Influence of monsoon-driven hydrographic features on siphonophore assemblages in the Taiwan Strait, western North Pacific Ocean

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Abstract.   The spatial patterns of siphonophores were analysed in relation to local hydrographic features during two different monsoon seasons (the north-easterly monsoon in winter *v.* the south-westerly monsoon in summer) in the Taiwan Strait. Forty-eight species were identified, with five types of calycophoran siphonophores (*Lensia subtiloides*, *Chelophyes appendiculata*, *Chelophyes contorta*, *Bassia bassensis*, and *Diphyes chamissonis*) being most common in both seasons. Significantly higher abundances of four of the five common species were recorded in summer than in winter. Differences in the siphonophore species compositions were also observed between the northern and southern part of Taiwan Strait, with significantly higher diversity occurring in the southern waters. The distribution patterns of siphonophore assemblages were closely linked to the hydrographic features, influenced by the dynamic nature of the currents in the study area, with temperature, salinity and zooplankton biomass being the three most important factors.

Additional keywords: composition, gelatinous, spatial variations, water masses, zooplankton.

Introduction

The Taiwan Strait (TS) is a shallow channel bounded by the Asian continent on the west and the island of Taiwan on the east, with a length of 350 km, width of 180 km and average depth of 60 m. It connects the East China Sea (ECS) in the north with the South China Sea (SCS) in the south and serves as an important pathway for the exchange of biota between those two seas (Fig. 1). The East Asian monsoons and bathymetric topography are the two major forces that determine the temporal and spatial variations of currents in the TS (Jan *et al.* 2002, 2006). Those currents are usually broadly divided into (1) the China Coastal Current (CCC), (2) the South China Sea Warm Current (SCSWC), and (3) the Kuroshio Branch Current (KBC) (Jan *et al.* 2002, 2006, 2010).

During winter (November to February), the prevailing north-easterly monsoon drives the cold, low-salinity and nutrient-rich CCC southward along the coast of China into the northern TS, and consequently, holds back the northward intrusion of the warm, highly saline and nutrient-poor KBC into the south-eastern TS. When the north-easterly monsoon weakens as winter becomes spring and summer, a south-westerly monsoon sets up that forces the penetration of the SCSWC into the TS and gradually replaces the KBC (Jan *et al.* 2002, 2006).

As the KBC and SCSWC alternately impinge on the Chan-gyun Ridge, the surface and subsurface waters from the Penghu Channel flow in different directions north of the ridge. The lighter surface water flows over the ridge and moves along the eastern side of the TS, whereas the heavier subsurface water is obstructed by the ridge and turns north-westward along local isobaths into the north-western TS (Wang and Chern 1988; Jan *et al.* 1994). The subsurface water was observed to diverge near the Penghu Islands, forming a cyclonic ring that upwelled cold water from below the mixed layer. These seasonally and locally varying currents, therefore, are expected to influence the distribution patterns and succession of plankton communities, as well as to create temporal and spatial variability in the planktonic ecosystem of the TS.

Siphonophores are widespread in the marine pelagic realm (Pugh 1999). These pelagic predators feed on zooplankton, particularly copepod crustaceans, and sometimes on fish larvae and young fishes (Purcell 1981; Alvariño 1985; Pagès *et al.* 2001). When conditions are favourable, they can reproduce rapidly and sometimes are the most abundant non-crustacean invertebrate predators (Pugh 1974; Robison *et al.* 1998; Hosia and Båmstedt 2007). Nevertheless, our understanding of sipho-nophore population and community ecology in the TS is very poor, with few surveys having been conducted in the ECS, SCS and the waters of northern Taiwan. For example, in the ECS, siphonophores were reported to be distributed mainly in
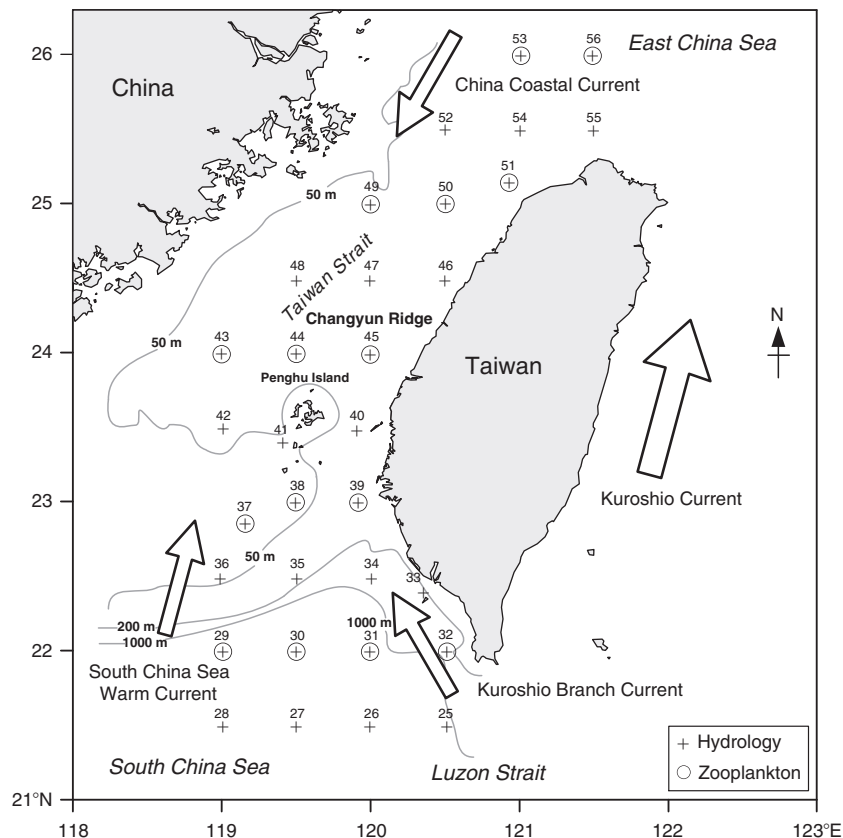
Fig. 1. Locations of sampling stations in the Taiwan Strait in January and July 2005.

southern and northern offshore areas, where *Muggiaea atlantica*, *Abylopsis eschscholtzi* and *Diphyes chamissonis* were the three most abundant species (Xu and Lin 2006). Zhang *et al.* (2005) recorded 31 siphonophore species in the Nanwan Bay of southern Taiwan during late autumn and early winter 2001, with *Chelophyes contorta*, *Diphyes bojani*, *Diphyes dispar*, *Chelophyes appendiculata*, *A. eschscholtzi* and *Bassia bassensis* being the five most common species. López-López *et al.* (2013) found indeed recurrent higher abundances on gelatinous carnivore zooplankton in the following month after a strong typhoon in northern Taiwan. On the north-western continental shelf of the SCS, Li *et al.* (2012) suggested that local coastal upwelling and surface ocean currents driven by south-westerly monsoon enhanced the species number and abundance of siphonophores in summer; in contrast, the north-easterly monsoon forced the cold coastal current into the study area, resulting in low species richness and abundance in winter.

In the present study, we identified and compared the taxonomic composition and abundance of siphonophores at hydrographic stations occupied during both monsoon seasons. We also analysed the distribution patterns of siphonophore assemblages in relation to changes in the local hydrographic conditions.

Materials and methods

Sampling

Siphonophores in the TS were sampled during two cruises of the R/V *Fishery Researcher I* on 3–24 January (hereafter winter)

and 9–14 July (hereafter summer) 2005. Zooplankton samples were taken at 15 of the 32 hydrographic stations (Fig. 1) by an Ocean Research Institute (ORI) net (1.6-m mouth diameter, 6-m long, and 330-μm mesh size), and preserved in a solution of 5% formaldehyde in sea water. The net was towed vertically at a speed of $1\,\mathrm{m\,s^{-1}}$ from 200 m (or 10 m above the bottom at stations with a depth of <210 m) to the surface. The water volume filtered was calculated using a Hydro-Bios mechanical flowmeter (Hydro-Bios, Kiel, Schleswing-Holstein, Germany) mounted at the centre of the net. At each station, vertical profiles of temperature and salinity were obtained with a General Oceanics SeaBird CTD (SEB-911 Plus, Sea-Bird Electronics, Inc., Bellevue, WA, USA). Water samples for measurements of Chlorophyll *a* concentration were collected at 5-, 25-, 50-, 75-, 100- and 150-m depths by using Go-Flo bottles (General Oceanics, Miami, Florida, USA).

In the laboratory, each zooplankton sample was divided into two subsamples with a Folsom splitter (Aquatic Research Instruments, Wellington, New Zealand). Siphonophores were sorted from one stochastic subsample, preserved in 70% alcohol after sorting, and identified to the lowest possible taxonomic level. Because of the polymorphic structure and fragile nature of most species, siphonopores usually fragment in net samples; therefore, the numbers of nectophores or bracts of the Physonectae and hippopodiids were counted and then divided by 10 to estimate their abundance, according to Pugh (1984). In general, species of the Calycophorae have two stages (polygastric and
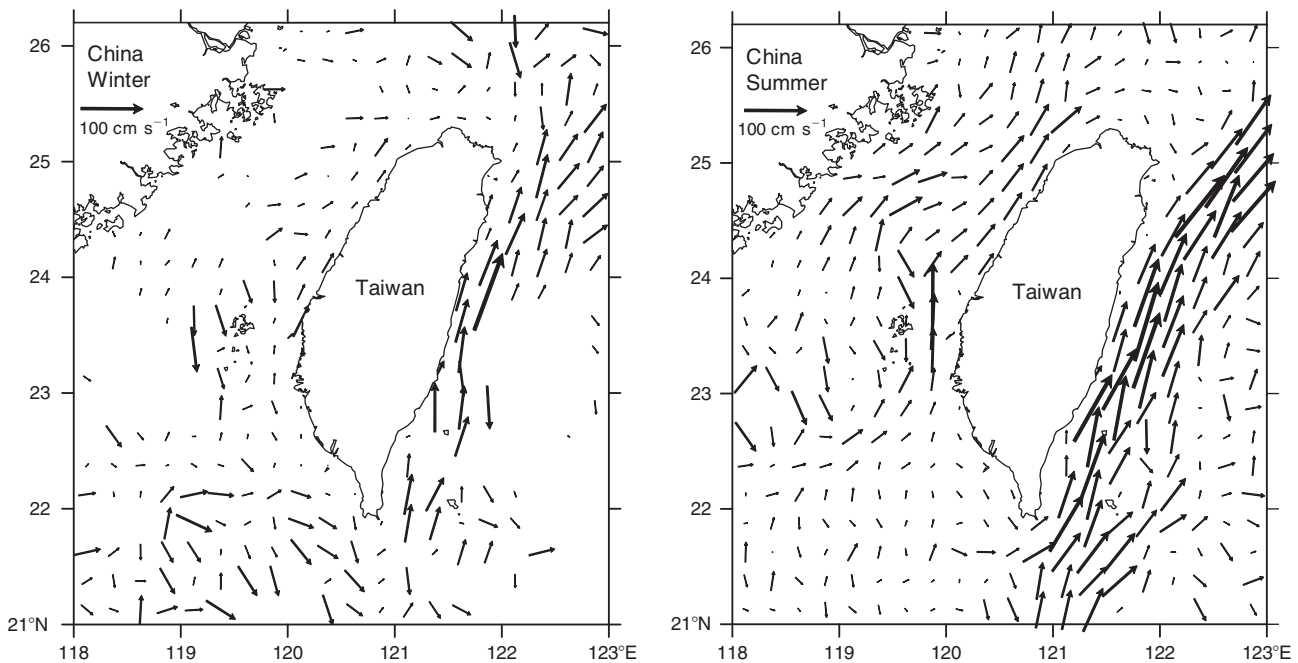
Fig. 2.   Surface-circulation patterns in the seas surrounding Taiwan during winter and summer. Data from the ocean databank of the National Center for Ocean Research (NCOR), Taiwan.

eudoxid stages) and each stage contains two distinct individuals (anterior and posterior nectophores); therefore, each kind of nectophore was counted separately and species abundance was given as the sum of the greater counts of both stages. The second subsample was repeatedly subdivided until the number of individual zooplankton in the last subsample was estimated to be 1000–2000 or fewer, and organisms in the entire subsample were counted to calculate the density of zooplankton at that station. Thirty zooplankton taxa were identified according to the classification of zooplankton in Kuroshio waters. Siphonophore and zooplankton abundances were standardised to the number of individuals (ind.) per $100\,\mathrm{m}^3$ and $1\,\mathrm{m}^3$, respectively.

Data analysis

Data on current velocity and direction were obtained from the ocean databank of the National Center for Ocean Research, Taiwan, for waters around Taiwan during the north-easterly monsoon and south-westerly monsoon (Fig. 2). The community structure of zooplankton from the samples was described with the Shannon diversity index (H'; Shannon 1948) and Pielou's index of evenness (J'; Pielou 1966). The Sørensen similarity index (SI; Sørensen 1948) of siphonophore assemblages between seasons was calculated by analysing the similarity of pairs of sites for presence or absence of species. Principal component analysis (PCA; Pielou 1984) was used to characterise hydrographic regions and to contrast seasonal variability from temperature, salinity and Chlorophyll *a* data collected at each hydrographic station in the two seasons. A non-parametric Mann–Whitney *U*-test was used to test for seasonal differences in siphonophore abundance and diversity (Mann and Whitney 1947).

The similarity of species compositions of siphonophores among sampling stations also was analysed by constructing a similarity matrix of $\log(x+1)$-transformed abundance of siphonophores (Bray and Curtis 1957). In addition, non-metric multi-dimensional scaling (MDS) was used to provide a two-dimensional visual representation of assemblage structure (Kruskal and Wish 1978). The similarity percentage (SIMPER) routine showed the percentage contribution of each taxon to the average similarities within the different siphonophore assemblages (Clarke 1993). In addition, non-linear relationships among sampling stations, dominant taxa and environmental variables were examined with canonical correspondence analysis (CCA), which is a statistical visualisation method (Ter Braak 1986).

Results

Physical environment

The maps of current direction and contours of temperature and salinity indicated the principal oceanographic features in the TS (Figs 2, 3). There was strong seasonality in the temperature of water masses across the sampling area, with temperature ranging from 14.6°C to 24.3°C in winter and from 25.1°C to 30.0°C in summer (Table 1). Although salinity varied by ~2 salinity units, the average salinity ranges were similar in winter (32.3–34.7) and summer (32.1–34.3, Table 1).

A strong temperature and salinity front was observed in the central TS (between 23°N and 24°N) during the north-easterly monsoon, reflecting two distinct water masses in the area (Fig. 3*a*). Significantly lower temperature and salinity were found off north-western Taiwan when the cold CCC flowed out from mainland China. In contrast, higher temperature and salinity occurred in the southern TS, implying penetration of the KBC via the Penghu Channel. The isotherms displayed a north-east–south-west gradient, with the difference between
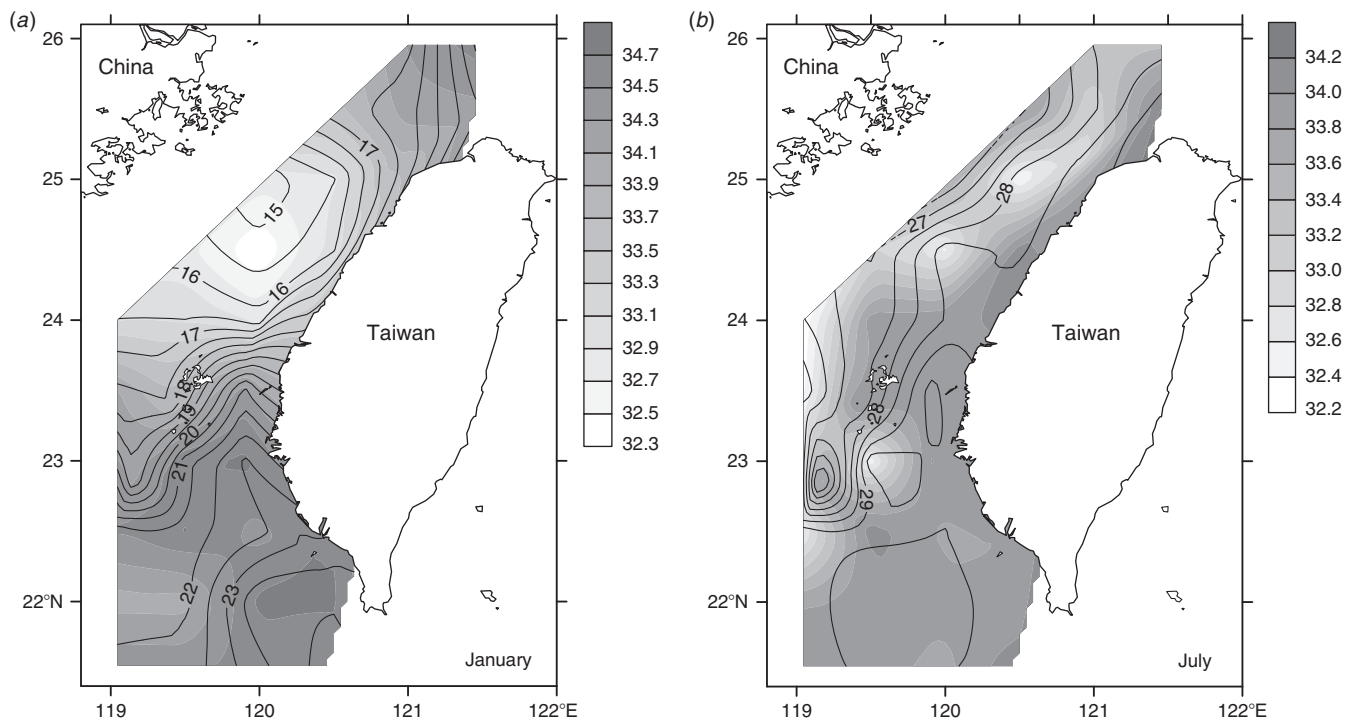
Fig. 3.   Distributions of temperature (°C, black lines) and salinity (grey scales) at 10-m depth in (*a*) January and (*b*) July 2005, in the Taiwan Strait.

Table 1.   Mean (± s.e.) of four environmental variables (temperature, salinity, Chlorophyll *a* concentration and zooplankton abundance) and abundances of five predominant siphonophore species (with the relative abundance, %, in parentheses), total abundance, species number, Shannon's diversity (*H′*), and Pielous's evenness (*J′*) of siphonophores in January and July 2005, in the Taiwan Strait

Variable	January	July
Temperature (°C)	19.61 ± 0.54	28.56 ± 0.22
Salinity	33.98 ± 0.13	33.50 ± 0.12
Chlorophyll *a* (μg L^{-1})	0.11 ± 0.02	0.08 ± 0.02
Zooplankton (individuals m^{-3})	115 ± 26	294 ± 63
Siphonophores		
Lensia subtiloides	5 ± 2 (2.7%)	1758 ± 624 (82.4%)
Chelophyes appendiculata	19 ± 7 (10.3%)	129 ± 50 (6.1%)
Chelophyes contorta	13 ± 5 (6.8%)	113 ± 28 (5.3%)
Bassia bassensis	17 ± 6 (9.3%)	26 ± 4 (1.2%)
Diphyes chamissonis	28 ± 14 (15.4%)	14 ± 4 (0.7%)
Total abundance (individuals 100 m^{-3})	184 ± 52	2134 ± 650
Species number (total)	13 ± 2 (41)	17 ± 2 (39)
H′	1.79 ± 0.17	1.44 ± 0.24
J′	0.76 ± 0.04	0.49 ± 0.07

Fig. 4.   Plots of a principal component analysis (PCA) based on temperatures (at 10-m depth), salinity (at 10-m depth) and Chlorophyll *a* (average concentration in the upper 150 m) at 32 surveyed stations in January and July 2005, in the Taiwan Strait.

these dense contours being up to 8°C. In contrast, warmer waters (>26°C; except at Station 37, 25.1°C) were widely distributed over the surveyed area during the south-westerly monsoon, and comparatively low-salinity waters were observed in the western part of the TS (Fig. 3*b*).
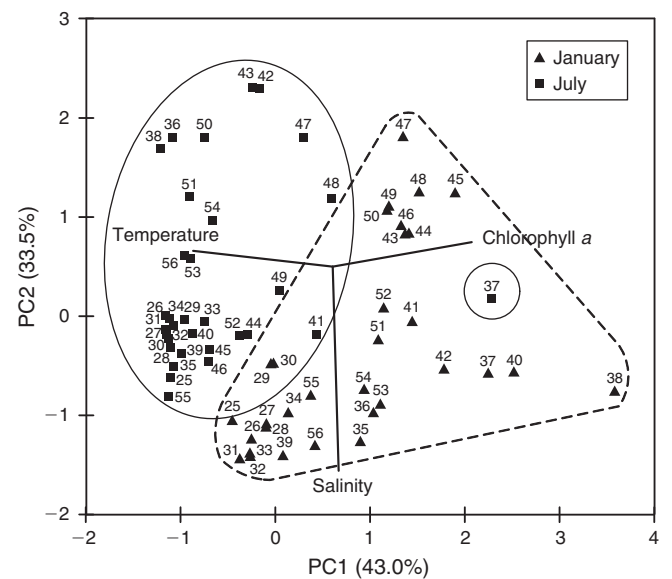
The sampling stations during the survey were categorised into two seasonal groups from the result of PCA of the three hydrographic variables (Fig. 4). In winter, Stations 43–50 had high Chlorophyll *a* concentrations, and the most stations in the southern TS showed positive correlations with salinity. In

Table 2. Alphabetical list of siphonophores collected in January and July 2005, in the Taiwan Strait

Physonectae	*Eudoxoides mitra* (Huxley, 1859)
Agalmatidae	*Eudoxoides spiralis* (Bigelow, 1911)
Agalma elegans (Sars, 1846)	*Lensia campanella* (Moser, 1925)
Agalma okeni Eschscholtz, 1825	*Lensia conoidea* (Keferstein & Ehlers, 1860)
Halistemma rubrum (Vogt, 1852)	*Lensia cossack* Totton, 1941
Halistemma striata Totton, 1965	*Lensia fowleri* (Bigelow, 1911)
Lychnagalma utricularia (Claus, 1879)	*Lensia hardy* Totton, 1941
Nanomia bijuga (Chiaje, 1841)	*Lensia hotspur* Totton, 1941
Nanomia cara Agassiz, 1865	*Lensia grimaldi* Leloup, 1933
Forskaliidae	*Lensia multicristata* (Moser, 1925)
Forskalia edwardsi Kölliker, 1853	*Lensia subtilis* (Chun, 1886)
Physophoridae	*Lensia subtiloides* Lens & van Riemsdijk, 1908
Physophora hydrostatica Forsskål, 1775	*Muggiaea atlantica* Cunningham, 1892
Calycophorae	*Muggiaea kochi* (Will, 1844)
Abylidae	*Sulculeolaria angusta* Totton, 1954
Abyla haeckeli Lens & van Riemsdijk, 1908	*Sulculeolaria chuni* (Lens & van Riemsdijk, 1908)
Abyla trigona Quoy & Gaimard, 1827	*Sulculeolaria monoica* (Chun, 1888)
Abylopsis eschscholtzi (Huxley, 1859)	*Sulculeolaria quadrivalvis* Blainville, 1834
Abylopsis tetragona Otto, 1823	*Sulculeolaria turgida* (Gegenbaur, 1853)
Bassia bassensis (Quoy & Gaimard, 1834)	Hippopodiidae
Enneagonum hyalinum Quoy & Gaimard, 1827	*Hippopodius hippopus* (Forskål, 1776)
Diphyidae	*Vogtia glabra* Bigelow, 1918
Chelophyes appendiculata (Eschscholtz, 1829)	*Vogtia microsticella* Zhang & Lin, 1991
Chelophyes contorta Lens & van Riemsdijk, 1908	Prayidae
Diphyes bojani (Eschscholtz, 1829)	*Amphicaryon acaule* Chun, 1888
Diphyes chamissonis Huxley, 1859	*Amphicaryon ernesti* Totton, 1954
Diphyes dispar Chamisso & Eysenhardt, 1821	*Amphicaryon peltifera* (Haeckel, 1888)
Eudoxia macra Totton, 1954	*Rosacea* sp.

summer, the stations sampled in the southern TS were clearly grouped and had high temperatures. Stations 36, 38, 41–43, 47–51 and 54 showed marked differences from the other stations, with lower salinity. In addition, Station 37 was distinguished from all other stations by having the lowest temperature and highest Chlorophyll *a* concentration, as was expected during upwelling there.

Seasonal changes in abundance and composition of siphonophore assemblages

Forty-eight species of siphonophores (39 calycophorans and 9 physonects) belonging to 22 genera and seven families were found in the present study (Table 2). The abundance of siphonophores was significantly higher in summer than in winter (Mann–Whitney U-test, $U = 31$, $P < 0.01$; Table 1). The overall abundance (mean ± s.e.) was 1159 ± 368 ind. 100 m^{-3}, ranging from 10 to 815 ind. 100 m^{-3} in winter and from 110 to 8233 ind. 100 m^{-3} in summer. In general, relatively higher abundances were observed in the southern TS in winter (Fig. 5*a*); however, significantly higher abundances occurred in the waters north of the Penghu Islands in summer, with a peak abundance of 8233 ind. 100 m^{-3} at Station 50 (Fig. 5*b*).

Siphonophores in 20 genera and 41 species were identified in winter. Winter siphonophore species diversity and evenness varied among stations, from 0.27 to 2.64 and from 0.24 to 0.93, respectively. In summer, 19 genera and 39 species were recorded, with species diversity and evenness ranging from 0.08 to 2.50 and from 0.04 to 0.76, respectively. Species evenness was

higher in winter than in summer (Mann–Whitney U-test, $U = 39$, $P < 0.01$), but species number (Mann–Whitney U-test, $U = 73$, $P = 0.101$) and species diversity (Mann–Whitney U-test, $U = 95$, $P = 0.468$) showed no significant seasonal differences (Table 1).

The calycophoran family Diphyidae was the most abundant family in our study, accounting for 95.4% of the total siphonophore numerical abundance (Table 2). At the species level, *Lensia subtiloides* constituted 76.1% of all siphonophores collected during the study, being the most abundant taxon. *Chelophyes appendiculata* (6.4%), *C. contorta* (5.4%), *B. bassensis* (1.9%) and *D. chamissonis* (1.8%) were the next four most abundant species of siphonophores. These five predominant species together constituted 91.6% of the total catch and they generally were present in >75% of the samples. Species composition of siphonophore assemblages showed a high similarity (SI = 80%; data not shown) between the two monsoon seasons, but the compositions of the predominant species (with relative abundances of >1%) were significantly different. *Diphyes chamissonis*, *Eudoxoides spiralis*, *C. appendiculata*, *Abylopsis eschscholtzi*, *D. dispar*, *B. bassensis*, *C. contorta*, *Eudoxoides mitra*, *A. tetragona*, *D. bojani*, *M. atlantica* and *L. subtiloides* were common in winter; whereas *L. subtiloides*, *C. appendiculata*, *C. contorta* and *B. bassensis* predominated in summer (Table 1). Among these species, *L. subtiloides* was sometimes extremely abundant, with eudoxid phase being twice more numerous than polygastric phase, particularly at Stations 49 and 50, contributing 82.4% of summer siphonophore numerical abundance.
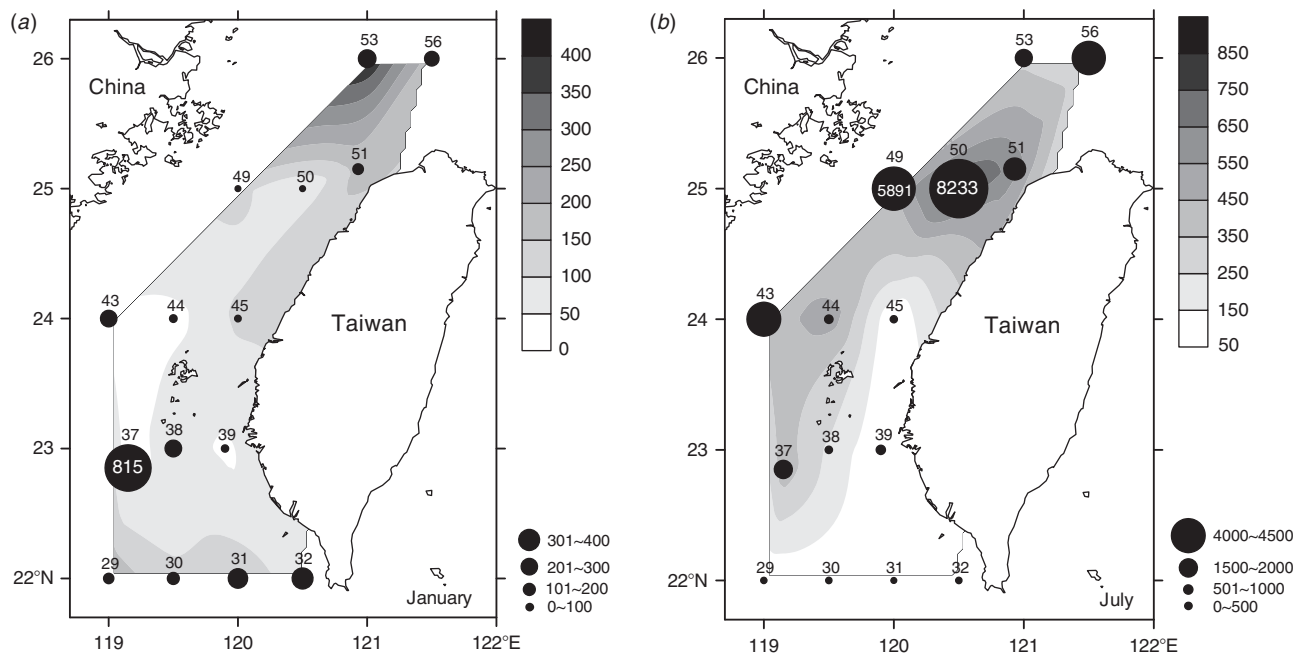
Fig. 5. Horizontal distributions of the integrated abundances of siphonophores (individuals (ind.) $100\,m^{-3}$, solid circles) and zooplankton (ind. m^{-3}, grey scales) in (*a*) January and (*b*) July 2005, in the Taiwan Strait.

Siphonophore assemblages

The hierarchical clustering and MDS analysis of siphonophore species composition showed that stations with similar geographic locations clustered together (Fig. 6). All sampling stations divided into two groups of stations (A and B) at a similarity level of 30%. Group B was further divided into two subgroups of stations, namely B1 and B2, and Group B2 was further divided into B2a and B2b. The characteristics of these groups are summarised in Table 3 and the species that contributed most (cut-off for low contributions at 90%) to their structure are listed in Table 4.

Group A comprised four winter stations, of which three (Stations 43–45) were adjacent to the Penghu Islands and the fourth (Station 49) was in the northern TS. Seven species were in this group, but only *D. chamissonis* was abundant, constituting 78.5% of the total siphonophores counted (Table 3). *Muggiaea atlantica* and *D. chamissonis* were the other two most important species in this group, contributing 57.1% and 29.4% to the within-group similarity, respectively (Table 4).

Group B1 included seven summer stations mostly located in the northern TS (Table 3). In total, 26 siphonophore species were in this group, which was characterised by high abundance, very low diversity and low evenness. Group B1 was typically dominated by *L. subtiloides*, which represented 89% of the total catch (Table 3) and >90% of within-group similarity (Table 4).

Group B2a contained 16 stations (eight winter and eight summer stations) that were located mainly in the southern and central TS, except for the winter Station 56 (Table 3). Forty-six siphonophore species were recognised, representing the highest diversity among the four station groups. *Chelophyes contorta*, *C. appendiculata*, *B. bassensis*, *A. eschscholtzi* and *E. spiralis*

were the five most abundant species in this group; the first four of these also contributed >10% to the within-group similarity (Table 4).

Group B2b consisted of three winter stations in the northern TS, with 18 identified siphonophore species (Table 3). It was dominated by *D. chamissonis*, *M. atlantica*, *L. subtiloides*, *C. appendiculata* and *C. contorta*. The two most important species were *M. atlantica* and *C. appendiculata*, which contributed 27.6% and 20.2% to the within-group similarity, respectively (Table 4).

Correlations between siphonophores and environmental variables

The CCA diagram derived from the abundances of the 10 most abundant siphonophore species illustrated the non-linear relationship between abundance and environmental variables (temperature, salinity, Chlorophyll *a* concentration and zooplankton abundance; Fig. 7). The first two canonical axes of the CCA explained 25.2% and 9.2% of the total variation in the distribution of species, respectively. The result showed a clear delineation between seasons, with winter having considerably more variability. Temperature was the most important variable to affect siphonophore abundance (Person and Kendall correlation with ordination axes, $r = 0.853$), followed by the zooplankton abundance ($r = 0.628$), salinity ($r = -0.620$) and Chlorophyll *a* concentration ($r = -0.097$). Among the 10 predominant species, *B. bassensis*, *D. bojani*, *Abylopsis tetragona*, *A. eschscholtzi* and *E. spiralis* were strongly and positively influenced by salinity and *L. subtiloides* was positively correlated with zooplankton abundance (Fig. 7).
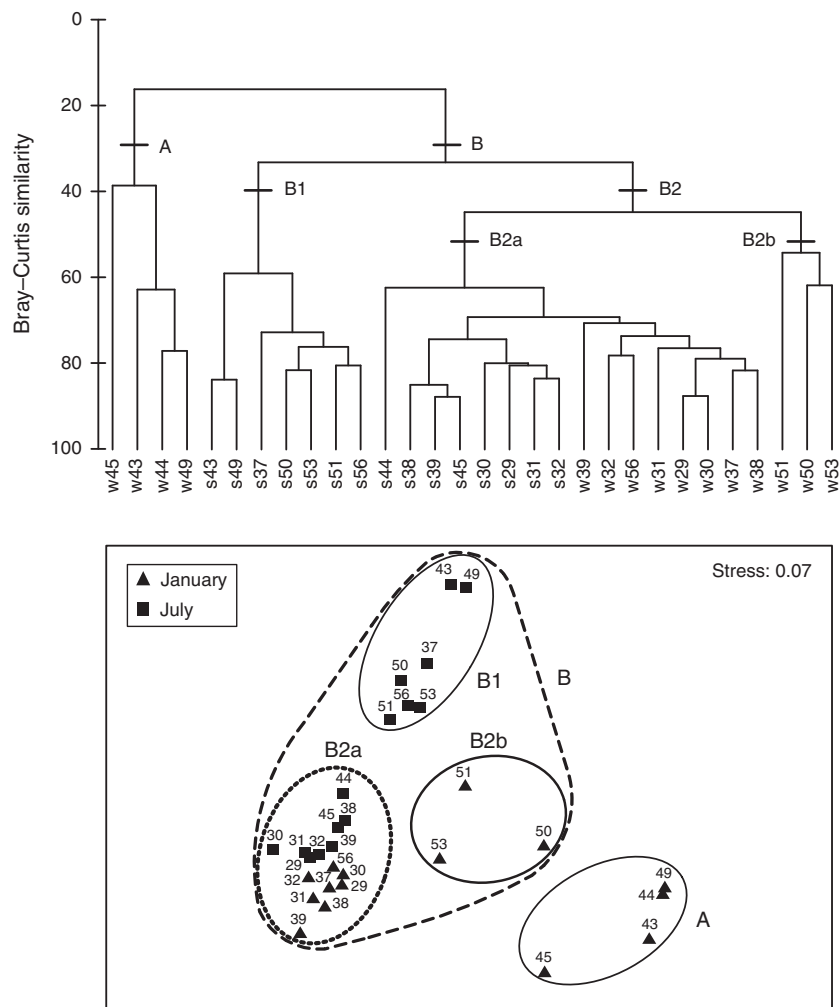
Fig. 6. Similarity dendrogram and multi-dimensional scaling (MDS) ordination of the station groups based on Bray–Curtis similarity matrix of $\log(x+1)$-transformed abundance of siphonophores in January and July 2005 in the Taiwan Strait.

Discussion

Effect of seasonal succession of currents on siphonophore composition

The seasonal monsoon system and bathymetric topography are the two main physical parameters that affect the spatio-temporal variations in water masses and determine the through-flow transports in the TS (Jan *et al.* 2002, 2006). In our study, monsoon-driven currents correlated with variations in the spatial distribution of siphonophores in the TS. In winter, the influence of the CCC extended north into the central TS, as evidenced by decreasing temperature and salinity from south-east to north-west. In the south-eastern TS, water of relatively high temperature (>23.5°C) and salinity (>34.7) flowed northward through the Penghu Channel, indicating penetration of the KBC into the south-eastern TS (Fig. 3*a*). However, in winter this northward flow of the KBC is largely inhibited by southerly flowing water of the CCC near the Penghu Channel,

which in turn reduces the transport of plankton from the SCS and KBC waters to the northern TS. In contrast, in summer an increase in 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 SCSWC, which was widely distributed from south of the Penghu Islands to the north-western part of the surveyed area (Jan *et al.* 2002, 2006; Fig. 3*b*).

Divergence of near-surface water (upwelling) and sharp gradients of temperature and salinity (fronts) may accumulate or separate different assemblages of siphonophores (Pagès and Gili 1991; Pagès *et al.* 2001). In our study area, the boundary of the frontal zone was dynamic in winter, with its location shifting temporally and spatially, depending on the extent of penetration of the CCC and KBC (Jan *et al.* 2006). Nevertheless, advection of siphonophore assemblages may be blocked by sharp frontal gradients and constrained by bottom topography. Because there, generally, is apparently a greater northward transport of the

Table 3. Abundance (individuals 100 m⁻³) and relative abundance (RA, %) of five predominant siphonophore species, and total abundance of siphonophores, species number, Shannon's diversity (H'), Pielou's evenness (J'), temperature and salinity of each station group in January and July 2005, in the Taiwan Strait

Values are means ± s.e., except for RA, which is %. Station groups are according to Fig. 6

Group A (winter: Stations 43, 44, 45, 49)			Group B1 (summer: Stations 37, 43, 49, 50, 51, 53, 56)			Group B2a (winter: Stations 29, 30, 31, 32, 37, 38, 39; summer: Stations 29, 30, 31, 32, 38, 39, 44, 45)			Group B2b (winter: Stations 50, 51, 53)		
Species	Mean ± s.e.	RA	Species	Mean ± s.e.	RA	Species	Mean ± s.e.	RA	Species	Mean ± s.e.	RA
Diphyes chamissonis	60 ± 50	78.53	*Lensia subtiloides*	3731 ± 855	88.58	*Chelophyes contorta*	56 ± 15	19.28	*Diphyes chamissonis*	34 ± 31	28.45
Muggiaea atlantica	11 ± 3	14.16	*Chelophyes appendiculata*	214 ± 99	5.07	*Chelophyes appendiculata*	43 ± 11	14.84	*Muggiaea atlantica*	24 ± 15	20.13
Diphyes dispar	2 ± 1	2.46	*Chelophyes contorta*	137 ± 54	3.26	*Bassia bassensis*	29 ± 5	10.14	*Lensia subtiloides*	15 ± 8	12.76
Eudoxia macra	1 ± 1	1.84	*Bassia bassensis*	24 ± 8	0.57	*Abylopsis eschscholtzi*	26 ± 7	9.07	*Chelophyes appendiculata*	14 ± 7	11.33
Nanomia bijuga	1 ± 0	1.57	*Diphyes chamissonis*	21 ± 8	0.50	*Eudoxoides spiralis*	24 ± 7	8.18	*Chelophyes contorta*	12 ± 7	10.10
Others (2 spp.)	1 ± 1	1.43	Others (21 spp.)	85 ± 48	2.01	Others (41 spp.)	111 ± 43	38.49	Others (13 spp.)	21 ± 19	17.23
Total abundance	76 ± 50			4212 ± 872			288 ± 53			120 ± 69	
Species number	4 ± 0			12 ± 2			20 ± 1			11 ± 3	
H'	0.85 ± 0.19			0.54 ± 0.14			2.25 ± 0.05			1.81 ± 0.07	
J'	0.65 ± 0.15			0.21 ± 0.05			0.76 ± 0.02			0.79 ± 0.05	
Temperature (°C)	15.94 ± 0.47			27.46 ± 0.51			25.46 ± 1.00			16.74 ± 0.65	
Salinity	32.94 ± 0.08			33.06 ± 0.24			34.10 ± 0.14			33.68 ± 0.44	

Table 4. List of predominant siphonophore species in January and July 2005, in the Taiwan Strait, identified by similarity percentage (SIMPER) routine, cutting off for low contributions at 90% as responsible for differences in the structure of the cluster shown in Fig. 6

MA, mean abundance (individuals 100 m⁻³); C, percentage contribution to within-group similarity

Species	MA	C (%)	Similarity (%)
Group A			23.39
Muggiaea atlantica	11	57.06	
Diphyes chamissonis	60	29.40	
Nanomia bijuga	1	11.58	
Total	–	98.04	
Group B1			60.44
Lensia subtiloides	3731	93.19	
Total	–	94.01	
Group B2a			45.77
Chelophyes appendiculata	43	16.03	
Chelophyes contorta	56	15.32	
Bassia bassensis	29	14.62	
Abylopsis eschscholtzi	26	11.55	
Eudoxoides spiralis	24	7.76	
Abylopsis tetragona	16	7.53	
Diphyes bojani	16	5.87	
Eudoxoides mitra	13	5.59	
Diphyes dispar	20	5.10	
Diphyes chamissonis	9	3.54	
Total	–	92.91	
Group B2b			20.32
Muggiaea atlantica	24	27.60	
Chelophyes appendiculata	14	20.20	
Lensia subtiloides	15	18.56	
Diphyes chamissonis	34	14.70	
Chelophyes contorta	12	13.10	
Total	–	94.16	

SCSWC in summer than there is in winter, the northward transport of siphonophores from southern to northern TS was most evident in summer.

Examination of the species compositions of siphonophores during two monsoon seasons showed that of the 43 species found in the southern stations (including Stations 29–32 and 37–39), 18 were absent from the northern stations (including Stations 43–45, 49–51, 53 and 56). This difference in siphonophore distribution between the northern and southern stations was due to the location of the winter frontal zone. The siphonophore assemblages at the northern and southern stations differed significantly from each other in species diversity (unpaired t-test, $t = 4.434$, $P < 0.001$; data not shown). We believe that these clear differences were due to the presence of both neritic and oceanic species in the southern stations, whereas primarily neritic species were present in the northern stations. For example, the neritic species *Muggiaea kochi* and *M. atlantica* were not found in the southern stations and the oceanic-epipelagic species *Lensia hotspur*, *Abyla haeckeli* and *Ceratocymba leuckarti* were absent from the northern stations.

The siphonophore assemblage of the southern stations closely resembled the siphonophore assemblage described for the northern SCS during 2005–2006 when the KBC prevailed,
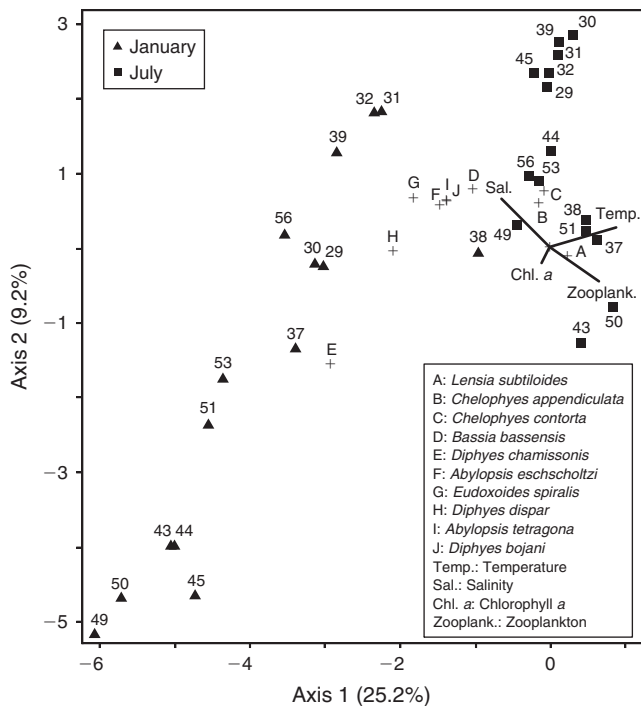
Fig. 7. Ordination diagram of the canonical correspondence analysis (CCA) based on four environmental variables and abundances of the 10 predominant siphonophore species in January and July 2005 in the Taiwan Strait.

including common taxa such as *C. contorta*, *C. appendiculata*, *B. bassensis* and *A. eschscholtzi* (Lo *et al.* 2013). In summary, the results of the present study indicated that regional differences in siphonophore compositions can primarily be attributed to mesoscale circulation in the TS. Seasonality, although important, plays a secondary role in structuring the mix of species assemblages.

Distribution of siphonophore assemblages

The mesoscale distribution of siphonophore assemblages in the TS was significantly influenced by the nature of surrounding water masses. The contrasting hydrography of the TS during the north-easterly and south-westerly monsoons led us to hypothesise that the different hydrographic conditions would be reflected by distinct assemblages of siphonophores during the two different monsoon seasons.

Group A was basically characterised by *Diphyes chamissonis*, the fifth most abundant siphonophore species in the present study (Table 3). *D. chamissonis* is largely a neritic Indo-Pacific species, with a relatively high tolerance to variations in temperature and salinity (Totton 1954). In our study, this species had widespread distributions in both seasons (Table 1), with the highest abundance at Station 43 in winter, when temperatures were below 17°C. During a survey of the ECS, Xu and Lin (2006) found an autumn aggregation of *D. chamissonis* in the Yangtze River estuary, indicating tolerance to a wide range of salinity.

Group B1 was confined mainly to the summer stations located north of the Penghu Islands, where temperature was

usually >28°C and salinity <33.5 (Table 3, Fig. 3*b*). Of the four station groups, B1 had the lowest mean diversity value because of the great numbers of *Lensia subtiloides* in these stations, associated with high zooplankton abundance, especially at Station 50 (Table 3). *L. subtiloides* is largely an Indo-Pacific neritic and warm-water species (Totton 1954). This species is usually rare or absent in the Gulf of Mexico (Gasca 1999; Sanvicente-Añorve *et al.* 2007), eastern South Pacific Ocean (Palma 1999; Pagès *et al.* 2001; Palma and Silva 2006) and Adriatic Sea (Lučić *et al.* 2005), but not in the coastal waters east of South Africa (Thibault-Botha *et al.* 2004). The distribution of *L. subtiloides* in the TS indicates a tolerance to a wide range of temperatures, but not to salinity lower than 33.

Group B2a was composed mainly of stations in the southern TS and associated with the KBC and SCSSC (Table 3). This area has low seasonal oscillations in temperature and salinity and the highest mean diversity and species number of siphonophores. *Chelophyes contorta*, *C. appendiculata* and *B. bassensis* were the predominant species in this group. According to Gibbons and Thibault-Botha (2002) and Thibault-Botha *et al.* (2004), these species are widely distributed in the oceanic realm and also in the near-shore waters around southern Africa. Off the coast of Chile, *B. bassensis* is most abundant at depths shallower than ~50 m, especially in oceanic waters with temperature >19°C (Pagès *et al.* 2001). Similarly, *C. contorta* and *B. bassensis* were the two most abundant siphonophores in surface waters adjacent to the Easter Island where temperature was ~21°C (Palma 1999; Palma and Silva 2006). Our results are consistent with the above studies, with *C. contorta* and *B. bassensis* occurring most abundantly when temperature in the TS was above 22°C.

Group B2b, similar to Group A, was dominated by *D. chamissonis* and *M. atlantica* (Table 3). Group B2b consisted of three winter stations located in the northern TS where the cold CCC was the main water mass (mean temperature only 16.7°C). *D. chamissonis* was widely distributed in our study area during both monsoon seasons and appeared to be highly tolerant to a wide range of temperature. In contrast, *M. atlantica* occurred mostly in the waters north of Penghu Islands during winter and was very rare in summer, being an indication of cold-water inhabitant. Russell (1934) found that *M. atlantica* is a common component of near-shore zooplankton assemblages in cool and productive waters. Thibault-Botha *et al.* (2004) also reported that *M. atlantica* was abundant in the inner stations along the eastern coast of South Africa, with an optimal thermal range of 16–19°C.

Factors affecting siphonophore abundance

The physical mechanisms that regulate the mesoscale spatio-temporal heterogeneity of zooplankton assemblages tend to be dominated by mesoscale variability (Denman and Powell 1984), especially for gelatinous zooplankton, which are weak swimmers and so depend on the dynamics of water masses, such as currents, fronts, upwelling and mixing of water masses (Lo and Biggs 1996; Gibbons and Thibault-Botha 2002; Thibault-Botha *et al.* 2004). At finer scales, biological processes, such as productivity or prey selection, could have more important effects on siphonophore distribution (Purcell 1997; Sanvicente-Añorve *et al.* 2007).

Hot spots of significantly higher zooplankton abundances were found in two areas during our investigation, namely, in waters around the Penghu Islands and in the northern half of the TS (Fig. 5). The former is an area of topographic upwelling as a result of the Changyun Ridge (Jan *et al.* 2006), whereas the north has more rivers that introduce nutrients via river runoff. In the present study, the distribution pattern of siphonophores is consistent with zooplankton abundance, especially in summer (Fig. 5). It is well known that siphonophores are carnivorous zooplankton, consuming mainly copepods, which in most areas of the world ocean are the major constituent of the zooplankton community (Purcell 1981, 1997). Thus, the distribution of zooplankton biomass in our study area was important to the spatial distribution of siphonophores. Similarly, Hosia and Båmstedt (2008) suggested that favourable prey concentrations contributed to the higher densities of eudoxid (sexual) and polygastric (asexual) stages of *Lensia conoidea* and *Dimophyes arctica* in summer and autumn in Norwegian fjords. The production and maturation times of the *M. atlantica* eudoxid stage increased with prey availability (Purcell 1982). Silguero and Robison (2000) speculated that the abundance peak in polygastric stage of *L. conoidea* and *Chuniphyes multidentata* in Monterey Bay, with a 6-week lag behind the phytoplankton bloom, could be due to the increased food availability, leading to liberation and maturation of eudoxids and subsequent production of polygastric colonies. In our study, the highest abundances of *L. subtiloides*, with eudoxids twice more numerous than polygastrics, were recorded at Stations 49 and 50 in summer and corresponded to higher zooplankton abundances. This result suggested that seasonality in zooplankton biomass is a control mechanism of seasonal cycles of the major gelatinous predators, and consequently, affects the abundance of siphonophores.

In addition to food availability, temperature and salinity are important factors affecting the distribution patterns of siphonophores (Buecher and Gibbons 2000; Pagès *et al.* 2001; Sanvicente-Añorve *et al.* 2009). Siphonophores are exclusively marine animals (Pugh 1999), and because most species inhabit pelagic rather than neritic areas, their populations can be enhanced or depressed by relatively small variations in temperature and salinity. In the temperate Mediterranean Sea, Carré and Carré (1991) reported that production of *M. kochi* varied seasonally with temperature, with shorter life cycles in warm temperatures, whereas subtropical siphonophore populations in the southern Gulf of Mexico were reduced when temperatures were higher than 28.1°C and/or when salinity values varied by more than 1–1.5 salinity units (>36.5 or <34) from the regional average of 35 there (Sanvicente-Añorve *et al.* 2007). In the Subarctic, Hosia and Båmstedt (2008) proposed that the locally higher densities of *D. arctica* and *L. conoidea* that occurred during the warmer seasons in Korsfjord were probably due to the warmer, more favourable temperature. During the summer surveys in the waters around Taiwan, W. T. Lo, S. F. Yu and H. Y. Hsieh (unpubl. data) found that temperature and zooplankton abundance were two important factors affecting the summer distribution of siphonophores; meanwhile, lower abundance of siphonophores and a slight increase in species diversity were observed after the passage of a typhoon. In the present study, although the CCC brought rich terrestrial nutrients to the northern TS in winter, the abundances of siphonophores were low because of the cold seawater temperatures (usually <18°C; Figs 3*a*, 5*a*). In contrast, in high seawater temperature (>27°C) in summer, the abundances of siphonophores, especially the predominant species, *L. subtiloides*, were markedly higher in this area. In addition, the results of CCA also showed that the abundance of some oceanic species, such as *B. bassensis*, *A. tetragona*, *D. bojani*, *C. appendiculata*, *C. contorta* and *A. eschscholtzi*, was strongly influenced by salinity (Fig. 7). These species were found in both seasons mainly in the southern TS, in salinities higher than 33.7 and in a wide range of temperatures (21–30°C).

In conclusion, in the TS, a significantly higher siphonophore abundance was observed in summer than in winter. The species compositions of siphonophores were different between the northern and southern TS, with significantly higher diversity in the southern waters. The distribution patterns of siphonophore assemblages were correlated with variations in temperature, salinity and zooplankton biomass. Furthermore, the monsoon-driven dynamics of the CCC, SCSWC and KBC in the study area determine seasonal variations in the distribution and abundance of siphonophore assemblages.

Acknowledgments

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