Zoological Studies

Siphonophores from a Transect off Southern Taiwan between the Kuroshio Current and South China Sea

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Wen-Tseng Lo, Pin-Ren Kang, and Hung-Yen Hsieh (2012) Siphonophores from a transect off southern Taiwan between the Kuroshio Current and South China Sea. *Zoological Studies* **51**(8): 1354-1366. Seasonal variations in the siphonophore community were related to the hydrography along a transect in the South China Sea (SCS) and Kuroshio Current off southern Taiwan from Jan. 2005 to Oct. 2006. In total, 55 siphonophore taxa were identified during the study period, comprising 44 calycophores and 11 physonects. The diphyids *Chelophyes contorta* and *C. appendiculata* and the abylids *Bassia bassensis*, *Abylopsis eschscholtzi*, and *A. tetragona* were the 5 most abundant species. Siphonophore abundances showed significant temporal and spatial differences, with higher abundances usually in summer at the western end of the transect line. Although species compositions of the predominant siphonophores were similar among seasons, the number of siphonophore species was higher during the warm season. Our results indicated that variations in seawater temperature had a minor effect on the distribution pattern of siphonophores in waters off southern Taiwan; however, seasonality in zooplankton biomass may be an important factor controlling seasonal cycles of siphonophore abundances. http://zoolstud.sinica.edu.tw/Journals/51.8/1354.pdf

Key words: Siphonophore, Community composition, South China Sea, Kuroshio.

The South China Sea (SCS), with an area of about 3.5×10^6 km^2, is a major marginal sea located in the tropical-subtropical belt of the western North Pacific extending from the equator to 25°N. A basin as deep as 5000 m is in the northeast and is bordered by broad shelves that are shallower than 100 m (Shaw and Chao 1994, Fang et al. 1998). The surface water of the SCS is generally warm, highly saline, and oligotrophic. The Luzon Strait (LS), located between Taiwan and the Philippines, is the principal deep channel allowing effective water exchange or transport between the SCS and the western North Pacific. Kuroshio waters usually intrude from the western Philippine Sea through the LS into the northern SCS and spread westward in the upper 300 m along the shelf slope of southern China (Shaw and Chao 1994). The surface circulation of the SCS changes seasonally in response to the prevailing monsoons. In winter and spring, the prevailing northeasterly monsoon induces the formation of eddies in the SCS, whereas an anticyclonic eddy occurs during the southwesterly monsoon in summer and autumn (Liu et al. 2002, Jia and Liu 2004).

Siphonophores are complex polymorphic pelagic cnidarians that are widespread in the marine pelagic realm (Pugh 1974). Most species are wholly oceanic, a few are mainly neritic, and some rarely appear inshore (Pugh 1999). These important pelagic predators feed on zooplankton, particularly copepod crustaceans, and also sometimes on larval and young fish (Purcell 1981 1997, Alvariño 1985, Pugh 1999). When

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conditions are favorable, they can reproduce rapidly and may occasionally become the most abundant non-crustacean invertebrate predators in the sea (Purcell 1982, Robison et al. 1998, Hosia and Båmstedt 2008). Due to limited mobility, siphonophores are often used as indicators of water masses and water mass movements (Alvariño 1971, Mapstone and Arai 1992, Pagès 1996, Gasca 1999).

Most previous studies on the oceanography of the SCS focused on the marine environment with circulation patterns strongly influenced by seasonal monsoons (Metzger and Hurlburt 2001, Li et al. 2002, Centurioni et al. 2004, Jia et al. 2005, Caruso et al. 2006) and seasonal dynamics of primary and new production (Chen et al. 2003 2007, Chen 2005, Chen and Chen 2006). Knowledge of the Siphonophora and indeed of most zooplankton is limited in waters off southern Taiwan. In the present study, we conducted an annual survey across the northern SCS and adjacent Kuroshio waters, where seasonal hydrographic variations were shown to be under the influence of the Kuroshio Current. The main objectives of this study were to investigate the abundance and species composition of siphonophores in waters off southern Taiwan and clarify the influence of the intruding Kuroshio waters on their distribution and abundance.

MATERIALS AND METHODS

Sample collection

Our siphonophore specimens came from plankton samples taken by the Taiwan Fisheries Research Institute during 8 seasonal cruises of the R/V *Fishery Researcher I* from Jan. (winter) 2005 to Oct. (autumn) 2006 in waters off southern Taiwan (Fig. 1). At each surveyed station, temperature and salinity at different depths were recorded with a General Oceanic SeaBird CTD (SBE-911 Plus, Bellevue, Washington, USA) lowered from the surface to 10 m above the bottom. Siphonophores were collected with a 6-m-long Ocean Research Institute (ORI; RIGO, Tokyo, Japan) net of 1.6-m mouth diameter and 330-μm mesh. The ORI net was towed vertically at a speed of 1 m/s from 200 m to the surface. A flow meter (Hydro-Bios, Kiel, Schleswing-Holstein, Germany) was centrally mounted in the mouth opening to estimate the volume of filtered water. Zooplankton samples were immediately fixed in a

5% solution of formalin in seawater.

Preparation of oceanographic and siphonophore data

We illustrated the current velocity and direction (data from the Ocean Data Bank of the National Center for Ocean Research, Taipei, Taiwan) in waters off southern Taiwan in each season to interpret the succession of water masses in our study area (Fig. 2). Each plankton sample was divided into 2 subsamples with a Folsom splitter (Aquatic Research Instruments, Wellington, New Zealand). Siphonophores were sorted from 1 subsample and identified to the lowest taxonomic level possible according to Bigelow (1911), Sears (1953), Totton (1965), and Pugh (1999). Because of their polymorphic structure and fragile nature, most siphonophores become fragmented in net samples, thus the numbers of nectophores (or bracts) of the Physonectae and hippopodiid Calycophorae were counted and then divided by 10 to estimate their abundance according to Pugh (1984). Calycophorae generally have 2 generations (polygastric and eudoxid phases), and each generation contains 2 distinct individuals (anterior and posterior nectophores of the polygastric phase, and a bract and gonophore of the eudoxid phase); therefore, nectophores (only anterior nectophores for diphyomorph calycophorans), bracts, and gonophores of each Calycophorae species were counted separately, and the species abundance was calculated from the sum of the greater number of both generations. The other subsample was repeatedly subdivided until zooplankton numbered 1000-2000 or less; counts of all taxa were used to estimate the zooplankton abundance. Thirty zooplankton taxa were identified according to the classification of zooplankton of Kuroshio waters. Data were converted to numbers of siphonophores (individuals; ind.)/100 m^3 and zooplankton/1 m^3 of water filtered through the net.

Data analysis

The Shannon-Weaver diversity index (H'; Shannon and Weaver 1963) was used to measure the species diversity of siphonophores. The Sørensen similarity index (SI) (Sørensen 1948) was calculated by analyzing the similarity of pairs of sites by the presence or absence of each siphonophore species. Differences in siphonophore abundances, species numbers, H'

values, seawater temperatures, salinities, and zooplankton abundances among seasons (4 levels) or station groups (3 levels, from results of the siphonophore assemblage analysis) were tested by a two-way analysis of variance (ANOVA; Dunn and Clark 1974). Siphonophores and zooplankton abundances were log(x+1)-transformed to normalize the data and homogenize residual variances. Statistical significance was accepted

at α = 0.05. If the ANOVA results indicated that significant treatment effects were at or above the 0.05 probability level (*p*), then a post-hoc Tukey's honest significant difference test was applied to determine which means significantly differed. Multivariate analyses were performed with the PRIMER (vers. 6.0) software package (Clarke and Gorley 2006). Cluster analysis with the Bray-Curtis similarity was used to measure levels of
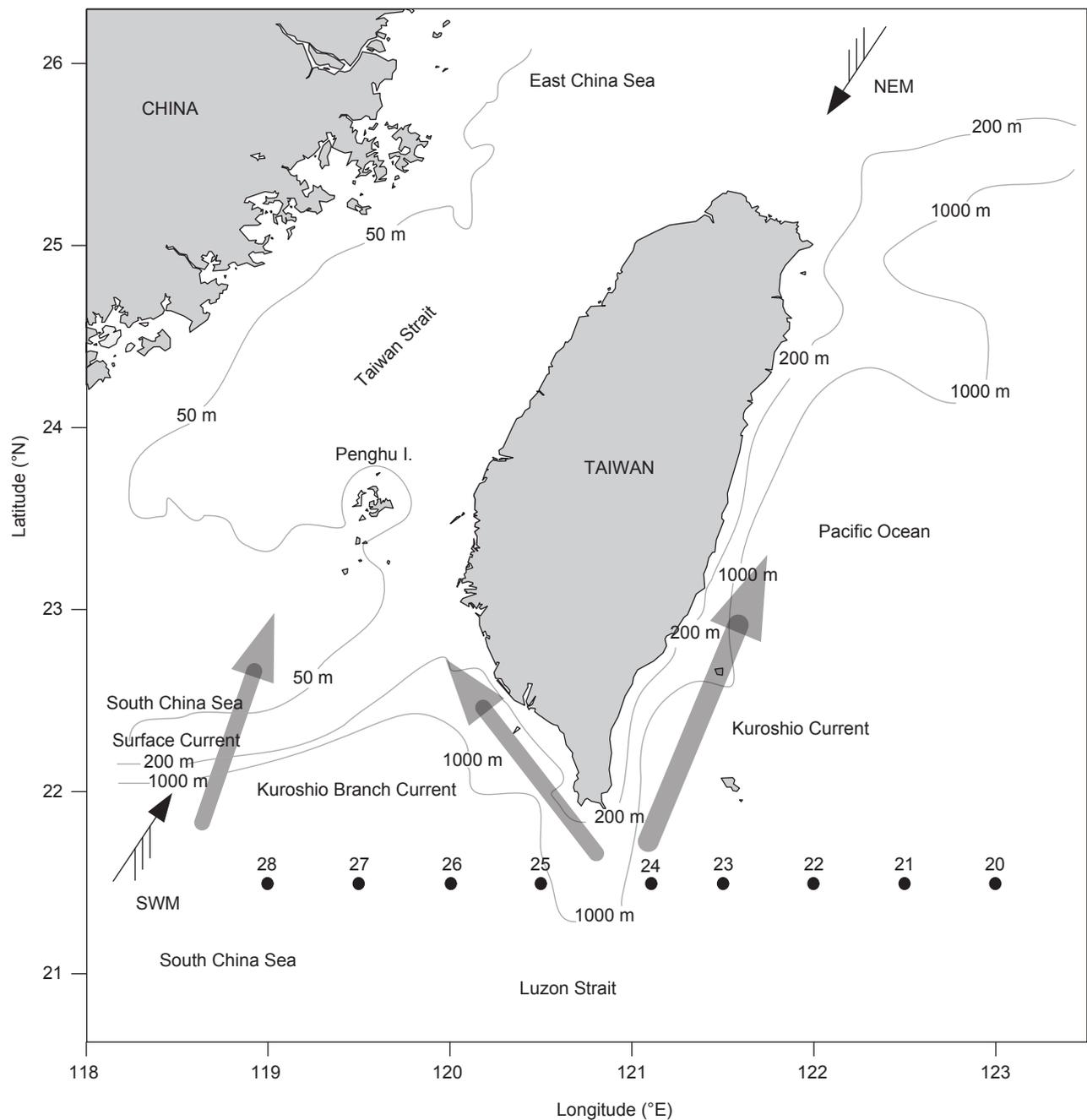

Fig. 1. Sampling stations 20 to 28 in waters off southern Taiwan during 2005-2006.

similarity in species compositions among sampling stations based on a similarity matrix of log(x+1)-transformed siphonophore abundances, and group-averaged linking was chosen to delineate groups with distinct community structures (Bray and Curtis 1957). Only 14 species accounting for > 1% of the total catch were included in the analysis to avoid any undue effect of rare species. In addition, we examined non-linear relationships between predominant species and environmental variables with a canonical correspondence analysis (CCA), a statistical visualization method (Ter Braak 1986). Data are presented as the mean ± standard error (SE).

RESULTS

Hydrographic conditions and zooplankton abundances

The mean water temperature at 10 m in depth varied seasonally (ANOVA, $F_{3,72}$ = 76.444,

$p < 0.001$), with the lowest temperature (23.7 ± 0.4°C) in Jan. 2005 and the highest (29.6 ± 0.1°C) in July 2006 (Fig. 3A). Mean water temperatures were usually below 25°C in winter and above 29.5°C in summer. The transitional periods, spring and autumn, had mean water temperatures of 26-28.5°C. Similarly, salinity varied seasonally during the survey period (ANOVA, $F_{3,72}$ = 3.960, $p < 0.05$, Fig. 3B). It fluctuated between 33 and 35 psu, being lowest (34.0 ± 0.1 psu) in Oct. 2006 and highest (34.5 ± 0.02 psu) in Apr. 2005. In addition, salinity significantly differed among stations (ANOVA, $F_{3,72}$ = 2.295, $p < 0.05$), with salinities at stations 27 and 28 lower (0.5-1 psu) than those at stations 20, 21, and 23 (by Tukey's test).

Maps of the current direction and vertical profiles of temperature and salinity illustrated the principal oceanographic features of the northern SCS and Kuroshio waters off southern Taiwan (Figs. 2, 4). The current direction was counterclockwise in waters southwest of Taiwan in winter. Waters off southeastern Taiwan were dominated by the Kuroshio waters throughout the
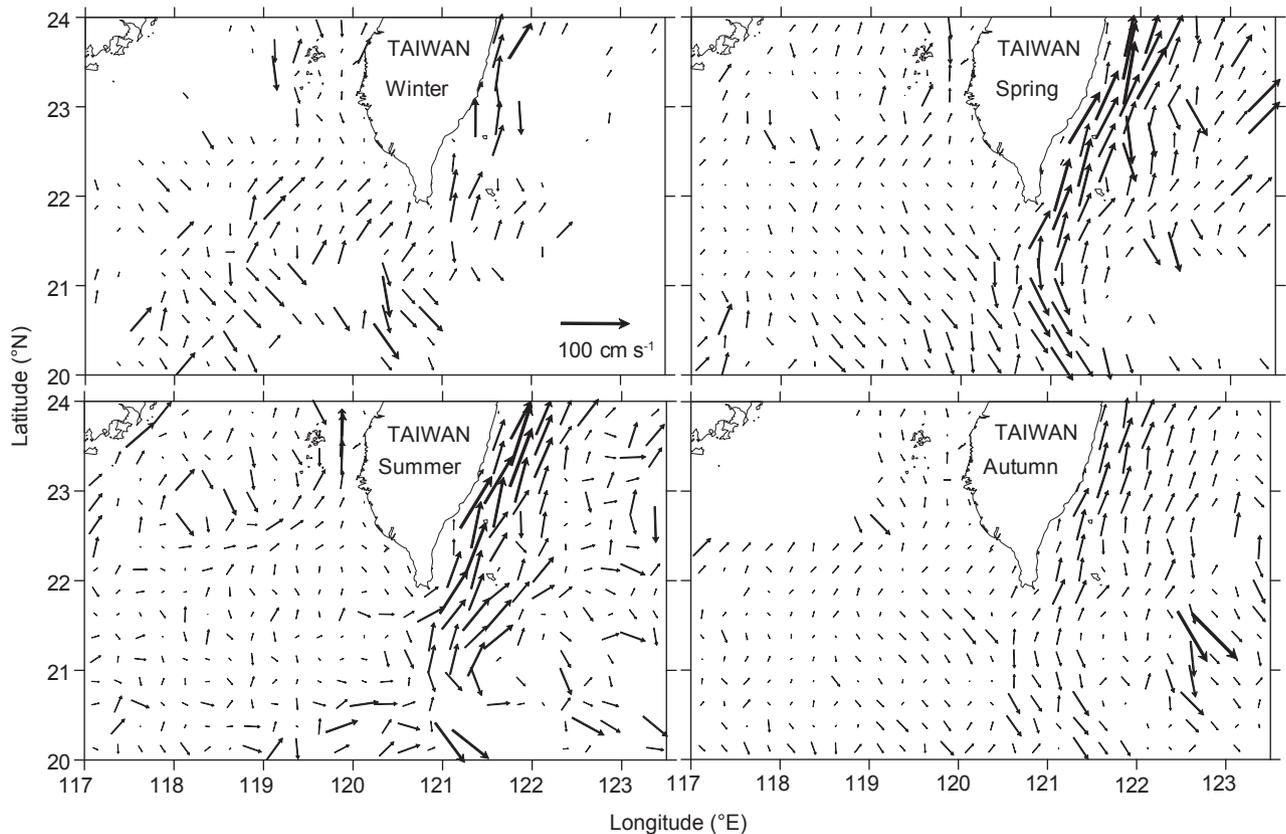

Fig. 2. Current direction and velocity in waters off southern Taiwan during the 4 seasons. (Data from the Ocean Data Bank of the National Center for Ocean Research, Taipei, Taiwan).

year (Fig. 2). Furthermore, analysis of vertical profiles of temperature and salinity in the study area (Fig. 4) showed that the upper 100-m layer of water off southern Taiwan was vertically well mixed in winter; conversely, during the warm seasons, this water was clearly stratified, and salinities at stations 25-28 were about 0.4-0.8 psu lower than those at stations 20-24. In addition, a downwelling site occurred between stations 22 and 26 southeast of Taiwan with relatively high temperatures and low salinities, particularly in winter and summer.

Zooplankton abundances varied from 1339 to 58,998 ind./m^3, with an overall mean of 12,155 ± 1217 ind./m^3. Zooplankton abundances differed seasonally (ANOVA, $F_{3,72}$ = 6.073, p < 0.01), with the lowest densities (26 ± 3 ind./m^3) in Jan. 2006 and the highest (198 ± 32 ind./m^3) in July 2006 (Fig. 3C). In general, abundances were significantly higher during the warm seasons than during the cold seasons, except in Jan. 2005.

Species composition of siphonophores

In total, 55 siphonophore taxa were identified in the study area (Table 1), comprising 44 calycophores and 11 physonects. The calycophoran families, Diphyidae and Abylidae, were the most abundant, together accounting for 99.3% of the total siphonophore catch. The Diphyidae had 27 species, or just under 1/2 (27/55) of the total number of identifiable species. Two of the diphyids, *Chelophyes contorta* and *C. appendiculata*, which respectively contributed 15.8% and 8.3% to total siphonophores, were the 1st and 5th most abundant species during the entire survey. The next most common family was the Abylidae, which was dominated by *Bassia bassensis*, *Abylopsis eschscholtzi*, and *A. tetragona*, together constituting 39.8% of the total catch.

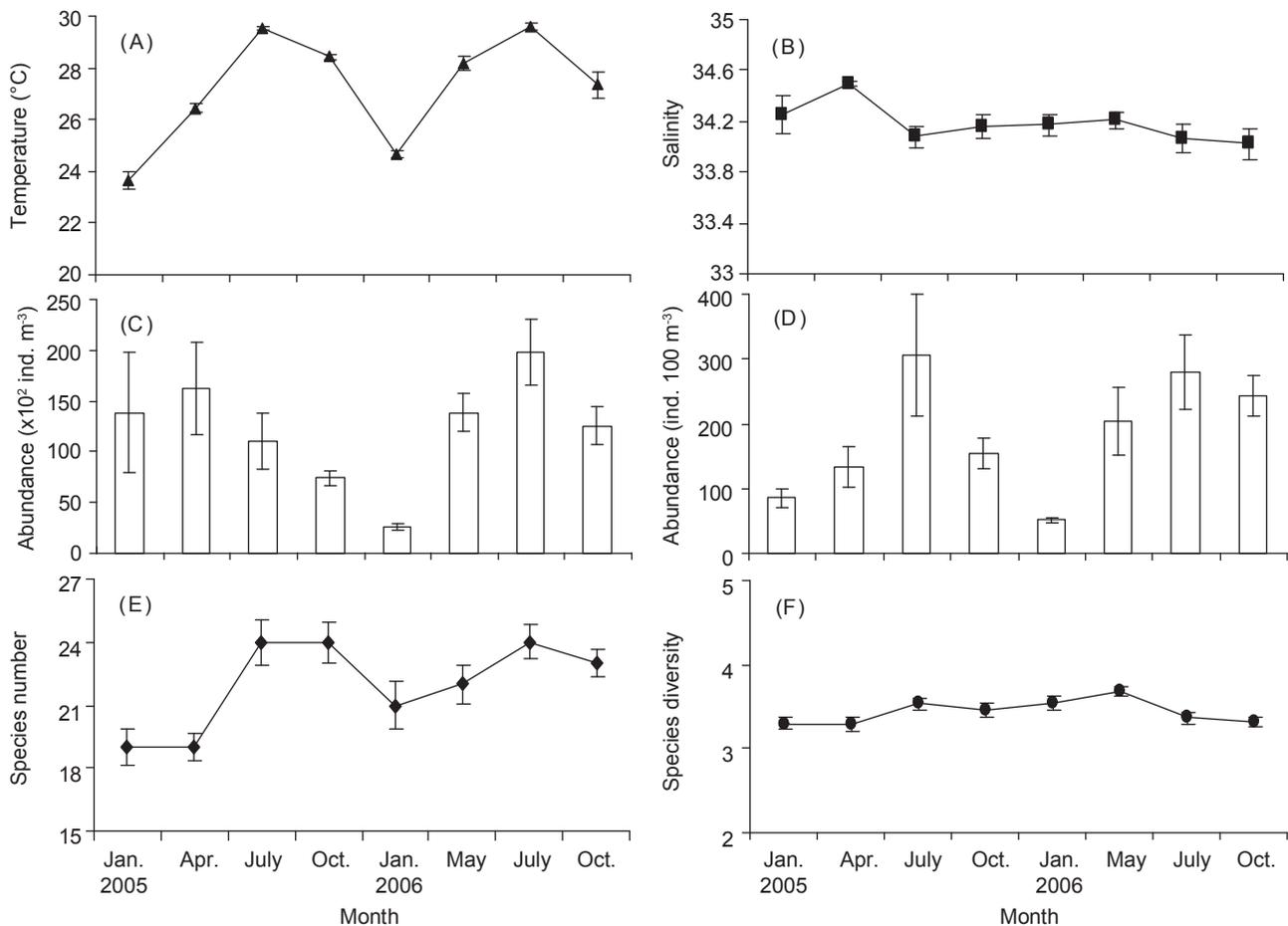The rankings of individual species varied with the season. Species compositions of dominant

Fig. 3. Variations in average (± standard error) (A) temperature, (B) salinity, (C) zooplankton abundance, (D) siphonophore abundance, (E) siphonophore species number, and (F) siphonophore species diversity in waters off southern Taiwan during 2005-2006.
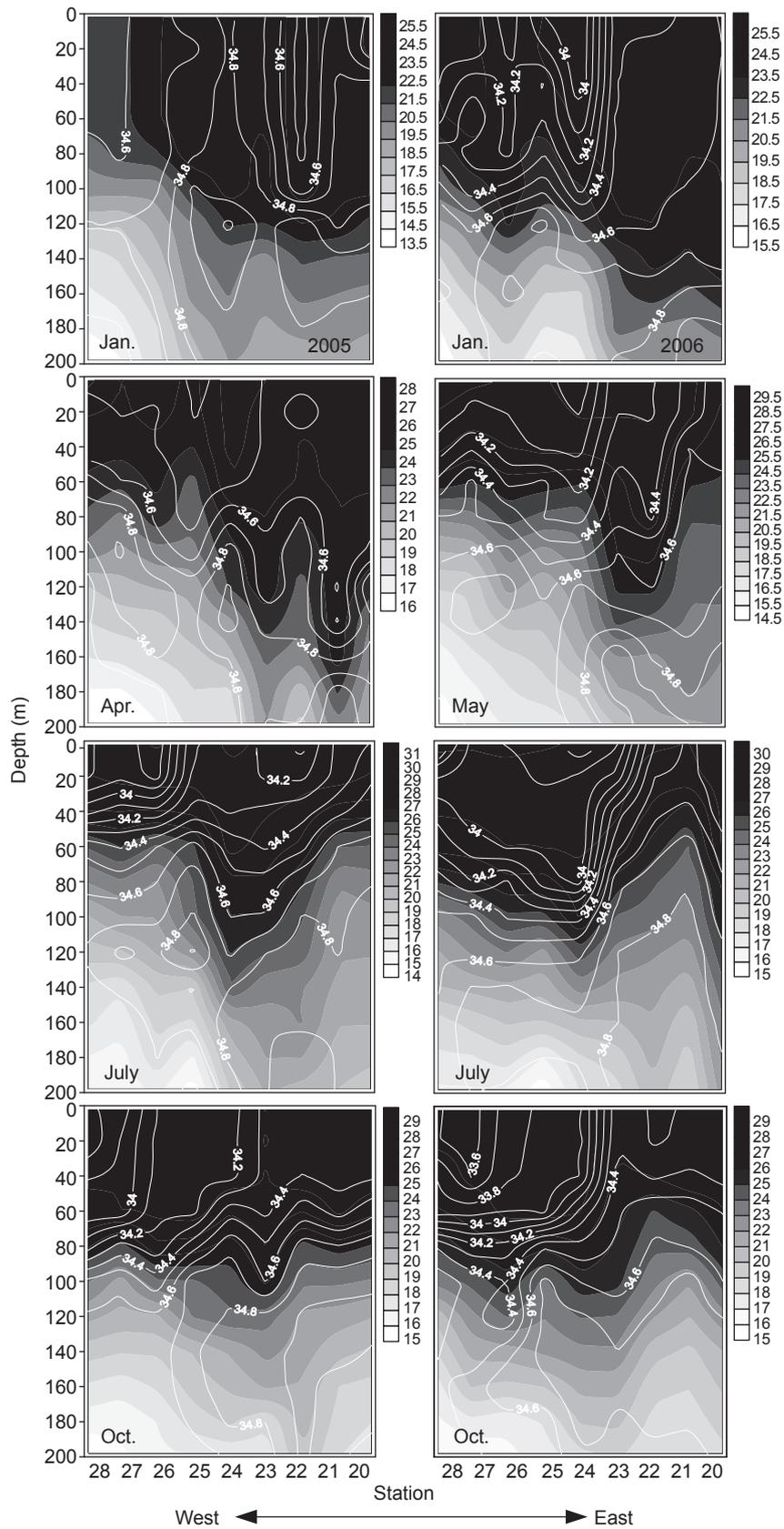
Fig. 4. Vertical profiles of temperature (gray shading) and salinity (white lines) in waters off southern Taiwan during 2005-2006.

siphonophores were similar among seasons, with 80%-91% similarities. The calycophores *C. contorta*, *B. bassensis*, and *A. eschscholtzi* were abundant in all seasons, usually constituting over 10% of the siphonophore catch each season. Apart the above species, the 5 most dominant species during the survey included the diphyids *Eudoxoides mitra* and *E. spiralis*, which were common in spring and winter.

Abundance and species diversity of siphonophores

The seasonal average abundance of siphonophores during the study period was 180 ± 19 ind./100 m^3. The abundance was significantly higher in summer (290 ± 52 ind./100 m^3) than in winter (68 ± 8 ind./100 m^3; ANOVA, $F_{3,72}$ = 13.072, $p < 0.001$, Fig. 3D), with the highest abundance recorded in July 2005 (305 ± 92 ind./100 m^3) and lowest abundance in Jan. 2006 (51 ±

5 ind./100 m^3). In addition, siphonophore abundances differed spatially (ANOVA, $F_{3,72}$ = 3.414, $p < 0.01$), with station 27 usually having a higher abundance (348 ± 101 ind./100 m^3) than at other stations, where abundances ranged 115 ± 41-228 ± 62 ind./100 m^3, Tukey's test). Numbers of siphonophore species were higher in summer and autumn than in winter and spring (ANOVA, $F_{3,72}$ = 9.490, $p < 0.001$, Fig. 3E), but there was no significant spatial difference among stations (ANOVA, $F_{3,72}$ = 1.367, $p > 0.05$). In contrast, species diversity of siphonophores ranged 2.99-3.99 among all sampling stations without a significant seasonal difference (ANOVA, $F_{3,72}$ = 0.318, $p > 0.05$, Fig. 3F).

Siphonophore assemblages

Three clusters (A, B, and C) of stations, using a similarity level of > 60%, were derived from the hierarchical clustering based on an analysis of

Table 1. Alphabetical list of siphonophores collected in waters off southern Taiwan during 2005-2006

Physonectae	*Eudoxia macra* Totton, 1954
Agalmatidae	*Eudoxoides mitra* (Huxley, 1859)
Agalma elegans (Sars, 1846)	*Eudoxoides spiralis* (Bigelow, 1911)
Agalma okeni Eschscholtz, 1825	*Gilia reticulata* (Totton, 1954)
Halistemma rubrum (Vogt, 1852)	*Lensia campanella* (Moser, 1925)
Halistemma striata Totton, 1965	*Lensia conoidea* (Keferstein & Ehlers, 1860)
Lychnagalma utricularia (Claus, 1879)	*Lensia cossack* Totton, 1941
Marrus sp. 1	*Lensia exeter* Totton, 1941
Marrus sp. 2	*Lensia fowleri* (Bigelow, 1911)
Nanomia bijuga (Chiaje, 1841)	*Lensia hardy* Totton, 1941
Nanomia sp.	*Lensia hotspur* Totton, 1941
Forskaliidae	*Lensia leloupi* Totton, 1954
Forskalia contorta Milne-Edwards, 1841	*Lensia meteori* (Leloup, 1934)
Forskalia edwardsi Kölliker, 1853	*Lensia multicristata* (Moser, 1925)
Calycophorae	*Lensia subtilis* (Chun, 1886)
Abylidae	*Lensia subtiloides* Lens & van Riemsdijk, 1908
Abyla bicarinata Moser, 1925	*Muggiaea kochi* (Will, 1844)
Abyla haeckeli Lens & van Riemsdijk, 1908	*Sulculeolaria biloba* (Sars, 1846)
Abyla trigona Quoy & Gaimard, 1827	*Sulculeolaria chuni* (Lens & van Riemsdijk, 1908)
Abylopsis eschscholtzi (Huxley, 1859)	*Sulculeolaria monoica* (Chun, 1888)
Abylopsis tetragona Otto, 1823	*Sulculeolaria quadrivalvis* Blainville, 1834
Bassia bassensis (Quoy & Gaimard, 1834)	*Sulculeolaria turgida* (Gegenbaur, 1853)
Ceratocymba dentata (Bigelow, 1918)	Hippopodiidae
Ceratocymba leuckarti (Huxley, 1859)	*Hippopodius hippopus* (Forskål, 1776)
Ceratocymba sagittata Quoy & Gaimard, 1827	*Vogtia glabra* Bigelow, 1918
Enneagonum hyalinum Quoy & Gaimard, 1827	*Vogtia* sp.
Diphyidae	Prayidae
Chelophyes appendiculata (Eschscholtz, 1829)	*Amphicaryon acaule* Chun, 1888
Chelophyes contorta Lens & van Riemsdijk, 1908	*Amphicaryon ernesti* Totton, 1954
Diphyes bojani (Eschscholtz, 1829)	*Amphicaryon peltifera* (Haeckel, 1888)
Diphyes chamissonis Huxley, 1859	*Rosacea plicata* Bigelow, 1911
Diphyes dispar Chamisso & Eysenhardt, 1821	

species compositions of siphonophores (Fig. 5). Cluster A contained only station 21 in Jan. 2006 (Table 2). Cluster B was comprised of 42 stations, mostly from spring, summer, and autumn in both years. This group was characterized by high temperatures (mean > 28°C) and high abundances of zooplankton and siphonophores (Table 2). The diphyids *C. contorta*, *C. appendiculata*, *E. mitra*,

and *Diphyes bojani* and the abylids *B. bassensis*, *A. eschscholtzi*, and *A. tetragona* were the most important species of this station group, contributing 8.0%-12.0% to the total average similarity (Table 3). Cluster C included 29 stations that mainly occurred in winter in both years, with a mean temperature of < 26°C (Table 2). Mean abundances of zooplankton and siphonophores in cluster C were
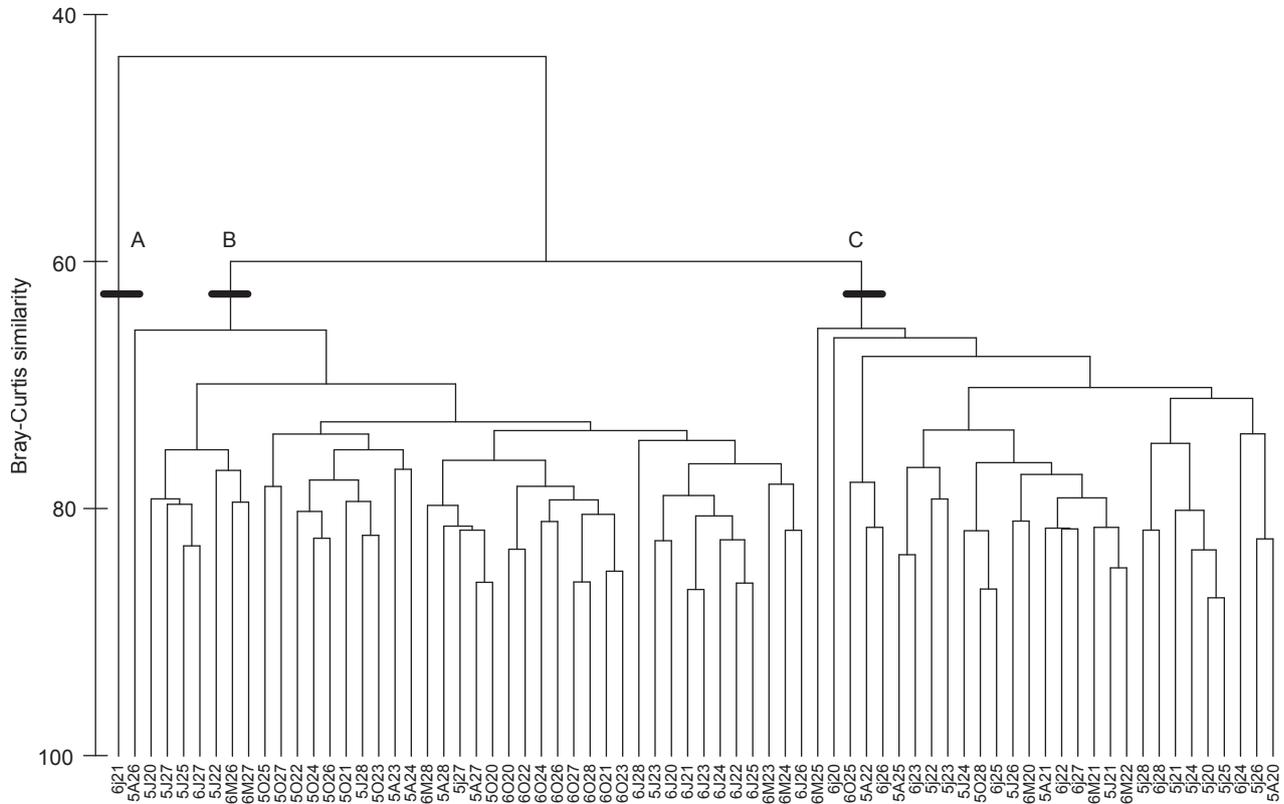

Fig. 5. Hierarchical clustering of station assemblages based on the Bray-Curtis similarity matrix of log(x+1)-transformed abundances of the 14 predominant siphonophore species (with a relative abundance of > 1%). 5, 2005; 6, 2006; j, Jan.; A, Apr.; M, May; J, July; O, Oct.

Table 2. Environmental variables (seawater temperature, salinity and zooplankton abundance) and mean values of abundance, species number, and species diversity (H') of siphonophores, within the 3 siphonophore assemblages. Station groups are according to those delineated in figure 5

Group	A	B	C
	Value	Mean ± S.E.	Mean ± S.E.
Temperature (°C)	24.86	28.26 ± 0.25	25.83 ± 0.39
Salinity (psu)	34.40	34.16 ± 0.04	34.21 ± 0.06
Zooplankton (ind./m³)	1339	16688 ± 1694	5964 ± 813
Siphonophore (ind./100 m³)	33	268 ± 24	62 ± 3
Species number (total)	18	23 ± 1 (53)	21 ± 1 (53)
H'	3.10	3.42 ± 0.04	3.48 ± 0.05

ind., individuals; S.E., standard error.

much lower than those in cluster B. The most important species in this group were the abylids *B. bassensis*, *A. eschscholtzi*, and *A. tetragona* and the diphyids *C. contorta* and *E. mitra*, with a combined contribution of > 60% (Table 3).

Relationships between siphonophores and environmental variables

We undertook a CCA to examine non-linear relationships between siphonophores (the 14 predominant species) and environmental variables (temperature, salinity, and zooplankton abundance) (Fig. 6). The 1st 2 canonical axes of the CCA explained 11.4% of the total variation in the distribution of species (Table 4). The eigenvalue indicated the influence of each axis on the ordination. Correlations between species and environmental axes were 0.646 and 0.509, respectively. Temperature was the most significant variable affecting siphonophore abundances. Species further from the center of the ordination diagram had stronger relationships with environmental variables than those nearer the center of the ordination. Among the 14 species, *C. appendiculata*, *D. chamissonis*, and *Lensia conoidea* were strongly and positively influenced by temperature; *D. dispar* and *A. tetragona* were significantly correlated with zooplankton abundances; and salinity had a positive effect on *A. eschscholtzi* and *D. bojani*.

DISCUSSION

Oceanographic conditions

Our study area extended westward from the western North Pacific (the Kuroshio water), through the LS, to the northern SCS. A branch of the Kuroshio enters the SCS from the southeast at 20°N, 121°E south of the LS, deflects at about 21°N, 118°E, and then flows out of the LS (Jia and Liu 2004, Jia et al. 2005). The deflected branch of the Kuroshio is called the Kuroshio Bend (Kuroshio Current Loop in Li et al. 1998), varies temporally, and sheds anticyclonic eddies periodically at the northern Kuroshio Bend, mainly near 20°-22°N, 117°-120.5°E. In the present study, a downwelling phenomenon, formed by an anticyclonic eddy, also usually occurred between stations 22 and 26, particularly in winter and summer (Fig. 4). In contrast to the intrusion pathway of the Kuroshio into the SCS proposed by Jia and Liu (2004) and Jia et al. (2005), Caruso et al. (2006) believed that the formation and characteristics of intrusions considerably vary from year to year. Typically, an intrusion originates in the central region of the LS and continues as an anticyclonic circulation in the northeastern SCS. However, in some years, the intrusion shifts to the northern portion of the LS and forms a small cyclonic circulation southwest of Taiwan. For example, in Jan. 2003, these authors observed the formation of a small cyclonic eddy

Table 3. Discriminating siphonophore species of the 3 station groups (from Fig. 5) based on abundances by the SIMPER analysis with a cutoff for low contributions at 90%. MA, mean abundance (individuals/100 m³); PC, percentage contribution to the within-group similarity

Similarity (%)	A (-)			B (75.32)			C (73.15)	
	MA	PC (%)		MA	PC (%)		MA	PC (%)
Fewer than 2 samples in a group			*Chelophyes contorta*	41	12.0	*Bassia bassensis*	12	14.8
			Abylopsis eschscholtzi	38	12.0	*Abylopsis eschscholtzi*	9	13.1
			Bassia bassensis	40	11.9	*Chelophyes contorta*	8	12.2
			Abylopsis tetragona	25	9.3	*Abylopsis tetragona*	5	10.8
			Chelophyes appendiculata	23	8.7	*Eudoxoides mitra*	5	9.6
			Eudoxoides mitra	21	8.4	*Diphyes bojani*	3	7.8
			Diphyes bojani	15	8.0	*Diphyes dispar*	2	7.1
			Diphyes dispar	14	7.5	*Eudoxoides spiralis*	4	7.3
			Lensia conoidea	6	3.6	*Chelophyes appendiculata*	2	5.9
			Diphyes chamissonis	4	3.2	*Sulculeolaria chuni*	1	2.3
			Eudoxoides spiralis	10	3.0			
			Lensia subtiloides	4	2.5			
			Total	-	90.1	Total	-	90.9

near the coast of Taiwan at 119.25°E, 21.5°N (adjacent to our stations 27 and 28), which drew cold shelf water into the basin, trapping Kuroshio water along the coast of Taiwan. We think that the periodic formation of cyclonic eddies (upwelling) may bring nutrient-rich subsurface water to surface waters in this area.

Temporal and spatial changes in abundances and species numbers

Siphonophores are exclusively marine animals, mostly oceanic, but a few are neritic (Pugh 1999). Extreme temperatures and salinities might not favor populations of siphonophores. In the past, some studies on siphonophore assemblages
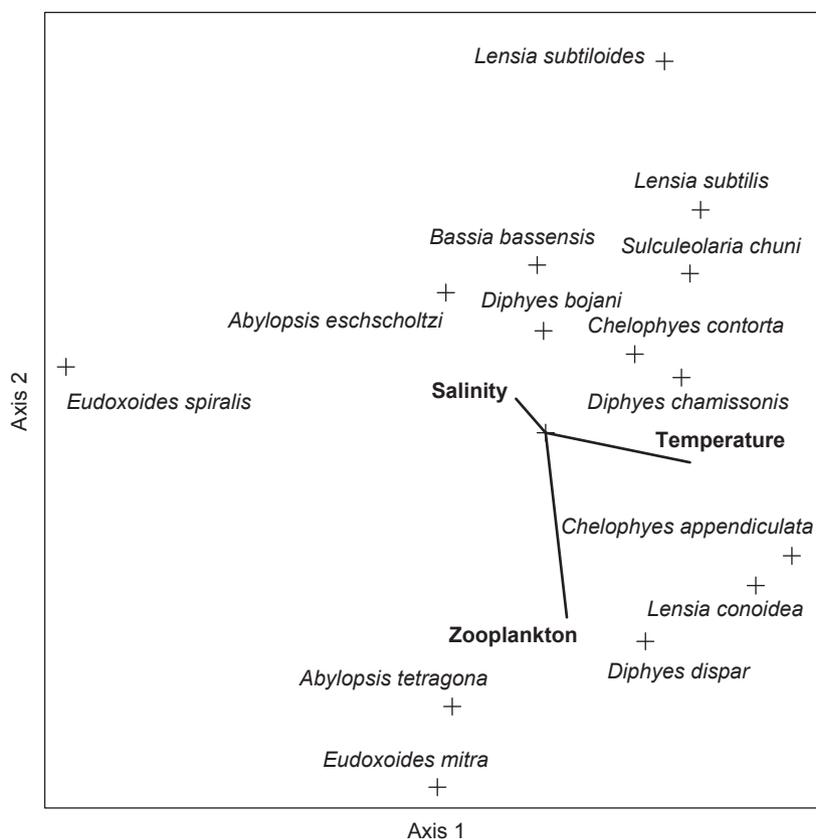

Fig. 6. Ordination diagram of the canonical correspondence analysis (CCA) based on hydrographic variables and abundances of the 14 predominant species.

Table 4. Summary of statistics for the canonical correspondence analysis of the 14 predominant siphonophore species (from Fig. 6)

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.039	0.011	0.004
Pearson correlations, Spp-Envt.	0.646	0.509	0.262
Percent of variance explained	8.8	2.6	0.9
Cumulative percent explained	8.8	11.4	12.3
Inter-set correlations of environmental variables with axes			
Temperature	0.617	-0.079	0.066
Salinity	-0.129	0.091	-0.253
Zooplankton	0.091	-0.504	0.001

Spp-Envt., species-environment.

in different regions of the world showed the influences of changes in temperature and salinity on temporal and spatial distribution patterns. For example, Carré and Carré (1991) found that production of *Muggiaea kochi* varied seasonally with temperature, with a shorter life cycle in warmer waters. Favorable temperatures probably contributed to the higher densities of *Lensia conoidea* and *Dimophyes arctica* observed during summer and autumn in Korsfjord (Hosia and Båmstedt 2008). In the southern Gulf of Mexico, most siphonophore populations were reduced by temperatures above 28.1°C (Sanvicente-Añorve et al. 2009) and extreme salinities (> 36.5 or < 34 psu) (Sanvicente-Añorve et al. 2007). In our study, higher abundances and species numbers of siphonophores occurred at stations 25-28 during the warm seasons (summer and autumn) when temperatures were usually > 28.5°C and salinities < 33.8 psu. In addition to total abundances of predominant species, species numbers of siphonophores were significantly and positively correlated with temperature. Our results were inconsistent with the above studies and indicated that the influence of salinity on siphonophore distributions in waters off southern Taiwan is minimal.

It is well known that siphonophores are carnivorous zooplankton, consuming mainly copepods, the major constituent of the zooplankton community (Purcell 1981 1997). In our study, consistent parallel trends in abundances of siphonophores and zooplankton were observed. We think that the seasonality in zooplankton biomass may be a control mechanism for seasonal cycles of the major gelatinous predators and may affect abundances of siphonophores. Similar conclusions were reached by several authors. Peaks in abundances of *L. conoidea* and *Chuniphyes multidentata* were observed 6 weeks behind the seasonal phytoplankton bloom in Monterey Bay, CA (Silguero and Robison 2000). In addition, Sreekumaran-Nair et al. (1992) assessed the response of phyto- and zooplankton to eutrophication along the west coast of India and found a peak in siphonophore abundance about 2-3 months after nutrient enrichment.

Siphonophore composition

Most siphonophore species collected in this study are widely distributed in tropic-equatorial waters (Gasca 1999, Pugh 1999, Pagès et al. 2001, Sanvicente-Añorve et al. 2007 2009).

Among the 2 major siphonophore assemblages (clusters B and C) in our study, compositions of the predominant species were the same despite an average abundance in cluster B 4-times higher than that in cluster C. Typical oceanic species, the diphyids, *C. contorta* and *C. appendiculata*, and the abylids, *B. bassensis*, *A. eschscholtzi*, and *A. tetragona*, were the 5 predominant species in our study, constituting 8%-16% of the total catch. These species are common in temperate waters of the Atlantic, Indian, and Pacific Oceans, including the SCS and Mediterranean Sea (Pugh 1974, Pagès and Gili 1991 1992).

Chelophyes contorta was the most common species in this study, with a significantly high abundance in summer. It is mostly a neritic Indo-Pacific species; however, in the North Pacific it extends northward to 36°N along the extension of the Davidson Current in the east and Kuroshio Current in the west. Its distribution appears to be limited by the 18°C isotherm at 200 m, except in the region of the Peru Current (Alvariño 1971). *Chelophyes contorta* was also most abundant in surface waters of Easter I. in the South Pacific (Palma 1999) and was found off South Africa in the western Indian Ocean due to intrusions of the Agulhas Current from the north (Thibault-Botha et al. 2004).

The 2nd-most abundant species, *B. bassensis*, generally appears to be distributed throughout tropical and subtropical belts of the Pacific, Atlantic, and Indian Oceans and almost exclusively resides in the upper 150-200 m (Alvariño 1971, Pugh 1999, Table 1). This species showed significantly higher abundances in summer and autumn than in winter and spring in our study, particularly in summer 2005. *Bassia bassensis* is one of the most abundant siphonophores in neritic and oceanic waters of the southern Gulf of Mexico (Gasca 1999) and mainly prefers the 20-80 m depth stratum (Sanvicente-Añorve et al. 2009). It is the most important secondary predator in the top 50 m of the water column, especially in oceanic waters off the Chilean coast (Pagès et al. 2001).

Distributions of the species *A. eschscholtzi* and *A. tetragona* extend in the Pacific from about 37°N to 35°S (Alvariño 1971) and appear year-round in the SCS. They were the 3rd and 4th most abundant species in our study and occurred mainly at stations 27 and 28 where salinities of < 34.2 psu were recorded during the warm season. These 2 species are widely distributed in oceanic waters and also in near-shore waters around southern Africa (Gibbons and Thibault-Botha

2002). Similarly, Sanvicente-Añorve et al. (2009) proposed that these species tolerated a wide range of salinities in the southern Gulf of Mexico; furthermore, *A. tetragona* had a high degree of uniformity in its distribution where salinities were > 33.4 psu.

Chelophyes appendiculata is one of the most common species in the upper 200-m layer in temperate to equatorial oceanic waters. It was abundant mainly in summer and autumn in our study area. In Kuroshio waters south of Japan and in several locations in the tropical-equatorial Pacific, *C. appendiculata* is widely present from the surface to 1000 m in depth (Alvariño 1971). It is among the 4 most important species in both neritic and oceanic environments in the Mexican Caribbean Sea (Gasca 1997). This species was common in our survey area, particularly at stations 20, 27, and 28, indicating that it has a wide salinity tolerance range. *Chelophyes appendiculata* is abundant in near-shore and shelf waters of the Gulf of Mexico, where extreme salinities were recorded (Sanvicente-Añorve et al. 2009).

In summary, siphonophore abundances showed significant temporal and spatial differences, with higher abundances usually in summer and in the SCS section of our transect. The predominant siphonophore species were similar among seasons, but species numbers of siphonophores were higher in summer and autumn than in winter and spring. Seawater temperatures and salinities showed slight effects on siphonophore distributions in waters off southern Taiwan. Conversely, the succession of zooplankton biomass may play a key role in seasonal cycles of siphonophore abundances.

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