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Comparison of Distribution Patterns of Larval Fish Assemblages in the Taiwan Strait between the Northeasterly and Southwesterly Monsoons

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Hung-Yen Hsieh, Wen-Tseng Lo, Long-Jing Wu, Dong-Chung Liu, and Wei-Cheng Su (2011) Comparison of distribution patterns of larval fish assemblages in the Taiwan Strait between the northeasterly and southwesterly monsoons. *Zoological Studies* **50**(4): 491-505. The objective of this study was to investigate the relationship between spatial patterns of larval fish assemblages and local hydrographic features during 2 distinct monsoon seasons (the northeasterly monsoon in winter vs. the southwesterly monsoon in summer) in the Taiwan Strait. In total, 234 taxa of larval fishes, belonging to 126 genera and 81 families, were identified. Families with higher numbers of species were the Myctophidae, Carangidae, Gobiidae, and Scombridae. Seasonal and spatial variations in larval fish assemblages were significant. Some species only occurred in a specific season with a peak abundance in some areas, for example, *Bleekeria mitsukurii*, *Benthosema pterotum*, *Trichiurus lepturus*, *Scomber* sp. 2, and *Scomber* sp. 1 dominated in winter, while *Encrasicholina punctifer*, *Auxis* sp., *Gunnellichthys* sp., *Selar crumenophthalmus*, and *Engraulis japonicus* were abundant in summer. The distribution pattern of larval fish assemblages was closely linked to the dynamic nature of the water currents in the study region, and high abundances of larval fish were generally restricted to a topographic upwelling area and well-matched with the abundances of phyto- and zooplankton. Food availability; therefore, may be an important factor affecting the distribution of larval fish assemblages in the Taiwan Strait. Intrusions of prevailing currents driven by seasonal monsoons may also transport different larval fish species, such as *Sigmops gracilis* and *Vinciguerria nimbaria*, from waters east of Taiwan into the Taiwan Strait. http://zoolstud.sinica.edu.tw/Journals/50.4/491.pdf

Key words: Larval fish composition, Monsoon, Water mass, Taiwan Strait.

Larval fish assemblages usually show considerably temporal and spatial scales of distribution in tropical and temperate continental shelf waters worldwide (Young et al. 1986, Doyle et al. 1993). Distribution patterns of larval fish communities, with respect to abundance and species composition, were traditionally a major issue of scientific research in fisheries oceanography (Govoni 2005). 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 special times of the year (Walker et al. 1987, McGowen 1993). Interactions between biological reactions and oceanographic processes determine the development and maintenance of larval fish assemblages by affecting the timing and location of spawning, larval mortality, advection, and behavior (Young et al. 1986, Doyle et al. 1993, Moser and Smith 1993, Hare et al. 2001). In addition, different assemblages are often representative of different water masses and currents, and membership in different assemblages and boundaries that separate assemblages can

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be static or dynamic (Doyle et al. 1993, Moser and Smith 1993).

The Taiwan Strait (TS), a shallow channel bounded by the southeastern Chinese coast on the west and the main island of Taiwan on the east, is an important pathway for the exchange of biota between the East (ECS) and South China Seas (SCS). East Asian monsoons and bathymetric topography are the 2 major forces influencing temporal and spatial variations in water masses and are associated with through-flow transport observed in the TS (Jan et al. 2002 2006 2010). The northeasterly monsoon (NEM), which prevails in winter, usually drives the cold, low-salinity, nutrient-rich China Coastal Current (CCC) which flows southward along the coast of China into the northern and central TS, and consequently holds back the northward intrusion of the Kuroshio Branch Current (KBC) through the Luzon Strait into the southeastern TS. When the NEM weakens in late winter and spring, the blocked KBC is then released and intrudes northward (via the Penghu Channel) into the ECS. In early summer, the southwesterly monsoon (SWM) begins to prevail, thus reducing the westward intrusion of the Kuroshio Current (KC), and forcing the SCS Surface Current (SCSSC) to penetrate into the TS, gradually replacing the KBC (Jan et al. 2002 2006 2010). Succession of these water masses driven by monsoons may potentially influence the distribution patterns of marine plankton (Hsieh et al. 2005, Hwang and Wong 2005, Hwang et al. 2006).

Research on the structure of larval fish communities and other groups of the zooplankton community in the TS has progressively developed in the last 2 decades. For example, Tzeng et al. (2002) found that monsoon-driven coastal currents may affect seasonal dispersal and communities of larval fishes in estuarine waters on the west coast of Taiwan, where species compositions of larval fish communities are more diverse in spring and autumn than in winter. Compositions and abundances of copepods and ichthyoplankton in the TS are closely related to oceanic variables, which, in turn, are heavily influenced by the monsoons (Hsieh et al. 2005). In coastal waters and estuaries of Taiwan, the distribution dynamics of larval fishes mostly conform to local hydrographic conditions, i.e., coastal currents and geographic gradients (Tzeng and Wang 1992 1993, Chang et al. 2002). Different stages of 3 dominant thaliacean species (*Doliolum denticulatum*, *Thalia democratic*, and *T. orientalis*) in southwestern Taiwan coastal waters had different preferences for water depth in different seasons, suggesting that the vertical distributions of these species might be related to reproduction and/or food (Tew and Lo 2005). The interactive effects of wastewater discharges and seawater intrusions are the main determinants of the community composition, distribution, and abundance of zooplankton in the Danshuei estuarine ecosystem of northern Taiwan (Hwang et al. 2010). The distribution patterns of larval fish assemblages were closely linked to hydrographic conditions and abundances of phyto- and zooplankton (Hsieh et al. 2010, Lo et al. 2010). In waters north of Taiwan, Hsieh et al. (2011) also found that 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.

This work is a part of the Taiwan Cooperative Oceanic Fisheries Investigation (TaiCOFI), a large-scale oceanographic and plankton survey around the island of Taiwan (21°-26°N, 119°-123°E) in Feb. and Aug. 2004, conducted by the Taiwan Fisheries Research Institute, Keelung, Taiwan. In this paper we identify and compare the taxonomic composition and abundance of larval fishes between the 2 distinct monsoon seasons and evaluate the persistence of distribution patterns of larval assemblages in relation to hydrographic conditions.

MATERIAL AND METHODS

Sample collection

Sampling of larval fishes in the TS was carried out during 2 cruises of the *R/V Fishery Researcher I* in winter (20-25 Feb., NEM) and summer (8-12 Aug., SWM) 2004. Among 32 stations, 15 were chosen for this study to analyze larval fish distributions (Fig. 1). Temperature and salinity at each station were recorded with a General Oceanic SeaBird CTD (SBE-911 Plus). Chlorophyll *a* (chl-*a*) concentrations at 5, 25, 50, 75, 100, and 150 m were measured from 1-L samples of seawater collected in Go-Flo bottles. Zooplankton samples were collected with a 6 m-long Ocean Research Institute (ORI) net with a 1.6-m mouth diameter and 330-μm mesh size. The water volume filtered through the net was calculated using a flow meter (Hydro-Bios) placed in the mouth of the net. The net was towed vertically at approximately 1 m/s from 200 m (or 10 m above the bottom at stations with a depth of < 200 m) to the surface. Zooplankton samples were immediately preserved in 5% seawater-buffered formalin. In the laboratory, each zooplankton sample was divided into 2 equal subsamples with a Folsom splitter. Larval fishes were sorted from 1 subsample, preserved in 70% alcohol after sorting, and identified to the lowest taxonomic level possible based on their morphological characteristics.

Data analysis

Current velocity and direction (data from the ocean databank of the National Center for Ocean Research, Taipei, Taiwan) in waters around Taiwan during the NEM and SWM are shown in

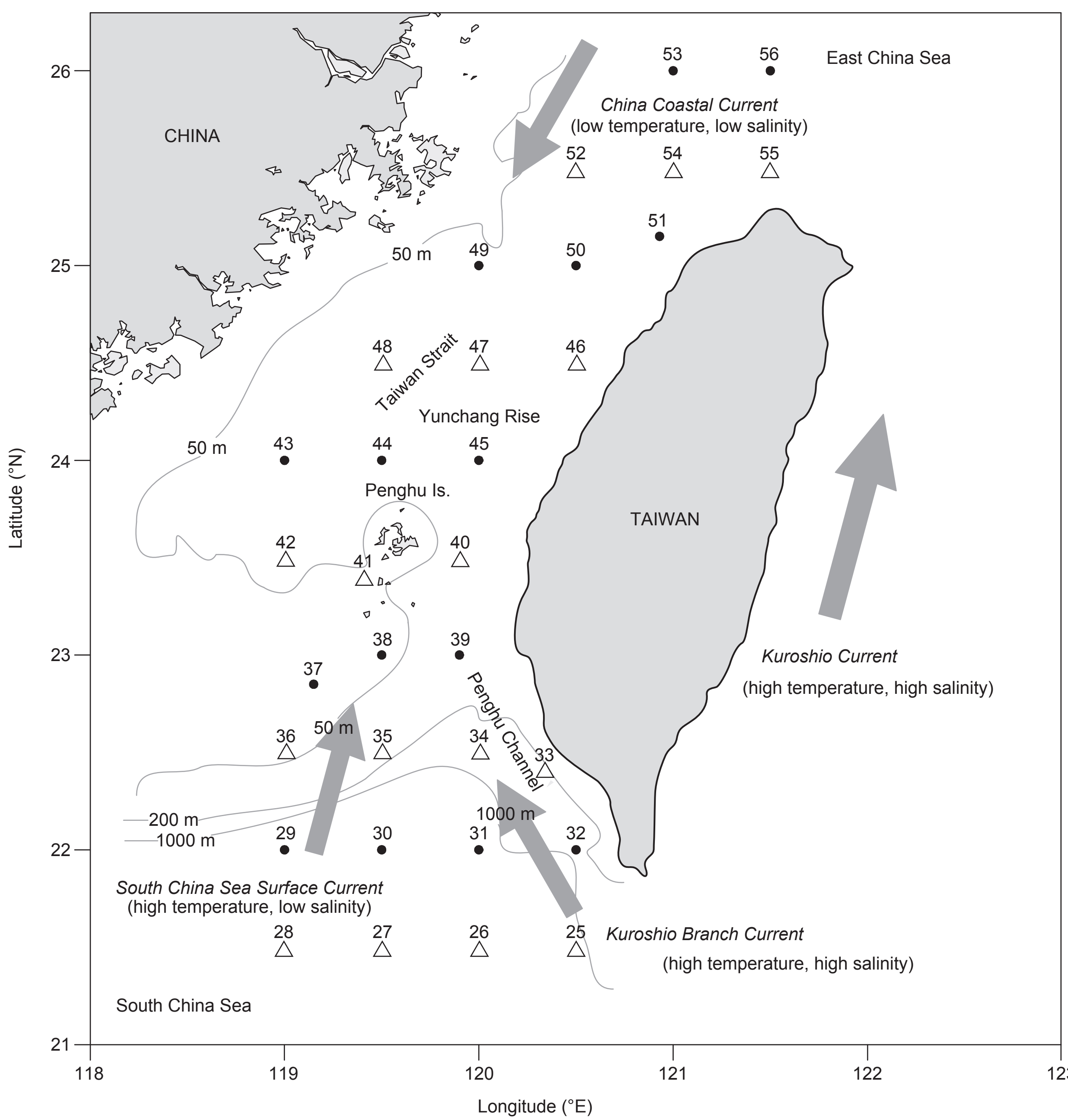

Fig. 1. Sampling stations in the Taiwan Strait. Triangles, stations with CTD data only; solid circles, stations with both CTD and larval fish samples.

figure 2. Larval abundance was standardized to numbers of individuals (ind.) per 1000 m^3. The Shannon diversity index (*H'*) (Shannon and Weaver 1963) and Pielou's index of evenness (*J'*) (Pielou 1966) were respectively used to calculate species diversity and evenness. A principal component analysis (PCA) was used to characterize hydrographic regions based on data of seawater temperature, salinity, and chl-*a* at each station (Pielou 1984). Student's *t*-test was used to determine the significance of seasonal variations in the abundance and diversity of larval fishes (Armitage and Berry 1994). Similarities among stations in the 2 monsoon seasons were measured based on quantitative data, and only taxa with a relative abundance ≥ 1% (22 in winter and 20 taxa in summer) were included in the analysis to avoid any undue effect of rare species. To reduce the weight of the most-abundant species, standardized data were 4th-root transformed. Hierarchical agglomerative clustering with group-averaged linking, based on the Bray-Curtis similarity measure, was used to delineate groups with a distinct community structure (Bray and Curtis 1957). A similarity percentage analysis (SIMPER), which identifies taxa most responsible for an assemblage, was used to determine the taxa that made the greatest contribution to each larval assemblage (Clarke 1993). Furthermore, in order to examine variations in larval fish compositions among stations, a canonical correspondence analysis (CCA), a statistical visualization method, was employed (Ter Braak 1986). Three environmental variables, temperature, salinity, and chl-*a* concentration, were the covariates. The 1st 2 CCA axes were then selected to illustrate seasonal variations in the scatter pattern of stations, larval fish taxa, and environmental variables.

RESULTS

Oceanography

The seawater at 10 m in depth in the TS showed clear spatial and seasonal changes in temperature, ranging 15.14-24.44°C in winter (NEM) and 26.81-29.83°C in summer (SWM),

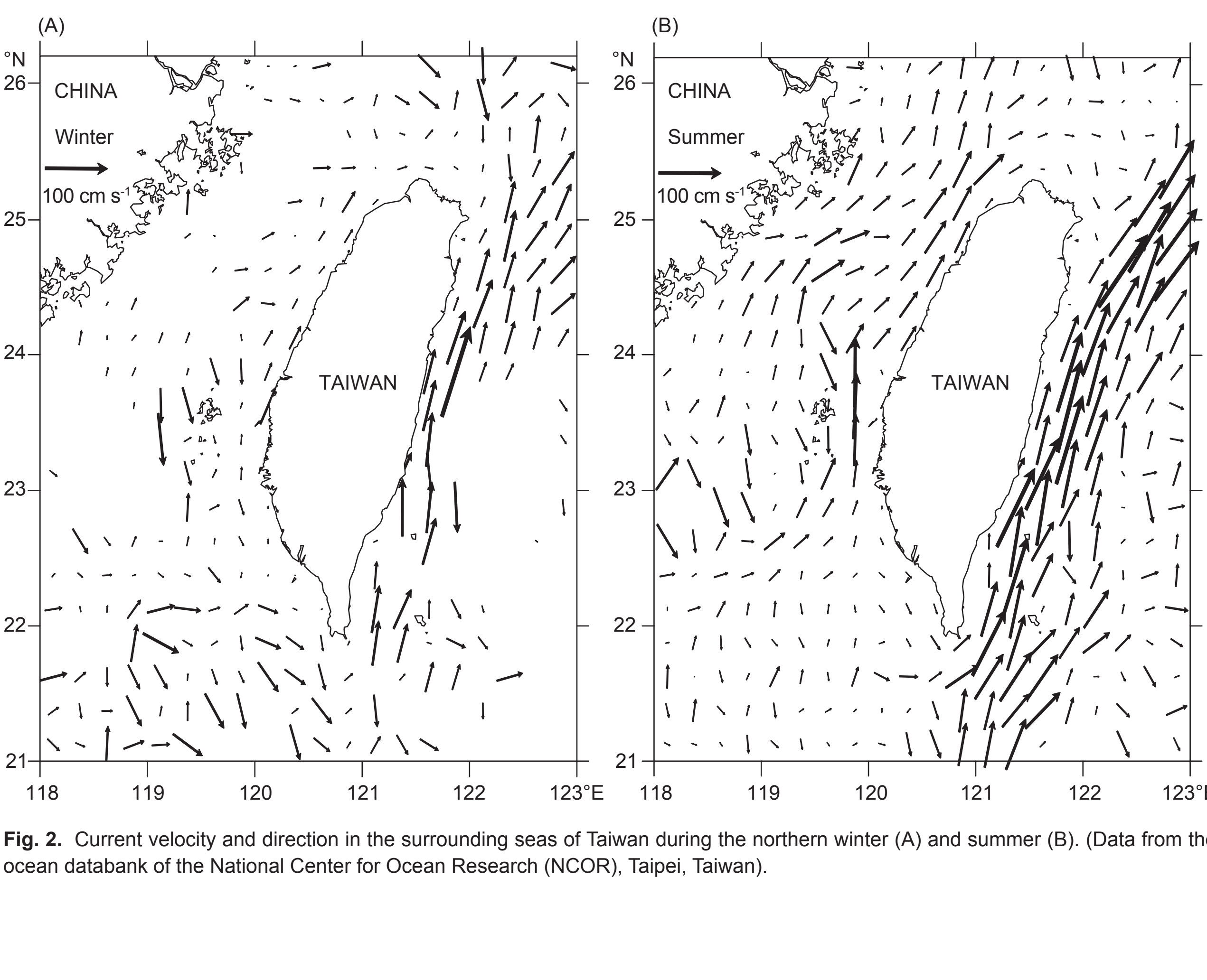

Fig. 2. Current velocity and direction in the surrounding seas of Taiwan during the northern winter (A) and summer (B). (Data from the ocean databank of the National Center for Ocean Research (NCOR), Taipei, Taiwan).

while salinity varied 32.21-34.47 psu in winter and 33.75-34.67 psu in summer (Table 1). Maps of the current direction and contours of surface temperature and salinity illustrate large-scale major oceanographic features in the TS (Figs. 2, 3). A strong temperature and salinity front was observed in the northern TS in winter. The isotherms displayed a northeast-southwest gradient, and temperatures gradually increased from high to low latitudes (from 15 to 21°C). In summer, high-temperature, low-salinity waters were widely distributed from south of the Penghu Is. to the northern TS and in the northwestern part of the study area (Fig. 3).

According to results of the PCA based on temperature, salinity, and chl-*a* concentration, different distribution patterns were observed in the 2 monsoonal seasons (Fig. 4). In winter, stations 37, 41-43, 49, 50, 52, 53, 55, and 56 were widely scattered in the diagram, while the others were closely grouped. Among the former, stations 43, 49, 50, 52, 53, 55, and 56 had negative correlations with all 3 hydrographic variables, and stations 37, 41, and 42 were heavily dominated by high salinities and chl-*a* concentrations. Most stations in summer were closely grouped; only stations 37, 41, 43, 44, and 52, due to higher chl-*a* concentrations, showed marked differences from the other stations. It is worth noting that several stations around the Penghu Is. (e.g., stations 37 and 41-44) usually had higher chl-*a* concentrations and lower temperatures (around 1-2°C lower) in both seasons, apparently due to the presence of upwelling (Fig. 5).

Larval fish abundances and compositions

In total, 3821 larval fishes were collected, and 234 taxa of larval fishes, belonging to 126 genera and 81 families, were identified in this study. Among these, 94 larvae (2.5% of the larval fish catch) in the yolk sac stage were unidentifiable. The overall mean abundance was 1262 (S.E. ± 244) ind./1000 m^3. The abundance was significantly higher in summer (1522 ± 355 ind./1000 m^3) than in winter (1001 ± 214 ind./1000 m^3) (*t*-test, $t = -2.142$, $p < 0.05$; not shown), but species number (*t*-test, $t = -0.073$, $p > 0.05$; not shown), species diversity (*t*-test, $t = 0.069$, $p > 0.05$; not shown), and species evenness (*t*-test, $t = 1.381$, $p > 0.05$; not shown) showed no significant seasonal differences (Table 1). Furthermore, the taxa were quite diverse and varied spatially in the 2 seasons. In winter, 145 taxa of larval fishes in 52 families and 87 genera were identified. The abundance, species diversity index, and evenness index of larval fishes varied 114-4678 ind./1000 m^3,

Table 1. Mean values (± standard error) of hydrographic variables, chlorophyll *a*, zooplankton abundance, larval fish abundance, species number, species diversity (*H'*), species evenness (*J'*), and abundances of predominant taxa during winter and summer in waters west of Taiwan

	Winter	Summer
Temperature (°C)	21.58 ± 0.49	28.82 ± 0.13
Salinity (psu)	34.08 ± 0.11	34.14 ± 0.05
Chlorophyll *a* (μg/L)	0.24 ± 0.06	0.08 ± 0.02
Zooplankton abundance (ind./m^3)	500 ± 90	1041 ± 610
Larval fish abundance (ind./1000 m^3)	1001 ± 335	1522 ± 355
Species number (total)	22 ± 4 (145)	22 ± 2 (157)
H'	3.45 ± 0.21	3.43 ± 0.19
J'	0.88 ± 0.03	0.82 ± 0.04
Encrasicholina punctifer	0	177 ± 89
Auxis sp.	0	163 ± 132
Bleekeria mitsukurii	139 ± 120	6 ± 5
Benthosema pterotum	111 ± 105	8 ± 6
Scomber sp. 1	39 ± 16	50 ± 37

ind., individuals.

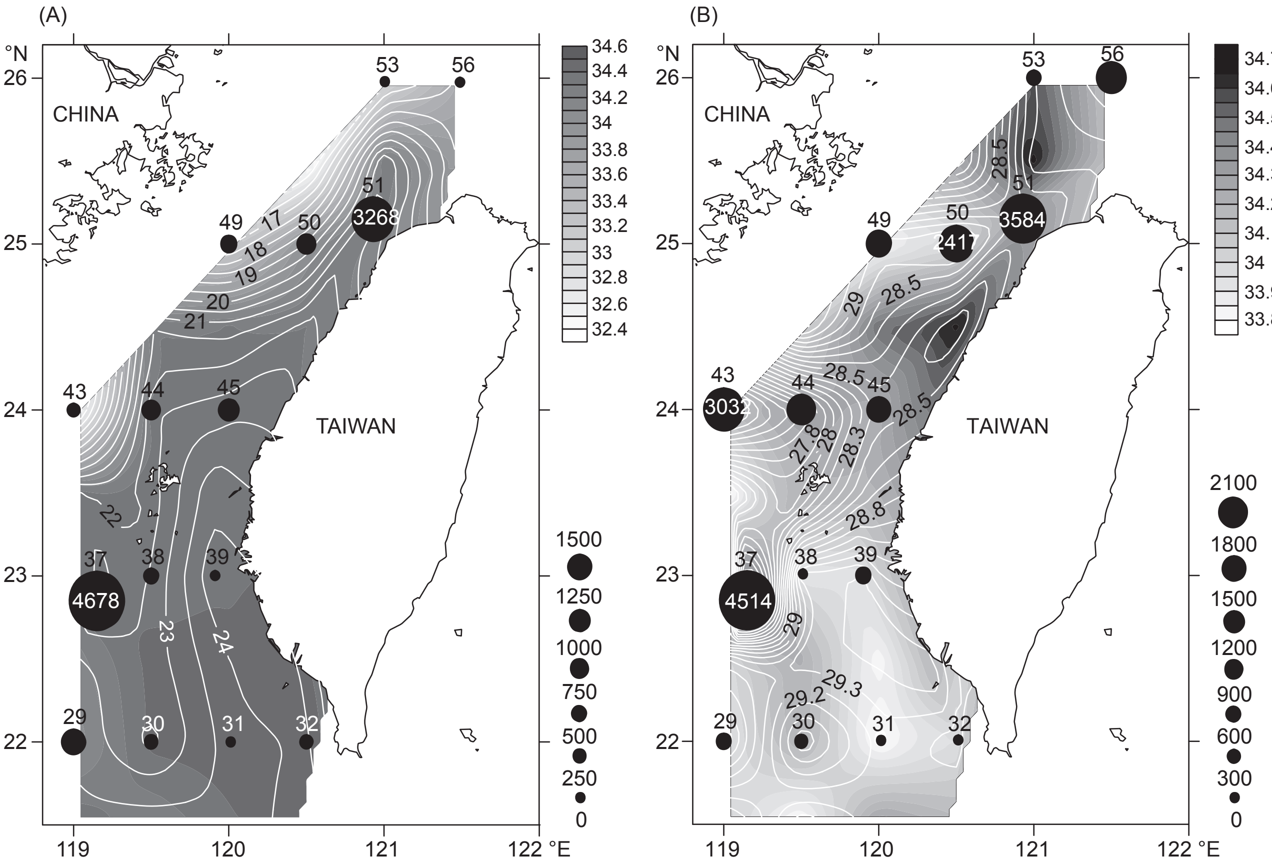

Fig. 3. Seawater temperatures (white lines) and salinities (gray scales) at 10-m depth and abundances (individuals (ind.)/1000 m^3) of larval fish (solid circles) in winter (A) and summer (B).

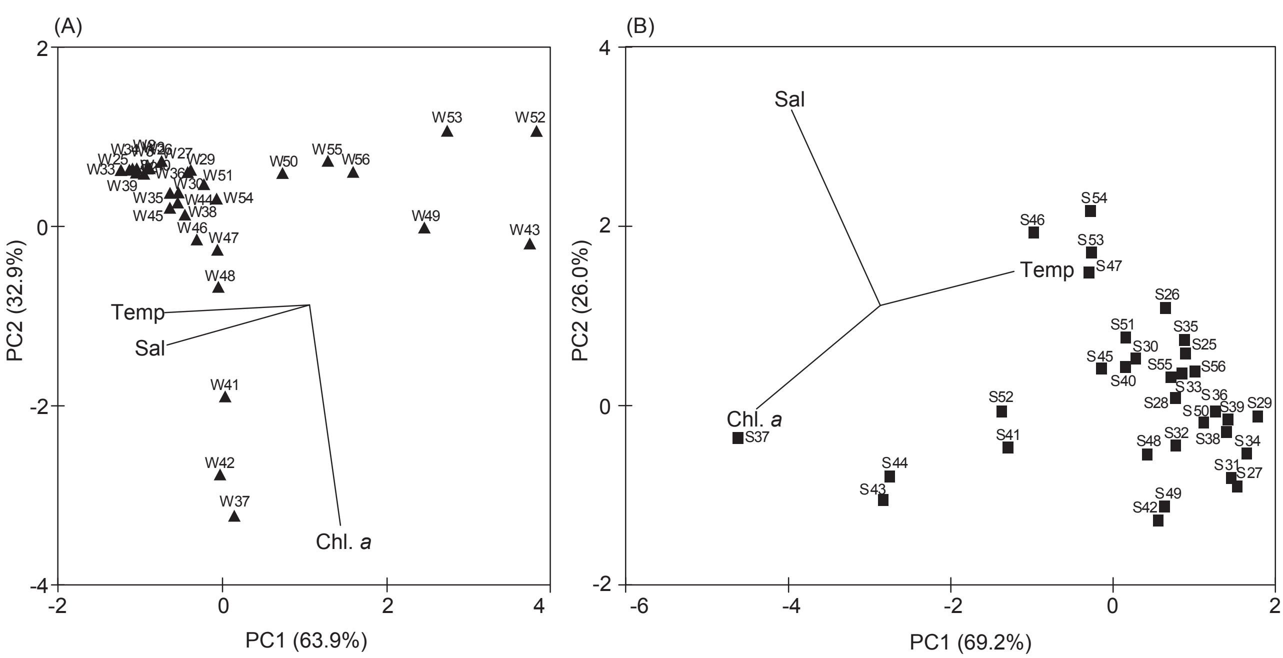

Fig. 4. Winter (A) and summer (B) plots of a principal component analysis based on seawater temperatures (at a 10-m depth), salinity (at a 10-m depth), and chlorophyll *a* (average concentration in the upper 150 m) at 32 surveyed stations.

2.03-5.04, and 0.65-0.99, respectively. In summer, 157 taxa of larval fishes in 67 families and 88 genera were recognized. Ranges of abundance, species diversity index, and evenness index were 136-4514 ind./1000 m^3, 1.24-4.42, and 0.39-0.99, respectively.

Families with the most species were the Myctophidae (33 spp.), Carangidae (11 spp.), Gobiidae (11 spp.), and Scombridae (9 spp.), while almost 1/2 (40/81) of families were represented by a single species. Six families, the Scombridae (12.5%), Myctophidae (12.3%), Engraulidae (11.1%), Carangidae (6.5%), Ammodytidae (5.8%), and Gobiidae (5.2%), accounted for 53.3% of the total larval fish catch. At the species level, *Encrasicholina punctifer* constituted 7.0% of the total larval fishes collected during this study, representing the most abundant taxon. *Auxis* sp. (6.5%), *Bleekeria mitsukurii* (5.8%), *Benthosema pterotum* (4.7%), *Scomber* sp. 1 (3.5%), *Gunnellichthys* sp. (3.5%), and *Engraulis japonicus* (3.3%) were also very common (with relative abundances of > 3%). These 7 species together comprised 34.3% of the total catch. Compositions of predominant taxa (with relative abundances of > 1%) significantly differed between the 2 monsoon seasons (Tables 2, 3), *Ble. mitsukurii*, *Ben. pterotum*, *Trichiurus lepturus*, *Scomber* sp. 2, and *Scomber* sp. 1 dominated in winter; while *Enc. punctifer*, *Auxis* sp., *Gunnellichthys* sp., *Selar crumenophthalmus*, and *Eng. japonicus* were very common in summer. Some species only occurred in a specific area in a season with a peak abundance.

Larval fish assemblages

The cluster analysis, based on larval fish compositions of 22 and 20 dominant species, defined 3 and 2 main groups of stations during the 2-season surveys at similarity levels of 60% in both seasons (Fig. 6). In winter, there were 3 station groups: W_A, W_B, and W_C. W_A comprised 1 station (station 39) in coastal waters of southwestern Taiwan. Eleven taxa were found at station 39, but only 1 mesopelagic fish, *Sigmops gracilis*, was abundant. W_B included 9 stations in the central and southern TS. In total, 133 taxa were identified in this group, with the highest mean abundance (1415 ind./1000 m^3) among the 3 groups. Some sandy-benthic species (such as *Ble. mitsukurii* and *Tri. lepturus*) and mesopelagic fish (such as *Ben.*

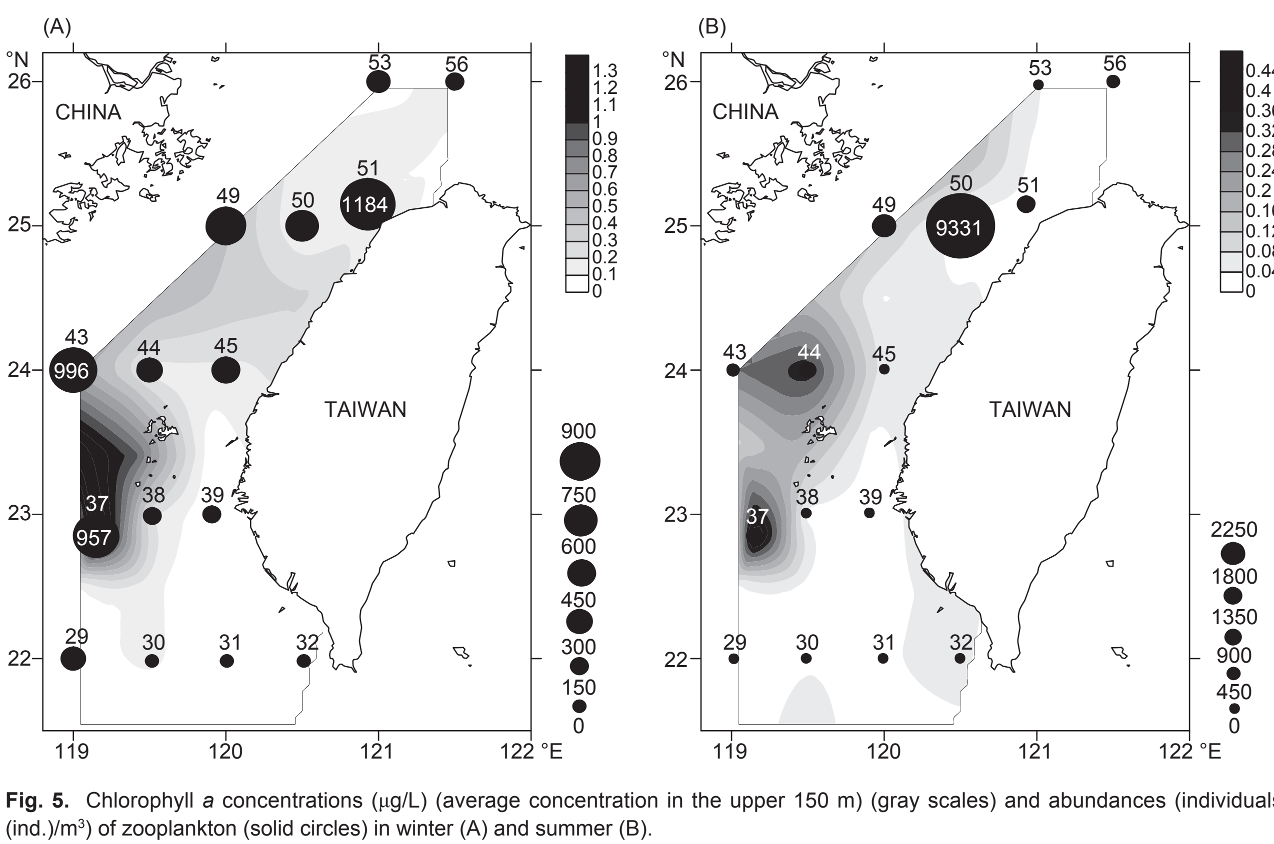

Fig. 5. Chlorophyll *a* concentrations (μg/L) (average concentration in the upper 150 m) (gray scales) and abundances (individuals (ind.)/m^3) of zooplankton (solid circles) in winter (A) and summer (B).

pterotum) were abundant in this group. Among these species, *Ble. mitsukurii* and *Tri. lepturus* were significantly more abundant at station 37 southwest of the Penghu Is., and *Ben. pterotum* was abundant (1586 ind./1000 m^3) at station 51 near the northwestern Taiwanese coast. However, the percentage contributions of the above 3 species (5.38%, 9.45%, and 0.57%, respectively) in group W_B were not high. On the other hand, 2 oceanic and mesopelagic species (*Sig. gracilis* and *Vinciguerria nimbaria*) were the top 2 most important taxa in this group, respectively contributing 16.34% and 11.73% to the within-group similarity. W_C, consisting of 5 stations, was in the northern TS and neighboring China. We identified 27 taxa in group W_C with a total mean abundance of 425 ind./1000 m^3. Three commercial species, *Carangoides ferdau*, *Eng. japonicus*, and *Scomber* sp. 2, were abundant in this group. Among these, *Scomber* sp. 2 and *Eng. japonicus* had high contributions (58.62% and 20.92%) to the within-group similarity (Table 2).

In summer, there were 2 station groups: S_A and S_B. Furthermore, 4 station subgroups (S_{A1}, S_{A2}, S_{B1}, and S_{B2}) were derived from S_A and S_B at similarity levels of 30% and 50%, respectively (Fig. 6). S_{A1} comprised 5 stations that were in the southern TS. Sixty-one species of larval fishes were recognized in subgroup S_{A1}, with a total mean abundance of 361 ind./1000 m^3. *Engraulis japonicus* was the most abundant species in this subgroup and had a high contribution (88.74%). S_{A2} contained 2 stations, one of which (station 53) was in the northern TS and the other (station 44) was in the central TS. Twenty-seven taxa were identified in this subgroup, and the total mean abundance (1168 ind./1000 m^3) was significantly higher than that of subgroup S_{A1}. The predominant taxa in this subgroup were *Eng. japonicus*, *Cryptocentrus* sp., an unidentified Gobiidae, *Scarus* sp., and *Terapon theraps*. Among these taxa, benthic *Cryptocentrus* sp. and reef-associated *Scarus* sp. were only found at station 44, and benthic *Ter. theraps* was only observed at

Table 2. Predominant taxa (with relative abundances of > 1%) of larval fishes of each station group in winter. (A, mean abundance within each group, individuals (ind.)/1000 m^3; C, percentage contribution to within-group similarity, %)

Group (similarity)	W_A (-)		W_B (18.33)		W_C (24.54)	
Taxa	A	C	A	C	A	C
Bleekeria mitsukurii			228	5.38	8	0
Benthosema pterotum			179	0.57	12	7.62
Trichiurus lepturus			86	9.45	2	0
Scomber sp. 2			19	1.47	109	58.62
Scomber sp. 1			57	6.24	14	
Engraulis japonicus			36	6.72	28	20.92
Lepidotrigla sp.			49	0.25		
Pagrus major			23	1.53	36	1.94
Carangoides ferdau			4	0	55	7.99
Trachurus japonicus			34	0.67		
Sigmops gracilis	13	-	30	16.34		
Gobiidae gen. spp.			22	4.58	15	2.91
Vinciguerria nimbaria			25	11.73	3	
Bregmaceros spp.			24	2.44		
Acanthocepola limbata			21	3.03		
Neoscopelus microchir			20	4.33		
Lampanyctus sp. 2			18	8.60		
Myctophum asperum			18	7.42		
Callionymidae gen. sp.			12	0.15	11	0
Bregmaceros nectabanus			18	2.13		
Trachinocephalus myops			17	5.99		
Hygophum proximum			17	0.99		
Number of stations	1		9		5	
Total abundance	159		1415		425	
Number of taxa	11		133		27	

station 53. Here, *Eng. japonicus* was still the most abundant species (contributing 50.0%); moreover, *Coryphaena hippurus* and the unidentified Gobiidae were also abundant, both contributing 25.0% to the within-group similarity. The total mean abundance of group S_B was much higher than that of group S_A. Among the 2 subgroups, S_{B1} included 5 stations that were in waters of northern Taiwan and northwest of the Penghu Is., and included 87 identified taxa. It was mainly dominated by some commercial (such as *Enc. punctifer*) and coastal (such as *Gunnellichthys* sp.) species. *Encrasicholina punctifer*, which mostly occurred at stations 49-51, was the most abundant and important species in this subgroup, with a mean abundance of 501 ind./1000 m^3 and a contribution of 49.25%. *Gunnellichthys* sp. was abundant at station 51 (866 ind./1000 m^3), with a contribution of 10.22%. In addition, the commercial species, *Scomber* sp. 1, was also abundant in this subgroup and was only found at station 43, but its percentage contribution was relatively low (0.28%).

S_{B2} contained 3 stations that were in waters between subroups S_{A1} and S_{B1}. In this subgroup, there were 52 taxa, with a total mean abundance of 2039 ind./1000 m^3. The oceanic-migratory species *Auxis* sp. was the most dominant taxon in this subgroup (with a high abundance at station 18), but its percentage contribution to the similarity was low (2.31%). The most important taxa in subgroup S_{B2} were the commercial-neritic species, *Sel. crumenophthalmus* and *Scomberoides lysan*, which respectively contributed 60.28% and 22.90% to the within-group similarity. Among these 2 taxa, *Sel. crumenophthalmus* was also abundant in this subgroup with a mean abundance of 232 ind./1000 m^3 (Table 3).

Relations of larval fish compositions and environmental variables

We performed a CCA to examine non-linear relationships between larval fish compositions and environmental variables (temperature,

Table 3. Predominant taxa (with relative abundances of > 1%) of larval fishes at each station group in summer. (A, mean abundance within each group, individuals (ind.)/1000 m^3; C, percentage contribution to the within-group similarity, %)

	S_A						S_B					
Group (similarity)	Total (24.95)		S_{A1} (33.26)		S_{A2} (15.69)		Total (15.96)		S_{B1} (26.98)		S_{B2} (8.18)	
Taxa	A	C	A	C	A	C	A	C	A	C	A	C
Encrasicholina punctifer	3	0	5	0			328	34.35	501	49.25	40	0
Auxis sp.	6	3.70	8	5.82			301	6.15	81	2.94	669	2.31
Gunnellichthys sp.							166	7.21	257	10.22	13	0
Selar crumenophthalmus							111	8.94	39	0.48	232	60.28
Engraulis japonicus	90	86.03	99	88.74	67	50.00	19	0	30	0		
Scomber sp. 1							94	4.01	110	0.28	69	0
Gobiidae gen. spp.	26	8.20	6	4.33	75	25.00	57	13.21	76	12.34	25	7.56
Mullidae gen. spp.	1	0	1	0			58	0.77	93	1.27		
Scarus sp.	19	0			66	0	40	2.15	64	3.57		
Scomberoides lysan							51	7.50	37	2.29	74	22.90
Acanthogobius spp.							45	1.41	72	2.33		
Trachinocephalus myops							44	6.84	51	4.80	33	4.63
Coryphaena hippurus	7	0.75			25	25.00	38	0.69	10	0	83	2.31
Scorpaenidae gen. spp.	3	0.70	4	1.11			36	1.12	57	1.85		
Encrasicholina heteroloba							37	0	59	0		
Lutjanus vitta							37	0	59	0		
Xyrichthys sp.	16	0.62	3	0	49	0	16	1.29	24	1.15	3	0
Terapon theraps	18	0			63	0	15	0.66	24	1.09		
Upeneus japonicus							29	3.71	46	6.14		
Cryptocentrus sp.	33	0			115	0						
Number of stations	7		5		2		8		5		3	
Total abundance	592		361		1168		2336		2515		2039	
Number of taxa	82		61		27		110		87		52	

salinity, chl-*a* concentration, and zooplankton abundance). The CCA diagram derived from the 19 predominant taxa of larval fishes indicated clear seasonal structures in which data from stations in the same season clustered together (Fig. 7). In the 1st 2-dimensional configuration, temperature was heavily loaded on the 1st axis and salinity on the 2nd axis. The larval fish composition was highly associated with environmental variables with respective canonical correlations of 0.941 and 0.928. Summer stations were found to be distinctively correlated with high water temperature and negatively correlated with chl-*a*. Winter station 37 was strongly influenced by chl-*a*, and highly

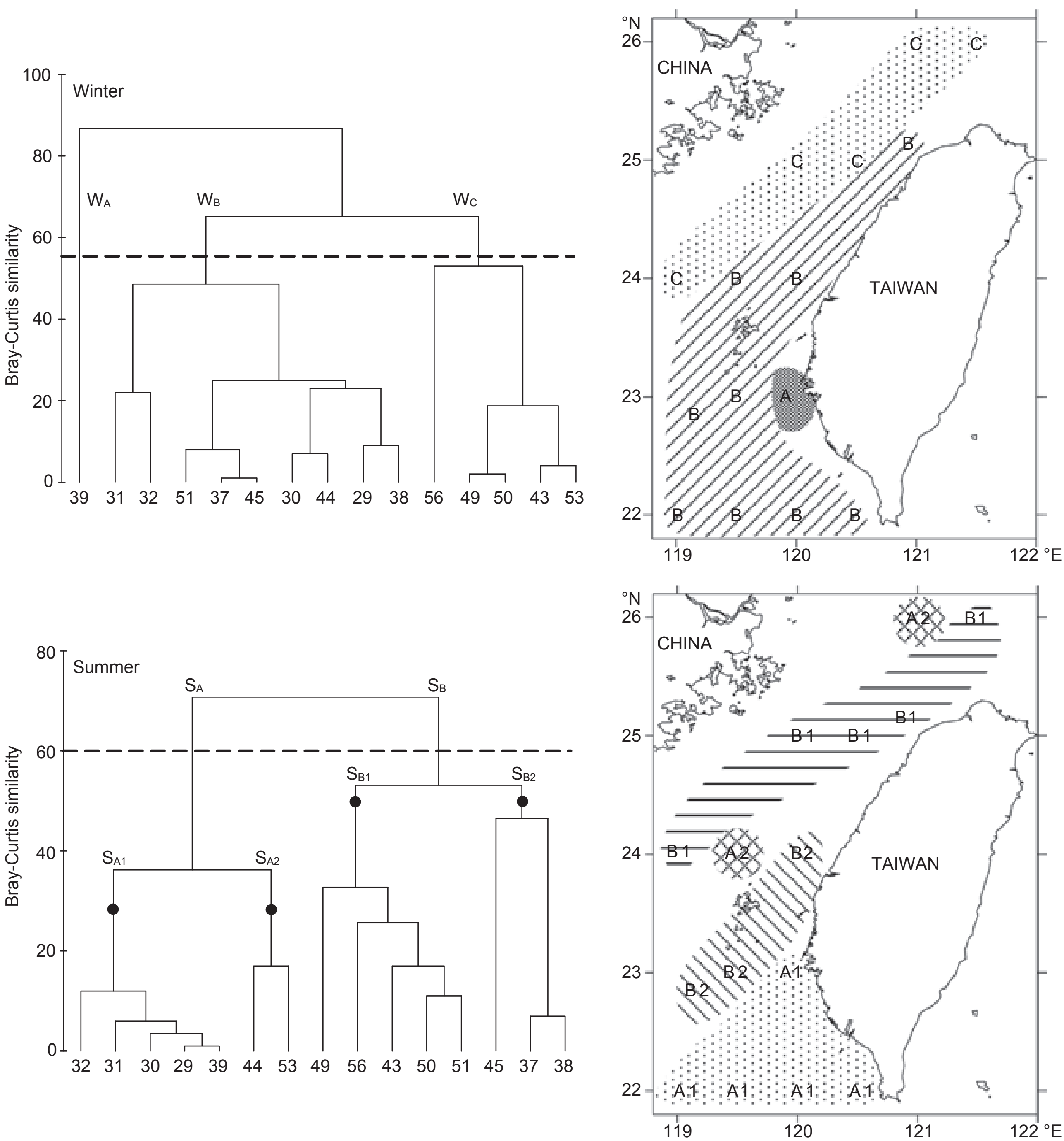

Fig. 6. Dendrograms of station groups defined by the Bray-Curtis similarity measure and their spatial locations in the sampling area in winter and summer.

correlated with *Lepidotrigla* sp. and *Ble. mitsukurii*. *Pagrus major*, *Ben. pterotum*, and *Scomber* sp. 2 were negatively influenced by temperature and significantly correlated with several winter stations (e.g., stations 43, 49-51, and 56). Temperature had an opposite effect on *Scarus* sp., *Sco. lysan*, *Gunnellichthys* sp., *Sel. crumenophthalmus*, and *Enc. punctifer*. Among these taxa, *Scarus* sp., *Enc. punctifer*, and *Gunnellichthys* sp. were correlated with summer stations 49 and 50, *Sco. lysan* with summer station 53, and *Sel. crumenophthalmus* with summer station 44. Salinity had a positive effect on *Coryphaena hippurus* and *Auxis* sp., which were heavily correlated with summer station 37.

DISCUSSION

Hydrographical conditions in the TS are strongly influenced by the monsoon-driven CCC, KBC, and SCSSC. During the NEM in winter, temperature and salinity showed significant decreasing trends from southeast to northwest in the northern TS, and a water tongue of relatively high temperature (> 23.6°C) and salinity (> 34.4 psu) flowed northward through the Penghu Channel and even into the northern TS. This phenomenon signals the presence of 2 distinct water masses in the study area: the cold, fresh CCC flows out from the coast of China and the

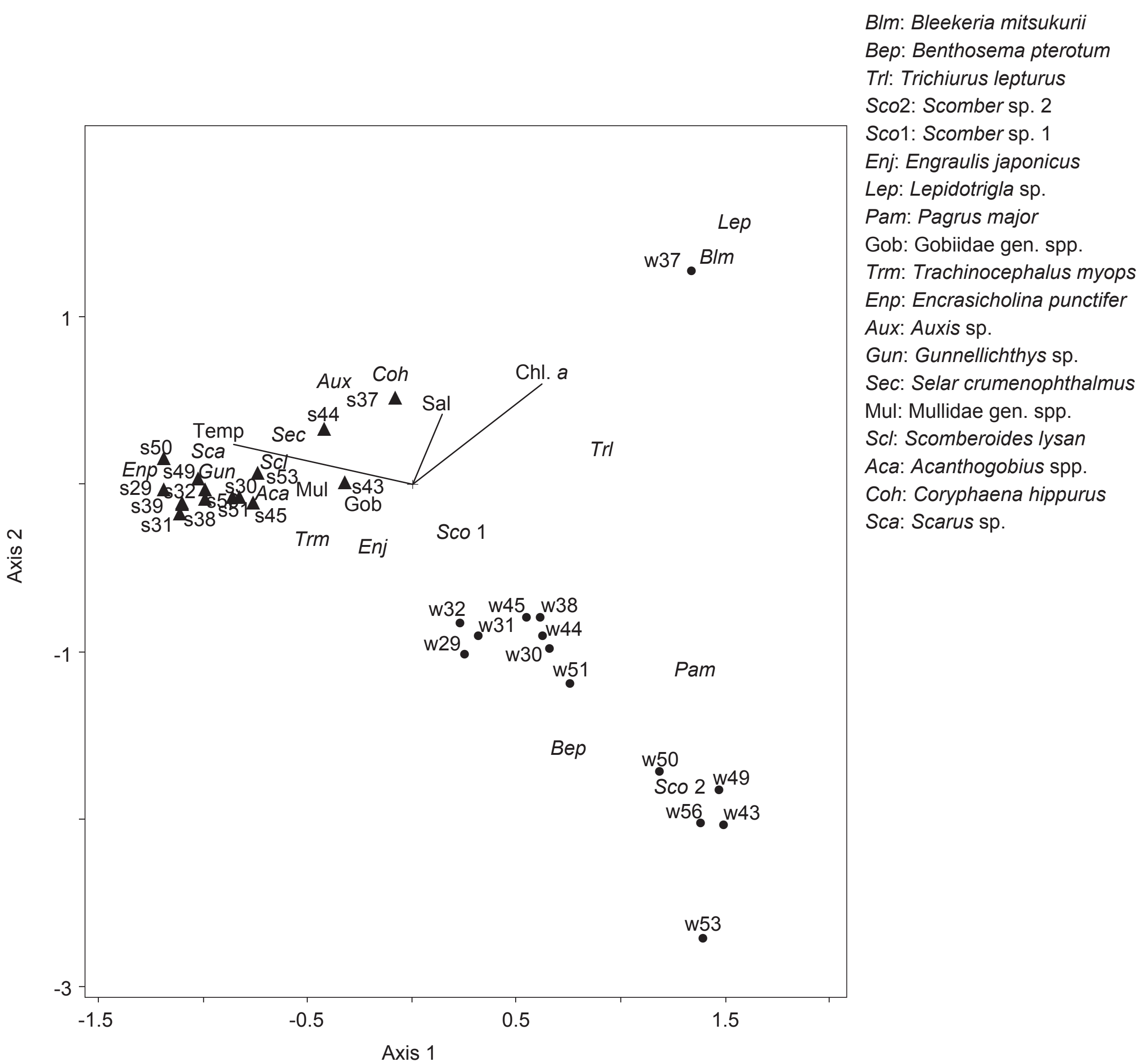

Fig. 7. Ordination diagram of the canonical correspondence analysis (CCA) based on hydrographic factors and abundances of the 19 predominant taxa of larval fishes (with relative abundances of > 1%). Circles, station in winter; triangles, stations in summer; numerals, station number.

warm, saline KBC penetrates into the TS along the southwestern coast of Taiwan. In summer, when the SWM prevailed, the warm, lower-salinity (about 0.4 psu lower than the salinity of the KBC) waters originating from the SCS were widely distributed from south of the Penghu Is. to the northwestern part of our surveyed area. The SCSSC replaced the KBC and dominated the summer oceanic conditions of the TS. Jan et al. (2002 2006 2010) also found a recurring pattern of a strong NEM driving the brackish CCC into the northern TS and limiting the northward intrusion of saline KBC in the southeastern TS from Dec. to Jan. The weakening of the NEM in Feb. and Mar.; however, made it possible for the KBC to intrude northward into the ECS. In June, the increase in this northerly transport accompanied by a decrease in the westward intrusion of the KC through the Luzon Strait led to the replacement of the KBC by the less-saline SCSSC. The onset of the NEM in Oct., on the other hand, marked the beginning of the change in the SCSSC to the KBC, the blocking of the northward currents in the Penghu Channel, and the southward intrusion of the CCC in the northwestern TS. Our results conform well to the circulation model proposed by Jan et al. (2002 2006 2010).

Significant higher chl-*a* concentrations were also observed in waters west of the Penghu Is. during our investigation. Topographic upwelling was formed due to the Changyun Ridge. As the KBC and SCSSC impinge on the Changyun Ridge, the surface and bottom waters flow in different directions upstream of the Changyun Ridge. The lighter surface water flows over the Changyun Ridge and moves along the eastern side of the TS. On the other hand, the heavier bottom water is obstructed by the ridge and turns northwestward along local isobaths into the northwestern TS (Jan et al. 1994). However, bottom water was observed to have risen near the Penghu Is., and formed a cyclonic ring which was characterized by upwelling of cold water from deep depths, which subsequently enriched the upper water with nutrients, therefore allowing phytoplankton to flourish, and finally increased the abundance of zooplankton and larval fishes. This recurring upwelling was well documented by Jan et al. (1994) and was found to be a site with high levels of nutrients (Chung et al. 2001). Thus, we suggest that food availability may be an important factor affecting the distribution patterns of larval fishes in the TS, similar to results revealed by Hsieh et al. (2010). Rodríguez et al. (1999) and Okazaki et al. (2002) also proposed that marine plankton ecosystems are deeply affected by mesoscale hydrographic features, such as fronts and eddies. These features act as mechanisms for enrichment, concentration, and retention of nutrients, and thereby contribute to increased biological production and the consequent survival of larval fishes (Bakun 1996).

Assemblages of larval fishes were found to reflect hydrographic and biological conditions of the world's oceans (Hare et al. 2001, Okazaki et al. 2002). Considering the contrasting hydrography of the TS between the NEM and SWM, we hypothesized that this switching of hydrographic conditions should be reflected in distinct assemblages of fish larvae between the 2 seasons. Thus the CCA was used to illustrate the correspondence of larval fish species with seasonal hydrographic conditions. Two different circumstances were observed in this study: larval fish assemblages with significant seasonal differences and the occurrence of several dominant species only in a specific season. Furthermore, we found *P. major* and *Scomber* sp. 2 to be representative of the cold-water environment influenced by the CCC; i.e., they were common at winter stations and were confined to the northern TS or north of the temperature and salinity front during winter. *Encrasicholina punctifer* and *Gunnellichthys* sp. were typical warm-water taxa, only found at summer stations dominated by the SCSSC. *Bleekeria mitsukurii* and *Lepidotrigla* sp., which nearly exclusively appeared in winter stations, were extremely abundant at station 37, corresponding to higher chl-*a* concentrations. Temperature and salinity, the 2 basic parameters of water masses, were equally loaded on the 1st and 2nd axes of the CCA. It is probable that the larval fish composition was effectively determined by seasonal variations in monsoon-driven water masses. Tzeng et al. (2002) reported that monsoon-driven coastal currents may influence seasonal dispersal and community structure of estuarine larval fishes in the 4 estuaries on the west coast of Taiwan. Shao et al. (1997) also noted that the latitudinal difference in fish fauna in coastal waters of western Taiwan was under the influence of monsoons, and found the boundary separating the northern and southern fish faunas to be located approximately at the Penghu Is. in the middle of the TS.

Results of the SIMPER analysis showed the contributions of the important taxa and also characterized seasonal changes in the species compositions in each season. Among the dominant winter species, in general, adults of the non-commercial species, *Ble. mitsukurii*, inhabit shallow waters with sandy bottoms, and dive into the sand when threatened (Shen et al. 1993). In this study, most larvae of *Ble. mitsukurii* were found in waters southwest of the Penghu Is., coinciding with the specific local topography. Another dominant species, the non-commercial *Ben. pterotum*, usually inhabits mesopelagic waters, mainly southwest and east of Taiwan, and its adults show clear diurnal vertical migration between 130 and 300 m during the day and 10 and 200 m at night (Shen et al. 1993). However, in the present study, most larvae of *Ben. pterotum* were found at station 51, probably indicating the entrance of the KBC through the Penghu Channel into the northern TS. In addition, we found some oceanic or mesopelagic species associated with the Kuroshio, such as *V. nimbaria* and *Sig. gracilis* (Nakabo 2000, Sassa et al. 2002), which were usually observed in waters east of Taiwan and also abundant in neritic waters of the central and northern TS. Thus, we propose that the intrusion of the KBC may bring oceanic species into the TS. The highly commercial fish, *Tri. lepturus*, is found throughout tropical and temperate waters of the world and is common in waters around Taiwan. Generally, adults of *Tri. lepturus* stay over muddy bottoms of shallow coastal waters and often enter estuaries (Nakamura and Parin 1993). In our survey, their larvae occurred mostly in the shallow basin around the Penghu Is. and coastal waters. Larvae of the 3 commercial species, *Scomber* sp. 2, *Scomber* sp. 1, and *Eng. japonicus*, were abundant in the central and northern TS in this study, especially in waters affected by the CCC. Among these species, adults of *Scomber* sp. 2 and *Scomber* sp. 1 mainly inhabit coastal waters and to a lesser extent epipelagic to mesopelagic waters over the continental slope (Collette and Nauen 1983). *Scomber* sp. 2 is an important species in group W_C where the CCC prevails. *Engraulis japonicus* occurs in large numbers near the surface, mainly in coastal waters but as far as over 1000 km from shore (Whitehead et al. 1988); meanwhile, it is abundant in all surrounding seas of Taiwan, especially in the north (Shen et al. 1993). This species was also important in group W_C. According to a previous study (Chiu et al. 1997), adult *Eng. japonicus* migrates annually from waters adjacent to Japan to northeastern Taiwan for spawning during Feb. and Mar. Therefore, we suggest that these larvae may be transported from north to south of the TS by the CCC during the NEM.

During the SWM in summer, the epipelagic commercial species, *Enc. punctifer*, was the most abundant species. Adults of *Enc. punctifer* are mainly found inshore but also occur in oceanic waters, hundreds of kilometers from land, and they sometimes enter large atoll lagoons or deep, clear bays (Whitehead et al. 1988). *Encrasicholina punctifer* is widely distributed in waters surrounding Taiwan, especially in waters around the Penghu Is. and northeastern Taiwan. In this study, its larvae were only found at stations 37, 49-51, and 56, and had a high contribution to subgroup W_{B1}. According to the degree of developmental condition, we found that larvae of *Enc. punctifer* at station 18 were in the early pre-flexion stage; whereas, most larvae at stations 49-51 and 56 belonged to the flexion and post-flexion stages. So, we suggest that these larvae are transported by the northerly flowing SCSSC from the central to the northern TS when the SWM prevails. The highly commercial *Auxis* sp., an epipelagic species in neritic and oceanic waters, is widespread in tropical and subtropical areas (Collette and Aadland 1996). It is also a common species, particularly in southern and eastern parts of Taiwan. The commercial species, *Sel. crumenophthalmus*, prefers clear oceanic waters around islands to neritic waters, and is occasionally found in turbid waters (Lin and Shao 1999). Its larvae were the most important species in subgroup W_{B2}. The topography of the main areas of distribution of its larvae in our study was consistent with their favorite environments. Adults of *Sel. crumenophthalmus* are very common in all seas surrounding Taiwan, and contribute to the largest quantity of the total catch of the Carangidae in Taiwan each year. Larvae of *Eng. japonicus* were also abundant in the summer survey and were mostly found in the central and southern TS. This result is consistent with studies by Chiu et al. (1997) and Chiu (1999), who noted that *Eng. japonicus* was occasionally abundant in waters off Fangliao in southern Taiwan in late spring and summer.

In conclusion, the distribution patterns of abundance and species assemblages of fish larvae were closely linked to hydrographic conditions, and well matched abundances of phyto- and zooplankton in the TS. The major currents in the TS are basically controlled by the timing and strength of the seasonal monsoons. This movement pattern of currents determines variations in the structures of larval fish assemblages. The results of this study showed that heterogeneity in the composition of larval fishes is apparently associated with prevailing hydrographic regimes in the TS during the 2 distinct monsoon seasons.

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