

Effects of summer mesoscale hydrographic features on epipelagic siphonophore assemblages in the surrounding waters of Taiwan, western North Pacific Ocean

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Received: 29 August 2012 / Revised: 17 June 2013 / Accepted: 19 June 2013 / Published online: 11 July 2013
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Abstract This is the first attempt to examine the relationship between the spatial distribution of siphonophores and mesoscale hydrographic features in the waters around Taiwan in summer. A total of 59 species of siphonophores, consisting of 12 Physonectae and 47 Calycophorae, were identified from our samples. The most abundant species were *Lensia subtiloides* (49.7 % of the total collection by number), *Diphyes chamissonis* (12.1 %), *Chelophyes appendiculata* (9.3 %), *C. contorta* (8.1 %), and *Bassia bassensis* (5.2 %). Two clear assemblages were associated with shelf waters (influenced by the South China Sea Surface Current) and oceanic waters (influenced by the Kuroshio Current), respectively. The shelf water assemblage was characterized by low diversity and high abundance of *L. subtiloides*, whereas the oceanic assemblage showed greater diversity and was dominated by *C. appendiculata*, *C. contorta*, and *B. bassensis*. We discovered strong correlations between temperature and zooplankton and siphonophore abundances, suggesting that temperature and prey concentration are important in determining the spatial distribution of siphonophores. In addition, lower abundance and higher species diversity of siphonophores were observed after the passage of typhoons. This study provides basic knowledge

on the distributional patterns of siphonophores, which is essential information to further understand the ecological roles played by siphonophores and their responses to the hydrological conditions in the waters surrounding Taiwan.

Keywords Siphonophores · Assemblage · Distribution · Hydrography · Typhoon

1 Introduction

Siphonophores are widespread in the marine pelagic realm (Pugh 1974). Most siphonophores are wholly oceanic, a few are mainly neritic, and rarely some are inshore species (Pugh 1999). They usually constitute one of the most important assemblages of predators in pelagic food webs by serving as a direct link between zooplankton and higher trophic levels (Graham et al. 2001; Pagès et al. 2001). Siphonophores either compete with fish by voraciously preying upon copepods (Purcell 1992) or feed almost exclusively on fish larvae (i.e. *Rhizophysa eysenhardti*, Purcell 1984). Some species prey on other gelatinous organisms (Purcell 1991). They can at times be the most abundant non-crustacean invertebrate predators (Purcell 1981; Gorsky et al. 2000; Hosia and Båmstedt 2007). Because of their limited mobility, siphonophores have been employed as indicators of water masses and water mass movement (Mapstone and Arai 1992; Pagès and Schnack-Schiel 1996; Gasca 1999).

The summer hydrologic features of the surrounding waters of Taiwan are mainly dominated by two oceanic currents: the South China Sea Surface Current (SCSSC) to the west of Taiwan and the Kuroshio Current (KC) to the east. During summer, when the southwesterly monsoon prevails, the warm, low salinity SCSSC flows northward into the northern Taiwan Strait (TS) through the Penghu Channel

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(Jan et al. 2002, 2006). However, the barrier of the Changyun Ridge causes the surface and bottom waters of the SCSSC to move in different directions north of the ridge. The surface SCSSC passes over the Changyun Ridge and continues to flow along the eastern side of the TS, while the bottom waters, blocked by the ridge, turn to the northwest along local isobaths into the northwestern TS (Jan et al. 1994). The bottom water diverges near the Penghu Islands, forming a cyclonic ring that induces an upwelling of cold water from below the mixed layer. The hydrography of waters east of Taiwan is much simpler than in the west. The KC, a strong western boundary current of the North Pacific, flows northward east of Taiwan throughout the year and shifts offshore during the southwesterly monsoon.

Except for the above oceanographic differences, summer hydrographic conditions in the waters around Taiwan are frequently affected by typhoons. Several studies have shown that typhoons can cause marked cooling of the sea surface, enhance nutrient pumping, and result in phytoplankton blooms along the paths of typhoons and in adjacent areas (Zheng and Tang 2007; Chen et al. 2009). Although typhoons considerably increase the primary productivity and the nutrient load in the upper water layers, their effect on the upper trophic levels is not clear. Therefore, the occurrence of typhoons and the distribution of water masses around Taiwan offer us an opportunity to study the effects of physical processes on the spatial distribution of siphonophores.

Our understanding of siphonophore population and community ecology in the waters around Taiwan is very limited. Zhang et al. (2005) reported that *Chelophyes contorta*, *C. appendiculata*, *Diphyes bojani*, *D. dispar*, *Abylopsis eschscholtzi*, and *Bassia bassensis* were the six most common species in the Nanwan Bay of southern Taiwan during late autumn and early winter of 2001. In the coastal waters of northern Taiwan, López-López et al. (2012) suggested that typhoons might act as resource pulse triggers for opportunistic carnivorous zooplankton groups. The objective of our study was to examine the spatial distribution of siphonophore abundance and composition in the waters around Taiwan during three summers. Furthermore, we intended to demonstrate how the distributional patterns of siphonophore assemblages vary with changes in the summer hydrographic conditions and, particularly, with the occurrence of typhoons.

2 Materials and methods

2.1 Field and laboratory work

Hydrographic data and zooplankton samples were obtained from three TaiCOFI summer cruises: August 2004 (from 4 August to 8 September, concurrent with typhoons

‘Rananim’ and ‘Aere’), July 2005 (5–15 July, no typhoons), and July 2006 (from 17 July to 7 August, typhoons ‘Bilis’ and ‘Kaemi’). Sixty-two sampling stations were surveyed in each cruise of the R/V “Fishery Researcher I” (Fig. 1). Zooplankton samples were collected with vertical tows from 200 m (or 10 m above the bottom at stations with depths <210 m) to the surface with an Ocean Research Institute (ORI) net (330- μ m mesh, 1.6-m mouth diameter) equipped with a Hydro-Bios flowmeter. They were preserved immediately after collection on board in 5 % buffered formalin–seawater solution. At each station, a General Oceanics SeaBird CTD (SBE-911 Plus) recorded vertical profiles of seawater temperature and salinity from the surface to 10 m above the bottom. Chlorophyll *a* concentrations at 5, 25, 50, 75, 100, and 150 m were measured from 1-l seawater samples collected with Go-Flo bottles. Among the 62 stations of each cruise, 34 were chosen to analyze siphonophore distributions (Fig. 1). In the laboratory, each zooplankton sample was divided into two subsamples with a Folsom splitter. Siphonophores were sorted from one stochastic subsample, preserved in 70 % alcohol after sorting, and identified to the lowest taxonomic level possible according to Bigelow (1911), Sears (1953), Totton (1965), and Pugh (1999). Because of the polymorphic structure and fragile nature of most species, siphonophores are usually fragmented in net samples; therefore, the numbers of nectophores of the Physonectae and Hippopodiidae were counted and then divided by ten to estimate their abundance, according to Pugh (1984). In general, species of the Calycophorae have two generations (anterior and posterior nectophores of the polygastric phase, bracts and gonophores of the eudoxid phase). Therefore, every nectophore of the Calycophorae was counted separately and then abundance of each species was represented by the sum of the greater counts of the two generations. In the present study, we identified two species of the genus *Nanomia* and were positive that one of them was *N. bijuga*. In our samples, we had other nectophores similar to those of *Nanomia* spp. but exact identification whether they were *N. bijuga* or *N. cara* was impossible, thus we grouped them under *Nanomia* spp. in the text. The other subsample was repeatedly subdivided until the number of individual zooplankton in the last subsample was estimated to be 1,000–2,000 or fewer, and then the entire subsample was counted in order to calculate the overall abundance of zooplankton. Siphonophores and zooplankton abundances were calculated to the number of individuals (ind.) per 100 and 1 m³, respectively.

2.2 Data analysis

Typhoon data were downloaded from the Central Weather Bureau of Taiwan website (Fig. 2, <http://rdc28.cwb.gov.tw/>).

Fig. 1 Geographic location of the sampling stations in the waters around Taiwan during the three summer cruises in 2004–2006. *Arrows* directions of currents; *triangles* stations with CTD data only; *circles* stations with both CTD and zooplankton samples

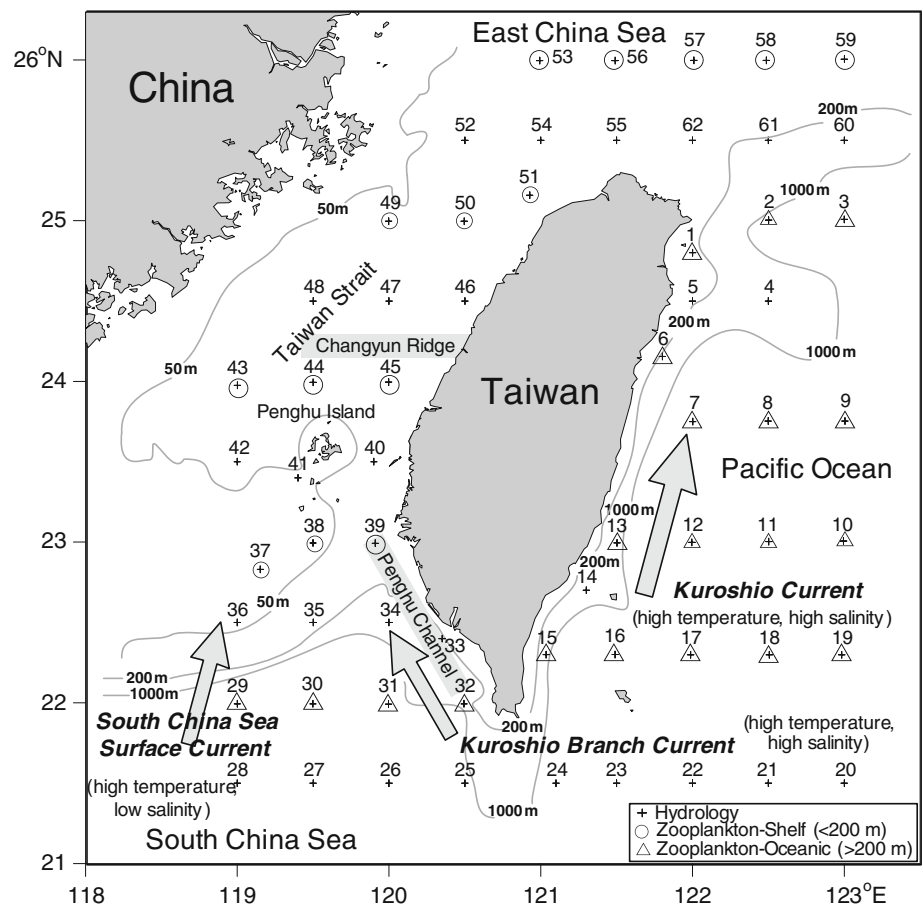
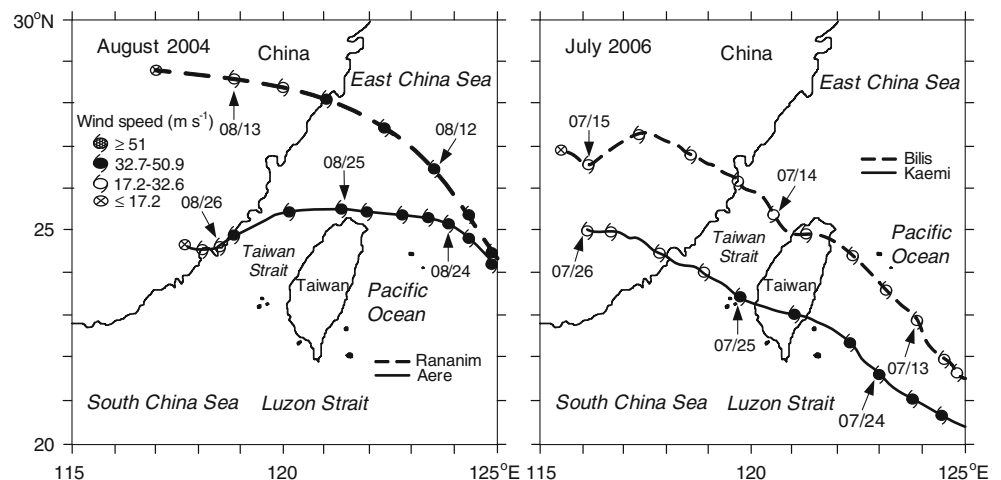


Fig. 2 Tracks of four typhoons in the waters around Taiwan in August 2004 (left) and July 2006 (right)



To describe the spatial variability of siphonophore community structure, we undertook the following analyses: Shannon–Weaver species diversity index (H' ; Shannon and Weaver 1963) was calculated for each station; Sørensen similarity index (SI; Sørensen 1948) of siphonophores between sampling cruises was calculated by analyzing the similarity of the same station in different cruises in terms of

presence or absence of a species; multivariate statistics were used to identify assemblages during the three cruises by examining the relationships among samples. A cluster analysis was made after transforming abundance data to $\log(n+1)$ to characterize assemblages of samples according to their affinity based on the species composition. The similarity coefficient of Bray–Curtis and the

complete linkage rule were used (Bray and Curtis 1957). To compare the values of chlorophyll *a* concentration, zooplankton abundance, siphonophore abundance, species number, and species diversity index between sampling locations and station groups, the non-parametric Mann–Whitney *U* test was employed (Mann and Whitney 1947). The differences in abundance, number of species, and species diversity of siphonophores among the three summers were tested by one-way ANOVA (Dunn and Clark 1974). In addition, we used canonical correspondence analysis (CCA; Ter Braak 1986) to examine non-linear relationships between the 10 predominant siphonophore species and environmental variables.

3 Results

3.1 Hydrographic and plankton conditions

Mean values of surface (10 m) water temperature, salinity, and chlorophyll *a* concentration (average concentration in the upper 150 m) were similar during the three summer surveys (Table 1). Surface water temperatures varied among stations, from 25.1 to 30.6 °C, with the lowest mean value (\pm SE, 28.5 ± 0.1 °C) recorded in July 2006 and the

highest mean value (28.9 ± 0.1 °C) in August 2004. Salinities varied between 32.1 and 34.7, the lowest mean value (33.8 ± 0.1) was in July 2006, and the highest mean value (34.2 ± 0.0) was in August 2004. Chlorophyll *a* concentration ranged between 0.003 and $0.638 \mu\text{g l}^{-1}$, with the highest concentration recorded in July 2006 at station 44. Contours of surface water temperature and salinity revealed the principal mesoscale oceanographic features in the waters around Taiwan (Fig. 3). During the three surveys, the TS shelf waters had lower surface water temperatures (0.5–1.5 °C) and salinities (0.5) than the ocean waters.

In contrast, chlorophyll *a* concentrations were higher in the TS shelf waters than in the ocean waters ($U = 653$, $p < 0.001$; Table 2), especially in the waters southwest and north of the Penghu Islands, e.g., stations 37 and 44 (Fig. 4). The temperatures at these stations were about 2–4 °C lower than surrounding waters. The chlorophyll *a* concentrations, between 0.3 and $0.7 \mu\text{g l}^{-1}$, were higher than the mean value of the shelf stations (Table 2). High zooplankton abundances were usually found in the northern TS and in the waters adjacent to the Penghu Islands, with the highest abundances at station 50 in all summers (Fig. 4). Significant differences in zooplankton abundance were noted between the shelf and oceanic stations

Table 1 Temperature (°C), salinity, chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), zooplankton abundance (ind. m^{-3}), total siphonophore abundance (ind. 100 m^{-3}), species number (S) of siphonophores, species diversity (H') of siphonophores, and abundance and relative

abundance (RA, %) of the 10 predominant species of siphonophore in the waters around Taiwan during the three summer cruises in 2004–2006

Sampling time	August 2004			July 2005			July 2006	
	Mean \pm SE	RA		Mean \pm SE	RA		Mean \pm SE	RA
Temperature	28.96 ± 0.10	–	Temperature	28.72 ± 0.14	–	Temperature	28.51 ± 0.14	–
Salinity	34.15 ± 0.03	–	Salinity	33.85 ± 0.08	–	Salinity	33.81 ± 0.05	–
Chlorophyll <i>a</i>	0.05 ± 0.01	–	Chlorophyll <i>a</i>	0.06 ± 0.01	–	Chlorophyll <i>a</i>	0.08 ± 0.02	–
Zooplankton	494 ± 277	–	Zooplankton	188 ± 33	–	Zooplankton	669 ± 165	–
Total siphonophore	545 ± 104	–	Total siphonophore	1059 ± 327	–	Total siphonophore	351 ± 140	–
S of siphonophores	22 ± 1	–	S of siphonophores	20 ± 1	–	S of siphonophores	20 ± 1	–
H' of siphonophores	3.11 ± 0.13	–	H' of siphonophores	2.71 ± 0.19	–	H' of siphonophores	3.24 ± 0.13	–
<i>Lensia subtiloides</i>	153 ± 91	28.10	<i>Lensia subtiloides</i>	792 ± 309	74.82	<i>Diphyes chammissonis</i>	155 ± 133	44.23
<i>Chelophyes appendiculata</i>	71 ± 13	13.13	<i>Chelophyes contorta</i>	77 ± 14	7.26	<i>Chelophyes appendiculata</i>	36 ± 7	10.17
<i>Diphyes chammissonis</i>	70 ± 34	12.93	<i>Chelophyes appendiculata</i>	75 ± 24	7.09	<i>Lensia subtiloides</i>	26 ± 8	7.47
<i>Chelophyes contorta</i>	55 ± 11	10.18	<i>Bassia bassensis</i>	25 ± 3	2.32	<i>Chelophyes contorta</i>	26 ± 4	7.29
<i>Bassia bassensis</i>	55 ± 6	10.02	<i>Abylopsis eschscholtzi</i>	17 ± 2	1.63	<i>Bassia bassensis</i>	22 ± 3	6.16
<i>Abylopsis eschscholtzi</i>	28 ± 4	5.12	<i>Diphyes chammissonis</i>	10 ± 2	0.96	<i>Abylopsis eschscholtzi</i>	15 ± 3	4.39
<i>Diphyes bojani</i>	23 ± 4	4.21	<i>Diphyes bojani</i>	9 ± 2	0.86	<i>Diphyes dispar</i>	11 ± 2	3.17
<i>Eudoxoides mitra</i>	18 ± 3	3.27	<i>Abylopsis tetragona</i>	9 ± 1	0.80	<i>Eudoxoides mitra</i>	11 ± 3	3.23
<i>Lensia subtilis</i>	15 ± 2	2.67	<i>Eudoxoides mitra</i>	8 ± 2	0.72	<i>Abylopsis tetragona</i>	11 ± 2	3.13
<i>Diphyes dispar</i>	14 ± 2	2.53	<i>Eudoxoides spiralis</i>	5 ± 1	0.50	<i>Diphyes bojani</i>	9 ± 2	2.65

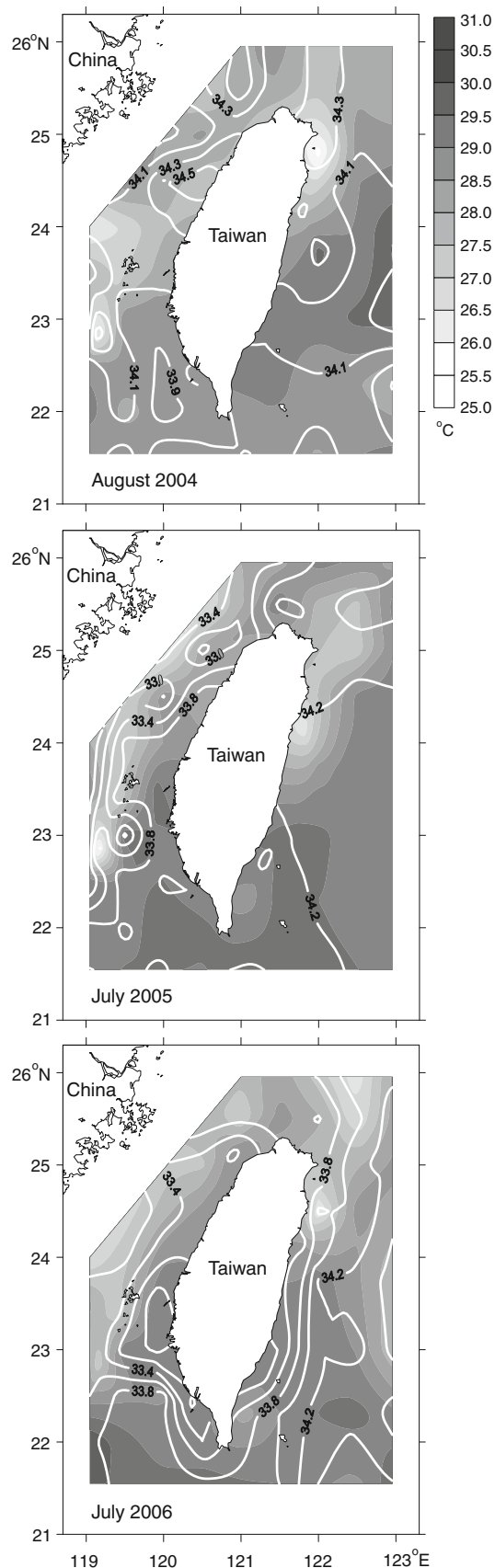


Fig. 3 Contour plots of temperature (°C, 10 m depth, gray scales) and salinity (10 m depth, black lines) during the three summer cruises in 2004–2006

($U = 368$, $p < 0.001$; Table 2), but differences among the three sampling cruises were not significant ($F_{2,34} = 1.689$, $p = 0.190$; Table 1).

3.2 Abundance and composition of siphonophores

Siphonophores of 26 genera and 59 species were identified in the present study, belonging to the suborders Physonectae (12 species) and Calycophorae (47 species) (Table 3). The overall mean abundance (\pm SE) was 652 ± 126 ind. 100 m^{-3} , ranging from 21 (station 1) in July 2006 to 8,233 ind. 100 m^{-3} (station 50) in July 2005. Although the abundance of siphonophores showed no significant difference among these three summers ($F_{2,34} = 2.913$, $p = 0.059$), comparatively higher abundances were observed in July 2005, which lacked typhoons. Similarly, there was no significant difference in species number ($F_{2,34} = 1.140$, $p = 0.324$); but species diversity was lowest in July 2005 ($F_{2,34} = 3.320$, $p < 0.05$; Tukey's test; Table 1). In general, higher abundances occurred in the TS shelf waters ($U = 745$, $p < 0.001$), especially in the waters north of the Penghu Islands, where peak abundance was 8,233 ind. 100 m^{-3} at station 50 in July 2005 (Table 2; Fig. 4). On the other hand, the distributions of species number ($U = 210$, $p < 0.001$) and species diversity ($U = 462$, $p < 0.001$) in siphonophores showed opposite trends to that of abundance, with higher values generally found in the oceanic waters east of Taiwan (Table 2). We did not find significant differences between day (sampling from 0530 to 1830 hours) and night (sampling from 1830 to 0530 hours) in siphonophore abundance ($U = 1,090$, $p = 0.174$) or species number ($U = 1,270$, $p = 0.880$) (not shown).

Species compositions of siphonophores showed high similarities among the three summers, which had similarity indices of 78 % (2004 vs. 2005), 82 % (2004 vs. 2006), and 90 % (2005 vs. 2006) (not shown). The calycophoran Diphyidae was the most abundant family of Siphonophora in our study, accounting for 90 % of the total numerical abundance. At the species level, the calycophoran *Lensia subtiloides* constituted 49.70 % of the total siphonophores, and was the most abundant species during the entire survey, followed by *Diphyes chamissonis* (12.07 %), *Chelophyes appendiculata* (9.32 %), *C. contorta* (8.08 %), and *Bassia bassensis* (5.15 %). Among these five species, some were abundant during only one cruise. The changes in the distribution patterns of abundances of the five predominant

Table 2 Temperature ($^{\circ}\text{C}$), salinity, chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), zooplankton abundance (ind. m^{-3}), and total siphonophore abundance ($\text{ind. } 100 \text{ m}^{-3}$), species number (*S*) of siphonophores, species diversity (*H'*) of siphonophores, and abundances of the 10

predominant species of siphonophore at different sampling locations and station groups (according to Fig. 6) in the waters around Taiwan during the three summer cruises in 2004–2006

	Location		Group	
	Shelf (<200 m)	Oceanic (>200 m)	SPI-ET	NPI
Temperature	28.21 \pm 0.12	29.08 \pm 0.08	28.87 \pm 0.11	27.65 \pm 0.29***
Salinity	33.72 \pm 0.07	34.08 \pm 0.03	34.01 \pm 0.04	33.55 \pm 0.17**
Chlorophyll <i>a</i>	0.120 \pm 0.024	0.035 \pm 0.005***	0.055 \pm 0.011	0.151 \pm 0.042***
Zooplankton	919 \pm 247	122 \pm 19***	293 \pm 69	1,295 \pm 554*
Total siphonophore	1,224 \pm 239	251 \pm 20***	310 \pm 22	2,667 \pm 567***
<i>S</i> of siphonophores	15 \pm 1	25 \pm 1***	22 \pm 1	11 \pm 1***
<i>H'</i> of siphonophores	2.39 \pm 0.14	3.46 \pm 0.04***	3.35 \pm 0.04	1.19 \pm 0.16***
<i>Lensia subtiloides</i>	774 \pm 256	8 \pm 1***	22 \pm 4	1,945 \pm 537***
<i>Diphyes chamissonis</i>	173 \pm 110	13 \pm 2***	17 \pm 2	410 \pm 268**
<i>Chelophyes appendiculata</i>	87 \pm 21	43 \pm 5	51 \pm 6	115 \pm 45
<i>Chelophyes contorta</i>	68 \pm 14	42 \pm 4	50 \pm 6	67 \pm 26
<i>Bassia bassensis</i>	30 \pm 5	36 \pm 3*	37 \pm 3	17 \pm 4**
<i>Abylopsis eschscholtzi</i>	17 \pm 3	23 \pm 2*	22 \pm 2	8 \pm 2***
<i>Diphyes bojani</i>	14 \pm 3	13 \pm 2	15 \pm 2	9 \pm 2*
<i>Eudoxoides mitra</i>	8 \pm 2	15 \pm 2***	14 \pm 2	4 \pm 2***
<i>Diphyes dispar</i>	11 \pm 2	10 \pm 1	12 \pm 1	5 \pm 2***
<i>Abylopsis tetragona</i>	6 \pm 1	11 \pm 2**	10 \pm 1	5 \pm 2**

Significant differences (Mann–Whitney *U* test): * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

siphonophore species are shown in Fig. 5. For example, *L. subtiloides* was sometimes extremely abundant, particularly at stations 44 and 50, contributing 28.1 and 74.8 % of the numerical abundance of siphonophores in the summers of 2004 and 2005, respectively. *Diphyes chamissonis* was the most abundant species in July 2006, with a peak of 4,539 ind. 100 m^{-3} at station 49 and constituting 44.23 % of the 2006 siphonophore catch.

3.3 Siphonophore assemblages

All sampling stations were divided into two groups at a similarity level of 45 % using the Bray–Curtis similarity analysis (Fig. 6). Two station groups were named according to their respective localities, i.e., south of Penghu Islands and east of Taiwan (SPI-ET) and north of Penghu Islands (NPI). Results of Mann–Whitney *U* tests showed clear spatial differences in abundance, species number, and species diversity of siphonophores, with significantly lower abundances ($U = 276$, $p < 0.001$) and higher species numbers ($U = 72$, $p < 0.001$) and species diversities ($U = 0$, $p < 0.001$) in the SPI-ET than in the NPI (Table 2). The SPI-ET was comprised of 86 stations that were widely distributed throughout the oceanic waters. Fifty-seven taxa of siphonophores were identified in this group. *Chelophyes appendiculata*, *C. contorta*, *Bassia*

bassensis, *Abylopsis eschscholtzi*, and *Lensia subtiloides* were the predominant species, constituting 59 % of the total siphonophores counted. Among these five species, *C. appendiculata* and *C. contorta* showed significantly higher abundances than the other species (Table 2). The NPI included 16 stations mainly located in the central and northern TS, except station 45. Only half (30 of 59) of the siphonophore taxa were collected in this group. The NPI was typified by the abundant *L. subtiloides* (1,945 \pm 569 ind. 100 m^{-3} and 73 % of the total siphonophores) and *Diphyes chamissonis* (410 \pm 285 ind. 100 m^{-3} and 15 % of the total catch) (Table 2). These two species had significantly higher abundances than others in this group. *C. appendiculata* and *C. contorta* were also abundant.

3.4 Correlations between siphonophores and environmental variables

The results of the CCA showed the relationships between siphonophores and the four environmental variables (Table 4). The first two canonical axes of the CCA explained 49.1 % of the total variation in the distribution of species, with the third axis contributing an additional 0.2 %. The eigenvalue provided an indication of the influence of each axis on the ordination. Correlations between species and environmental axes were 0.806 and

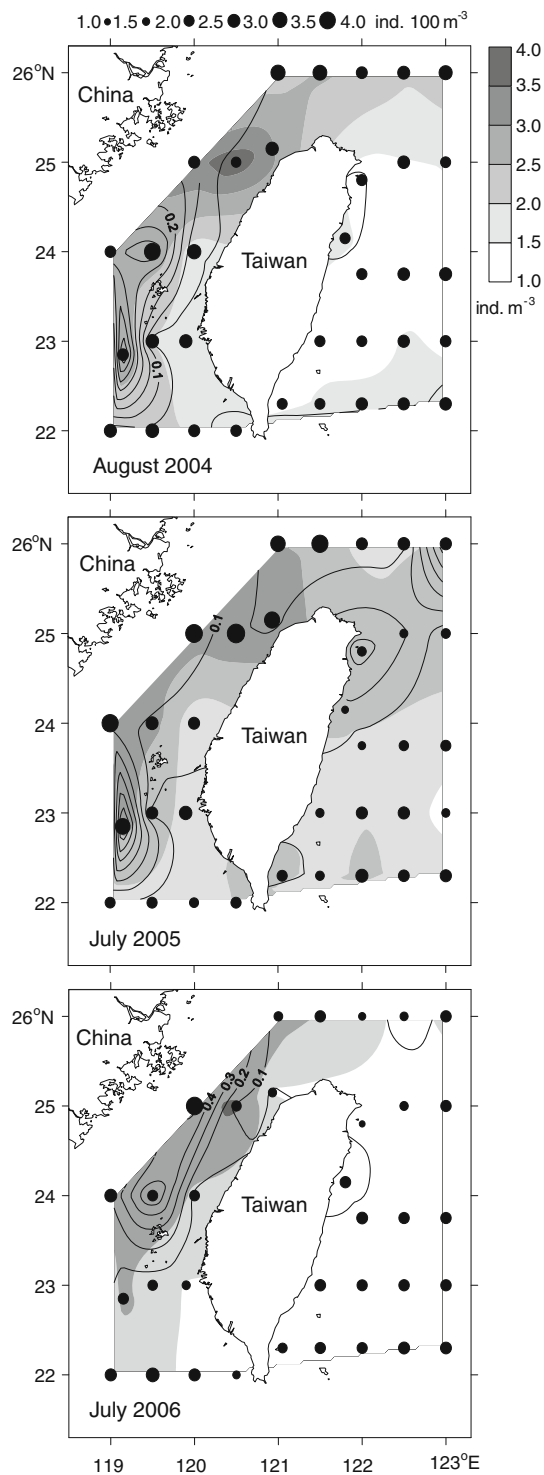


Fig. 4 Contour plots of chlorophyll *a* concentration ($\mu\text{g l}^{-1}$, 150 m average concentration, black lines), log zooplankton abundance (ind. m^{-3} , gray scales), and log siphonophore abundance ($\text{ind. } 100 \text{ m}^{-3}$, solid circles) during the three summer cruises in 2004–2006

0.713, respectively. In the list of inter-set correlations of environmental variables with axes, we found that temperature, zooplankton abundance, and salinity were important

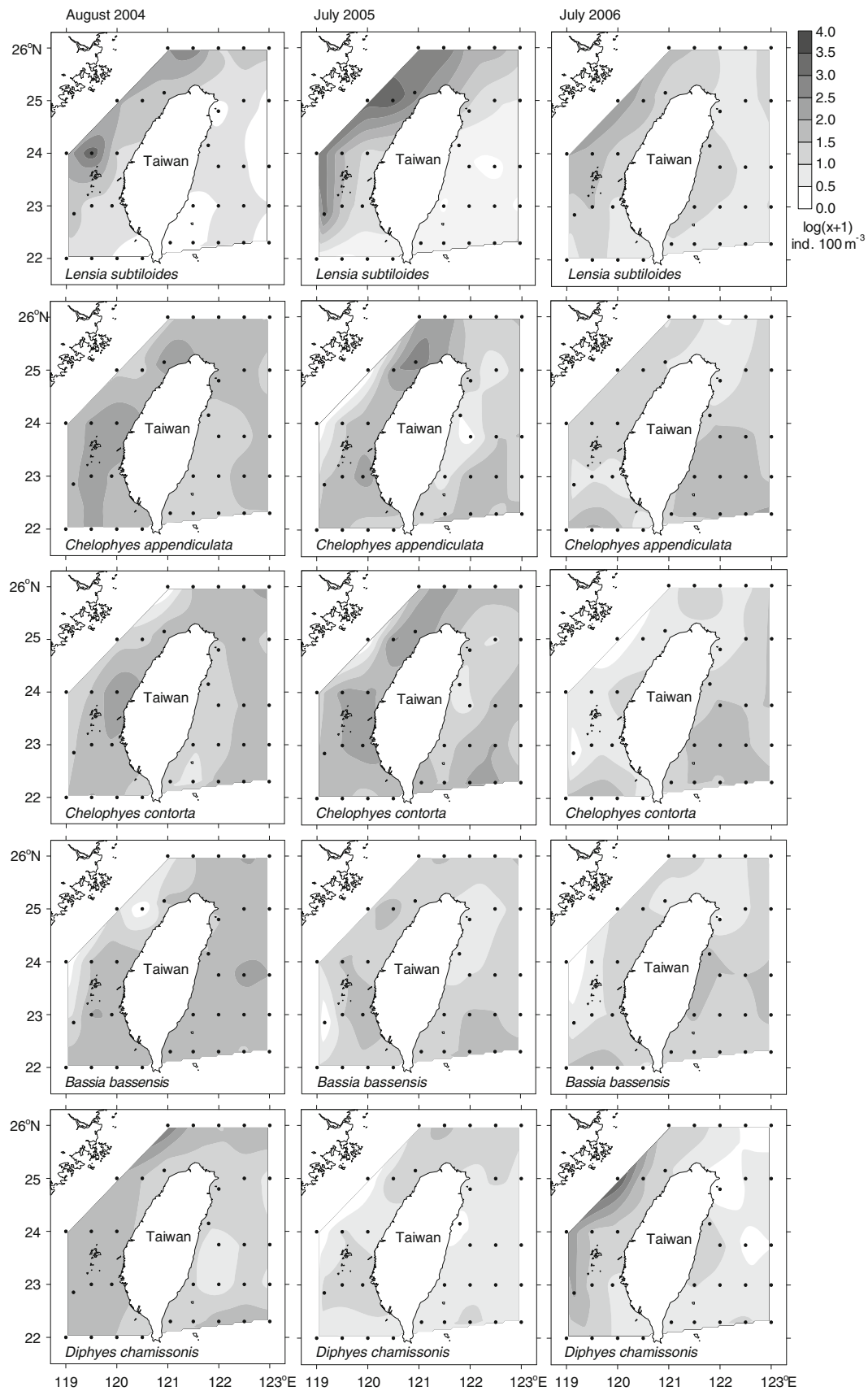
variables affecting the distribution of siphonophores. Temperature was significantly negatively correlated with *Lensia subtiloides* and positively correlated with *Chelophyes appendiculata*, *C. contorta*, and *Bassia bassensis* (Fig. 7). Log zooplankton abundance correlated significantly and positively with *L. subtiloides* and *Diphyes chamissonis* and negatively with *C. contorta* and *B. bassensis* (Fig. 8). Salinity had a significant negative correlation with *L. subtiloides* (Fig. 9).

4 Discussion

4.1 Factors affecting siphonophore distribution

Studies concerning zooplankton distribution at large spatial scales, particularly for weak swimmers like gelatinous zooplankton, emphasizes the importance of physical oceanographic variability, such as currents, fronts, mixing of water masses, upwellings, and eddies (Denman and Powell 1984; Lo and Biggs 1996; Gasca 1999; Gibbons and Thibault-Botha 2002; Thibault-Botha et al. 2004). At fine scales, or within homogeneous waters, biological processes, such as food availability or prey selection, may have a more significant effect on the distribution of siphonophores (Purcell 1997; Sanvicente-Añorve et al. 2007). However, information about the distributional pattern of siphonophores and the relationship between siphonophores and biophysical processes in the waters around Taiwan was lacking.

Because most siphonophores inhabit oceanic rather than neritic waters, their populations can be enhanced or depressed by relatively small variations in temperature and salinity. Molinero et al. (2008) also advocated that gelatinous carnivores are sensitive to environmental conditions and that their annual peaks are substantially enhanced by favorable conditions. In the present study, the CCA indicated that temperature is an important factor in determining the abundance of siphonophores (Table 4). We noted that higher siphonophore abundances, mostly in the NPI, were usually in relatively lower temperatures ($<28.5^\circ\text{C}$; Figs. 3, 4). When the temperature was higher than 28.5°C (recorded mainly in the SPI-ET), the abundances of most siphonophore populations were significantly lower. In the southern Gulf of Mexico, Sanvicente-Añorve et al. (2009) found that the subtropical siphonophore population was reduced when the temperature was higher than 28.1°C . Carré and Carré (1991) reported that production of *Mugilgiaea kochi* varied seasonally with temperature, with shorter life cycles in warm temperature in the temperate Mediterranean Sea. Favourable temperature and prey concentrations probably contributed to the higher densities of *Lensia conoidea* and *Dimophyes arctica* eudoxids and



abundances of siphonophores and zooplankton were observed in the shelf waters north of the Penghu Islands and northern Taiwan (Figs. 3, 4). A similar trend was reported in the abundance and diversity of siphonophores along a coastal-oceanic gradient in the southern Gulf of Mexico (Sanvicente-Añorve et al. 2007, 2009). A cross-shelf gradient in the structure of siphonophore assemblages also was found by Thibault-Botha et al. (2004) and Li et al.

(2012), with the neritic assemblage supporting greater densities of siphonophores.

It is well known that siphonophores are carnivorous zooplankton, consuming mainly copepods, the major component of the zooplankton community (Purcell 1981). In the Humboldt Current system, *Bassia bassensis* consumed up to 69.3 % of the small copepod biomass (Pagès et al. 2001). Silguero and Robison (2000) speculated that

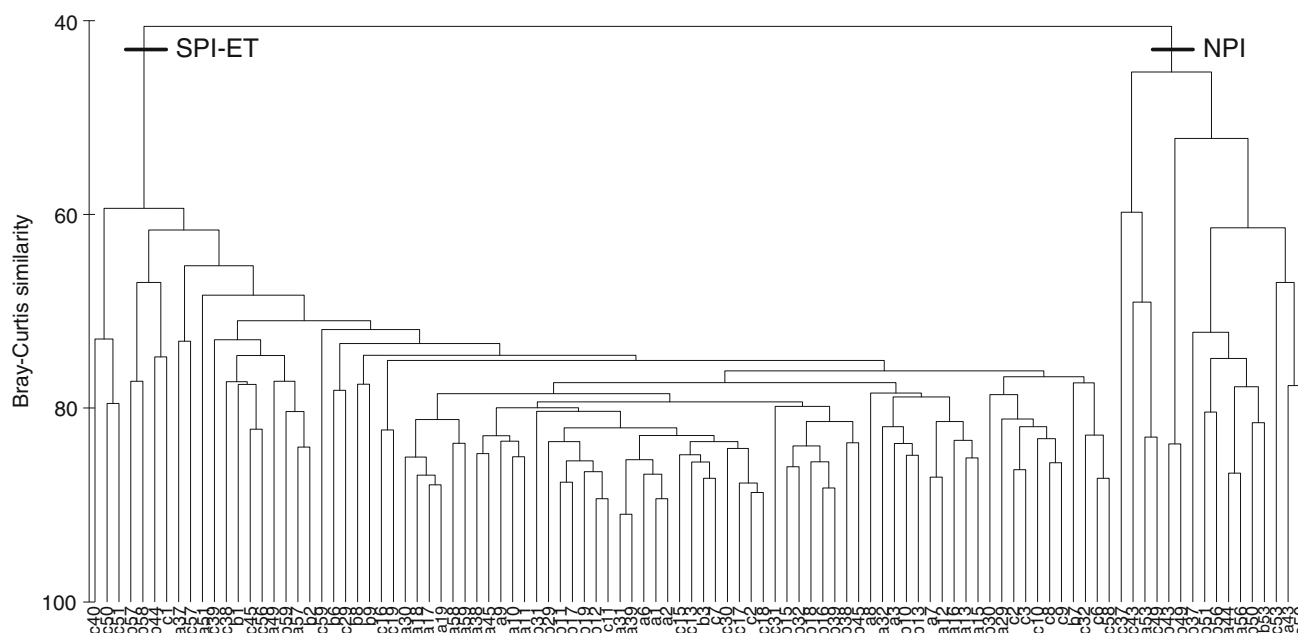


Fig. 6 Similarity dendrograms between all sampling stations during the three summer cruises in 2004–2006. a: 2004; b: 2005; c: 2006

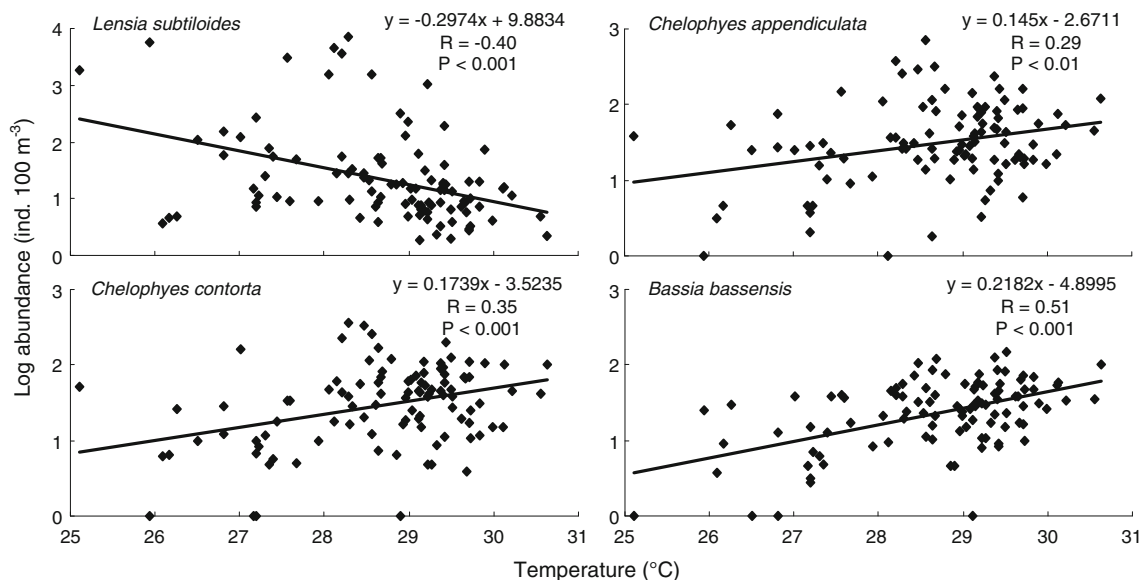


Fig. 7 Linear regression by least squares between temperature and log siphonophore abundance for the predominant species with significant relationships during the three summer cruises in 2004–2006

the abundance peaked in polygastric phase of *Lensia co-noidea* and *Chuniphyes multidentata*, which lagged 6 weeks 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 Monterey Bay. In the NW Mediterranean Sea, Sabatés et al. (2010) reported that high concentrations of coastal and offshore species of siphonophores were found close to the shelf/slope front, which could be related to increased primary and secondary productions in the frontal area. Similarly, copepod abundance appeared to be the most significant factor to influence the distribution and abundance of nearshore siphonophore species in the northwestern South China Sea (Li et al. 2012). These results are consistent with present result that zooplankton abundance plays an important role in determining the spatial distribution of the siphonophores.

Table 4 Summary of statistics for the canonical correspondence analysis (CCA) of the 10 predominant siphonophore species in the waters around Taiwan during the three summer cruises in 2004–2006

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.436	0.325	0.002
Pearson correlations, Spp-Envt.	0.806	0.713	0.162
% of variance explained	28.2	21.0	0.2
Cumulative % explained	28.2	49.1	49.3
Inter-set correlations of environmental variables with axes			
Temperature	−0.547	0.020	0.155
Salinity	−0.430	−0.192	−0.118
Chlorophyll <i>a</i>	0.431	−0.253	−0.130
Zooplankton	0.571	−0.154	0.137

4.2 Composition of siphonophore assemblages

The two siphonophore assemblages in our study, identified by the Bray–Curtis ordination (Fig. 6), reflected the summer hydrographic conditions of the waters around Taiwan and the corresponding siphonophore communities. The NPI was confined to depths <100 m, where variations in temperature and salinity were great. This area was characterized by an ample supply of food, as indicated by the highest chlorophyll *a* concentrations and zooplankton abundances observed in our study. The SPI-ET, demonstrated by high temperature, high salinity, and high species diversity but low abundance in siphonophores (Table 2), was definitely a stable oceanic assemblage. It was apparent that the changes in siphonophore abundance and composition were correlated closely with the distance to shore and the effect of mesoscale oceanographic features. Because of the contrasting hydrography of the SPI-ET and NPI, we hypothesized that the distinct composition of siphonophores between these two assemblages reflected the differences in hydrographic conditions. The similarity of siphonophore compositions between the two station groups was 60 % (not shown).

The SPI-ET was composed mainly of stations in the waters east of Taiwan, as well as in the southern TS associated with the KC and KBC. *Chelophyes appendiculata*, *C. contorta*, and *Bassia bassensis*, the three most abundant siphonophore species in the present study, dominated this group (Table 2). These three species are common in the tropical–equatorial oceanic belt of the Atlantic, Pacific, and Indian oceans (Alvarinho 1971). In the present study, they were widespread not only in the eastern oceanic

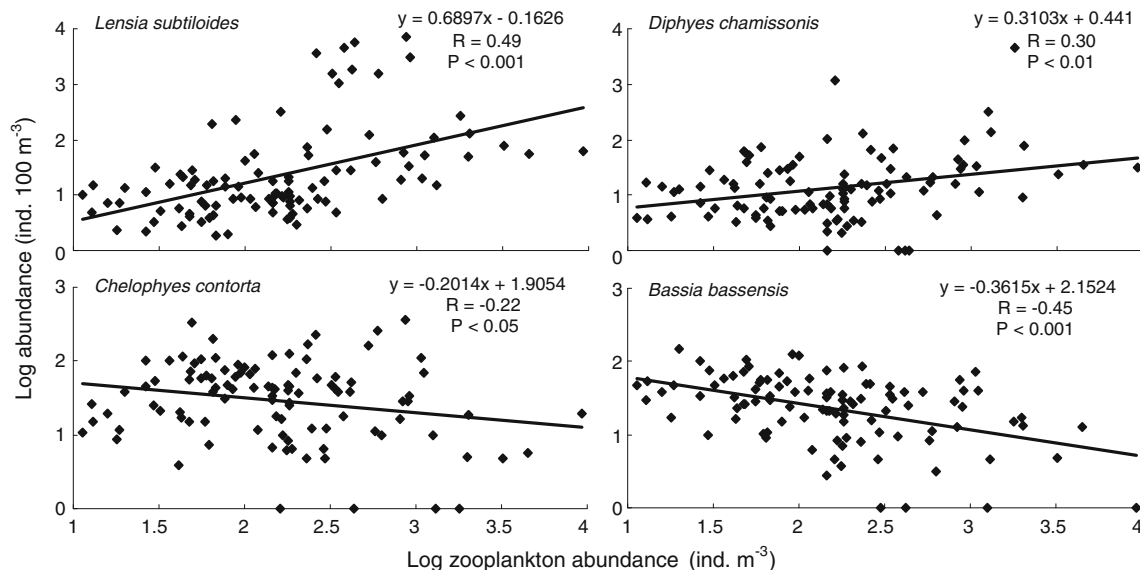


Fig. 8 Linear regression by least squares between log zooplankton abundance and log siphonophore abundance for the predominant species with significant relationships during the three summer cruises in 2004–2006

stations but also in the western shelf stations. In surface waters adjacent to the Easter Island, *C. contorta* and *B. bassensis* were the two most abundant siphonophores, where the temperature was about 21 °C (Palma 1999; Palma and Silva 2006). Off the coast of Chile, Pagès et al. (2001) reported that *B. bassensis* was most abundant at depths shallower than about 50 m, especially in oceanic waters where the temperature was >19 °C. Zhang et al. (2005) found that *C. appendiculata*, *C. contorta*, and *B. bassensis* were the predominant species in the Nanwan Bay of southern Taiwan in late autumn and early winter. Hsieh et al. (2013) observed that *C. contorta* and *B. bassensis* were most abundant in the southern TS when the temperature was higher than 22 °C and were associated with the KBC and SCSSC. Likewise, the species composition of the siphonophore assemblage of the northern South China Sea (Lo et al. 2013) closely resembled that found in our surveys. These phenomena seem to indicate that the northward flow of the SCSSC and/or KBC may transport these oceanic species from the northern South China Sea or east of Taiwan into the TS.

The NPI was confined mainly to the shelf stations located north of the Penghu Islands where the temperature was usually <28.5 °C and salinity <34. Low species

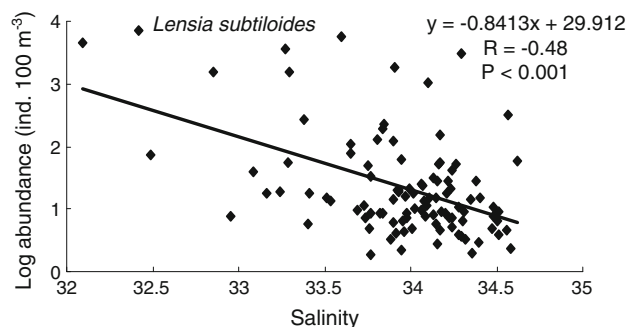


Fig. 9 Linear regression by least squares between salinity and log siphonophore abundance for the predominant species with significant relationship during the three summer cruises in 2004–2006

diversity values were usually recorded at these stations due to high numbers of *Lensia subtiloides* or *Diphyes chamissonis*, especially at stations 49 and 50. *Lensia*, including both epipelagic and deep-living species, is the most diverse calyphoran genus and some of its species have a complex taxonomy (Pugh and Pagès 1997). *L. subtiloides* is principally an Indo-Pacific neritic and warm water species (Totton 1954). In the Changjiang River estuary, China, it usually occurs in large numbers in the estuary and adjacent waters in summer and autumn, indicating its wide tolerance to temperature and salinity (Xu and Lin 2006; Lun et al. 2008). In the TS, *L. subtiloides* was distributed widely (Zhang and Lin 2001; Hsieh et al. 2013), but was less tolerant of waters with salinities less than 33 (Hsieh et al. 2013). However, in the present study, we speculate that its high abundance in the NPI was probably due to favorable population growth as a consequence of the relatively low temperature (<28.5 °C) and an abundance of food. *D. chamissonis* was the second most abundant siphonophore species in our study area, also mainly a neritic Indo-Pacific species, with relatively high tolerance to variations in temperature and salinity (Totton 1954). Along the southwest coast of India and the Laccadive Sea, *D. chamissonis* is the predominant species, constituting 35 % of the total catch, and is equally distributed in the neritic and oceanic provinces, coinciding with high plankton production (Rengarajan 1983). *D. chamissonis* is usually abundant in summer, based on a series of surveys along the east coast of China from the East China Sea to Taiwan Strait, such as the western waters of Taiwan Strait (Zhang and Lin 2001), Changjiang River Estuary (Xu and Lin 2006; Lun et al. 2008), Qujiang River Estuary (Gao and Xu 2009), Zhou-shan fishing ground (Chen et al. 2010; Yu et al. 2011), Jiaojang Estuary (Du et al. 2011), and Shenzhen Bay (Zhang et al. 2010). These results agree with our study that this species was widely distributed in the three summers, with the highest abundance at station 49 in 2006 (4,539 ind. 100 m⁻³).

Table 5 Comparisons on temperature (°C), salinity, chlorophyll *a* concentration (μg l⁻¹), zooplankton abundance (ind. m⁻³), and abundance of siphonophores (ind. 100 m⁻³), species number (*S*) of

siphonophores, species diversity (*H'*) of siphonophores in the waters around Taiwan between 2005 (non-typhoon period) and 2006 (after passages of typhoons 'Bilis' and 'Kaemi', respectively)

Stations	Sts. 1–30 and 55–60 2005/2006 (typhoon 'Bilis')	Sts. 31–54 2005/2006 (typhoon 'Kaemi')
Temperature	28.96 ± 0.14/28.71 ± 0.18	28.34 ± 0.27/28.20 ± 0.20
Salinity	34.15 ± 0.04/34.02 ± 0.05	33.38 ± 0.14/33.47 ± 0.06
Chlorophyll <i>a</i>	0.04 ± 0.01/0.04 ± 0.01	0.10 ± 0.02/0.13 ± 0.04
Zooplankton	107 ± 15/285 ± 54	336 ± 73/1,372 ± 391
Abundance of siphonophore	398 ± 192/231 ± 32	2271 ± 759/572 ± 396
<i>S</i> of siphonophores	22 ± 1/23 ± 1	17 ± 2/14 ± 1
<i>H'</i> of siphonophores	3.12 ± 0.14/3.53 ± 0.08	1.95 ± 0.39/2.70 ± 0.28

4.3 Preliminary observations on the effect of typhoons on siphonophores

There were two typhoons ('Rananim' and 'Aere') during our cruise in 2004; however, their paths did not pass our sampling area directly (Fig. 2). Accordingly, we compare the difference in composition and abundance of siphonophores between non-typhoon (2005) and typhoon (2006) periods. In 2006, we collected samples at stations 1–30 and 55–62 (mostly located in the waters east of Taiwan) and stations 31–54 (located in the waters west of Taiwan) 3 and 8 days after typhoons 'Bilis' and 'Kaemi' passed, respectively (Fig. 2). According to Zheng and Tang (2007) and Chen et al. (2009), noticeably higher concentrations of surface nutrients and phytoplankton productivities, due to the run-off inputs and vertical mixing or upwelling, occurred in the sea surface after the typhoons and might subsequently lead to more favorable conditions for the higher trophic groups, including copepods and gelatinous carnivore populations. López-López et al. (2012) found recurrent higher abundances of siphonophores in the month following a strong typhoon in northern Taiwan. Our results, however, were inconsistent with the above studies: no significant enhancement in chlorophyll *a* concentration was observed after the passages of the two typhoons in our study (Table 5). In addition, the abundance of siphonophores was significantly lower during the typhoon period, even if zooplankton abundance noticeably increased, especially after the passage of typhoon 'Kaemi'. In contrast, a slight increase in species diversity of siphonophores was observed after typhoons, but the reason which caused the above phenomenon is uncertain.

5 Conclusion

This study demonstrated spatial differences in siphonophore composition in summer in the waters of Taiwan. Siphonophores were more diverse east of Taiwan and in the southern TS than in the TS NPI. Meanwhile, we recorded significantly lower abundances of siphonophores and a slight increase in species diversity after the passage of a typhoon. The distribution patterns of siphonophore assemblages were closely correlated with summer meso-scale hydrographic characteristics and food availability. Temperature and zooplankton abundance were two important factors affecting the summer distribution of siphonophores. In addition, salinity gradients may also play an important role in the abundance and composition of siphonophores. The present study has broadened our knowledge on the distribution of siphonophores in the waters surrounding Taiwan.

Acknowledgments We thank the crew of the "Fishery Researcher I" for their assistance in collecting zooplankton samples and specified environmental data. We are also grateful to Prof. C.-T. Shih of the National Taiwan Ocean University and two anonymous referees for their critical reviews and valuable comments on the manuscript. Editing was provided by Sea Pen Scientific Writing. This work was supported by grants from the National Science Council and the Ministry of Education of the Republic of China to W.-T. Lo. [NSC99-2611-M 110-014 and 00C030203 (Kuroshio Project)].

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