

Spatio-temporal variations in the siphonophore community of the northern South China Sea*

LI Kaizhi (李开枝)¹, YIN Jianqiang (尹健强)^{1, **}, HUANG Liangmin (黄良民)¹, LIAN Shumin (练树民)², ZHANG Jianlin (张建新)¹

¹ Key Laboratory of Marine Bio-Resources Sustainable Utilization, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China

² State Key Laboratory of Tropical Oceanography, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China

Received Apr. 19, 2012; accepted in principle May 30, 2012; accepted for publication Oct. 17, 2012

© Chinese Society for Oceanology and Limnology, Science Press, and Springer-Verlag Berlin Heidelberg 2013

Abstract To understand how hydrological and biological factors affect near- to off-shore variations in the siphonophore community, we sampled zooplankton at 82 stations in the northern South China Sea during summer, winter, and spring. Forty-one species of siphonophore were collected by vertical trawling. The species richness of siphonophores increased from the nearshore to offshore regions in all three seasons of investigation, with maximum richness in summer and minimum richness in winter. The abundance of siphonophores was also higher in summer than in spring and winter, concentrated in the nearshore region in the warm season and scattered in the offshore region in the cold season. Four siphonophore groups were classified according to the frequency of occurrence: nearshore, near-offshore, offshore, and tropical pelagic. Among them, the nearshore group had higher abundance nearshore compared with the offshore. The tropical pelagic group had higher species number offshore than nearshore. Spatial and temporal fluctuations in taxonomic composition and abundance of siphonophores were due to the influence of the coastal upwelling and surface ocean currents of the South China Sea, driven by the East Asia monsoonal system.

Keyword: siphonophore; species composition; abundance; ocean current; monsoon; South China Sea

1 INTRODUCTION

The South China Sea (SCS), in an area of about 3.5×10^6 km², is the largest semi-enclosed sea in the tropical western Pacific Ocean. Sea surface circulations in the SCS are driven mostly by the prevailing East Asian monsoon (Li et al., 2000; Li, 2002). The summer southwesterly (SW) monsoon pushes high-temperature and high-salinity water originating from the southern SCS northward to the coast bordering the northern South China Sea (nSCS). The winter northeasterly (NE) monsoon usually drives the cold, low-salinity and nutrient-rich China coastal current southward along the coast of continental China into the nSCS (Li et al., 2000; Li, 2002; Su, 2004). Summer upwelling along the coast of the nSCS is very common, especially along the east coast of Hainan Island (Wu and Li, 2003). These

oceanographic features, driven by the SW and NE monsoons, play important roles in the zooplankton distribution in the nSCS (Zhang et al., 2009; Li et al., 2010, 2011; Yin et al., 2011).

Siphonophores, a major constituent of the zooplankton community, are a widespread and abundant group of colonial gelatinous cnidarians that play important roles in the trophic web of the pelagic realm (Alvarino, 1971; Mackie et al., 1987; Pugh, 1999). The distribution of siphonophores is generally restricted to certain water masses, and some species of siphonophores can be used to indicate movement

* Supported by the Key Knowledge Innovation Program of Chinese Academy of Sciences (No. KZCX2-YW-Q07), the National Natural Science Foundation of China (Nos. 31101619, 41130855), and the Chinese Offshore Investigation and Assessment (No. 908-01-ST08)

** Corresponding author: jqyin@scsio.ac.cn

of water masses (Alvariño, 1971). Studies of siphonophore assemblages at large scales have emphasized the importance of hydrological features, such as currents, water masses, upwelling, eddies, and coastal processes in the spatial distribution of siphonophores (Gasca, 1999; Gibbons and Thibault-Botha, 2002; Thibault-Botha et al., 2004; Palma and Silva, 2006; Sanvicente-Añorve et al., 2007). Some species of siphonophore can be used to indicate certain types of water in a particular region (Alvariño, 1971; Gasca and Suárez, 1991; Thibault-Botha et al., 2004). Studies at smaller scales have focused on biological processes, such as productivity and prey selection, which can have a more important impact on siphonophore abundance (Mackie et al., 1987; Gasca, 1999; Pagés et al., 2001). Sanvicente-Añorve et al. (2007) found that both hydrological features and food availability affected the structure and distribution of siphonophores in the southern continental waters of the Gulf of Mexico.

The siphonophores in the SCS have been well described taxonomically, with 89 species recorded (Hong and Zhang, 1981; Chen, 1983; Zhang and Lin, 1997; Gao et al., 2002; Zhang, 2005). However, siphonophores have usually been considered as an unimportant component of zooplankton because of their gelatinous and fragile bodies. Therefore, because they have often been neglected in past studies of zooplankton biomass and abundance in the southern SCS (Nansha Islands and adjacent waters) and the central SCS (Xisha and Zhongsha Islands) (Chen, 1983), data about their quantity and distribution in the SCS is limited. This study aims to reveal the temporal and spatial variations of the siphonophore community on the continental shelf of the nSCS during the periods of summer (typical SW monsoon), winter (NE monsoon) and spring (inter-monsoon), and to understand how environmental factors affect siphonophore abundance and distribution.

2 MATERIAL AND METHOD

2.1 Study area

The survey region was located on the northwestern continental shelf of the SCS (17°17.10'–21°25.62'N, 109°28.74'–113°13.26'E). It included coastal waters east of the Leizhou Peninsula and the continental shelf from the eastward mouth of Qiongzhou Strait to the east and southeast of Hainan Island (Figs. 1 and 2). The Guangdong Coastal Current (GCC), coastal upwelling (CU), surface circulation of SCS and the SCS Warm

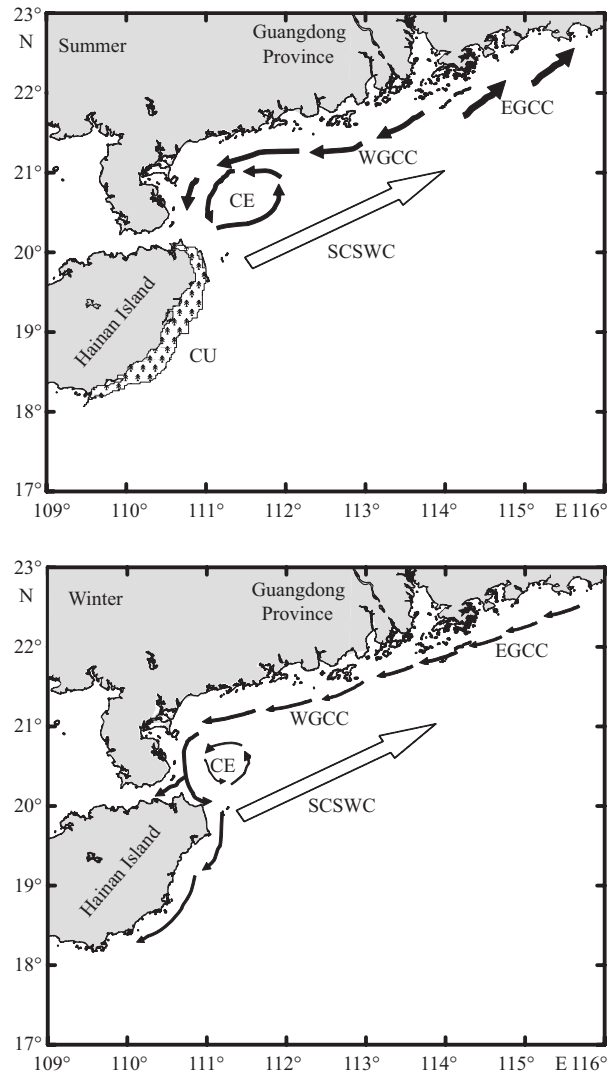


Fig.1 Sketch map of ocean currents in the study area during summer and winter

EGCC, WGCC, CE and SCSWC represent the east Guangdong Coastal Current, the west Guangdong Coastal Current, cold eddy (cyclonic circulation), and South China Sea Warm Current, respectively, and CU indicates regions of coastal upwelling.

Current (SCSWC) all control water movements in the study area (Huang et al., 1992; Yang et al., 2003; Guan and Yuan, 2006; Chiang et al., 2008; Jing et al., 2009; Wang et al., 2010). The GCC is divided traditionally into the east GCC (EGCC) and the west GCC (WGCC) by the Pearl River estuary. Forced by the winter NE monsoon, both the EGCC and WGCC move southwestward. They bring low salinity waters from the East China Sea to the SCS shelf. The EGCC flows northeastward under the influence of the summer SW monsoon, but the WGCC still passes southwestward to the Leizhou Peninsula due to the large Pearl River discharge (Huang et al., 1992; Yang et al., 2003). The

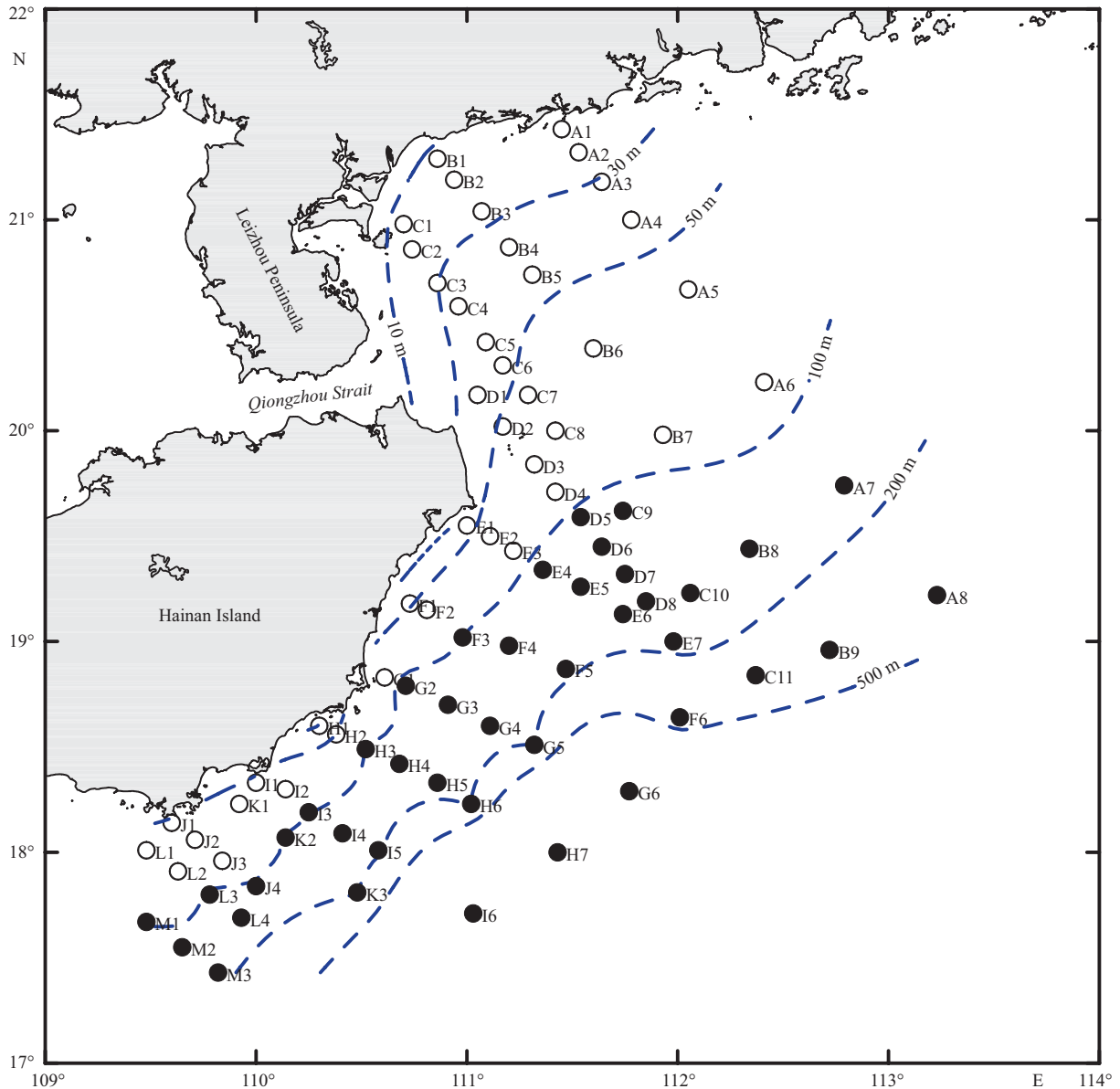


Fig.2 Map showing the positions of sampling stations (○: nearshore stations; ●: offshore stations) and underlying bathymetry on the northwest continental shelf of the South China Sea

offshore surface current east of the Leizhou Peninsula flows northeastward (driven by the SW monsoon), in an opposite direction to the southwesterly WGCC near the coast of Leizhou Peninsula. The two opposite currents cause the formation of a cold eddy (CE). This cyclonic circulation persists throughout the year with its intensity being determined by SW monsoonal strength and the flux of the Pearl River (Huang et al., 1992; Yang et al., 2003; Guan and Yuan, 2006). During summer, coastal upwelling dominates the east and southeast coasts of Hainan Island, driven by the strong SW monsoon and the topography. The SCSWC is a consistent northeastward current straddling the shelf-

break region where depths range from 100–300 m (Guan, 1978, 1998; Li et al., 2000; Chiang et al., 2008).

2.2 Field sampling and laboratory procedures

Three cruises were carried out along the northwest continental shelf of the nSCS during July 19 to August 6, 2006 (summer), December 26, 2006 to January 18, 2007 (winter) and April 12 to April 25, 2007 (spring). At 82 stations (Fig.2), zooplankton were sampled with a vertical tow from 1 m above the bottom (depth < 200 m) or from 200 m (depth > 200 m) to the surface, using a plankton net with 505- μ m mesh

(mouth diameter: 50 or 80 cm). The net mouth was fitted with a flow-meter (Hydro-Bios) to determine the volume of water filtered in each tow (unit: m³). Trawl winch speed was about 1 m/s. Samples collected were preserved immediately in 5% formaldehyde. Using a stereomicroscope, all siphonophores were identified and counted based on current taxonomy (Gao et al., 2002; Zhang, 2005). The abundance of calyphophoran species was determined from the counts of anterior nectophores only, and eudoxids were enumerated separately. For physonect abundance, pneumatophores and nectophores and/or bracts were all counted (Pugh, 1999).

A SeaBird CTD probe was used to measure temperature and salinity of the seawater from the surface to near the bottom at each station. Water samples for the measurement of chlorophyll *a* (Chl *a*) concentration were collected using a 5-L Niskin bottle at 0, 10, 30 m, and bottom levels where the depth was ≤ 50 m, or 0, 10, 30, 50, 75, 100, 150 and 200 m where the depth was >50 m. For the determination of Chl *a* concentration, a 500-mL water sample was filtered through a 0.70- μ m cellulose filter and chlorophyll was extracted in 90% acetone for 24 h, in darkness at 4°C. The mean of water column Chl *a* concentration (unit: mg/m³) was then determined fluorometrically (by a Turner designs 10AU fluorometer) before and after acidification (Parsons et al., 1984).

2.3 Data analysis

To understand the spatial distribution of siphonophores, we divided the 82 sampling sites into nearshore (41 stations) and offshore (41 stations) regions, demarcated by the 100 m contour line (Fig.2). The nearshore region included the coastal waters east of the Leizhou Peninsula and Hainan Island, while the offshore region included the offshore waters from the Leizhou Peninsula to Hainan Island. Transects C and E, located off the eastern coasts of the Leizhou Peninsula and Hainan Island respectively, were selected to show vertical distribution of temperature and salinity in the region. The Shannon-Wiener diversity index (H') was used to calculate the species diversity (Shannon and Weaver, 1963) and the Pielou evenness index (J) was employed to measure the relative abundances of species in a community (Omori and Ikeda, 1984).

A two-way analysis of variance (ANOVA) was used to test differences in physical and biological parameters among different regions and seasons

(using SPSS 15.0 package). Multivariate analyses were performed with PRIMER (Ver. 6.0) (Clarke and Gorley, 2006). Species abundances above 25% in each season were presence/absence transformed before analysis. A one-way analysis of similarities (ANOSIM) was performed to detect the effect of the sampling sites on the composition and distribution of siphonophores among three seasons. The similarity percentage (SIMPER) routine was selected to show the percentage contribution of each taxon to the average dissimilarities between nearshore and offshore regions. We also examined Pearson correlations between the abundance of siphonophores and physical and biological factors (surface sea temperature, salinity, Chl *a*, and copepod abundance).

3 RESULT

3.1 Environmental conditions

The values of surface sea temperature (SST) and salinity (SSS) differed significantly among seasons and regions (Table 1). The mean SST's were 28.62(± 1.53)°C, 22.95(± 1.54)°C and 25.32(± 2.06)°C in summer, winter and spring, respectively. During winter and spring, horizontal distribution of SST increased gradually from the north to south and from the nearshore to the offshore regions. The minimum temperature (~ 27 °C) was found nearshore. High values (>30 °C) were found offshore, between the Leizhou Peninsula and the Hainan Island in the summer, when the SW monsoon prevails (Fig.3a). The mean SSS's in summer, winter, and spring were 33.99(± 0.26)°C, 33.72(± 0.56)°C and 34.01(± 0.57)°C respectively. The values of SSS varied less in the offshore region, but they changed markedly in the nearshore waters east of the Leizhou Peninsula, in all three seasons (Fig.3b). Both SST and SSS were higher offshore than nearshore, regardless of the season.

At stations from transects C and E, temperature of nearshore waters was not stratified during winter or spring, but offshore waters were generally stratified in spring (Fig.4a, 4c). Salinity in offshore waters was low (below 34) in spring and winter. Seasonal variations were obvious when the surface was covered by low salinity waters at transects C and E (Fig.4b, 4d). At both transects in the summer, the isopleths of temperature and salinity rose, as would be expected, from the bottom to surface waters, and from nearshore to offshore (Fig.4a–d).

Chl *a* concentration did not vary significantly among seasons, but did among regions (Table 1).

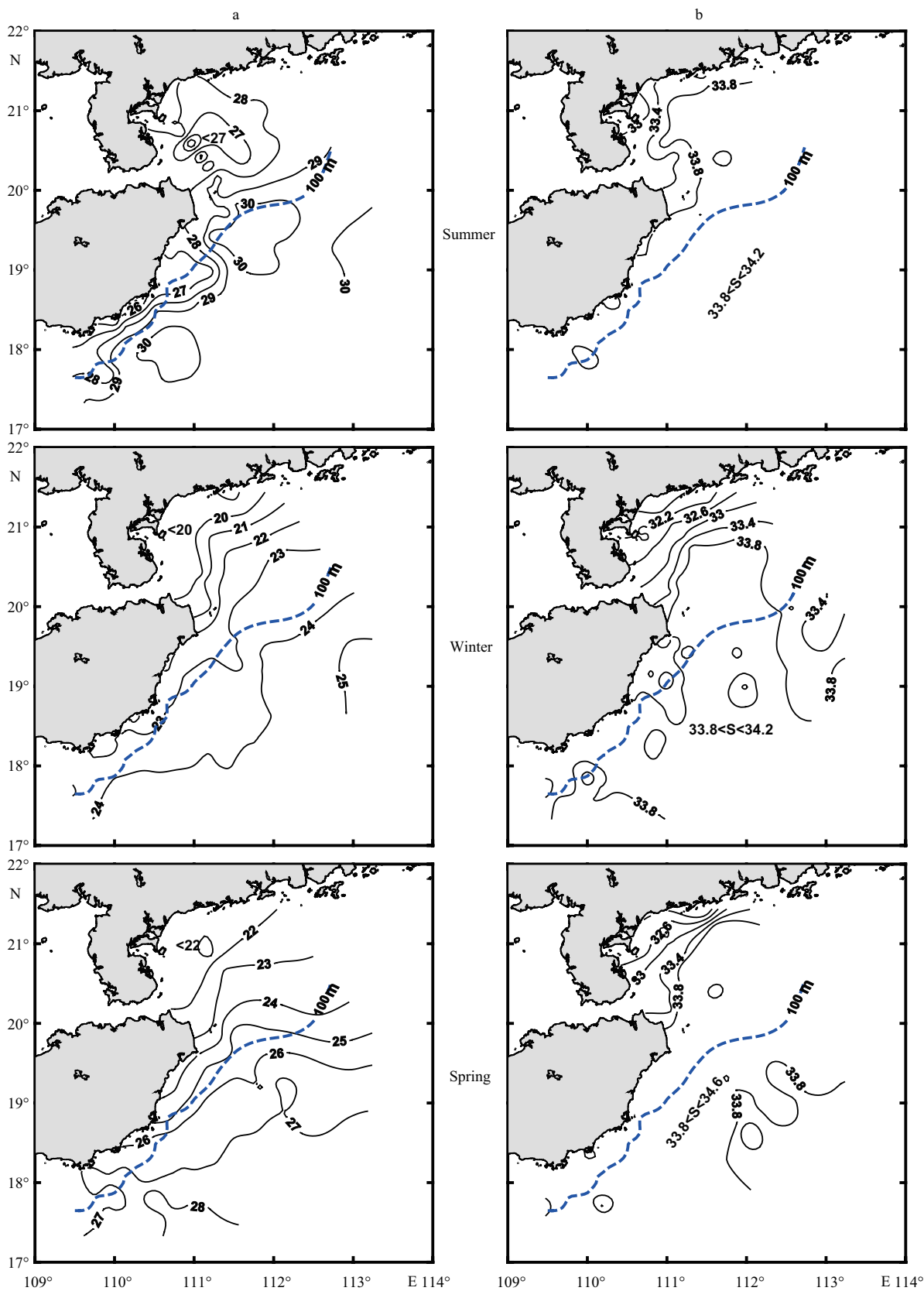


Fig.3 Horizontal distribution of surface sea temperature (SST, °C) and salinity (SSS) in the northern South China Sea during summer, winter and spring

a: SST; b: SSS

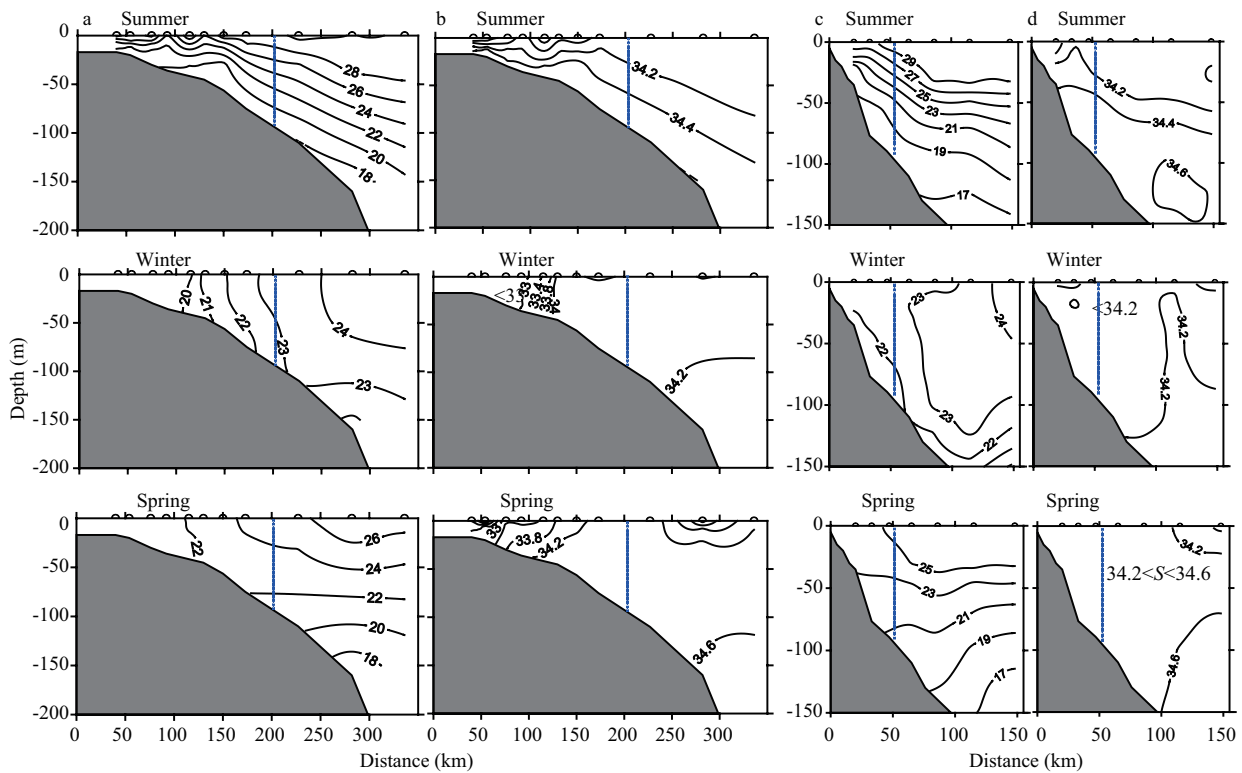


Fig.4 Vertical distribution of temperature (°C) and salinity at transects C and E during summer, winter and spring
 a and b: transect C temperature and salinity; c and d: transect E temperature and salinity. The dashed line indicates the 100 m depth contour.

Table 1 A two-way ANOVA result for physical and biological parameters

Variables	Season					Region					Season vs. region				
	df	MS	F_s	P	Sig.	df	MS	F_s	P	Sig.	df	MS	F_s	P	Sig.
Temperature	2	668.35	357.71	0.000	***	1	307.06	164.34	0.000	***	2	6.42	164.34	0.034	*
Salinity	2	7.88	7.31	0.001	**	1	5.34	20.82	0.000	***	2	0.18	0.71	0.492	n.s.
Chl <i>a</i>	2	0.41	0.23	0.792	n.s.	1	9.08	66.84	0.000	***	2	0.66	4.99	0.008	**
Copepods	2	60 210	6.21	0.002	**	1	415 478	49.16	0.000	***	2	55 000	7.21	0.001	**
Richness	2	222.04	26.33	0.000	***	1	1 410.25	167.24	0.000	***	2	24.96	2.96	0.054	n.s.
Abundance	2	5 191.24	7.98	0.000	***	1	16 089.88	24.73	0.000	***	2	3 870.65	5.95	0.003	**
Diversity index	2	5.12	9.08	0.000	***	1	89.52	158.67	0.000	***	2	2.37	4.20	0.016	*
Evenness index	2	0.095	3.13	0.046	n.s.	1	1.23	40.56	0.000	***	2	0.34	1.12	0.328	n.s.
Group A1	2	4 216.69	6.54	0.002	**	1	16 633.74	25.81	0.000	***	2	3 427.26	5.32	0.005	**
Group A2	2	3.58	4.51	0.012	*	1	17.64	22.18	0.000	***	2	8.72	10.98	0.000	***
Group B	2	9.21	11.67	0.000	***	1	1.53	1.94	0.165	n.s.	2	4.33	5.49	0.005	**
Group C	2	5.00	12.02	0.000	***	1	1.84	4.42	0.037	*	2	2.84	6.83	0.001	**

df: degrees of freedom; MS: mean square; F_s : test value; P : probability value; *: $0.05 > P > 0.01$; **: $0.01 > P > 0.001$; ***: $P < 0.001$; n.s.: $P > 0.05$.

Chl *a* concentration generally decreased from nearshore to offshore regardless of the season (Fig.5a–c). A region of high Chl *a* was observed between the east of the Leizhou Peninsula and the Qiongzhou Strait in summer (with the maximum of 3.25 mg/m³ at station C4) and also in the nearshore

waters east and southeast of Hainan Island. The abundance of copepods varied significantly with season and region (Table 1). It generally decreased from nearshore to offshore during the three seasons, but high abundances of copepods were found east of the Leizhou Peninsula in the summer (Fig.5a–c).

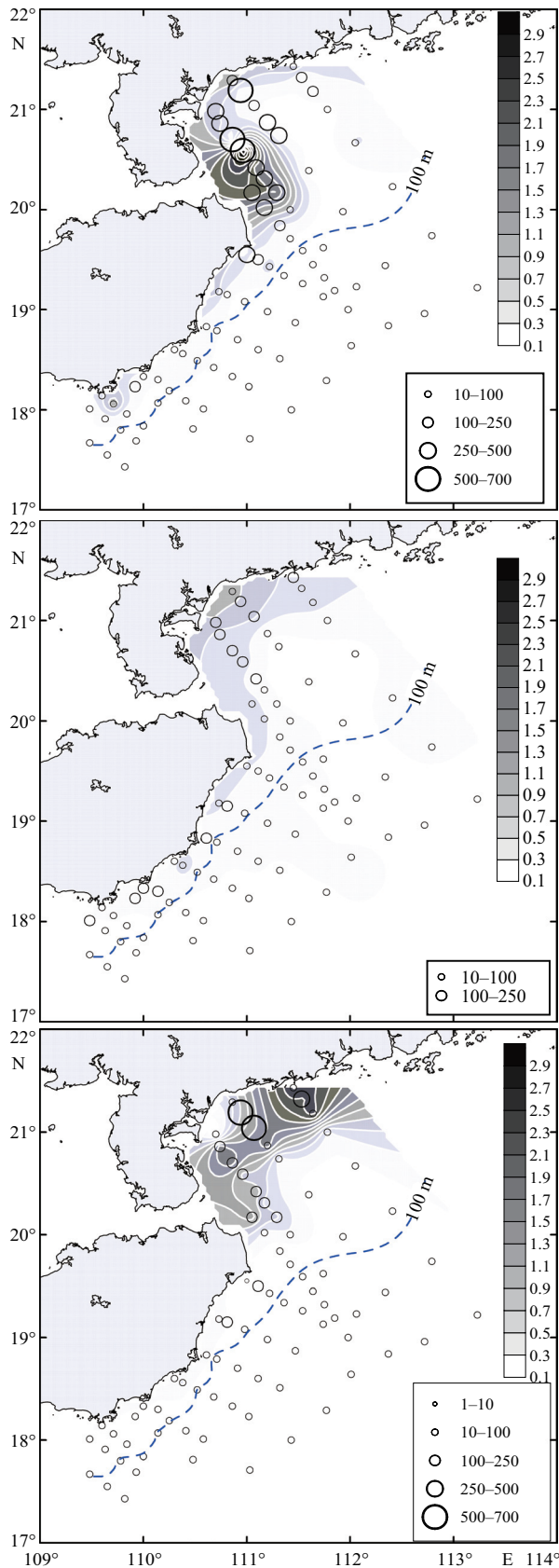


Fig.5 Chlorophyll *a* concentration (mg/m^3) (gray scales) and abundance of copepods ($\text{ind.}/\text{m}^3$) (blank circles) in summer, winter and spring

3.2 Species composition and distribution

Forty-one species of siphonophores were collected in the study (Table 2), of which 36 (88%) were calyphoran species and only 5 (12%) were physonect species. The greatest number of species was observed in summer (37 species), with 25 in winter and 26 in spring. Of all the collected species, half of them were found in all the seasons and 20% of them in two seasons: the rest were found in one season. 30 species were common to both nearshore and offshore regions, with 10 only found offshore and one only found nearshore (Table 2).

The species present at >25% of stations were clustered into three groups (Fig.6). Three distinct assemblages of species were arranged at the 35% similarity level (Fig.6). All the species of Group A were found in every season in both the nearshore and offshore regions. Group A1 is termed the 'nearshore' group, and includes three species with higher occurrence (>50%) in the nearshore than the offshore. Species of Group A2, termed the 'near-offshore' group, were assembled mainly in the offshore waters, and their occurrences were generally <50% in the nearshore region. The species in Group B, the 'offshore' group, were occasionally distributed in the offshore region at >25% of stations (Table 2). The rest (occurrence <25%) were considered as a 'tropical pelagic' group (Group C), which intruded into the nearshore and offshore regions in the surface ocean currents from the southern SCS, in summer.

The number of siphonophore species generally increased from north to south, and from nearshore to offshore, in all seasons (Fig.7a). Species richness of siphonophores in summer was greater than in winter and spring. The species richness changed significantly with season and region (Table 1). The species richness was correlated positively to the SST and SSS in summer (SST, $R=0.522$; SSS, $R=0.425$), winter (SST, $R=0.762$; SSS, $R=0.515$) and spring (SST, $R=0.482$) at $P<0.001$ in all cases.

3.3 Siphonophore abundance and distribution

The mean abundance of siphonophores was $17.9(\pm 38.7)$, $2.2(\pm 2.7)$ and $10.7(\pm 26.8)$ $\text{ind.}/\text{m}^3$ in summer, winter, and spring, respectively. Abundance was high (>49.9 $\text{ind.}/\text{m}^3$) in the nearshore waters east of the Leizhou Peninsula in summer and spring, and slightly lower in the nearshore waters east and southeast of Hainan Island in summer (Fig.7b). In winter, the abundance was generally low (<10 $\text{ind.}/\text{m}^3$)

Table 2 Alphabetical list of siphonophore species arranged by Order, collected in the nearshore and offshore regions during summer, winter, and spring

	Summer		Winter		Spring		Group
	Nearshore	Offshore	Nearshore	Offshore	Nearshore	Offshore	
Physonectae							
<i>Agalma elegans</i>	•	•		•		•	C
<i>Agalma okeni</i>		•	•	•	•	•	C
<i>Halistemma rubrum</i>	•	•	•	•		•	C
<i>Nanomia bijuga</i>	•••	•••	••	•••	••	••	A1
<i>Physophora hydrostatica</i>	•	•	•	•		•	C
Calycephorae							
<i>Abyla carina</i>		•					C
<i>Abyla haeckeli</i>		•					C
<i>Abyla schmidti</i>	•						C
<i>Abyla trigona</i>	•	•				•	C
<i>Abylopsis eschscholtzi</i>	•••	•••	••	•••	•	•••	A2
<i>Abylopsis tetragona</i>	•••	•••	•••	•••	••	•••	A2
<i>Amphicaryon acaule</i>		•				•	C
<i>Amphicaryon peltifera</i>		•					C
<i>Bassia bassensis</i>		••	••	•••	•	•••	A2
<i>Ceratocymba leuckarti</i>		•					C
<i>Chelophyes appendiculata</i>				•			C
<i>Chelophyes contorta</i>	•	•••	••	•••	•	•••	A2
<i>Diphyes bojani</i>	•	•	•	•••	•	•••	A2
<i>Diphyes chamissonis</i>	•••	•••	•••	••	•••	•	A1
<i>Diphyes dispar</i>	•	••	•	•••	•	•••	A2
<i>Enneagonum hyalinum</i>	•	•					C
<i>Enneagonum searsae</i>	•	•					C
<i>Eudoxiodes spiralis</i>	•	•••		•	•	•••	A2
<i>Eudoxiodes mitra</i>						•	C
<i>Hippopodius hippopus</i>	•	•	•	•		•	C
<i>Lensia campanella</i>	•	•••	•	•		••	B
<i>Lensia conoides</i>	•	•					C
<i>Lensia cossack</i>	•	••				••	B
<i>Lensia fowleri</i>				•		•	C
<i>Lensia hotspur</i>	•	••		•		•••	B
<i>Lensia meteori</i>		•				•	C
<i>Lensia multicristata</i>	•					•	C
<i>Lensia subtilis</i>	••	••	•	•		••	B
<i>Lensia subtiloides</i>	•••	•••	•••	••	•••	•	A1
<i>Lensia tottoni</i>						•	C
<i>Muggiaea atlantica</i>	•••	•••	•	•••	•	•••	A2
<i>Sulculeolaria chuni</i>	•••	••		•			B
<i>Sulculeolaria monoica</i>			•	•			C
<i>Sulculeolaria quadrivalvis</i>	•	•	•	•		•	C
<i>Vogtia glabra</i>	•	•		•		•	C
<i>Vogtia spinosa</i>		•					C

• indicates species found at <25% of the 82 sampling stations; •• indicates 25%–50%, ••• indicates >50% in the nearshore and offshore regions.

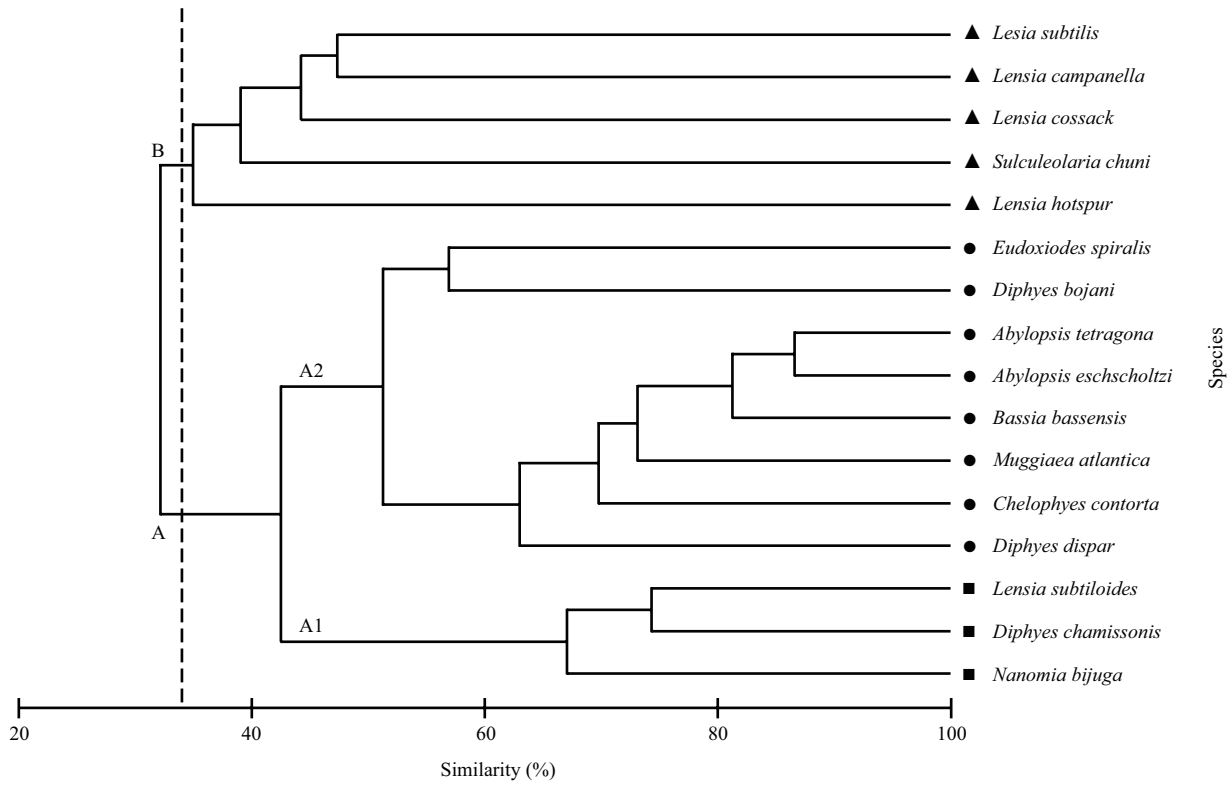


Fig.6 Dendrogram, based on the Bray-Curtis Similarity Index, of the siphonophores species with occurrence >25%

A1: nearshore group; A2: near-offshore group; B: offshore group.

Table 3 Correlation coefficients between abundance of siphonophores (ind./m³) and surface sea temperature (SST), surface sea salinity (SSS), Chl *a* concentration (mg/m³) and copepod abundance (ind./m³) during summer, winter and spring

Variables	Summer	Winter	Spring
SSS	-0.165**	-0.408*	-0.625**
SST	-0.714**	-0.335**	-0.730**
Chl <i>a</i>	0.247*	0.298**	0.621**
Copepods	0.476**	0.269**	0.404**

* 0.05>P>0.01; ** 0.01>P>0.001.

in both nearshore and offshore regions. Siphonophore abundance differed significantly with seasons and regions (Table 1).

The abundance of Group A1, which accounted for 88% in summer, 66% in winter, and 92% in spring of total siphonophores, varied seasonally and regionally: higher in the nearshore than offshore in any season, with a maximum in summer and a minimum in winter (Fig. 8a). The abundances of other groups (A2, B and C) were higher in the nearshore than offshore in

summer (Fig. 8b, 8c, 8d). SST and SSS were negatively correlated to the abundance of siphonophores during all seasons; Chl *a* and copepods were positively correlated (Table 3).

The ANOSIM based on the abundances of species revealed significant differences between regions (summer: $R=0.415$, $P<0.001$; winter: $R=0.425$, $P<0.001$; spring: $R=0.157$, $P<0.001$). The SIMPER results show that, at about a 90% cutoff level for cumulative dissimilarity, 14, 9 and 6 species contribute to the nearshore-offshore division of different groups in summer, winter, and spring, respectively (Table 4). Among them, *Diphyes chamissonis*, *Nanomia bijuga*, and *Lesia subtiloides* were the major contributing species to the dissimilarity between the nearshore and offshore regions (Tables 2 and 4).

4 DISCUSSION

4.1 Taxonomic composition

Some 175 species of siphonophore have been described so far, and they are grouped into three orders: Cystonectae, Physonectae, and Calycophorae (Pugh, 1999). Although half of them has been

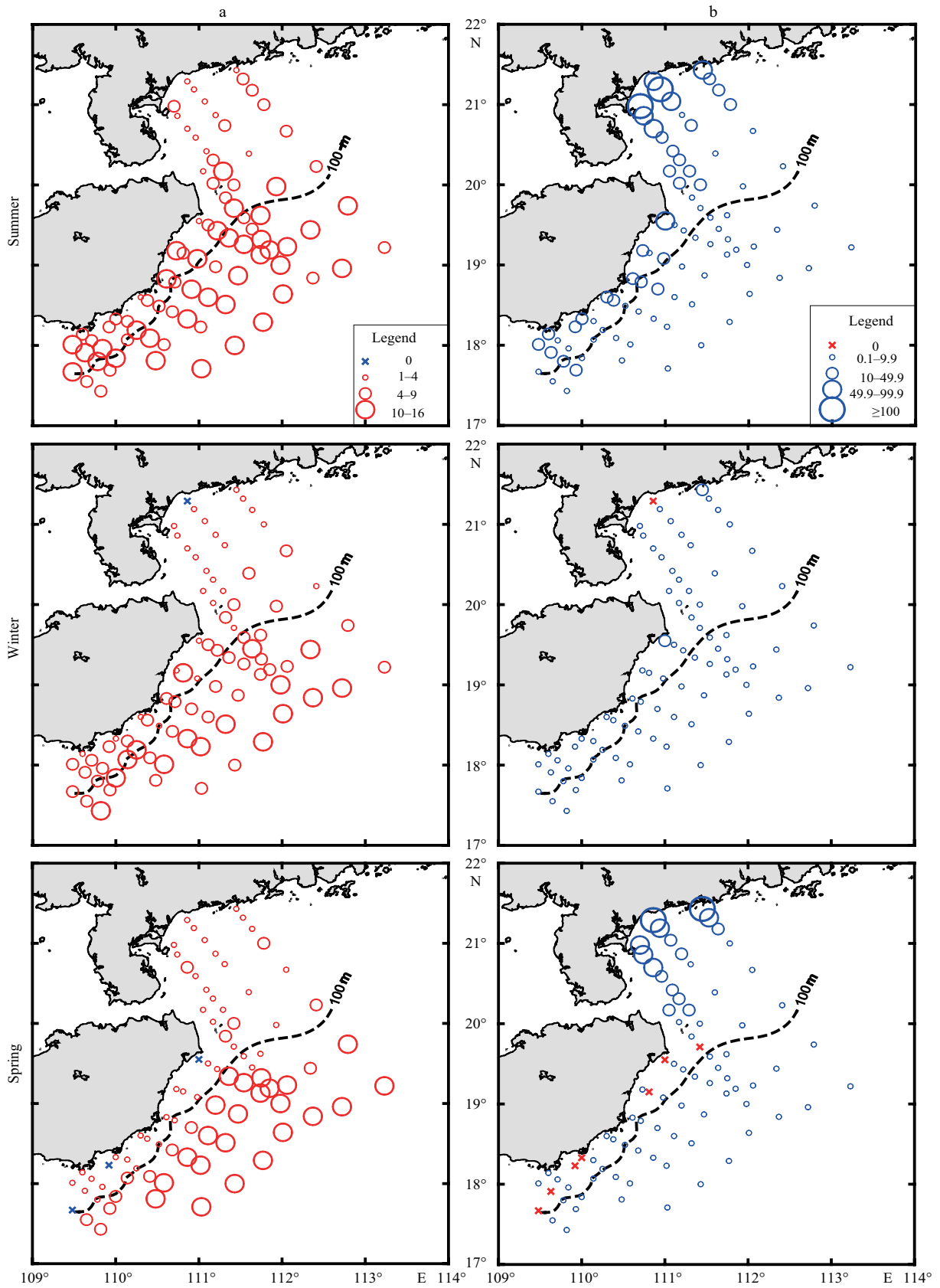


Fig.7 Species richness and abundance (ind./m³) of siphonophores in the northern South China Sea during summer, winter and spring

Panel a: species richness; Panel b: abundance.

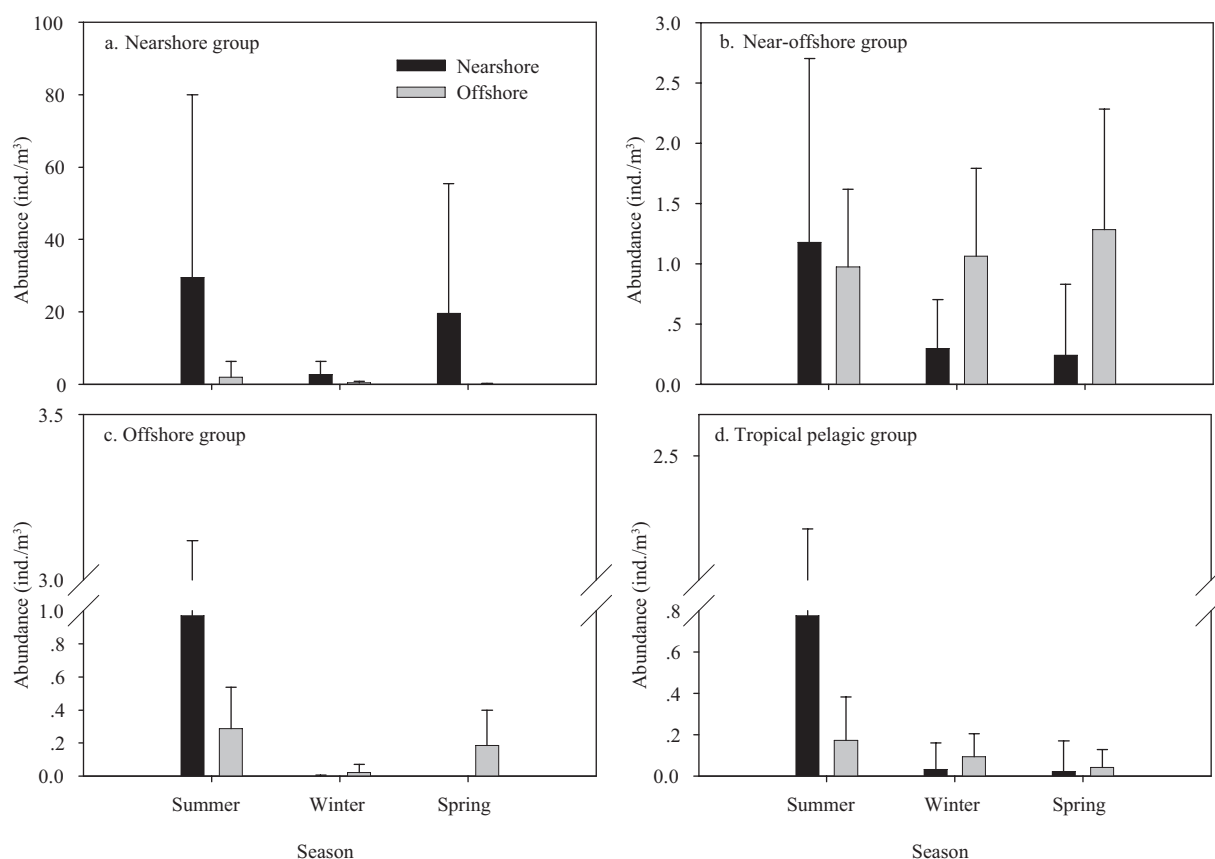


Fig.8 Seasonal variability in the abundance of nearshore, near-offshore, offshore and tropical pelagic groups in nearshore and offshore regions

recorded in the SCS (Zhang, 2005), quantitative data about their abundance in the epipelagic zone is currently limited. Only 41 species of siphonophore were collected in this study. Although information about siphonophores in the SCS is limited, most of them are thought to be widely distributed (Hong and Zhang, 1981). Of the 41 species recorded during this survey (Table 2), 30 species have been found in the East China Sea (Xu et al., 2003) and 37 species in the Taiwan Strait (Huang et al., 1991) and all have been found in the central and southern SCS (Chen, 1983; Lin, 1992; Zhang and Lin, 1997; Gao et al., 2002; Zhang, 2005). The order Calycophorae is the most diverse and widely distributed group of Siphonophora in the study area. Some species, including *Abylopsis tetragona*, *Bassia bassensis*, *Chelophyes appendiculata*, *Diphyes dispar*, *Enneagonum hyalinum*, *E. searsae*, and *Eudoxiodes spiralis*, have been found to be widely distributed in the open ocean and also in the nearshore waters of southern Africa and the southern Gulf of Mexico (Gibbons and Thibault-Botha, 2002; Sanvicente-Añorve et al.,

2007). One of the limitations of the sampling methodology of this study was that a plankton net with 505- μm mesh size was used: some small-sized siphonophores were ignored.

4.2 Species distribution and ocean currents

To date, no study has been conducted to investigate spatio-temporal changes in the siphonophore community of the SCS, except that of Lin (1992). He found that the distribution of siphonophores in the central SCS was influenced by coastal waters from the Java Sea and Sunda shelf and also by the uplifted subsurface waters of low temperature and high salinity from the southern SCS. It has also been observed that different water masses over the continental shelf of the nSCS result from the SW and NE monsoons (Fan et al., 1988; Li et al., 2002; Su, 2004). Therefore, we need to understand clearly how variations of ocean currents in the nSCS affect siphonophore distribution and abundance.

The three assemblages indicated by the cluster analysis reflect differences in siphonophore

Table 4 Results of SIMPER analysis, showing species contributing most to dissimilarity between nearshore and offshore regions in summer, winter and spring

Season	Species	Av.abund. nearshore	Av.abund. offshore	Av.Diss	Diss./SD	Contrib.%
Summer	<i>Diphyes chamissonis</i>	2.14	0.40	24.99	1.67	32.12
	<i>Nanomia bijuga</i>	1.28	0.20	14.28	1.25	18.35
	<i>Lensia subtiloides</i>	0.50	0.12	6.38	1.08	8.20
	<i>Abylopsis tetragona</i>	0.24	0.25	4.56	0.89	5.85
	<i>Sulculeolaria chuni</i>	0.35	0.06	4.47	0.72	5.74
	<i>Abylopsis eschscholtzi</i>	0.18	0.20	3.35	1.07	4.30
	<i>Muggiaea atlantica</i>	0.19	0.10	2.99	0.73	3.85
	<i>Bassia bassensis</i>	0.08	0.10	2.03	0.76	2.61
	<i>Physophora hydrostatica</i>	0.15	0.01	1.52	0.37	1.96
	<i>Chelophyes contorta</i>	0.01	0.07	1.46	0.49	1.88
	<i>Lensia campanella</i>	0.01	0.08	1.43	0.65	1.84
	<i>Lesia subtilis</i>	0.04	0.06	1.33	0.67	1.71
	<i>Eudoxiodes spiralis</i>	0.01	0.06	1.15	0.49	1.48
	<i>Diphyes dispar</i>	0.04	0.03	0.99	0.56	1.28
Winter	<i>Diphyes chamissonis</i>	0.66	0.06	20.36	1.06	25.39
	<i>Lensia subtiloides</i>	0.38	0.09	12.59	1.03	15.70
	<i>Abylopsis tetragona</i>	0.11	0.19	7.72	1.15	9.63
	<i>Nanomia bijuga</i>	0.15	0.11	7.24	0.94	9.03
	<i>Bassia bassensis</i>	0.06	0.20	7.24	1.10	9.03
	<i>Chelophyes contorta</i>	0.03	0.16	6.09	1.09	7.59
	<i>Abylopsis eschscholtzi</i>	0.03	0.10	4.12	1.10	5.14
	<i>Muggiaea atlantica</i>	0.01	0.09	3.49	0.78	4.35
Spring	<i>Diphyes dispar</i>	0.01	0.10	3.39	0.72	4.23
	<i>Diphyes chamissonis</i>	1.54	0.09	29.07	1.10	34.79
	<i>Nanomia bijuga</i>	0.76	0.08	15.22	1.03	18.22
	<i>Abylopsis tetragona</i>	0.16	0.11	9.55	0.71	11.48
	<i>Lensia subtiloides</i>	0.42	0.01	8.22	0.84	9.84
	<i>Chelophyes contorta</i>	0.10	0.14	7.75	0.72	9.27
	<i>Eudoxiodes spiralis</i>	0.10	0.12	7.49	0.73	8.96
					92.55	

Av.Abund. represents the abundance (ind./m³) after log(x+1) transformation. Contrib.% means contribution to the nearshore and offshore dissimilarities. Av.Diss. represents average Bray Curtis dissimilarity, and Diss./SD represents the ratio of the dissimilarity to the standard deviation.

distribution. Group A consisted of three coastal species, *Diphyes chamissonis*, *Nanomia bijuga*, and *Lensia subtiloides* (Fig.6). Zhang and Lin (1997) reported that these three coastal species occurred in all seasons in the nearshore waters of less than 100 m in depth—they are generally considered as a characteristic species of coastal waters of the China Sea (Hong and Zhang, 1981; Zhang and Lin, 1997). The WGCC flows southwestward along the eastern nearshore waters of the Leizhou Peninsula during

summer when the SW monsoon prevails (Huang et al., 1992; Su, 2004; Yang et al., 2003). Therefore, we suggest that the distribution range of *D. chamissonis* could extend to the offshore region due to the large amount of Zhujiang River (Pearl River) runoff during summer (Fig.1). Apparently, species of Groups A2 and B are more common in the offshore region than in the nearshore (Table 2). Groups A2 and B are dominated by *Chelophyes contorta*, *C. appendiculata*, *Bassia bassensis*, *Eudoxiodes mitra*, *Abylopsis*

tetragona, *A. eschscholta*, and *Eudoxoides spiralis* (Lin, 1992). These species have been shown to be widely distributed in the oceanic waters off the eastern coast of South Africa (Thibault-Botha et al., 2004) and the southern Gulf of Mexico (Sanvicente-Añorve et al., 2007), with a preference for high temperature and salinity. During summer, Groups A2 and B are generally present in the nearshore waters off Hainan Island and are transported from the central SCS (Zhang and Lin, 1997). The tropical pelagic group, which appeared occasionally in the nearshore and offshore regions (Table 2), is limited to the areas of high salinity (above 33.8). Lin (1992) reported that *Abyla carina*, *A. haeckeli*, *Enneagonum hyalinum*, *E. searsea*, and *Vogtia spinosa* were transported to the nSCS from the south by surface circulation in summer. The survey time in the summer cruise was from July 19 to August 6, 2006, when southwesterly winds prevailed over the entire SCS. Coastal upwelling in the east and southeast of Hainan Island in summer is strong (Han et al., 1990; Wu and Li, 2003) and carries tropical pelagic species into the investigation area. Nine species occurred only in summer, confirming that tropical pelagic species had reached the surveyed region (Table 2).

Siphonophores can be used as indicators for particular ocean currents in a region (Alvariño, 1971). The variations in species of Groups A1 and C were due to movement of coastal and surface oceanic waters. *Chelophyes contorta* is an indicator of tropical water in the Atlantic, Pacific, and Indian Oceans (Alvariño, 1971). It was very common in offshore waters with occurrences >50% in all three seasons (Table 2) and has been associated with SCSWC throughout the year (Chiang et al., 2008; Wang et al., 2010). *C. contorta* is an indicator of the intrusion of subtropical waters to Easter Island in the eastern South Pacific Ocean (Palma and Silva, 2006). *Bassia bassensis*, *Eudoxoides spiralis*, *Lensia companella*, and *L. subtilis* are typical oceanic species with wide geographic distributions. They appeared in the offshore waters of the study area and may indicate the intrusion of oceanic waters towards the nearshore zone in summer. Species of Group C could be used to indicate the movement of warm pelagic water into the nearshore region of Hainan Island during summer. The continental shelf east of the Leizhou Peninsula, which is broader than that along the southeast of Hainan Island, limits the mixing of oceanic and coastal waters, causing very low species richness (Fig. 7a). Across the southeast continental shelf of the

Hainan Island, the SCSWC is present all year. This holds high temperature and salinity water which supports the greater number of siphonophore species observed in this study.

4.3 Distribution of siphonophore abundance and coastal upwelling

The distribution of siphonophore abundance in summer is characterized by aggregation (Fig. 7b). High abundances (>100 ind./m³) were recorded mainly at stations within 50 m depth, where *Diphyes chamissonis*, *Nanomia bijuga*, and *Lensia subtiloides* (Group A1 species) were found in summer and spring. During summer, the nearshore region was covered by coastal upwelling waters due to the effect of the SW monsoon and the topography in the east and southeast of Hainan Island (Guan and Yuan, 2006; Jing et al., 2009). The presence of local upwelling might result in high Chl *a* and copepod abundance in the nearshore region (Fig. 5). High potential food availability would increase the abundance of siphonophores. The local distribution and abundance of siphonophores were found to be strongly influenced by upwelling off the Yucatan Peninsula and in the Mexican Caribbean Sea (Gasca and Suárez, 1991; Gasca, 1999). The abundances of Group A1 species were always higher nearshore than offshore in all three seasons because of their coastal intimacy (Fig. 8a). Although the abundances of Groups A2, B, and C species were higher in the offshore region during winter and spring, in summer they were all higher nearshore than offshore (Fig. 8b–d). Species of Groups A2, B, and C were transported from the offshore and pelagic waters into the nearshore zone. The abundance of these species was boosted by the high Chl *a* concentration and copepod abundance in the nearshore region, particularly in summer (Tables 1 and 3), in turn due to the local upwelling. Therefore, the abundances were more geography-related for Group A1 and more season-affected for Groups A2, B, and C.

During winter, the siphonophore abundance was less than 10 ind./m³ in the study area (Fig. 7b). Temperature and salinity were hydrographically homogeneous in winter, and species abundance showed little variation, indicating a degree of homogeneity in the siphonophore community.

5 CONCLUSION

The composition and abundance of siphonophores were closely linked to mesoscale hydrographic and

biological conditions in the nSCS. The nearshore region was characterized by moderately low diversity and high abundance of *Diphyes chamissonis*, *Nanomia bijuga*, and *Lensia subtiloides*, while high diversity and low abundance was typical of the offshore region. Our results suggest that spatial and temporal changes in the composition and distribution of the siphonophore community were due to the impact of ocean currents driven by the SW and NE monsoonal winds.

References

- Alvariño A. 1971. Siphonophores of the Pacific with a review of the world distribution. *Bull. Scripps Inst. Oceanogr.*, University of California Press. **16**: 1-432.
- Chen Q C. 1983. Siphonophores in the central and northern parts of the South China Sea. *In*: South China Sea Institute of Oceanology, Chinese Academy of Science ed. Contributions on Marine Biological Research of the South China Sea. China Ocean Press. p.7-16. (in Chinese)
- Chiang T L, Wu C R, Chao S R. 2008. Physical and geographical origins of the South China Sea Warm Current. *J. Geophys. Res.*, **113**: C08028, <http://dx.doi.org/10.1029/2008JC004794>.
- Clarke K R, Gorley R N. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Fan L Q, Su Y S, Li F Q. 1988. Analysis on water mass in the northern South China Sea. *Acta Oceanol. Sin.*, **10**: 136-145. (in Chinese with English abstract)
- Gao S W, Hong H Q, Zhang S M. 2002. Phylum Cnidaria. Science Press. p.1-275. (in Chinese)
- Gasca R, Suárez E. 1991. Siphonophores of upwelling areas of the Campeche Bank and the Mexican Caribbean Sea. *Hydrobiologia*, **216/217**: 419-502.
- Gasca R. 1999. Siphonophores (Cnidaria) and summer mesoscale features in the Gulf of Mexico. *Bull. Mar. Sci.*, **65**: 75-89.
- Gibbons M J, Thibault-Botha D. 2002. The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. *J. Mar. Biol. Ass. U.K.*, **82**: 801-810.
- Guan B X. 1978. The warm current in the South China Sea—A current flowing against the wind in winter in the open sea off Guangdong Province. *Oceanol. Limnol. Sin.*, **9**: 117-127. (in Chinese with English abstract)
- Guan B X. 1998. A review of study on the South China Sea Warm Current. *Oceanol. Lim. Sin.*, **29**: 322-329. (in Chinese with English abstract)
- Guan B X, Yuan Y C. 2006. Overview of studies on some eddies in the China Seas and their adjacent seas I. The South China Sea and the region east of Taiwan. *Acta Oceanol. Sin.*, **28**: 1-16. (in Chinese with English abstract)
- Hong H Q, Zhang S M. 1981. A preliminary study on the fauna of the siphonophores in the China sea. *J. Xiamen Fish. College*, **1**: 46-56. (in Chinese with English abstract)
- Huang Q Z, Wang W Z, Li Y S, Li C W, Mao M. 1992. General situations of the current and eddy in the South China Sea. *Advance Earth Sci.*, **7**: 1-9. (in Chinese with English abstract)
- Jing Z Y, Qi Y Q, Hua Z L, Zhang H. 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, Liu C. 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. (in Chinese)
- Li K Z, Yin J Q, Huang L M, Lian, S M, Zhang J L, Liu C G. 2010. Monsoon-forced distribution and assemblages of appendicularians in the northwestern coastal waters of South China Sea. *Estuarine, Coastal Shelf Sci.*, **89**: 145-153.
- Li K Z, Yin J Q, Huang L M, Lian S M, Zhang J L, Liu C M. 2010. Distribution and abundance of thaliaceans in the northwest continental shelf of the South China Sea, with response to environmental factors driven by monsoon. *Cont. Shelf Res.*, **31**: 979-989.
- Li L. 2002. Advance in observational studies of upper layer circulations of South China Sea. *J. Oceanogr. Taiwan Strait*, **21**: 114-125. (in Chinese with English abstract)
- Li L, Wu R S, Guo X G. 2000. Seasonal circulation in the South China Sea—a TOPEX/POSEIDON satellite altimetry study. *Acta Oceanol. Sin.*, **22**: 13-26. (in Chinese with English abstract)
- Lin M. 1992. Primary study on siphonophores in the central South China Sea. *Acta Oceanol. Sin.*, **14**: 99-105. (in Chinese)
- Mackie G O, Pugh P R, Purcell J E. 1987. Siphonophore biology. *Advances in Mar. Biol.*, **24**: 97-262.
- Omori M, Ikeda T. 1984. Methods in Marine Zooplankton Ecology. Wiley, New York. p.332.
- Pagès F, González H E, Ramón M, Sobarzo M, Gili J M. 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). *Mar. Ecol. Prog. Ser.*, **210**: 13-24.
- Palma S, Silva N. 2006. Epipelagic siphonophore assemblages associated with water masses along a transect between Chile and Easter Island (eastern South Pacific Ocean). *J. Plankton Res.*, **28**: 1 143-1 151.
- Parsons T R, Maita Y, Lalli C M. 1984. A Manual of Chemical and Biological Methods for Seawater Analyses. Pergamon Press, Oxford. p.173.
- Pugh P R. 1999. Siphonophorae. *In*: Boltovskoy D ed. South Atlantic Zooplankton. Backhuys Publishers. Leiden. p.467-511.
- Sanvicente-Añorve L, Alba C, Alatorre M A, Flores-Coto C. 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.
- Shannon C E, Weaver W. 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, p.144.

- 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**: 1 745-1 760.
- Thibault-Botha D, Lutjeharms J R E, Gibbons M J. 2004. Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. *J. Plankton Res.*, **26**: 1 115-1 128.
- Wang D X, Hong B, Gan J P, Xu H Z. 2010. Numerical investigation on propulsion of the counter-wind current in the northern South China Sea in winter. *Deep-Sea Res. I*, **57**: 1 206-1 221.
- Wu R S, 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)
- Xu Z L, Zhang J B, Jiang M. 2003. Ecological study on Siphonophora in the East China Sea. *J. Fish. China*, **27**(Suppl.): 82-90. (in Chinese with English abstract)
- Yang S Y, Bao X W, Chen C S, Chen F. 2003. Analysis on characteristics and mechanism of current system in west coast of Guangdong Province in the summer. *Acta Oceanol. Sin.*, **25**: 1-8. (in Chinese with English abstract)
- Yin J Q, Huang L M, Li K Z, Lian S M, Li C L, Lin Q. 2011. Abundance distribution and seasonal variations of *Calanus sinicus* (Copepoda: Calanoida) in the northwest continental shelf of South China Sea. *Cont. Shelf Res.*, **31**: 1 447-1 456.
- Zhang W C, Tang D L, Yang B, Gao S W, Sun J, Tao Z C, Sun S, Ning X R. 2009. Onshore-offshore variations of copepod community in northern South China Sea. *Hydrobiologia*, **636**: 257-269.
- Zhang J B, Lin M. 1997. The ecogeography of siphonophores in the South China Sea. *Acta Oceanolog. Sin.*, **19**: 121-131. (in Chinese with English abstract)
- Zhang J B. 2005. Pelagic Siphonophora in China Sea. Ocean Press, Beijing. p.1-151. (in Chinese)