidae, Sillaginidae, Sciaenidae, Myctophidae, and Leiognathidae were the five most abundant, accounting for 43.68% of the total larval fish. In addition, in the study the larvae of unidentified yolk sac stage were also numerous, comprising 30.84% of the total catch. At the species level, *Engraulis japonicus* was the most dominant species and constituted 11.92% of all larval fish collected during the survey. The next four predominant taxa were *Sillago sihama* (8.09%), *Pennahia argentata* (7.07%), *Equulites rivulatus* (4.82%), and unidentified Engraulidae (3.11%). The five larval fish taxa together constituted 35.01% of the total catch. Nonetheless, the occurrence rate of the five dominant taxa was low (< 20%), which were only found in the specific cruise and station. Although the species number of larval fish that occurred in each cruise was equal, the similarity of composition between cruises was only 34.67% (calculated by Sørensen similarity index; data not shown). The predominant taxa in different sampling times and locations were significantly different (Table 3), and the proportions

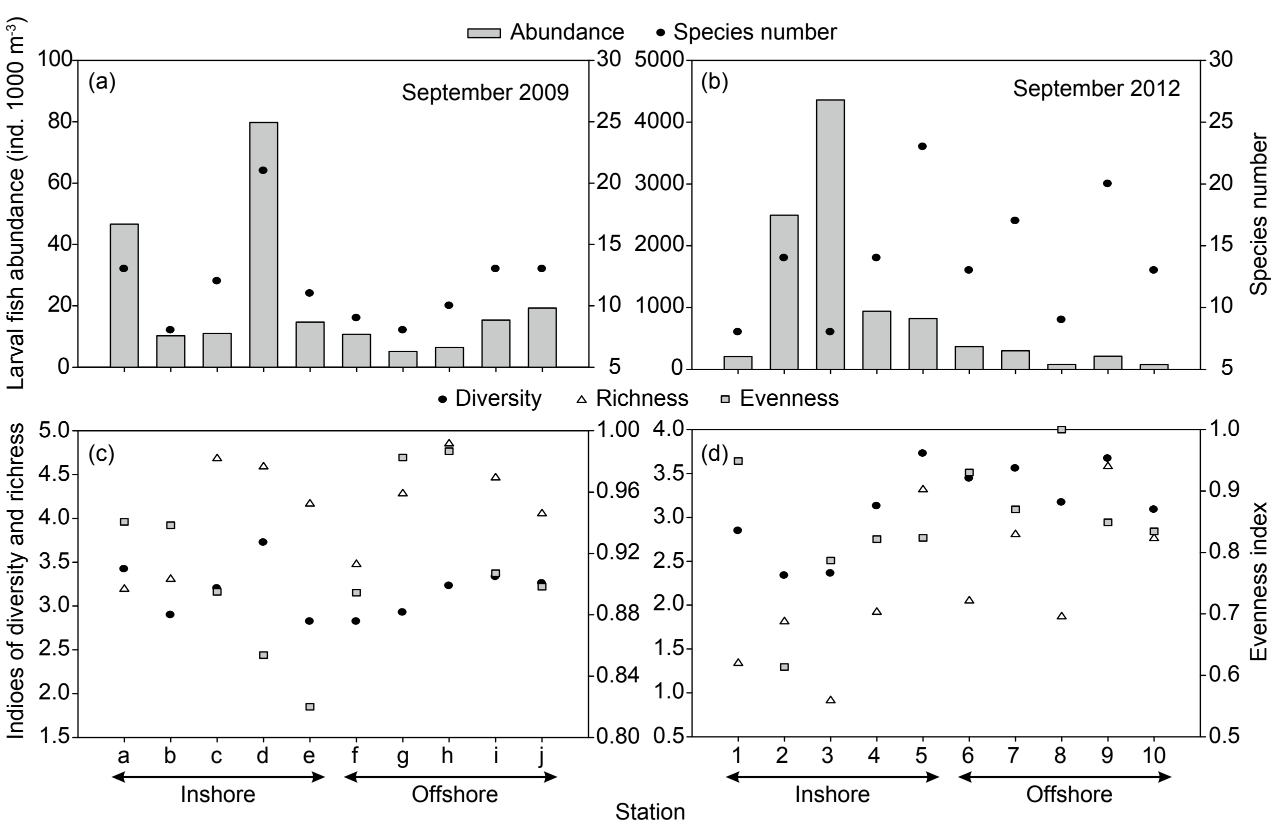


Fig. 6. Larval fish abundance, species number, and indices of diversity, richness, and evenness at each sampling station.

of the ten predominant taxa at each station during the study are shown in figure 7.

Assemblages of larval fish

A distinct difference of assemblage structure in which stations of the same cruise clustered together, except for Stations i and j of 2009, was derived from the hierarchical clustering and MDS by analyzing species compositions of larval fish (Fig. 8). All sampling stations were divided into two main groups of stations (A and B) at a similarity level of 10%, which respectively represented 2009 and 2012 cruises. Among the two assemblages, Group A was further divided into two subgroups of stations, namely A1 and A2, and Group A1 was further divided into A1a and A1b. Similarly, Group B was further divided into B1 and B2, and furthermore Group B2 was divided into B2a and B2b.

Group A1a comprised Stations b and c, which were characteristic of the inshore and northern study area. Seventeen larval fish taxa were found in the assemblage of which *Ceratoscopelus warmingi* was the most abundant species, with the mean of 1.57 ± 1.57 (SE) ind. 1000 m^{-3}. *Benthosema pterotum*, *Cyclothone* spp., and *Decapterus macarellus* were the three most important taxa in the assemblage, all contributing 33.33% to the within-group similarity (Table 4).

Group A1b consisted of four stations that were located mainly in the central and southern offshore areas, except for the inshore Station e. In total, 27 larval fish taxa were found in the group. Similar to Group A1a, the abundance of taxa identified in the group was low. It was dominated by *Encrasicholina heteroloba* and *Gempylus serpens*. The three most important species in the group were *G. serpens*, *Coryphaena hippurus*, and *E. heteroloba*, which contributed 37.31%, 20.12%, and 12.79% to the within-group similarity, respectively (Table 4).

Group A2 contained two inshore stations. One

Table 3. Mean abundance and relative abundance (RA) of the ten dominant larval fish taxa

	Inshore 2009 (Stns: a-e)			Offshore 2009 (Stns: f-j)	
Species	Mean ± SE (ind. 1000 m^{-3})	RA (%)	Species	Mean ± SE (ind. 1000 m^{-3})	RA (%)
Encrasicholina heteroloba	5.30 ± 4.18	16.32	*Trachinocephalus myops*	1.22 ± 0.78	10.73
Sparidae gen. spp.	2.42 ± 1.64	7.45	*Diaphus* A group	0.98 ± 0.70	8.63
Nuchequula nuchalis	1.66 ± 1.66	5.12	*Iniistius* spp.	0.95 ± 0.78	8.31
Cyclothone spp.	1.57 ± 0.91	4.83	*Encrasicholina heteroloba*	0.71 ± 0.71	6.27
Equulites rivulatus	1.51 ± 1.51	4.66	*Bregmaceros* spp.	0.56 ± 0.42	4.94
Sillago japonica	1.26 ± 1.26	3.88	*Naso unicornis*	0.54 ± 0.39	4.78
Decapterus macarellus	1.20 ± 0.28	3.68	*Gempylus serpens*	0.52 ± 0.26	4.53
Nibea sp.	1.01 ± 1.01	3.11	*Coryphaena hippurus*	0.51 ± 0.13	4.45
Bothidae gen. spp.	1.00 ± 1.00	3.07	*Cyclothone* spp.	0.43 ± 0.29	3.77
Gobiidae gen. spp.	0.96 ± 0.49	2.95	*Bregmaceros nectabanus*	0.43 ± 0.43	3.77
	Inshore 2012 (Stns: 1-5)			Offshore 2012 (Stns: 6-10)	
Species	Mean ± SE (ind. 1000 m^{-3})	RA (%)	Species	Mean ± SE (ind. 1000 m^{-3})	RA (%)
Engraulis japonicus	240.26 ± 142.85	13.62	*Cyclothone alba*	27.43 ± 13.87	12.55
Sillago sihama	163.02 ± 157.46	9.24	*Diaphus* A group	26.46 ± 15.37	12.55
Pennahia argentatus	142.53 ± 121.32	8.08	*Iniistius* spp.	18.82 ± 9.02	9.08
Equulites rivulatus	95.64 ± 48.14	5.42	*Bregmaceros* spp.	14.06 ± 5.99	6.79
Engraulidae gen. sp.	62.74 ± 55.20	3.56	*Vinciguerria nimbaria*	11.37 ± 5.21	5.49
Cyclothone alba	32.48 ± 21.50	1.84	*Cyclothone pallida*	9.54 ± 9.54	4.60
Gobiidae gen. spp.	32.19 ± 14.18	1.82	*Diaphus* B group	6.84 ± 6.26	3.30
Pagrus sp.	22.65 ± 22.65	1.28	*Benthosema* sp.	6.20 ± 5.62	2.99
Diaphus A group	19.42 ± 16.18	1.08	*Diplophos orientalis*	6.04 ± 3.71	2.91
Evynnis sp.	19.36 ± 19.36	1.08	*Trachinocephalus myops*	3.73 ± 3.73	1.80

(Station a) was located in the northernmost of the study area and the other (Station d) was adjacent to the estuary of the Kaoping River. Thirty-one larval fish taxa were recognized in the group. The dominant taxa were *E. heteroloba*, unidentified Sparidae, *Nuchequula nuchalis*, *E. rivulatus*, and *Sillago japonica*. Unidentified Sparidae, unidentified Gobiidae, and *D. macarellus* were the three most important taxa, contributing between 20.44% and 47.31% to the within-group similarity (Table 4).

Group B1 was represented by two inshore stations (Stations 2 and 3). Twenty larval fish taxa were recorded in the group which was characterized by high abundance and low richness. Group B1 was mainly dominated by *E. japonicus*,

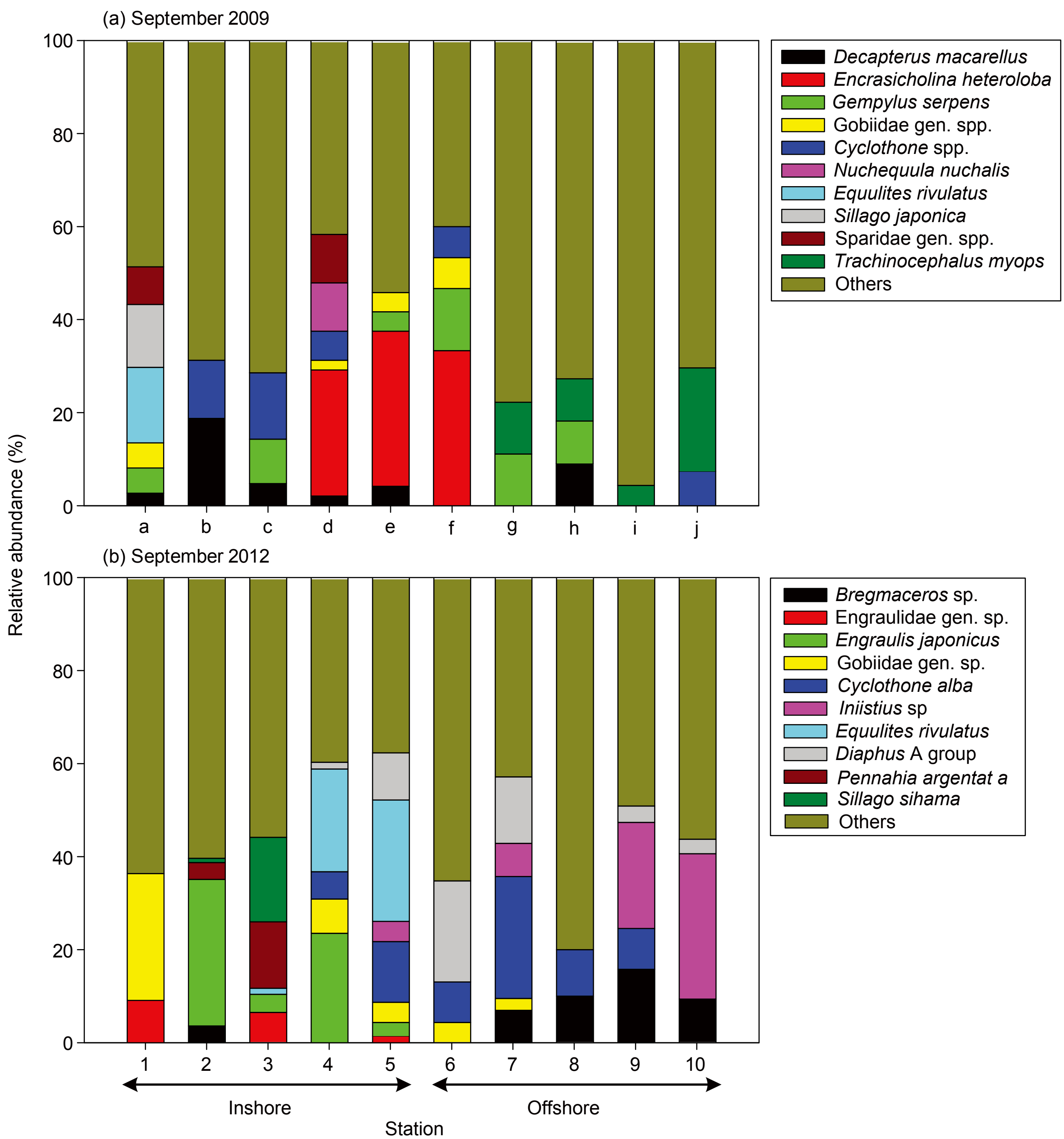


Fig. 7. Proportions (%) of the ten dominant larval fish taxa at each sampling station.

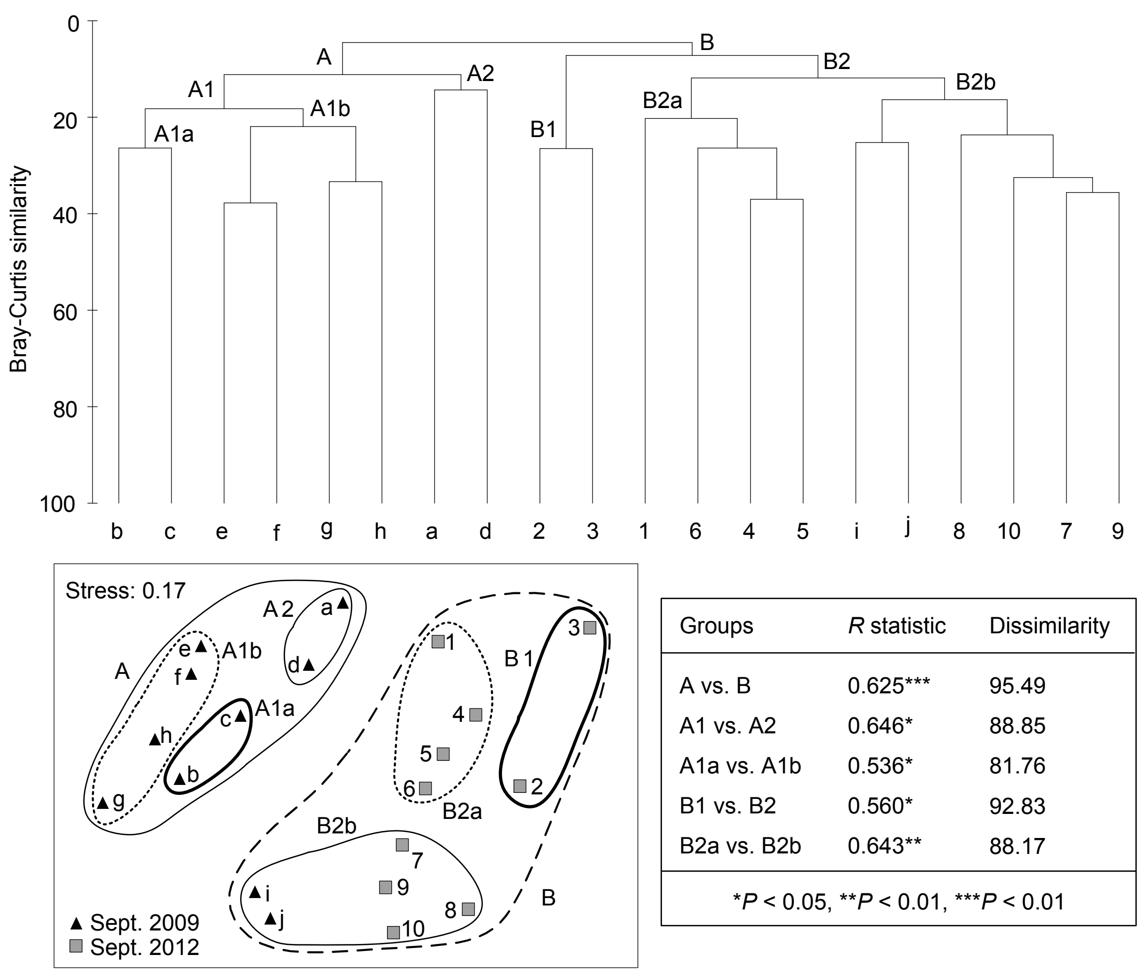
S. sihama, and *P. argentata*, which together represented 71.44% of the total catch. They were also the most important taxa for the group, respectively with the percentage contributions of 40.09%, 24.57%, and 35.24% (Table 4).

Group B2a included Stations 4-6 situated in the southernmost of the study area, with 41 identified larval fish taxa. *Equulites rivulatus*, *E. japonicus*, *Cyclothone alba*, unidentified Gobiidae, and *Diaphus* A group were the five most abundant taxa in the group; the last three of these contributed more than 10% to within-group similarity (Table 4). In addition, *Diaphus* B group and *Pagrus major* were also important for the group, contributing 12.72% and 12.38% to the within-group similarity, respectively.

Group B2b comprised six stations (two in 2009 and four in 2012) that were distributed across the offshore area. Fifty-three larval fish taxa were found in the group, representing the most abundant species number among all station groups. The top three dominant species of Group B2b were *Bregmaceros* spp., *Iniistius* spp., and *C. alba*. *Bregmaceros* spp., *Iniistius* spp., *Diaphus* A group, and *Vinciguerria nimbaria* were the four most important taxa in the group, with the contribution between 14.18% and 26.73% (Table 4).

Environmental effects on the distribution of larval fish

The bi-plot of CCA derived from the abundances of the 20 most dominant larval fish taxa illustrated the non-linear relationship between larval fish abundance and environmental variables (Fig. 9). The first and second canonical axes accounted together for 49.6% of the constrained



Groups	*R* statistic	Dissimilarity
A vs. B	0.625***	95.49
A1 vs. A2	0.646*	88.85
A1a vs. A1b	0.536*	81.76
B1 vs. B2	0.560*	92.83
B2a vs. B2b	0.643**	88.17

*P < 0.05, **P < 0.01, ***P < 0.01

Fig. 8. Hierarchical clustering, multidimensional scaling (MDS) ordination, and similarity results of Bray-Curtis similarity. The classification diagrams of percentage similarity between stations were diagramed by the similarity matrix of log(x+1)-transformed abundances of larval fish at each sampling station in the 2009 and 2012 cruises.

variance, with the third axis contributing an additional 14.7% (Table 5). Correlations between species and environmental axes were 0.978 and 0.994, respectively. The first canonical axis, which explained 28.5% of the variance, was negatively correlated with phosphate (r = -0.908) and zooplankton (r = -0.912). The second axis, accounting for 21.1%, was positively associated with chlorophyll *a* (r = 0.941), nitrate-nitrite combined (r = 0.876), and silicate (r = 0.886). According to the species distribution (Fig. 9), at the inshore waters, *P. argentata* was strongly and positively influenced by zooplankton. Temperature and salinity had positive effects on *E. rivulatus*, unidentified Gobiidae, and *B. pterotum*. The abundance of *E. japonicus* was highest at

Table 4. Taxa of larval fish regarded as representative of each station group (from Fig. 8). Representatives were identified by SIMPER cutting off for low accumulated contributions at 90%. Mean abundance and percentage contribution (C) to within-group similarity were shown

Group A/Species	Mean ± SE (ind. 1000 m^{-3})	C (%)	Group B/Species	Mean ± SE (ind. 1000 m^{-3})	C (%)
Group A1a (26.4)			Group B1 (26.5)		
Benthosema pterotum	0.58 ± 0.06	33.33	*Engraulis japonicus*	478.10 ± 308.25	40.09
Cyclothone spp.	1.42 ± 0.15	33.33	*Pennahia argentata*	356.33 ± 266.46	35.24
Decapterus macarellus	1.22 ± 0.70	33.33	*Sillago sihama*	407.55 ± 385.09	24.57
Group A1b (26.5)			Group B2a (25.1)		
Gempylus serpens	0.80 ± 0.21	37.31	Gobiidae gen. spp.	44.22 ± 11.68	29.34
Coryphaena hippurus	0.47 ± 0.16	20.12	*Cyclothone alba*	48.55 ± 22.56	13.66
Encrasicholina heteroloba	2.12 ± 1.25	12.79	*Diaphus* B group	15.60 ± 6.64	12.72
Trachinocephalus myops	0.29 ± 0.17	6.98	*Pagrus major*	11.63 ± 4.12	12.38
Nealotus tripes	0.32 ± 0.19	6.23	*Diaphus* A group	44.15 ± 21.70	12.07
Benthosema pterotum	0.44 ± 0.28	5.57	*Equulites rivulatus*	105.39 ± 60.86	5.93
Decapterus macarellus	0.30 ± 0.17	5.56	*Benthosema pterotum*	15.84 ± 9.29	3.65
Group A2 (14.3)			Engraulidae gen. sp.	7.65 ± 4.63	3.64
Sparidae gen. spp.	6.04 ± 2.26	47.31	Group B2b (21.9)		
Gobiidae gen. spp.	2.09 ± 0.43	32.29	*Bregmaceros* spp.	12.19 ± 5.23	26.73
Decapterus macarellus	1.46 ± 0.20	20.44	*Iniistius* spp.	16.47 ± 7.72	19.85
			Diaphus A group	9.61 ± 6.74	14.72
			Vinciguerria nimbaria	4.29 ± 1.50	14.18
			Cyclothone alba	17.56 ± 12.58	6.47
			Trachinocephalus myops	3.94 ± 3.02	4.64
			Ceratoscopelus warmingi	2.64 ± 1.57	4.31

Table 5. Correlations of environmental variables with axes using the canonical correspondence analysis (CCA)

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.751	0.557	0.387
% of variance explained	28.5	21.1	14.7
Cumulative % explained	28.5	49.6	64.3
Pearson correlations, Spp-Envt.	0.978	0.994	0.955
Inter-set correlations of environmental variables with axes			
Temperature	0.502	-0.399	0.554
Salinity	0.503	0.026	-0.750
Chlorophyll *a*	0.046	0.941	-0.027
NO_2+NO_3	-0.042	0.876	-0.380
SiO_2	-0.056	0.886	-0.405
PO_4	-0.908	0.202	0.165
Zooplankton	-0.912	-0.178	-0.074

inshore Station 2, with the high concentrations of chlorophyll *a*, nitrate-nitrite combined, and silicate.

DISCUSSON

Changes of hydrographic and biological variables

Significantly higher concentration of nitrate-nitrite combined was recorded in the inshore area even through the non-typhoon period in the study. The terrestrial runoff was the main sources of nutrients in the coastal waters off southwestern Taiwan. The large river runoff during summer period was caused by two main reasons: (1) the warm and wet southwesterly monsoon blows from the ocean to the land and produces plentiful precipitation (>100 mm per month) and (2) the passage of typhoon carries the heavy rainfall. Of the two reasons, the passage of typhoon is of the greatest importance. In the study, heavy precipitation, more than 600 mm in one day (Fig. 3) brought by the typhoon Tembin, was responsible

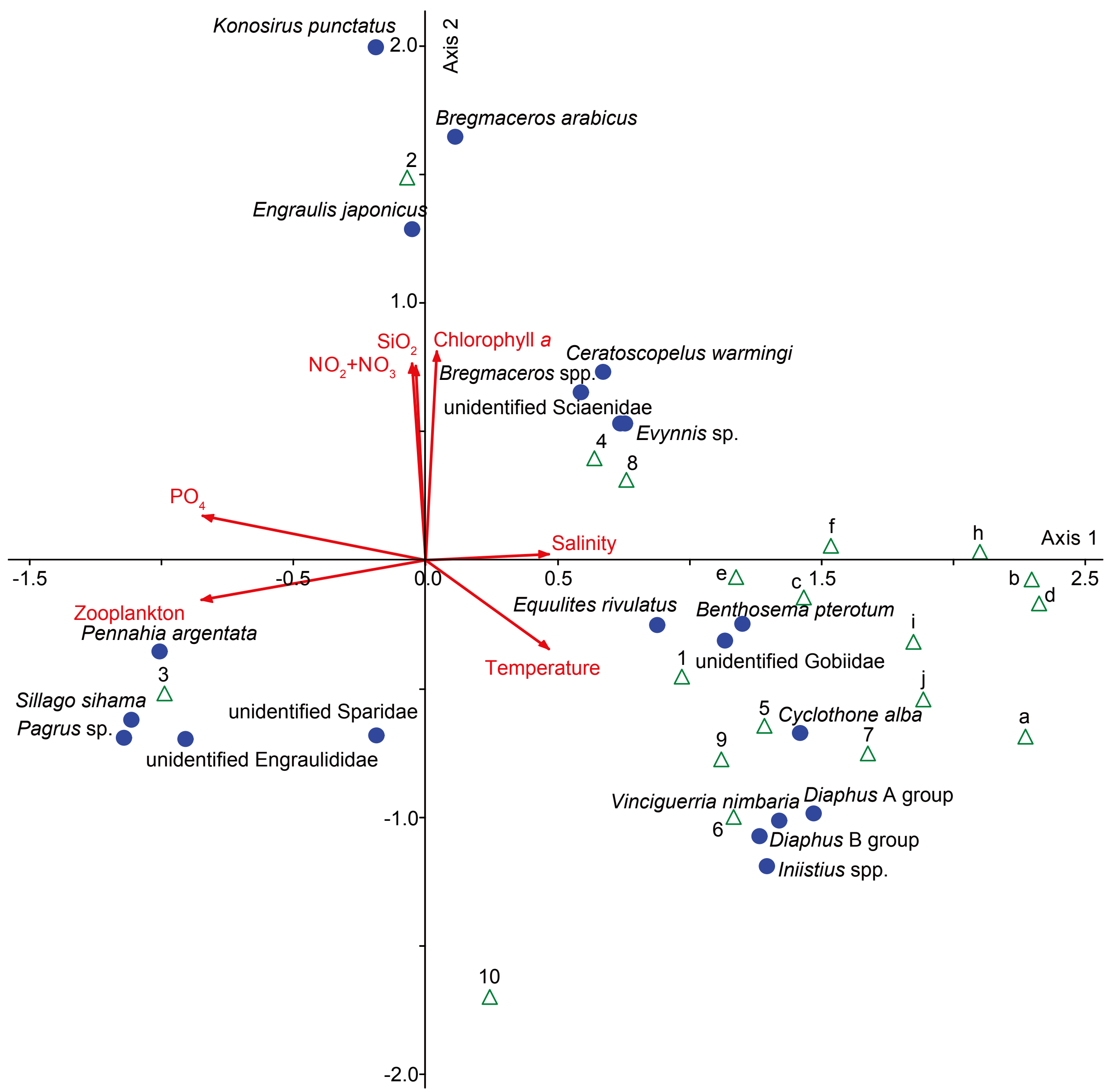


Fig. 9. Ordination diagram of canonical correspondence analysis (CCA). The dendrogram is diagramed based on the hydrographic variables and abundances of 20 dominant larval fish of each sampling station in the 2009 and 2012 cruises.

for the significant increases of nutrients (Table 6) through flood in Kaoping River.

Population growth of phytoplankton unexpectedly did not occur simultaneously with the nutrient uptake processes. In contrast to previous studies showing nutrient and phytoplankton flush shortly after typhoon passage (Chen et al. 2009; Zhao et al. 2008), our results indicated slight decline of chlorophyll *a* after the typhoon Tembin (Table 6). We speculated that the decline in chlorophyll *a* concentration must have been caused by other typhoon-related factors. For example, Thomas and Gibson (1990) have proposed that phytoplankton cells are known to be damaged by strong shear. In addition, zooplankton grazing would become more active in a turbulent environment (Kiørboe 1993; Hwang et al. 1994). However, more work is required to clarify how these factors may negatively affect the phytoplankton abundance at the study area.

Larval fish assemblages

Diverse assemblages of larval fish in this study confirmed that the TS is a major transition zone between tropical and subtropical faunas (Hsieh et al. 2010, 2012). Changes in the assemblage of larval fish are often observed along water depth gradient from shallow coastal waters to the marine shelf (Doyle et al. 1993; Gray and Miskiewicz 2000; Paulic and Papst 2013). In the study, significant variability in the horizontal structure of larval fish assemblage was also observed in the cross-shelf (onshore-offshore) direction. We speculated that this was related to the spawning location of the adult fishes and also due to the fact that the main physical features which influenced the horizontal distribution of larval fish and which maintained larval fish assemblage boundaries were found in this direction (Sabatés 1990; Doyle et al. 2002; Rodriguez et al. 2009). However, the tidal cycles or front associated with wind stress may transport fish eggs and larvae to the inshore waters and increase their abundance in adjacent regions.

The understanding of effect of the typhoon on larval fish assemblage in the waters of southwestern Taiwan is still insufficient. However, the contrasting hydrography of the waters between the non- and post-typhoon periods, particularly at

Table 6. Comparisons of hydrographic and biological variables at Station d (non-typhoon) and Station 2 (post-typhoon)

	Station d		Station 2
Environmental variables		Environmental variables	
Temperature (°C)	29.18	Temperature (°C)	27.84
Salinity	33.54	Salinity	32.84
Chlorophyll *a* (mg m^{-3})	0.65	Chlorophyll *a* (mg m^{-3})	0.46
NO_2+NO_3 (μM)	1.25	NO_2+NO_3 (μM)	13.82
PO_4 (μM)	0.16	PO_4 (μM)	1.08
SiO_2 (μM)	2.55	SiO_2 (μM)	13.98
Zooplankton (ind. 100 m^{-3})	2963.64	Zooplankton (ind. 100 m^{-3})	25163.17
Larval fish		Larval fish	
Abundance (ind. 1000 m^{-3})	79.74	Abundance (ind. 1000 m^{-3})	2493.85
Species number	21	Species number	14
Species diversity (H')	3.75	Species diversity (H')	2.34
Species evenness (J')	0.85	Species evenness (J')	0.61
Species richness (d)	4.59	Species richness (d)	1.81
Encrasicholina heteroloba	21.60	*Engraulis japonicus*	786.35
Nuchequula nuchalis	8.31	*Bregmaceros* sp.	89.87
Sparidae gen. spp.	8.31	*Pennahia argentatus*	89.87
Bothidae gen. spp.	4.98	*Konosirus punctatus*	67.40
Cyclothone spp.	4.98	*Bregmaceros arabicus*	44.93
Apogonidae gen. spp.	3.32	*Ceratoscopelus warmingi*	44.93
Muraenesocidae gen. sp.	3.32	*Encrasicholina heteroloba*	22.47
Ctenochaetus binotatus	1.66	*Sillago sihama*	22.47
Psettina gigantea	1.66	*Acanthopagrus schlegeli*	22.47
Decapterus macarellus	1.66	*Trichiurus lepturus*	22.47

the inshore stations, leads to the hypothesis that distinct assemblage of larval fish reflects different hydrographic conditions. According to the study of McKinnon et al. (2003) in shelf and slope waters of the southern Northwest Shelf, the abrupt changes observed in the composition of zooplankton and larval fish assemblages following passage of tropical cyclone Tiffany demonstrated that tropical cyclones could be important agents for distribution and dispersal of plankton and pelagic larvae in shallow shelf systems. The lower fish diversity after the typhoon Tembin accompanied by the great dominance of *E. japonicus* population indicates that after the typhoon Tembin the system was at a more unsteady status than that of the normal summer condition.

Factors controlling larval fish abundance

Highly productive nature of estuarine and coastal waters and their role as spawning grounds or nursery grounds to fish are well evidenced for temperate and tropical areas (McGowen 1993; Whitfield 1999; Sanvicente-Añorve et al. 2000; Franco-Gordo et al. 2008). Since early life stages of fish are a particularly vulnerable phase, it is hypothesized that marine larval fish and juveniles migrate into estuarine and coastal waters to make use of the high food abundance and refuge against predators, in order to maximize survival (Van der Veer et al. 2001; Olivar et al. 2010). The hydrographic data in nutrients showed that river runoff from the southwestern coast of Taiwan brought rich nutrients into this study area (Table 1 and Fig. 5). Although phytoplankton production did not respond to nutrient inputs yet, the zooplankton abundance increased significantly. This phenomenon was thought not to have been a population response in the time frame of the present study, but to have represented enhanced growth and survival of individual plankters.

In the northwestern Mediterranean Olivar et al. (2010) proposed that variation in zooplankton abundance could further affect larval fish populations and a positive correlation was expected when zooplankton was considered to be food for larval fish. Similarly, in the eastern Mediterranean Somarakis et al. (2006) suggested that actively selecting sites with increased zooplankton and feeding plasticity of *Sardina pilchardus* were interpreted as adaptations to grow and reproduce optimally at varying prey conditions. In the study, the CCA bi-plot showed that the chlorophyll *a*, phosphate, nitrate-nitrite combined, silicate, and zooplankton were the major factors in shaping the larval fish assemblages (Table 5 and Fig. 9). The results indicated that food availability was important in the distribution pattern of larval fish assemblage in the waters of southwestern Taiwan. The aggregation of zooplankton at the inshore waters after the typhoon Tembin passed by (Fig. 5) seemed to attract the predation of larval fishes.

Compared to food availability, in the study the effects of seawater temperature and salinity on the distribution of larval fish assemblages are relatively small. In the Skagerrak and Kattegat, which were situated between the saline waters of the North Sea and the brackish waters of the Baltic Sea, Munk et al. (2014) found that the ichthyoplankton abundances showed linkage to environmental characteristics described by surface temperature, salinity and bottom-depth. Hsieh et al. (2009) reported that the CPUE (catch per unit of fishing effort) of larval anchovy showed an apparent correlation with combination of water temperature and river runoff in the coastal waters southwest of Taiwan. In the study, it was found that the most taxa that appeared at the same side of variables of temperature and salinity were oceanic taxa, such as *B. pterotum*, *C. alba*, *V. nimbaria*, *Diaphus* A group, and *Diaphus* B group (Fig. 9). In general, these taxa mainly inhabit the deeper oceanic waters (Nakabo 2002) and their larvae are most abundant in the Kuroshio Current and offshore oceanic water (Sassa et al. 2002, 2004; Okazaki and Nakata 2007).

CONCLUSIONS

The present study suggests that the effects of typhoons on the hydrographic and biological conditions are great. After the typhoon event, high nutrient concentrations revealed the rich terrestrial runoff from the Kaoping River; in addition, high abundance and low diversity of larval fish further indicate that the ecosystem of the coastal waters of southwestern Taiwan is at an unsteady status. The great difference of larval fish assemblage determined between the non- and post-typhoon periods mainly results from the different species present at the two sampling cruises. The larval fish assemblage is closely correlated with the chlorophyll *a*, nutrients, and zooplankton, suggesting food availability is important in the distribution pattern of larval fish, particularly after the passage of the typhoon.

List of abbreviations

South China Sea Surface Current (SCSSC); Kuroshio Branch Current (KBC); Ocean Research Institute (ORI); Sørensen similarity index (SI); non-metric multi-dimensional scaling (MDS); similarity percentage (SIMPER); canonical correspondence analysis (CCA)

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