

# SHORT COMMUNICATION

## Comparison of siphonophore distributions during the southwest and northeast monsoons on the northwest continental shelf of the South China Sea

KAI Z. LI, JIAN Q. YIN\*, LIANG M. HUANG AND XING Y. SONG

KEY LABORATORY OF MARINE BIO-RESOURCES SUSTAINABLE UTILIZATION, SOUTH CHINA SEA INSTITUTE OF OCEANOLOGY, CHINESE ACADEMY OF SCIENCE, 164 WEST XINGANG ROAD, GUANGZHOU, 510301 GUANGDONG, CHINA

\*CORRESPONDING AUTHOR: jqyin@scsio.ac.cn

Received August 19, 2011; accepted in principle April 5, 2012; accepted for publication April 11, 2012

Corresponding editor: Mark J. Gibbons

Differences in siphonophore communities between summer and winter in the northern South China Sea and the influence of environmental conditions on their variations were studied. Our results suggested that local coastal upwelling and surface ocean currents driven by the southwest monsoon enhanced the species number and abundance of siphonophores in summer, while the northeast monsoon forced the cold coastal current into the study area, resulting in low species richness and abundance in winter.

**KEYWORDS:** upwelling; ocean current; zooplankton; distribution; northern South China Sea

The South China Sea (SCS), with a total area of  $\sim 3.5 \times 10^6 \text{ km}^2$ , is the largest semi-enclosed sea in the tropical western Pacific Ocean. The surface oceanic current in the SCS is controlled by the East Asian monsoonal winds, with the southwesterly (SW) monsoon prevailing in summer and the northeasterly (NE) monsoon in winter (Liang, 1991). The SW summer monsoon pushes the high temperature and high salinity waters from the southern SCS northward to the coast bordering the northern SCS (nSCS). The NE winter monsoon usually drives the cold, low-salinity and nutrient-rich China Coastal Current southward along the coast of mainland China into the nSCS (Su, 2004).

These oceanographic features driven by the SW and NE monsoons could be important in determining plankton distribution in the nSCS. Siphonophores usually have been neglected in zooplankton research in the SCS in the past because of their fragile, gelatinous bodies. We hypothesize that in the northwest continental shelf of the SCS, the different environmental conditions during the SW and NE monsoon seasons influence the taxonomic composition and abundance distribution of siphonophores.

To test this idea, two cruises were conducted from 19 July to 6 August 2006 (summer) during the SW monsoon and from 26 December 2006 to 18 January

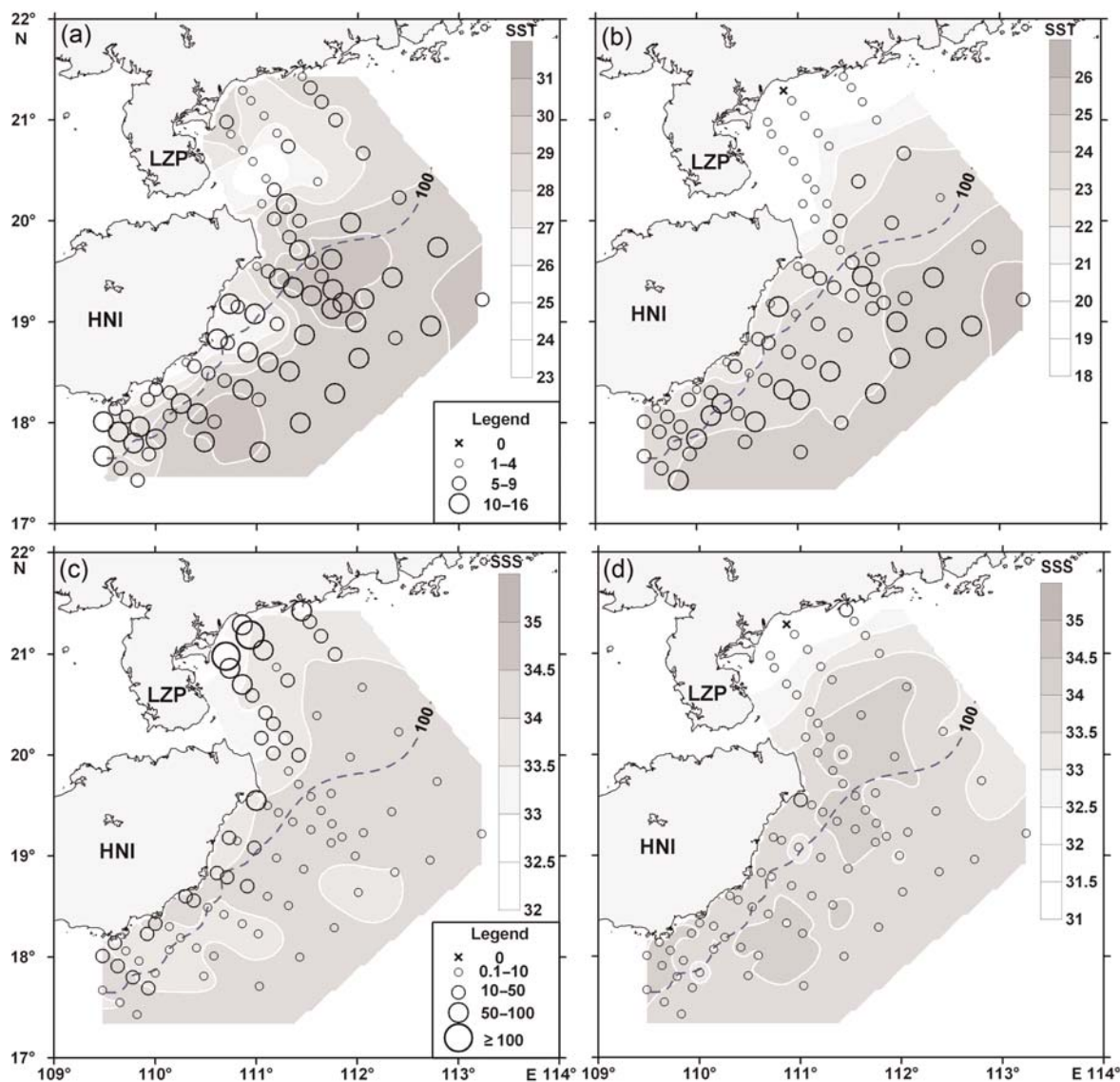
2007 (winter) during the NE monsoon along the north-western coastal waters of the SCS (109–113°E, 17–21°N). The sampling regime was identical during both cruises. Zooplankton was sampled by vertical tows from 1 m above the bottom (bottom depth < 200 m) or from 200 m (bottom depth > 200 m) to the surface using a plankton net of 505- $\mu\text{m}$  mesh (mouth diameter: 50 or 80 cm) at 82 stations. The net mouth was fitted with a Hydro-Bios flowmeter. Trawl winch speed was about  $1 \text{ m s}^{-1}$ . The samples collected were immediately preserved in 5% formaldehyde. All siphonophores and copepods were identified and counted with the aid of a dissecting microscope and current taxonomic information (Chen and Zhang, 1965; Gao *et al.*, 2002; Zhang, 2005). The abundance of Calycophorae was determined from counts of the anterior nectophores only, which were enumerated separately for the eudoxids. For physonect abundance, the pneumatophores and nectophores and/or bracts were counted (Pugh, 1999). A SeaBird CTD was used to measure the temperature and salinity of seawater from the surface to near the bottom of the water column at each station. Water samples for the measurement of chlorophyll *a* (Chl *a*) concentration were collected by 5-L Niskin bottles at depths of 0, 10 and 30 m, and bottom layer if the station depth was less than 50 m, or from 0, 10, 30, 50, 75, 100, 150 and 200 m, if it was more than 50 m. For the determination of Chl *a* concentration, a 500-mL water sample was gently filtered through a 0.70- $\mu\text{m}$  cellulose filter that then was extracted in 90% acetone for 24 h in darkness. The mean water column Chl *a* concentration ( $\text{mg m}^{-3}$ ) was then determined fluorometrically (Turner designs 10AU fluorometer) before and after acidification (Parsons *et al.*, 1984).

In order to further understand the spatial distribution of siphonophores, we divided the 82 sampling sites into nearshore (41 stations) and offshore (41 stations) regions based on the 100-m isobath (Fig. 1). Independent samples *t*-tests were used to test for significant differences in physical and biological parameters between summer and winter seasons, and between nearshore and offshore regions. Multivariate analyses were performed with the PRIMER (vers. 6.0) software package (Clarke and Gorley, 2006). Prior to the analyses, data on siphonophore species abundance were  $\log(x + 1)$  transformed. A one-way layout of ANOSIM was performed to detect the effect of the sampling sites on the composition and distribution of siphonophores during the SW and NE monsoons. The similarity percentage (SIMPER) routine was selected to show the percentage contribution of each taxon to the average dissimilarities within the nearshore and offshore regions. The distribution of siphonophore abundance in relation to physical

and biological factors was explored by canonical correspondence analysis (CCA) with CANOCO 4.5. Physical and biological factors (surface sea temperature, salinity, Chl *a* and copepod abundance) were used to examine their relationships with species richness and abundance of siphonophores. Data on the number of species and density are reported as means  $\pm$  standard error.

A total of 38 species of siphonophores were collected during the study (Table 1). The greatest number of species was observed in summer (36 species), with 24 species in winter. Thirteen species were recorded at frequencies higher than 25% of all sampling stations, of which *Nanomia bijuga*, *Abylopsis eschscholtzi*, *A. tetragona*, *Diphyes chamissonis* and *Lensia subtiloides* appeared at the nearshore and offshore regions with frequencies of >50% (Table 1). Another 25 species, mostly belonging to the genera *Abyla*, *Amphicaryon*, *Ceratocymba* and *Enneagonum* appeared sporadically in the nearshore or offshore regions in the summer. Species richness was lowest in the east inshore waters of the Leizhou Peninsula and highest in the regions with depths greater than 100 m during summer and winter (Fig. 1a and b). Species richness differed significantly between nearshore and offshore regions during both summer ( $t = -6.418$ ,  $P < 0.001$ ) and winter ( $t = 4.567$ ,  $P < 0.001$ ). Species richness was positively correlated with the sea surface temperature (SST) and sea surface salinity (SSS) in the summer (SST,  $r = 0.522$ ; SSS,  $r = 0.425$ ) and winter (SST,  $r = 0.762$ ; SSS,  $r = 0.515$ ;  $P < 0.001$  for all).

Mean siphonophore density was  $17.9 (\pm 38.7) \text{ ind. m}^{-3}$  in summer, which was significantly higher than in winter with  $2.2 (\pm 2.7) \text{ ind. m}^{-3}$  ( $t = 3.664$ ,  $P < 0.001$ ). The highest densities of siphonophores ( $>50 \text{ ind. m}^{-3}$ ) were mainly found at the east of Leizhou Peninsula and east and southeast of Hainan Island in summer (Fig. 1c), while densities generally were  $<10 \text{ ind. m}^{-3}$  in winter (Fig. 1d). Siphonophore densities in the offshore region were lower than in nearshore waters, both in summer ( $t = 3.652$ ,  $P < 0.001$ ) and in winter ( $t = 2.531$ ,  $P < 0.05$ ). The ANOSIM analysis based on the densities of 36 species in summer and 24 species in winter also confirmed the significant difference between regions (summer:  $R = 0.415$ ,  $P < 0.001$ ; winter:  $R = 0.425$ ,  $P < 0.001$ ). The SIMPER results indicated that 14 (91.17% cutoff) and 9 (90.09% cutoff) species contributed to the nearshore and offshore regions in summer and winter, respectively (Table 1). Negative correlations of SST ( $r = -0.165$ ,  $P < 0.01$ , summer;  $r = -0.408$ ,  $P < 0.05$ , winter) and SSS ( $r = -0.714$ ,  $P < 0.01$ , summer;  $r = -0.335$ ,  $P < 0.01$ , winter), and positive correlations of Chl *a* ( $r = 0.247$ ,  $P < 0.05$  summer;  $r = 0.298$ ,  $P < 0.01$ , winter) and copepod densities ( $r = 0.476$ ,  $P < 0.01$ , summer;  $r = 0.269$ ,  $P <$



**Fig. 1.** Distribution of the surface sea temperature (SST), salinity (SSS), species richness and density (ind. m<sup>-3</sup>) on the northwest continental shelf of the SCS during summer and winter [(a) summer SST and richness, (b) winter SST and richness, (c) summer SSS and abundance, and (d) winter SSS and abundance]. The dashed lines represent 100 m depth. The white contour lines represent SST (a and b) and SSS (c and d). LZP, Leizhou Peninsula; HNI, Hainan Island.

0.05, winter) with siphonophore densities were found. Results from CCA ordination of most abundant species in both summer and winter indicated that they could be divided into two groups (Fig. 2). One group included the most frequent nearshore species such as *Diphyes chamissonis*, *Nanomia bijuga* and *Lensia subtiloides* and the other consisted mainly of infrequent offshore species (Table I, Fig. 2). The CCA also revealed that copepod abundance appeared to be the most significant factor influencing the distribution and abundance of the nearshore species, while the offshore species generally were associated with warm, deep waters (Fig. 2a and b).

The differences in species composition and distribution between the nearshore and offshore, and the summer and winter, is mainly due to hydrographic features. The nearshore region was generally controlled by the coastal mixed water mass and surface water mass of the SCS in summer with the SW monsoon, but by the mixed water mass from China Coastal Current and surface water mass of the SCS during winter with NE monsoon (Wu and Li, 2003). The nearshore region was also influenced by coastal upwelling in the summer (Jing et al., 2009). The offshore region was controlled by the surface water mass of the SCS throughout the year

Table I: Alphabetical list of siphonophore species by order, collected at the nearshore and offshore region during summer and winter, respectively

Species	Summer				Winter			
	Nearshore		Offshore		Nearshore		Offshore	
	Freq.	Dens.	Freq.	Dens.	Freq.	Dens.	Freq.	Dens.
Physonectae								
<i>Agalma elegans</i>	+	<0.1	+	<0.1	–	0	+	<0.1
<i>Agalma okeni</i>	–	0	+	<0.1	+	<0.1	+	<0.1
<i>Halistemma rubrum</i>	+	0.2	+	<0.1	+	<0.1	+	<0.1
<b><i>Nanomia bijuga</i><sup>s,w</sup></b>	+++	<b>10.0</b>	+++	<b>0.3</b>	++	<b>0.2</b>	+++	<b>0.1</b>
<i>Physophora hydrostatica</i> <sup>s</sup>	+	0.4	+	<0.1	+	<0.1	+	<0.1
Calycophorae								
<i>Abyla haeckeli</i>	–	0	+	<0.1	–	0	–	0
<i>Abyla schmidtii</i>	+	<0.1	–	0	–	0	–	0
<i>Abyla trigona</i>	+	<0.1	+	<0.1	–	0	–	0
<i>Abylopsis eschscholtzi</i> <sup>s,w</sup>	+++	0.2	+++	0.2	++	<0.1	+++	0.1
<b><i>Abylopsis tetragona</i><sup>s,w</sup></b>	+++	<b>0.4</b>	+++	<b>0.3</b>	+++	<b>0.1</b>	+++	<b>0.2</b>
<i>Amphicaryon acaule</i>	–	0	+	<0.1	–	0	–	0
<i>Amphicaryon peltifera</i>	–	0	+	<0.1	–	0	–	0
<b><i>Bassia bassensis</i><sup>s,w</sup></b>	+	<b>0.1</b>	++	<b>0.1</b>	++	<b>0.1</b>	+++	<b>0.2</b>
<i>Ceratocymba leuckarti</i>	–	0	+	<0.1	–	0	–	0
<i>Chelophyes appendiculata</i>	+	<0.1	+	<0.1	–	0	+	<0.1
<i>Chelophyes contorta</i> <sup>s,w</sup>	+	<0.1	+++	0.1	++	<0.1	+++	0.2
<i>Diphyes bojani</i>	+	<0.1	+	<0.1	+	<0.1	+++	0.1
<b><i>Diphyes chamissonis</i><sup>s,w</sup></b>	+++	<b>18.5</b>	+++	<b>1.5</b>	+++	<b>1.7</b>	++	<b>0.1</b>
<i>Diphyes dispar</i> <sup>s,w</sup>	+	<0.1	++	<0.1	+	<0.1	+++	0.1
<i>Enneagonum hyalinum</i>	+	<0.1	+	<0.1	–	0	–	0
<i>Enneagonum searsae</i>	+	<0.1	+	<0.1	–	0	–	0
<i>Eudoxiodes spiralis</i> <sup>s</sup>	+	<0.1	+++	<0.1	–	0	+	<0.1
<i>Hippopodius hippopus</i>	+	<0.1	+	<0.1	+	<0.1	+	<0.1
<i>Lensia campanella</i> <sup>s</sup>	+	<0.1	+++	<0.1	+	<0.1	+	<0.1
<i>Lensia conoides</i>	+	<0.1	+	<0.1	–	0	–	0
<i>Lensia cossack</i>	+	<0.1	++	<0.1	–	0	–	0
<i>Lensia fowleri</i>	–	0	–	0	–	0	+	<0.1
<i>Lensia hotspur</i>	+	<0.1	++	<0.1	–	0	+	<0.1
<i>Lensia meteori</i>	–	0	+	<0.1	–	0	–	0
<i>Lensia multicristata</i>	+	<0.1	–	0	–	0	–	0
<i>Lensia subtilis</i> <sup>s</sup>	++	0.1	++	0.1	+	<0.1	+	<0.1
<b><i>Lensia subtiloides</i><sup>s,w</sup></b>	+++	<b>1.0</b>	+++	<b>0.2</b>	+++	<b>0.7</b>	++	<b>0.1</b>
<i>Muggiaea atlantica</i> <sup>s,w</sup>	+++	0.4	+++	0.1	+	<0.1	+++	0.1
<i>Sulculeolaria chuni</i> <sup>s</sup>	+++	0.9	++	0.1	–	0	+	<0.1
<i>Sulculeolaria monoica</i>	–	0	–	0	+	<0.1	+	<0.1
<i>Sulculeolaria quadrivalvis</i>	+	0.1	+	<0.1	+	<0.1	+	<0.1
<i>Vogtia glabra</i>	+	<0.1	+	<0.1	–	0	+	<0.1
<i>Vogtia spinosa</i>	–	0	+	<0.1	–	0	–	0

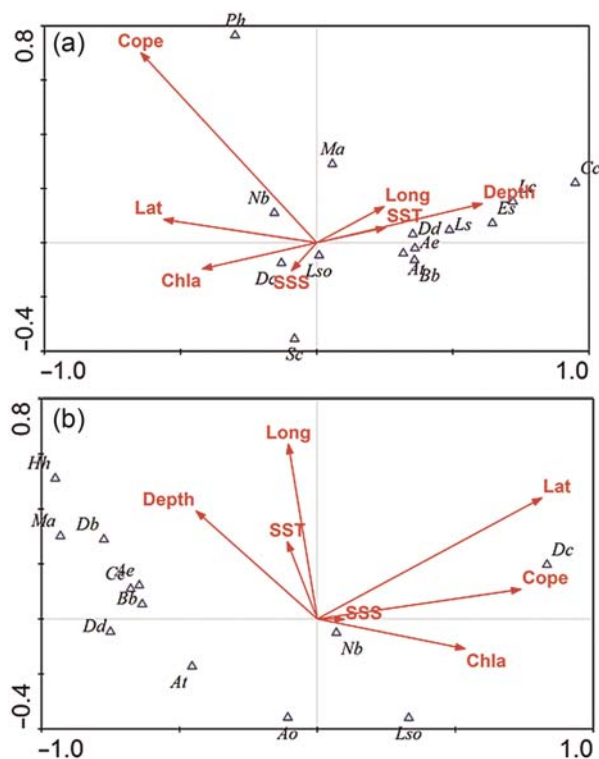
‘+’ represents the frequency of species <25%, ‘++’ meaning 25–50%, ‘+++’ >50% in the nearshore and offshore waters, respectively. ‘–’ represents no occurrence. The species contribution to the division of the nearshore and offshore group by SIMPER analysis is given as superscripts summer (S) and winter (W).

Freq.: frequency and Dens.: average abundance (ind. m<sup>−3</sup>). Species and abundance in **bold** refer to an abundance > 0.1 ind. m<sup>−3</sup> for the species in the nearshore and offshore region in both summer and winter.

(Li *et al.*, 2002). The distribution of SST and SSS in the summer and winter also confirmed that the nearshore region was characterized by low temperature and salinity, and the offshore region by high temperature and salinity (Fig. 1). Some siphonophore species such as *Chelophyes contorta*, *C. appendiculata*, *Bassia bassensis*, *Eudoxiodes mitra*, *E. spiralis*, *Abylopsis tetragona* and *A. eschscholtzi* that occurred in the warm, deep, saline waters resulted in higher species richness in the offshore region than in the nearshore region (Table I). Those

species are also widely distributed in the oceanic waters off the east coast of South Africa (Thibault-Botha *et al.*, 2004) and in the southern Gulf of Mexico (Sanvicente-Añorve *et al.*, 2007). The coastal upwelling and surface ocean current driven by the SW monsoon made a remarkable difference in species composition between summer and winter. It was worth-noting that 13 species were only present in the summer (Table I). Lin (Lin, 1992) reported that tropical pelagic species such as *Abyla carina*, *A. haeckeli*, *Enneagonum hyalinum*,





**Fig. 2.** CCA biplots of siphonophore density (triangles) in relation to environmental factors (arrows) in the northwest continental shelf of the SCS [(a) summer and (b) winter]. Note: SST, sea surface temperature; SSS, sea surface salinity; Long, longitude; Lat, latitude; Chl *a*, Chlorophyll *a* concentration; Cope, copepod abundance; Ae, *Abylopsis eschscholtzi*; Ao, *Agalma okeni*; At, *Abylopsis tetragona*; Bb, *Bassia bassensis*; Cc, *Chelophyes contorta*; Dc, *Diphyes chamissonis*; Dd, *Diphyes dispar*; Es, *Eudoxides spiralis*; Hh, *Hippopodius hippopus*; Lc, *Lensia campanella*; Ls, *Lensia subtilis*; Lso, *Lensia subtiloides*; Ma, *Muggiaea atlantica*; Nb, *Nanomia bijuga*; Ph, *Physophora hydrostatica*; Sc, *Sulculeolaria chuni*.

*E. searsea* and *Vogtia spinosa* were transported from the southern to the northern SCS by the surface circulation in summer. A coastal upwelling appeared in the east of Leizhou Peninsula and Hainan Island in summer (Wu and Li, 2003), which brought these tropical pelagic species into the offshore and nearshore waters. In contrast, the China Coastal Current brought low temperature and low salinity waters into the study area during the NE monsoon, which resulted in low species numbers in winter. The result may, to some extent, suggest that the species composition and distribution of siphonophore resulted from hydrological conditions driven by SW and NE monsoons.

The densities and distribution of siphonophores along the northwest continental shelf of the SCS were significantly different during the summer (SW monsoon) and winter (NE monsoon). The horizontal distribution of siphonophore abundance was clearly heterogeneous in summer, while homogeneous in winter. The

siphonophore densities decreased from the nearshore to the offshore regions, with high values ( $>100 \text{ ind. m}^{-3}$ ) mainly recorded from the east Leizhou Peninsula to the east and southeast of Hainan Island where local coastal upwelling dominated in the summer. The elevated nearshore densities might be supported by the high food production due to local coastal upwelling (Fig. 2a). High Chl *a* concentrations and copepod densities appeared east of Leizhou Peninsula and Hainan Island due to coastal upwelling (Li *et al.*, 2010). Results of the correlation and CCA analysis suggested that high food availability driven by the SW monsoon was the main reason for the high densities of *Diphyes chamissonis*, *Nanomia bijuga* and *Lensia subtiloides* in summer. During winter, the densities of siphonophores decreased in a gradient from the north to south, and from the nearshore to offshore region. Results of the SIMPER analysis showed the contributions of the important species differed between the nearshore and offshore regions. The nearshore region was characterized by moderately low diversity and high densities of *D. chamissonis*, *N. bijuga* and *L. subtiloides*, while the offshore region typically had high diversity and low overall abundance. The spatial pattern of these results is generally in good agreement with those observed in the southern Benguela upwelling region (Pagès and Gili, 1991) and the east coast of South Africa (Thibault-Botha *et al.*, 2004), as well as upwelling areas elsewhere (Gasca and Suárez, 1991). The difference in physical and biological features between summer and winter driven by SW and NE monsoons resulted in the different distribution patterns for siphonophores. The presence of coastal upwelling driven by SW monsoon is one of the most important physical processes contributing to the high diversity and abundance of siphonophores in the nearshore region in summer.

We demonstrated that the species number and abundance distribution were high in summer, but low in winter. The surface ocean currents and coastal upwelling driven by the SW monsoon increased the species number and abundance of siphonophores in summer. Siphonophores are a major constituent of the zooplankton community and we suggest that their role in the trophic web of the pelagic realm and other members of the zooplankton community would be regulated by the SW and NE monsoons in the SCS.

## ACKNOWLEDGEMENTS

We would like to thank the editor and three anonymous reviewers for comments that helped to improve the manuscript, and Sea Pen Scientific Writing for editing services.

## FUNDING

This study was supported by Key Innovation Project of the Chinese Academy of Sciences (KZCX2-YW-Q07), the Natural Science Foundation of China (Nos 31101619 and 41130855) and Chinese Offshore Investigation and Assessment (No. 908-01-ST08).

## REFERENCES

- Chen, Q. C. and Zhang, S. Z. (1965) The planktonic copepods of the Yellow Sea and the East China Sea. I. Calanoida. *Stud. Mar. Sin.*, **7**, 20–131 (in Chinese).
- Clarke, K. R. and Gorley, R. N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Gao, S. W., Hong, H. Q. and Zhang, S. M. (2002) *Phylum Cnidaria*. Science Press, Beijing, pp. 1–275.
- Gasca, R. and Suárez, E. (1991) Siphonophores of upwelling areas of the Campeche Bank and the Mexican Caribbean Sea. *Hydrobiologia*, **216/217**, 419–502.
- Jing, Z. Y., Qi, Y. Q., Hua, Z. L. *et al.* (2009) Numerical study on the summer upwelling system in the northern continental shelf of the South China Sea. *Cont. Shelf Res.*, **29**, 467–478.
- Li, F. Q., Li, L., Wang, X. Q. *et al.* (2002) Water masses in the South China Sea and water exchange between the Pacific and the South China Sea. *J. Ocean Uni. Qingdao*, **1**, 19–24.
- Li, K. Z., Yin, J. Q., Huang, L. M. *et al.* (2010) Monsoon-forced distribution and assemblages of appendicularians in the northwestern coastal waters of South China Sea. *Estuarine Coastal Shelf Sci.*, **89**, 145–153.
- Liang, B. Q. (1991) *Tropical Atmospheric Circulation System over the South China Sea*. China Meteorology Press, Beijing, 224 pp (in Chinese).
- Lin, M. (1992) Primary study on siphonophores in the central South China Sea. *Acta Oceanol. Sin.*, **14**, 99–105 (in Chinese).
- Pagès, F. and Gili, J. M. (1991) Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.*, **75**, 205–215.
- Parsons, T. R., Maita, Y. and Lalli, C. M. (1984) *A Manual of Chemical and Biological Methods for Seawater Analyses*. Pergamon Press, Oxford, 173 pp.
- Pugh, P. R. (1999) Siphonophorae. In Boltovskoy, D. (ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 467–511.
- Sanvicente-Añorve, L., Alba, C., Alatorre, M. A. *et al.* (2007) Cross-shelf and vertical distribution of siphonophore assemblages under the influence of freshwater outflows in the southern Gulf of Mexico. *Hydrobiologia*, **586**, 69–78.
- Su, J. L. (2004) Overview of the South China Sea circulation and its influence on the coastal physical oceanography outside the Pearl River Estuary. *Cont. Shelf Res.*, **24**, 1745–1760.
- Thibault-Botha, D., Lutjeharms, J. R. E. and Gibbons, M. J. (2004) Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. *J. Plankton Res.*, **26**, 1115–1128.
- Wu, R. S. and Li, L. (2003) Summarization of study on upwelling system in the South China Sea. *J. Oceanogr. Taiwan Strait*, **22**, 269–277 (in Chinese with English abstract).
- Zhang, J. B. (2005) *Pelagic Siphonophora in China Sea*. Ocean Press, Beijing, pp. 1–151.