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Community Structure of Larval Fishes from the Southeastern Taiwan Strait: Linked to Seasonal Monsoon-driven Currents

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Hung-Yen Hsieh, Wen-Tseng Lo, and Long-Jing Wu (2012) Community structure of larval fishes from the southeastern Taiwan Strait: linked to seasonal monsoon-driven currents. *Zoological Studies* **51**(5): 679-691. This study analyzed the spatiotemporal patterns of larval fish assemblages in relation to hydrographic conditions during 2 distinct monsoon seasons (Sept. 2009 vs. Apr. 2011) in the southeastern Taiwan Strait. In total, 128 taxa of larval fishes belonging to 76 genera and 61 families were identified. Larvae collected in the study were a combination of neritic and oceanic species. The Clupeidae, Siganidae, Bregmacerotidae, Myctophidae, and Trichiuridae were the 5 most dominant families. *Encrasicholina heteroloba* (13.7%) and *Sardinops* sp. (26.3%) were the most abundant taxa in Sept. and Apr., respectively. Larval fish assemblages showed significant seasonal and spatial differences. The distribution pattern of larval fish assemblages was closely linked to local hydrographic conditions, with high abundances in Apr. and at inshore stations. The mechanism of spring spawning of coastal fishes and the input of rich nutrients from the southwestern coast of Taiwan may be 2 important factors affecting the distribution of larval fish assemblages in the study area. Some oceanic larvae, such as *Sigmops gracilis* and *Vinciguerria nimbaria*, may also be carried by the penetrating Kuroshio Branch Current driven by the seasonal monsoon from waters east of Taiwan into the southeastern Taiwan Strait.
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Key words: Larval fish, Composition, Monsoon, Kuroshio, Taiwan Strait.

The Taiwan Strait (TS), a shallow channel sandwiched between southeastern China and the island of Taiwan which connects the East and South China Seas, serves as a pathway for faunal exchange between these 2 waters on the margin of the western North Pacific. Wind patterns in this region are determined by the typical East Asian monsoon, i.e., the northeasterly monsoon during winter (Oct.-Mar.) and the southwesterly monsoon during summer (May-Aug.). Three main currents, the China Coastal Current (CCC), Kuroshio Branch Current (KBC), and South China Sea Warm Current (SCSWC), affect hydrographic conditions in the TS (Jan et al. 2002 2006). In winter, the northeasterly monsoon usually drives the colder and fresher CCC which flows southward along the coast of China into the northern and central TS, and consequently holds back the northward intrusion of the warm and highly saline KBC through the Luzon Strait into the southeastern TS (Jan et al. 2010). When the northeasterly monsoon weakens in late winter and spring, the blocked KBC is then released and intrudes into the TS (via the Penghu Channel) and along the coast of southwestern Taiwan. When the southwesterly monsoon prevails in summer, the KBC does not enter the TS; instead, the monsoon-

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driven northeasterly flowing currents on the continental shelf of southern China push the less-saline SCSWC to penetrate into the TS, gradually replacing the KBC (Jan et al. 2002).

Distribution patterns of larval fish assemblages are quite complex in tropical and temperate continental shelf waters worldwide (Young et al. 1986, Doyle et al. 1993, Olivar et al. 2010). Investigations of assemblages of larval fishes help elucidate their early life history strategies, and also reveal characteristics and short-term biological properties of different water masses (Sherman et al. 1984, Doyle et al. 1993, Moser and Smith 1993). Many larval fish assemblages in shelf waters undergo significant temporal changes in composition, particularly on a seasonal basis, with many taxa and distinct groups occurring only at specific times of the year (Walker et al. 1987, McGowen 1993). The composition of larval fish assemblages varies spatially and temporally because of the behavior of larvae (Gray and Miskiewicz 2000), and due to oceanographic transport and mixing processes (Auth 2008, Muhling et al. 2008). Most previous studies on larval fish communities mainly focused on how biological processes such as food availability, timing and location of spawning, predator stocks, and behavior regulate the distribution and abundance of larval fishes (Young et al. 1986, Doyle et al. 1993, Moser and Smith 1993, Somarakis et al. 2006, Olivar et al. 2010). However, relationships between larval fish assemblages and biological-physical processes are considered to be more important in ecosystem-based fishery management and fishery-independent stock assessments than purely biological forcing mechanisms (Sabatés et al. 2004, Bakun 2006, Olivar et al. 2010).

Research on the structure of larval fish communities in the TS has progressively developed in the last 2 decades. However, most previous studies were concentrated in the northern TS, estuarine and coastal waters of western Taiwan, or the entire waters of the TS. In contrast, investigations of larval fish communities, particularly those focused on the southeastern TS, are scarce. In coastal waters of northern Taiwan, Tzeng and Wang (1993) and Chang et al. (2002) reported that the distribution dynamics of larval fish mostly conform to local hydrographic conditions such as coastal currents and geographic gradients, but their relationships with plankton and copepods varied temporally and spatially (Hsieh and Chiu 2002). The succession of water masses induced by monsoon systems and rich nutrients due to frontal turbulence and topographic upwelling may determine distributions of the abundances and compositions of larval fishes (Hsieh et al. 2011a). In estuarine waters of the west coast of Taiwan, Tzeng et al. (2002) found that monsoon-driven coastal currents may influence the seasonal dispersal patterns of larval fish assemblages, and larval fish communities were generally more diverse in spring-autumn than in winter. The temporal succession and spatial segregation of sympatric clupeoid larvae may lead to avoidance or reduced competition for habitat and thus to maximized utilization of resources in the waters off the Tanshui River estuary (Wang and Tzeng 1997). In the TS, compositions and abundances of copepods and larval fishes are closely related to oceanic variables, which in turn, are heavily influenced by the monsoons (Hsieh et al. 2005). Distribution patterns of larval fish assemblages are closely linked to the dynamic nature of water currents, and high abundances of larval fishes are generally restricted to a topographic upwelling area and well-matched the abundances of phyto- and zooplankton (Lo et al. 2010, Hsieh et al. 2011b).

Coastal waters of southwestern Taiwan are one of the most important fishing grounds around Taiwan. The objectives of this study were to investigate the abundance, composition, and distribution of the larval fish community in the southeastern TS and its relationship with local hydrographic conditions between the 2 distinct monsoon seasons.

MATERIALS AND METHODS

Data collection

Sampling of larval fishes in the southeastern TS was carried out during 2 cruises of the R/V *Hai-Fu* on 21-23 Sept. (late summer) 2009 and 7-8 Apr. (spring) 2011 (Fig. 1). Zooplankton samples were collected at 10 stations in the daytime using a 6 m-long Ocean Research Institute net with a 1.6-m mouth diameter, a 330-μm mesh size, and a Hydro-Bios flow meter (Hydro-Bios, Kiel, Schleswing-Holstein, Germany) placed in the mouth of the net. The net was towed obliquely at approximately 1 m/s from 100 m (or 10 m above the bottom at stations with a depth of < 100 m) to the surface. Zooplankton samples were immediately preserved in 5% seawater-buffered formalin. Prior to zooplankton sampling, the temperature and salinity at each station were recorded with a General Oceanics SeaBird CTD (SEB-911 Plus, Bellevue, Washington, USA). Vertical water samples for chlorophyll (chl)-*a* and nutrient (phosphate, silicate, and nitrite-nitrate combined) concentrations were collected at 5-, 25-, 50-, and 75-m depths using Go-Flo bottles, and the value of chl-*a* at each station was represented by calculating the average concentration in the upper 75 m. In the laboratory, larval fishes were sorted, preserved in 70% alcohol after sorting, and identified to the lowest taxonomic level possible based on their morphological characteristics according to Leis and Rennis (1983), Ozawa (1986), Okiyama (1988), Leis and Trnski (1989), and Neira et al. (1998). In addition, all samples were repeatedly subdivided until the number of individuals remaining in the last subsample was 1000-2000 or fewer, from which the abundance of zooplankton was calculated.

Statistical analysis

Spatial 2D-maps of temperature, salinity, chl-*a*, total fish larval abundance, species number, Shannon-Wiener diversity index (Shannon and Weaver 1963), Pielous's evenness index J' (Pielou 1966), and zooplankton abundance were obtained with SURFER 8.01 software. Abundances of larval fishes and zooplankton were standardized to numbers of individuals (ind.) per 1000 and 100 m^3, respectively. The Shannon diversity index (H') (Shannon and Weaver 1963) and J' (Pielou 1966) were calculated to assess the diversity of larval fishes in the samples. The non-parametric Mann-Whitney *U*-test was selected to test for seasonal differences in abundance and diversity (Mann and Whitney 1947). The Sørensen similarity index (SI) of larval fishes between sampling seasons and among locations 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 structure, a cluster analysis was performed with the PRIMER-6 software package. 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) and ordinated by non-metric multi-dimensional scaling (MDS) (Kruskal and Wish 1978). SIMPER (similarity percentage analysis) was used to examine the contribution of taxa to average similarities within different larval fish assemblages (Clarke 1993). Finally, relationships between biotic (chl-*a* and zooplankton) and abiotic (temperature, salinity, phosphate, silicate, and nitrite-nitrate combined) matrices were explored through the BIOENV procedure by maximizing Spearman's rank correlations (r_s) between a similarity matrix (of Bray-Curtis similarities) of the abundance of larval fishes and a matrix (of Euclidean distances) of environmental similarities based on normalized selected variables (Clarke and Ainsworth 1993).

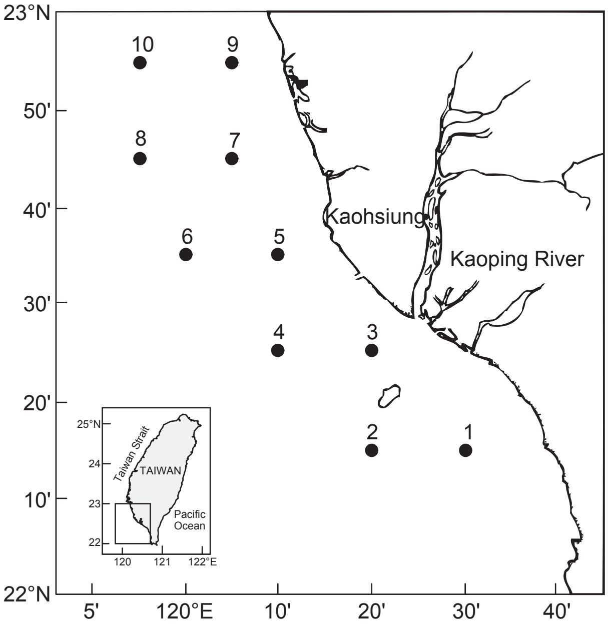

Fig. 1. Topography and sampling grid of the surveyed area in Sept. 2009 and Apr. 2011.

RESULTS

Hydrographic conditions

Satellite images showed different patterns of the horizontal distribution of sea surface temperatures during the study period (Fig. 2). In Sept., high-temperature waters were widely distributed in the TS; conversely, western and eastern portions of the TS were respectively controlled by the cold CCC and warm KBC in Apr. The seawater at 10 m in depth in the southeastern TS showed clear seasonal changes in temperature (Mann-Whitney *U*-test, $U = 0$, $p < 0.001$) and salinity (Mann-Whitney *U*-test, $U = 0$, $p < 0.001$, Table 1). In Sept. the temperature ranged 29.07-

29.97°C, compared to Apr. when it ranged 22.76-24.30°C; while salinity varied 33.43-33.58 psu in Sept. and 34.10-34.50 psu in Apr. No significantly spatial differences in temperature (Mann-Whitney *U*-test, $U = 34$, $p = 0.226$) or salinity (Mann-Whitney *U*-test, $U = 48$, $p = 0.880$) were observed between inshore and offshore stations (Table 1), but comparatively lower temperatures and salinities were recorded in inshore waters in our study (Fig. 3). The isotherms displayed a northwest-southeast gradient, and temperatures gradually increased with the offshore distance.

The distribution of chl-*a* concentrations (the average concentration of the top 75 m) showed a trend opposite to those of temperature and salinity, with higher values generally found in nearshore waters (Mann-Whitney *U*-test, $U = 16$, $p < 0.05$, Table 1, Fig. 4). Notably, the highest chl-*a* concentration was recorded at station 3 (0.446 μg/L) adjacent to the estuary of the Kaoping River in Sept.; in Apr., the highest value was found at northern station 9 (0.829 μg/L). Concentrations of phosphate and silicate showed significant differences between seasons. Phosphate concentrations were significantly higher in Apr. than in Sept. (Mann-Whitney *U*-test, $U = 17$, $p < 0.05$), and the opposite was observed for silicate concentrations (Mann-Whitney *U*-test, $U = 20.5$, $p < 0.05$, Table 1). In addition, slightly higher phosphate concentrations were found at

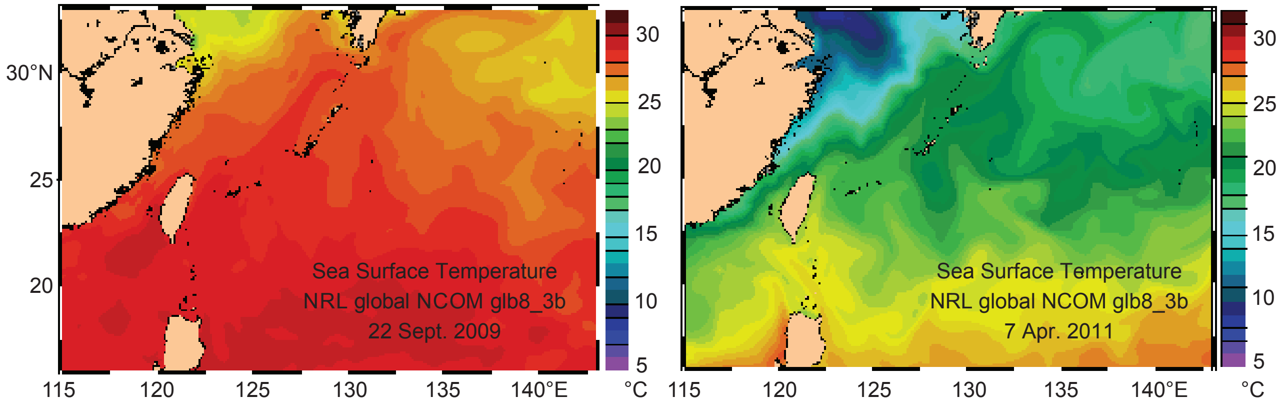

Fig. 2. Satellite images of sea surface temperature (SST, °C) around Taiwan on 22 Sept. 2009 and 7 Apr. 2011. (Data are from the 1/8° global Navy Coastal Ocean Model of the U.S. Naval Research Laboratory).

Table 1. Mean values (mean ± S.E.) of abundance, species number, species diversity (H'), and species evenness (J') of larval fishes, and temperature (10 m), salinity (10 m), chlorophyll *a* (average concentration at 0-75 m), nutrients (average concentrations at 0-75 m), and zooplankton abundances at different sampling times and locations in waters southwest of Taiwan

	Time		Station	
	Sept. 2009	Apr. 2011	Inshore (Stns. 1, 3, 5, 7, 9)	Offshore (Stns. 2, 4, 6, 8, 10)
Abundance (ind./1000 m^3)	22 ± 7	390 ± 142**	318 ± 152	94 ± 41
Species number	12 ± 1	15 ± 2	14 ± 1	13 ± 2
H'	2.21 ± 0.07	2.05 ± 0.21	2.17 ± 0.11	2.09 ± 0.19
J'	0.91 ± 0.02	0.77 ± 0.08	0.84 ± 0.04	0.84 ± 0.07
Temperature (°C)	29.57 ± 0.10	23.61 ± 0.17***	26.37 ± 1.03	26.81 ± 0.97
Salinity (psu)	33.51 ± 0.02	34.29 ± 0.04***	33.87 ± 0.12	33.92 ± 0.15
Chlorophyll *a* (μg/L)	0.07 ± 0.04	0.20 ± 0.08	0.23 ± 0.08	0.05 ± 0.02*
NO_2+NO_3 (μg/L)	13.47 ± 3.41	7.53 ± 1.47	12.59 ± 3.63	8.40 ± 1.26
PO_4 (μg/L)	3.48 ± 0.26	6.58 ± 0.83*	5.96 ± 0.86	4.11 ± 0.61*
SiO_2 (μg/L)	77.30 ± 9.12	23.34 ± 4.59*	55.55 ± 12.77	45.09 ± 9.83
Zooplankton (ind./100 m^3)	1891 ± 280	5511 ± 2550	5696 ± 2528	1707 ± 179**

* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$, significantly differ by the Mann-Whitney *U*-test.

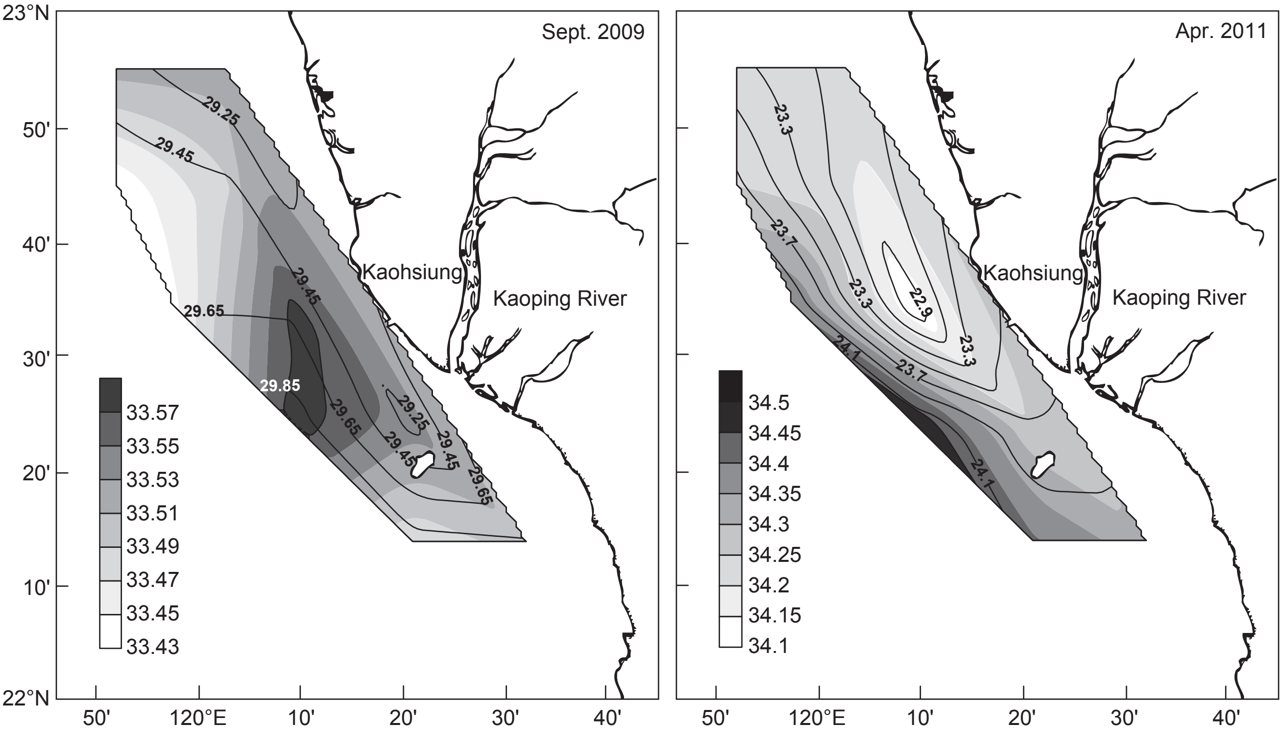

Fig. 3. Seawater temperatures (black lines) and salinities (gray scales) at 10 m in depth in Sept. 2009 and Apr. 2011.

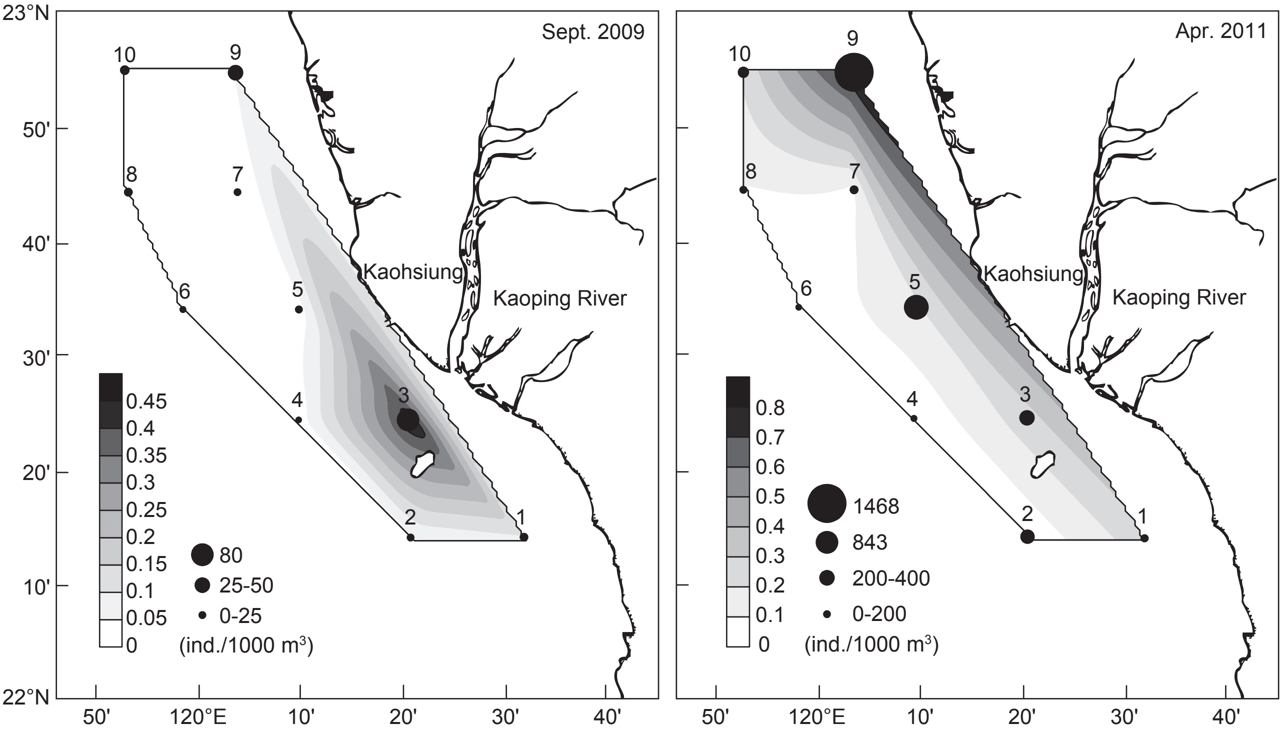

Fig. 4. Chlorophyll *a* concentrations (μg/L) (average concentration in the upper 75 m) (gray scales) and abundances (individuals (ind.)/1000 m^3) of larval fishes (solid circles) in Sept. 2009 and Apr. 2011.

inshore stations than at offshore stations (Mann-Whitney *U*-test, $U = 23$, $p < 0.05$, Table 1).

Abundances of larval fishes and zooplankton

The abundance of larval fishes was significantly higher in Apr. than in Sept. (Mann-Whitney *U*-test, $U = 4$, $p < 0.01$), but there were no significant seasonal differences in number (Mann-Whitney *U*-test, $U = 30$, $p = 0.128$), diversity (Mann-Whitney *U*-test, $U = 42.5$, $p = 0.571$), or evenness (Mann-Whitney *U*-test, $U = 38$, $p = 0.364$) of species (Table 1). The mean abundances in Sept. and Apr. were 22 ± 7 (mean ± S.E.) and 390 ± 142 ind./1000 m^3, respectively, and ranged 5-1468 ind./1000 m^3 in both seasons. The highest abundance was found at station 9 in Apr. In a comparison of spatial differences in sampling stations, the abundance (Mann-Whitney *U*-test, $U = 34$, $p = 0.226$), number (Mann-Whitney *U*-test, $U = 35.5$, $p = 0.270$), diversity (Mann-Whitney *U*-test, $U = 48$, $p = 0.880$), and evenness (Mann-Whitney *U*-test, $U = 31$, $p = 0.151$) of larval fishes did not significantly differ between inshore and offshore stations. Even so, comparatively higher abundances of larval fishes were observed at inshore stations in both seasons (Table 1, Fig. 4). On the other hand, the horizontal distribution of zooplankton abundances showed a decreasing gradient towards offshore stations (Mann-Whitney *U*-test, $U = 14$, $p < 0.01$), with a mean abundance of 5696 ± 2528 ind./100 m^3 for inshore and 1707 ± 179 ind./100 m^3 for offshore stations; but there was no significant difference between the seasons (Mann-Whitney *U*-test, $U = 28$, $p = 0.096$, Table 1).

Compositions of larval fishes

In total, 128 taxa of larval fishes were identified in this study, belonging to 76 genera and 61 families. Among the 61 families, only 18 exceeded 1% of the total larval fish catch. Over 1/2 (35/61) of families were represented by a single taxon. Larvae of the families Clupeidae, Siganidae, Bregmacerotidae, Myctophidae, and Trichiuridae were the most abundant, accounting for 59% of total fish larvae. Among these families, the Myctophidae had the largest number of species (19). At the species level, *Sardinops* sp. was the most abundant species and constituted 24.9% of the total larval fishes collected, followed by *Siganus* sp. (8.4%), *Trichiurus lepturus* (6.3%), an unidentified Clupeidae (4.8%), and *Bregmaceros* spp. (4.6%), together comprising 49.0% of the total catch. The similarity of larval fish compositions between the 2 seasons was only 35% (calculated by similarity indices, data not shown), and the 10 predominant taxa significantly differed (Table 2). In Sept., the 5 most dominant taxa were *Encrasicholina heteroloba*, an unidentified Sparidae, *Cyclothone* spp., *Nuchequula nuchalis*, and *Equulites rivulatus*; in Apr., they were *Sardinops* sp., *Siganus* sp., *T. lepturus*, an unidentified Clupeidae, and *Bregmaceros* spp. In addition, compositions of larval fishes between inshore and offshore stations also significantly differed, with a similarity of only 40% (data not shown). *Sardinops* sp., *T. lepturus*, an unidentified Clupeidae, *Bregmaceros* spp., and an unidentified Carangidae were abundant at inshore stations; while, *Siganus* sp., *Sardinops* sp., *Lutjanus* spp., *Lampanyctus* sp. 7, and *Vinciguerria nimbaria* dominated offshore stations (Table 2).

Larval fish assemblages

A seasonal structure in which stations of the same season clustered together was derived from the hierarchical clustering and MDS by analyzing species compositions of larval fishes (Fig. 5). Two main groups of larval fish were defined by a cluster analysis at the 5% similarity level. These station groups were denoted according to their major season of occurrence as “spring” and “late summer”. Meanwhile, species contributing to similarities within the larval fish assemblages are shown in table 3. The spring group was represented by all Apr. stations and 1 Sept. station (stn. 3). The dominant larval fish taxa in this station group were an unidentified Clupeidae, an unidentified Carangidae, *Scomber australasicus*, *E. heteroloba*, and an unidentified Sparidae. Two commercial species, *Gempylus serpens* and *Decapterus macarellus*, and 1 mesopelagic taxon, *Cyclothone* spp., were the most important taxa in this group, with percentage contributions of 13%-18%. The late-summer group was comprised of 9 Sept. stations. This group was dominated mainly by *Sardinops* sp., *Siganus* sp., *T. lepturus*, *Bregmaceros* spp., and *Lampanyctus* sp. 7. Among these taxa, *Bregmaceros* spp., *Lampanyctus* sp. 7, and *T. lepturus* had the higher contributions, respectively contributing 19.7%, 11.9%, and 11.2% to the within-group similarity. In addition, the oceanic and mesopelagic species, *V. nimbaria*, was also important in this group, with a percentage contribution of 16.7%.

Relations of larval fish compositions and environmental variables

Results of the BIOENV analysis showed that the combination of 4 variables (temperature, salinity, phosphate, and zooplankton) best explained the relationship between environmental and biotic ordinations (Spearman's rank correlation, $n = 20$, $r_s = 0.528$, $p < 0.05$, Table 4). The single variable which yielded the best rank correlation between matrices was salinity ($r_s = 0.492$). Log values of larval fish abundances showed significant negative correlations with seawater temperature and positive correlations with salinity, phosphate, and log (zooplankton abundance) (Fig. 6). These results indicated that seasonal changes in temperature, salinity, and food availability play important roles in determining distributions of larval fishes in the study area.

DISCUSSION

Hydrographic conditions in the southeastern TS are strongly influenced by the monsoon-driven KBC and SCSWC (Jan et al. 2002 2006 2010). During the northeasterly monsoon in winter, the KBC, carrying high-temperature and high-salinity water, flows northward through the Penghu Channel into the southeastern TS. In summer, the southwesterly monsoon prevails, and the warm low-salinity SCSWC flows northeasterly, replacing the KBC, and intrudes into the southern East China Sea where it dominates summer oceanic conditions of the TS. The alternation of hydrographic conditions in the study area may greatly affect distribution patterns and succession of larval fish communities and the entire ecosystem on a seasonal scale. Considering the contrasting hydrography of the southeastern TS between

Table 2. Mean (mean ± S.E., individuals/1000 m^3) and relative abundances (RAs, %) of the 10 predominant taxa of larval fishes at different sampling times and locations in waters southwest of Taiwan

Sept. 2009	Mean ± S.E.	RA	Apr. 2011	Mean ± S.E.	RA
Encrasicholina heteroloba	3 ± 2	13.72	*Sardinops* sp.	102 ± 89	26.30
Sparidae gen. spp.	1 ± 1	5.51	*Siganus* sp.	35 ± 35	8.87
Cyclothone spp.	1 ± 0	4.55	*Trichiurus lepturus*	26 ± 20	6.68
Nuchequula nuchalis	1 ± 1	3.79	Clupeidae gen. sp.	20 ± 16	5.03
Equulites rivulatus	1 ± 1	3.45	*Bregmaceros* spp.	19 ± 14	4.76
Gempylus serpens	1 ± 0	3.08	Carangidae gen. spp.	16 ± 16	4.12
Decapterus macarellus	1 ± 0	2.99	*Lampanyctus* sp. 7	10 ± 7	2.64
Sillago japonica	1 ± 1	2.88	*Auxis rochei*	10 ± 9	2.54
Trachinocephalus myops	1 ± 0	2.79	*Vinciguerria nimbaria*	8 ± 5	2.08
Gobiidae gen. spp.	1 ± 0	2.51	*Bregmaceros* sp. 3	7 ± 6	1.73
Total		45.27	Total		64.75

Inshore (Stns. 1, 3, 5, 7, 9)	Mean ± S.E.	RA	Offshore (Stns. 2, 4, 6, 8, 10)	Mean ± S.E.	RA
Sardinops sp.	90 ± 90	28.32	*Siganus* sp.	35 ± 35	36.85
Trichiurus lepturus	26 ± 20	8.10	*Sardinops* sp.	12 ± 12	13.28
Clupeidae gen. sp.	19 ± 16	6.04	*Lutjanus* spp.	4 ± 4	4.69
Bregmaceros spp.	17 ± 14	5.28	*Lampanyctus* sp. 7	3 ± 1	3.47
Carangidae gen. spp.	16 ± 16	5.12	*Vinciguerria nimbaria*	3 ± 1	3.18
Auxis rochei	9 ± 9	2.98	*Bregmaceros* spp.	2 ± 1	2.35
Lampanyctus sp. 7	7 ± 7	2.24	*Trachinocephalus myops*	2 ± 1	2.23
Bregmaceros sp. 3	7 ± 6	2.16	*Diaphus* sp. 5	2 ± 1	2.19
Scomber australasicus	6 ± 4	1.88	Tetraodontidae gen. sp.	2 ± 2	1.84
Champsodon sp.	6 ± 6	1.83	Myctophidae gen. spp.	2 ± 1	1.65
Total		63.95	Total		71.73

the northeasterly and southwesterly monsoons, we anticipated that larval fish assemblages off southeastern TS would reflect this switching of hydrographic conditions between the 2 seasons.

Coastal areas often constitute favorable habitats for early life stages of fishes living in different marine ecosystems (McGowen 1993). Oceanographic data show that river runoff from the southwestern coast of Taiwan brings rich nutrients into the southeastern TS. Accordingly, nutrient inputs result in phytoplankton blooms in coastal waters as represented by higher chl-*a* concentrations, and ultimately increase the abundance of zooplankton. According to results of the BIOENV analysis, we noted that zooplankton abundances were one of the major factors that best explained the relationship between hydrographic conditions and larval compositions. Furthermore, the abundances and distributions of larval fishes in both seasons well matched the distribution pattern of chl-*a* concentrations and zooplankton abundances. A similar association of larvae of the Engraulidae and Myctophidae with increased plankton production was also reported off the northwestern US coast (Doyle et al. 1993).

Generally, spring is a crucial period for the

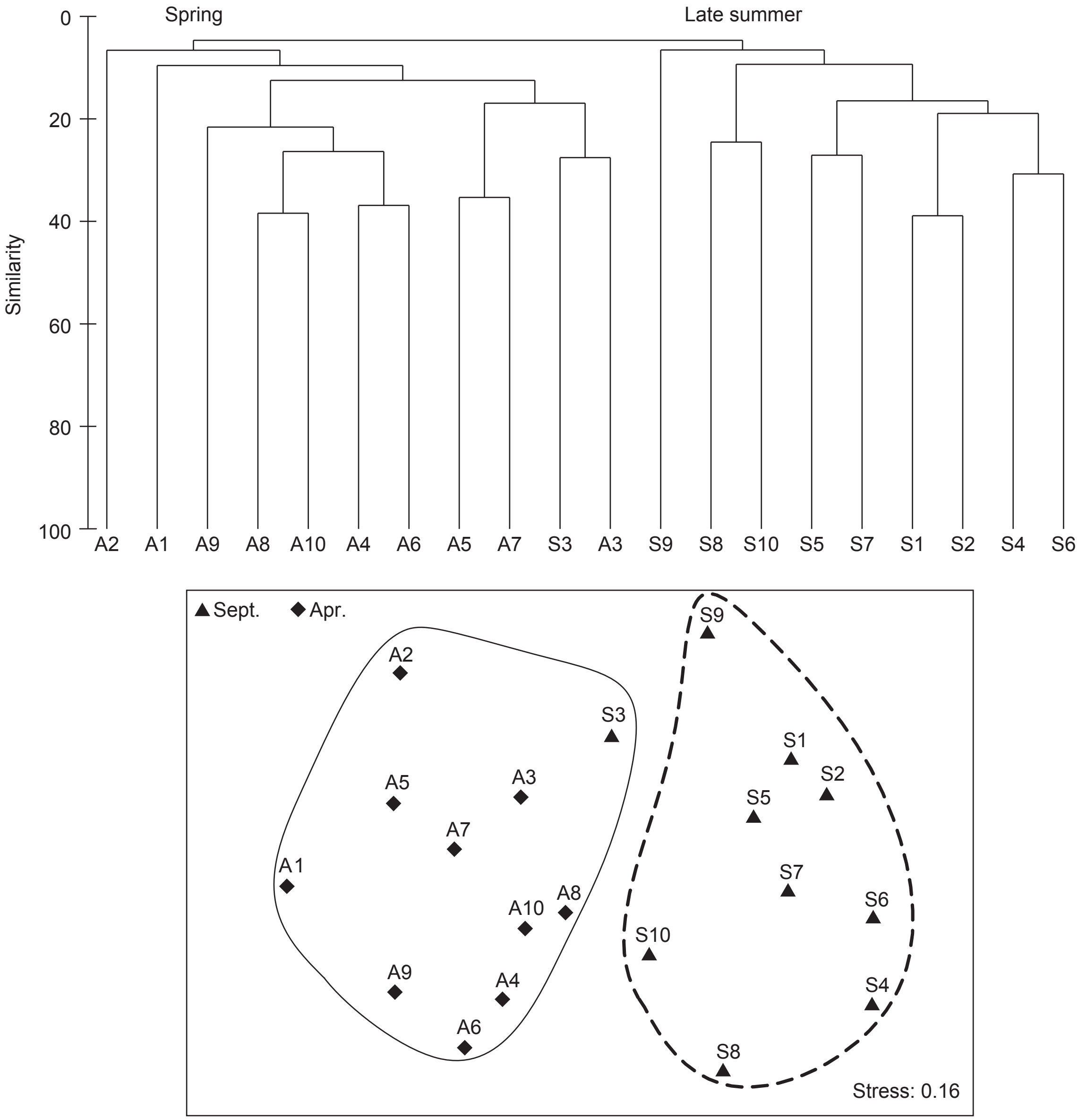

Fig. 5. Cluster dendogram and 2-dimensional MDS ordination of the Bray-Curtis similarity, based on a matrix of log(x+1)-transformed abundances of larval fishes at each station in Sept. 2009 and Apr. 2011. A, Apr.; S, Sept.

reproductive success of fishes (Bruno et al. 2001, Sabatés et al. 2007). In this study, many coastal spring-spawning fishes also reached maximum abundances during the Apr. sampling period. The high abundances of some larval fish taxa, such as *E. heteroloba*, *Sardinops* sp., *T. lepturus*, and an unidentified Clupeidae, can likely be linked to the spread of floating eggs synchronized with primary production and cycles of zooplankton. Thus, we suggest that food availability may be important in the seasonal distribution patterns of larval fishes in the southeastern TS.

According to previous studies on waters around Taiwan, Hsieh et al. (2011a) and Su et al. (2011) proposed that the timing of spawning of most important commercial fishes, such as *E.*

Table 3. Mean abundances (mean ± S.E., individuals/1000 m^3) and percentage contributions of predominant larval fish taxa to the average similarity within the 2 larval fish assemblages (from Fig. 5, values in parentheses are the mean percent similarity), as determined by a SIMPER analysis with a cutoff for low contributions at 90%

	Spring (14.0)			Late summer (15.3)	
	Mean ± S.E.	Contribution (%)		Mean ± S.E.	Contribution (%)
Gempylus serpens	0.6 ± 0.2	17.7	*Bregmaceros* spp.	20.2 ± 15.7	19.7
Decapterus macarellus	1.0 ± 0.4	14.4	*Vinciguerria nimbaria*	9.0 ± 5.0	16.7
Cyclothone spp.	1.3 ± 0.5	13.3	*Lampanyctus* sp. 7	11.4 ± 7.6	11.9
Trachinocephalus myops	0.6 ± 0.4	6.7	*Trichiurus lepturus*	28.5 ± 22.1	11.2
Coryphaena hippurus	0.2 ± 0.1	6.7	Scorpaenidae gen. sp.	4.2 ± 3.1	5.1
Benthosema pterotum	0.3 ± 0.1	6.5	Gobiidae gen. spp.	4.6 ± 3.1	4.4
Gobiidae gen. spp.	0.9 ± 0.4	6.3	*Diaphus* sp. 5	4.9 ± 2.7	4.2
Encrasicholina heteroloba	2.7 ± 2.0	5.4	*Sardinops* sp.	113.8 ± 99.2	3.0
Benthosema fibulatum	0.2 ± 0.1	3.2	*Trachinocephalus myops*	2.7 ± 1.4	2.8
Bregmaceros spp.	0.8 ± 0.4	2.9	*Apogon* spp.	6.1 ± 3.9	1.7
Sparidae gen. spp.	1.8 ± 1.0	2.1	*Decapterus* spp.	5.8 ± 5.2	1.7
Carangidae gen. spp.	14.4 ± 14.1	2.1	*Sigmops gracilis*	0.8 ± 0.4	1.6
Ceratoscopelus warmingi	0.7 ± 0.4	1.6	*Leptostomias* sp.	1.1 ± 0.9	1.4
Maurolicus sp.	0.1 ± 0.1	1.4	*Bregmaceros* sp. 3	7.5 ± 6.4	1.3
			Myctophidae gen. spp.	1.7 ± 1.1	1.0
			Diaphus spp.	4.8 ± 3.4	1.0
			Bleekeria mitsukurii	4.3 ± 3.3	1.0
			Lutjanus spp.	5.4 ± 4.8	0.9
Total		90.2	Total		90.5

Table 4. Correlations of larval fishes with environmental variables in waters southwest of Taiwan in Sept. 2009 and Apr. 2011, according to the BIOENV routine

Correlation with each variable	Correlation value
1. Temperature	0.468
2. Salinity	0.492
3. Chlorophyll *a*	0.208
4. $NO_2 + NO_3$	-0.037
5. PO_4	0.285
6. SiO_2	0.076
7. Zooplankton	0.144
Best combination of one or more variables	1, 2, 5, 7 $r_s = 0.528$ $p = 0.01$*

*Significant at < 5%.

heteroloba, *Scomber* sp. 1, *Scomber* sp. 2, and *T. lepturus*, may be synchronized with seasonal plankton blooms. This finding was consistent with results of the present study. Similarly, in the northwestern Mediterranean Sea, Sabatés (1990) and Koutrakis et al. (2004) proposed that larvae of some coastal fishes feed on abundant plankton in the spring bloom and grow rapidly through the early summer. Peaks in larval fish abundances in the central Mexican Pacific Ocean coincided with primary and secondary production patterns and reproductive seasonality of the fish community (Franco-Gordo et al. 2001 2008), corroborating that the spawning strategies of fish populations evolved in synchrony with prevailing oceanographic processes. Also, the development of the subsurface chl-*a* maximum during the spring-summer stratification period and the associated high zooplankton biomass offers an important food source for larval fishes in the northwestern Mediterranean Sea (Sabatés et al. 2007).

Larval fishes collected during this investigation are a combination of neritic and oceanic species. Compositions of the larval fish communities between the 2 seasons were dissimilar, with a similarity of only 35%. Results demonstrated that temporal compositions of the larval fish community in the southeastern TS changed between the distinct monsoon seasons. *Encrasicholina heteroloba*, an important commercial fish in coastal waters off Taiwan from May to Sept., particularly in

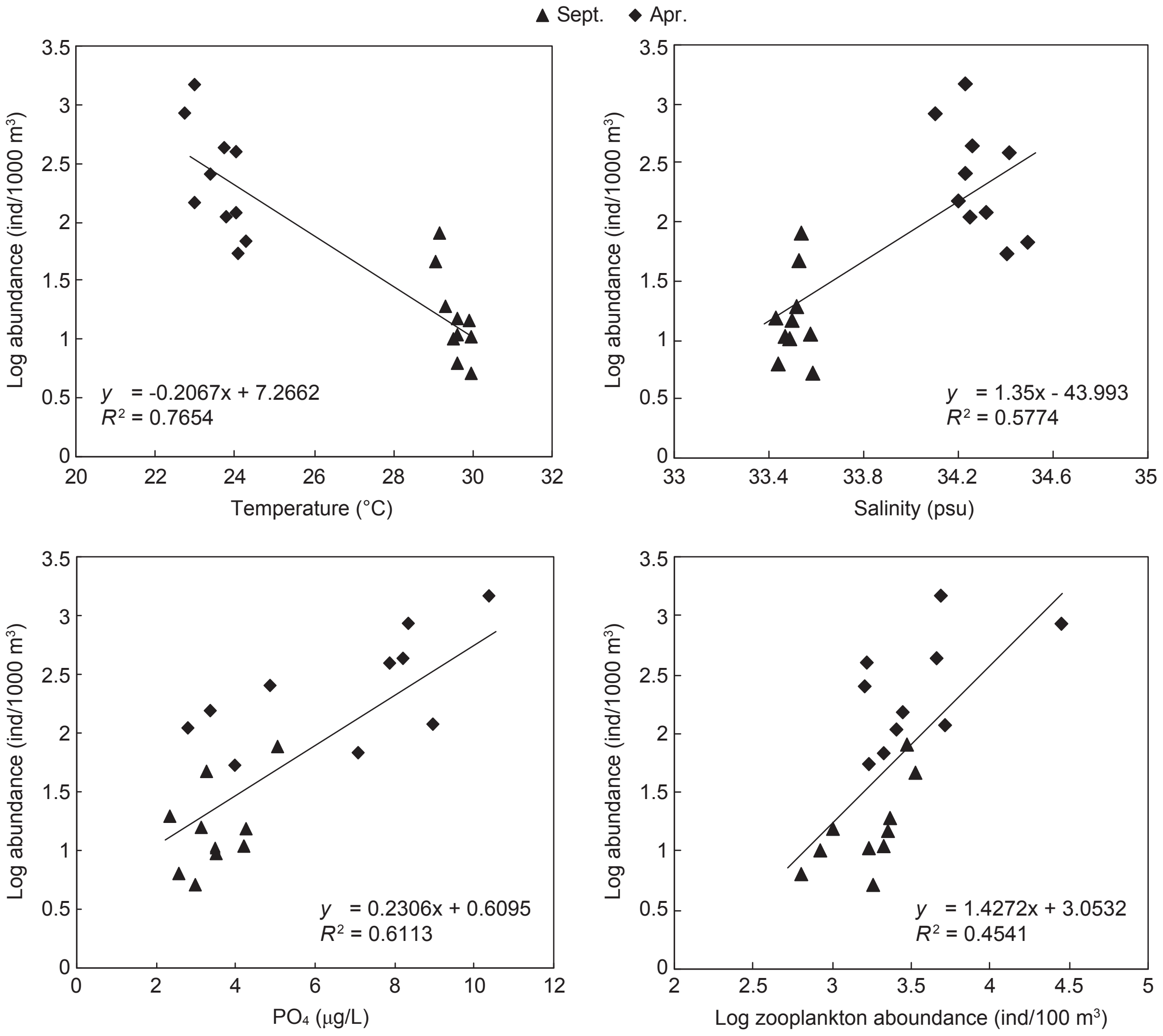

Fig. 6. Correlations of larval fish abundances and 4 environmental variables (temperature, salinity, phosphate, and zooplankton abundance).

the northeast and around the Penghu Is. (Huang and Chiu 1998), was the most dominant taxon in Sept. in this study. In coastal waters off the Tanshui River estuary in northern Taiwan, Wang and Tzeng (1997) observed that *E. heteroloba* exhibited a distinct temporal succession associated with seasonal temperature changes, with a peak abundance in early Oct. Hsieh and Chiu (2002) also found larvae of *E. heteroloba* to be abundant in the northern TS in summer. The timing of the occurrence of *E. heteroloba* larvae in the study area was similar to the above-described studies.

In Apr., *Sardinops* sp., *Siganus* sp., and *T. lepturus* were the 3 most dominant taxa. Among these 3 taxa, epipelagic commercial species, adults of the genus *Sardinops*, are mainly found inshore but also occur in oceanic waters, hundreds of kilometers from land (Whitehead et al. 1988). Syahailatua et al. (2011) proposed that *Sardinops sagax* could serve as an abundant and general marker of inner-shelf waters. In our study, *Sardinops* sp. was mainly recorded at inshore stations, which was also consistent with a study by Wang and Tzeng (1997), who noted that *Sardinops* spp. had a peak abundance in May and were mainly distributed at water depths of 10-20 m in coastal waters off the Tanshui River estuary of northern Taiwan. Juveniles of the genus *Siganus* are mainly found in mangrove areas and seagrass flats; adults remain in protected waters such as lagoons and bays in the vicinity of rocky substrata and reefs (Woodland 1997). However, in this study, larvae of *Siganus* sp. were only found at offshore station 2 in Apr. In addition, the important commercial fish, *T. lepturus*, is found throughout tropical and temperate waters of the world and is common in waters around Taiwan. Generally, adults of *T. lepturus* stay over muddy bottoms of shallow coastal waters and often enter estuaries (Nakamura and Parin 1993). Similarly, their larvae also mostly occurred in inshore coastal waters in the present survey.

In addition to the above-mentioned neritic taxa, larvae of some oceanic spawning fishes, such as *G. serpens*, *V. nimbaria*, and *Sigmops gracilis*, were also observed in this area. We speculated that these tropical-oceanic species, which originate in the KBC and/or SCSWC, may be carried to the subtropical-neritic southeastern TS by the northward advection of larvae and early juveniles. Previous studies by Nakabo (2002), Sassa et al. (2002), and Okazaki and Nakata (2007) found that *V. nimbaria* and *Sig. gracilis* mainly inhabit deeper oceanic waters, and their larvae are most abundant in Kuroshio waters and offshore oceanic water. Therefore, they usually are good indicators for intrusion of the KBC into the southeastern TS. These species together with coastal species can tolerate high temperatures and salinities and form a combined assemblage with high diversity in this study area. Also similar results were revealed by Lo et al. (2010) and Hsieh et al. (2011b). In the central Mexican Pacific, Franco-Gordo et al. (2003) found that during the transitional period between June and Dec., a high species richness of larval fishes was due to the mixing of tropical (from the Equatorial Countercurrent) and subtropical (from the California Current) species. Likewise, increasing zooplankton diversity due to mixing of Kuroshio and coastal assemblages was also observed in a coastal area in southern Japan (Noda et al. 1998).

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