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Seasonal and spatial distribution of chaetognaths on the north-west continental shelf of the South China Sea

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The seasonal variation and spatial distribution of chaetognaths were studied based on samples collected from July to August 2006 (summer), December 2006 to January 2007 (winter), and in April 2007 (spring) on the north-west continental shelf of the South China Sea. A total of 19 species of chaetognaths were identified. The average chaetognath abundances (mean ±SD) were 54.0 ± 44.5, 36.8 ±16.7 and 48.9 ± 95.5 ind. m^{-3} in summer, winter and spring, respectively. Flaccisagitta enflata *and* Serratosagitta pacifica *were the dominant species during the whole sampling period, and* F. enflata *determined the spatial distribution of total chaetognath abundance. According to the topography and hydrological conditions, the survey area was divided into three sub-regions: inshore waters of the western Guangdong (Region I), inshore waters to the east of Hainan Island (Region II) and offshore waters from the western Guangdong to Hainan Island (Region III). The community structure and abundance distribution of chaetognaths varied significantly between the three sub-regions. The species richness was significantly different among the three sub-regions, with the lowest in Region I and the highest in Region III. The species richness was correlated positively with temperature and salinity. The abundance of chaetognaths was significantly higher in Region I than in both Regions II and III in summer and spring. The increasing food availability caused by the cold eddy, coastal upwelling and the western Guangdong coastal current was able support a greater abundance of chaetognaths during warm seasons on the north-west continental shelf of the South China Sea.*

Keywords: Chaetognatha, community structure, cold eddy, coastal upwelling, South China Sea, continental shelf

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INTRODUCTION

Although small-sized (2–120 mm), chaetognaths are often abundant and an important component in ocean biomass (up to 30% of the biomass of copepods in the global oceans (Reeve, 1970)). Chaetognaths often compose the second most abundant mesozooplanktonic group after copepods in the zooplankton of marine environments (Feigenbaum & Maris, 1984; Shannon & Pillar, 1986; Gibbons, 1992). The exact position of chaetognaths remains uncertain for genomic data show affinities of chaetognaths to protostomes and yet chaetognaths show features of deuterostome-like embryology (Marlétaz *et al.*, 2006). Classical taxonomy divides chaetognaths into nine genera and about 110 species (Tokioka, 1965). After Tokioka, Bieri (1991) divided the genus *Sagitta* into 14 new genera and recognized 23 genera and 113 species. In this paper we are following Bieri's classification.

Chaetognaths can be found in all kinds of marine habitats and play important roles in the food webs (Bone *et al.*, 1991). In pelagic waters they are predators mainly of copepods, whereas in benthopelagic layers they are detritus feeders (Casanova, 1986). Their position in the pelagic food web makes them important controllers of energy flow to higher consumers, including several species of commercial fish (Kimmerer, 1984; Baier & Purcell, 1997), and they are thus considered a good indicator of potentially important fishery areas (Boltovskoy, 1981).

Like other zooplankton organisms, chaetognaths are subjected to dispersion and changing physical–chemical conditions of the water (e.g. salinity, temperature and dissolved oxygen) (Ulloa *et al.*, 2000). Furthermore, several species of chaetognaths are strongly related to specific water masses (Ulloa *et al.*, 2000), and thus are very useful as indicators of water mass movements (Russell, 1935, 1936, 1937; Mulkana & Mcllwain, 1973; Cheney, 1985; Pierrot-Bults, 2008). Chaetognaths appear to be suitable for the study of the effects of physical processes acting at the mesoscale on the dynamics and variability of zooplankton populations (Duró & Saiz, 2000).

Composition, spatial and temporal variations of Chaetognatha have been carried out all around the world (e.g. Bieri, 1959; Terazaki, 1989; Kruse *et al*, 2009; Bohata & Koppelmann, 2013). Although several previous studies have dealt with the species distribution of chaetognaths in the South China Sea (SCS) (e.g. Zhang & Chen, 1991; Du *et al.*, 2003; Tse, 2007; Lin *et al.*, 2010), there is little information on their distribution on the north-west continental shelf of the SCS, where mesoscale physical processes are determining factors. The present study is the first effort to determine how the monsoon affects the species composition, distribution and abundance, as well as the main assemblages of chaetognaths

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on the north-west continental shelf of the SCS during summer, winter and spring. Our hypothesis is that the density of chaetognaths is higher on the north-west continental shelf of the SCS than in the other regions of China as a result of greater food supply.

MATERIALS AND METHODS

Study area

The SCS is a large semi-enclosed marginal sea in the north-west Pacific Ocean with a total area of 3.5 million km². Liu found 41 species of chaetognaths belonging to 17 genera in oceanic waters around China (2008). Only *Aidanosagitta crassa* and *A. umida* could not be found in the SCS. The SCS is generally recognized as having the greatest diversity and density of chaetognaths in China's seas (Xiao, 2004). The surveyed region is located in the north-western SCS (17°17.10′–21°25.62′N 109°28.74′–113°13.26′E), which is affected by the Guangdong coastal current (GCC), the Qiongdong coastal upwelling, cyclonic circulation and the SCS warm current (Figure 1). Its main feature is a broad continental shelf with depths less than 200 m, while the east and south-east coasts of Hainan Island run parallel to the continental slope with a maximum depth of 1900 m. The climate in the SCS is dominated by the East Asian Monsoon system. In winter the north-east monsoon prevails in the SCS, whereas in summer the winds reverse direction to south-west (Su, 2004).

The GCC is under the combined influence of the East Asia Monsoon and the Pearl River. Due to the large discharge of the Pearl River in summer, the GCC flows south-westerly around the east coast of the Leizhou Peninsula. The SCS surface current flows north-easterly, driven by the south-west monsoon. The current flows north-eastward, impacted by the south-west monsoon on the eastern side of Guangzhou Bay, whereas on the western side of Guangzhou Bay, it flows south-westward. Hence, a cold eddy is formed along the eastern waters of the Leizhou Peninsula (20°20′–21°10′N 110°50′–112°00′E) (Huang *et al.*, 1992). The cold eddy exists all year and varies seasonally, from strong in summer to weak in winter. Factors including the south-west monsoon and bottom topography can cause intense upwelling during the summer in the eastern waters of Hainan Island (Jing *et al.*, 2009; Su & Pohlmmann, 2009). The Qiongdong upwelling near the coast is concentrated between 18°30′–20°30′N and 110°–111°30′E, located within 30 m water depth. The upwelling lasts about 150 d, from April to October and peaks from June to August. There is a consistent north-eastward SCS warm current located in the east of the survey areas (Guan, 1998).

We divided the surveyed region into three sub-regions based on the different topography and hydrological conditions (Figure 2): Region I (inshore waters of the western Guangdong); Region II (inshore waters to the east of Hainan Island); and Region III (offshore waters from the western Guangdong to Hainan Island). Region I (with water depth <50 m) is influenced by the Pearl River discharge and coastal mixing water. Region II is under the influence of the SCS surface water throughout the year, and is affected by upwelling in summer and by the GCC in spring and winter, with water depths greater than 100 m. Region III ranging in depth from 56 m to 1980 m is controlled by the SCS surface water all year (Li, 2002).

Field sampling

The study was conducted during three different periods: July–August 2006 (summer); December 2006–January 2007 (winter); and April 2007 (spring). Zooplankton samples were taken at 82 stations along 13 transects (Figure 2). Zooplankton was sampled by vertical tows from 1 m above the bottom (depth <200 m) or from 200 m (depth >200 m) to the surface using plankton net of 169 μm mesh size (mouth diameter: 0.5 m) and plankton net of 505 μm mesh size (mouth diameter: 0.5 m). In this paper most data are based on the samples obtained with the 169 μm net (mouth diameter: 0.5 m). The net opening was fitted with a flow meter to determine the volume of water filtered during each tow (unit: m³). Trawl winch speed was about 1 m.s^{-1}. Samples were fixed immediately after collection and preserved

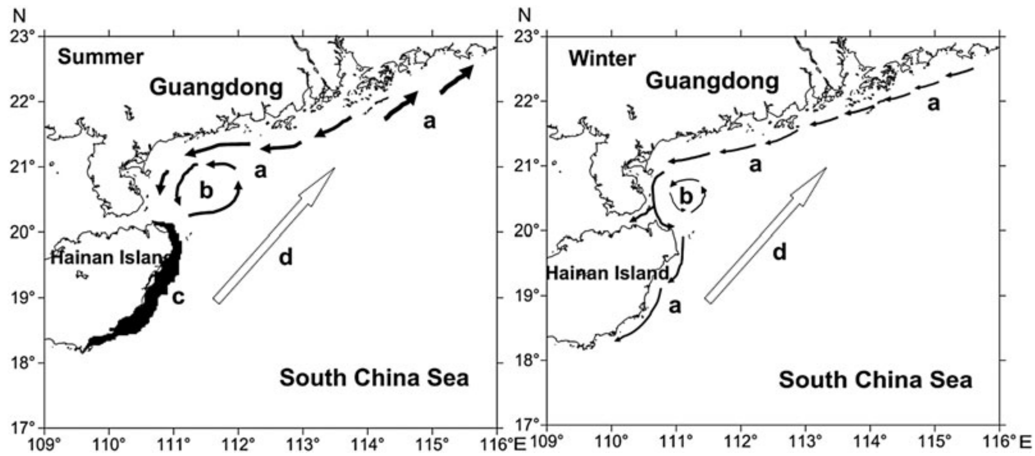

Fig. 1. Ocean currents diagrams of the north-west continental shelf of the South China Sea (SCS): (A) the Guangdong coastal current; (B) cyclonic circulation; (C) the Qiongdong coastal upwelling; (D) the SCS warm current (from Li *et al.*, 2010).

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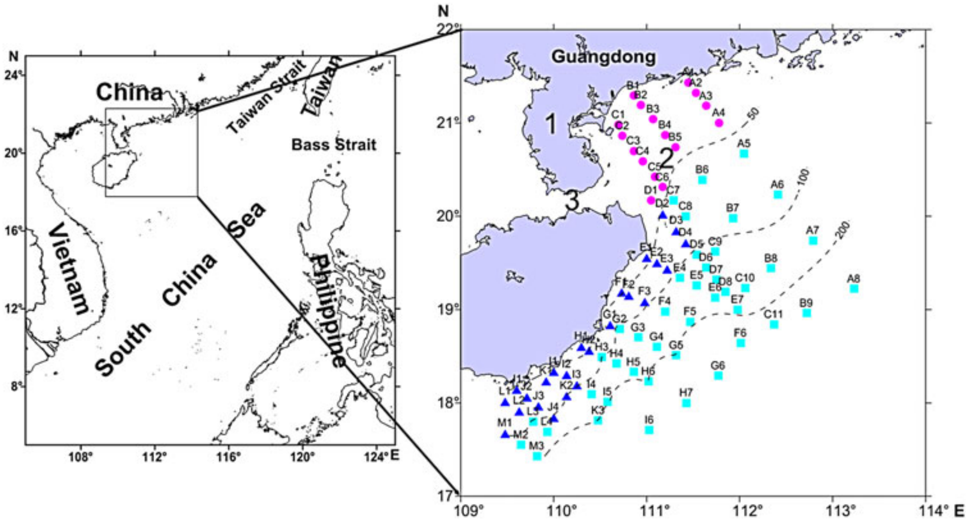

Fig. 2. Map of the north-west continental shelf of the South China Sea showing the sampling locations. 1, the Leizhou Peninsula; 2, Guangzhou Bay; 3, the Qiongzhou Strait. Region I has 16 stations, shown as circles; Region II has 24 stations, shown as triangles; Region III has 42 stations, shown as squares (Li *et al*., 2011).

in 5% formaldehyde solution. All chaetognaths were sorted from the samples and identified to species level according to Xiao (2004); copepods were also counted. Chaetognaths were classified into larvae, which contain no visible reproductive organs, and adults, which contain developing or mature reproductive organs. Most of the larvae could not be assigned to a species, so were counted as larvae. The counts of all species were converted to densities per m^3 of water sampled (ind. m^{-3}). Water temperature and salinity were measured by a CTD on-board.

Data analyses

The dominance indicator was estimated by use of Xu's equitability (Y) (Xu & Chen, 1989):

$$Y = \frac{n_i}{N} f_i,$$

in which, n_i is the abundance of the species i, f_i is the occurrence frequency (the number of the stations with species i/the number of total stations) of species i, N is the total abundance. A species was defined as dominant when $Y \geq 0.02$.

A one-way ANOVA on ranks test was used to test for significant differences between the three regions and between different seasons. Bivariate correlation was used to determine the relationship between chaetognath and environmental factors. All statistical analyses were performed using SPSS software.

RESULTS

Hydrography

The average surface temperature was higher in summer (28.34 $\pm$3.24°C) than winter (22.95 $\pm$1.54°C) and spring (25.32 $\pm$2.06°C). The surface temperatures differed significantly between seasons ($F = 129.38$, $P < 0.001$), ranging from 23.71 to 30.74°C, 18.77 to 25.27°C and 20.73 to 28.79°C in summer, winter and spring, respectively. The distribution of surface temperature was uneven, with lower values normally found in the intersection between Guangzhou Bay and the east mouth of the Qiongzhou Strait, where the cold ring was located (Figure 3A). During the summer, surface temperature of offshore waters was generally higher than inshore waters. The distribution of temperature in winter and spring showed a gradual increase corresponding to the latitude (Figure 3C, E).

The average salinity in the surface layer was 33.95 ($\pm$0.26), 33.72 ($\pm$0.57) and 34.01 ($\pm$0.57) in summer, winter and spring, respectively. The maximum (34.78) and the minimum (31.51) of salinity were in spring. Salinity was higher in offshore waters than in inshore waters (Figure 3B, D, F). Differences in salinity between seasons was significant ($F = 10.05$, $P < 0.001$).

Copepods

Average density (means $\pm$SD) of copepods in summer (1675.39 $\pm$1904.43 ind. m^{-3}) was significantly higher than winter (916 $\pm$643.04 ind. m^{-3}) and spring (815.68 $\pm$994.13 ind. m^{-3}) with significance $P < 0.001$. Difference of density of copepods among three regions was relatively more distinct in summer ($P < 0.001$) and spring ($P < 0.001$) than in winter ($P < 0.05$). During three seasons, the distribution of the density of copepods showed a same trend: highest in Region I and lowest in Region III (Figure 4A–C). All maximum density in three seasons was found in Region I.

Species composition

In total nineteen chaetognath species were identified in this study (Table 1), with 18 species occurring in summer, 16 species in winter, and 17 species in spring. *Aidanosagitta delicata* and *A. johorensis* were found exclusively in summer, while *Mesosagitta decipiens* was found only in spring. The specific composition displayed no clear seasonal changes. *Flaccisagitta enflata* was the most abundant and

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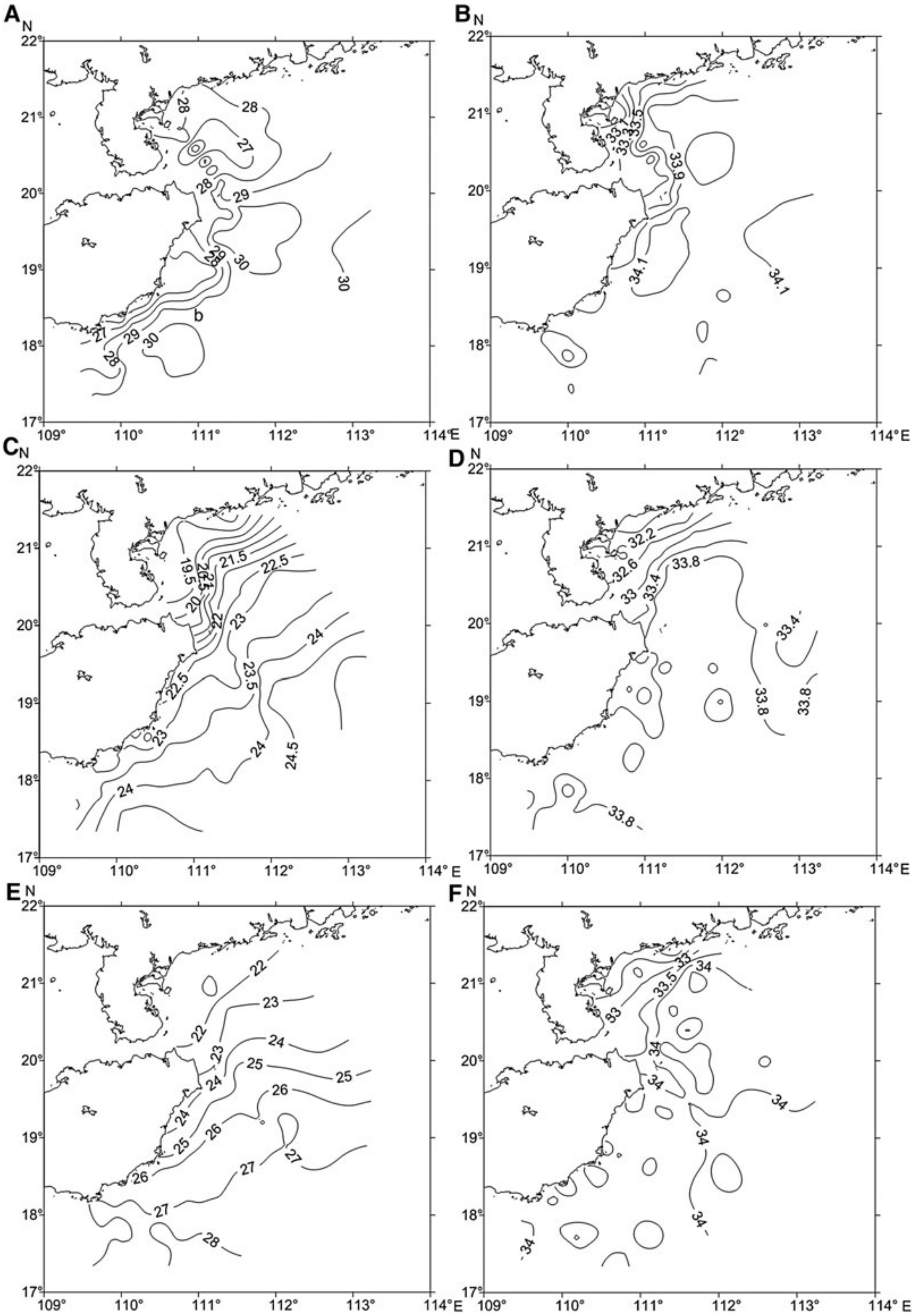

Fig. 3. Distribution of surface temperature (°C) and surface salinity in the north-western coastal waters of the South China Sea: left column = temperature; right column = salinity; row 1 = summer; row 2 = winter; row 3 = spring.

frequent species. This species was distributed throughout the study area and was the most abundant in all study areas. *F. enflata*, *Mesosagitta Minima* and *Serratosagitta pacifica* occurred with a frequency of more than 80% in summer and winter, respectively; as did *F. enflata*, *A. regularis*, *Ferosagitta ferox* and *S. pacifica* in spring. The frequency of occurrence of chaetognath larvae was higher in summer and winter than in spring (Table 1).

All species were divided into three groups according to their distribution and ecological characteristics: (1) warm water euryhaline species were the most widely distributed, with high densities, and found from high salinity offshore waters to low salinity coastal waters; (2) pelagic warm water species were typical tropical oceanic species found in high temperatures and at high salinity; and (3) warm water coastal species found in low densities in high temperatures and in low salinity waters (Du *et al.*, 2004). The

Table 1. The occurrence and average density (ind. m^{-3}) of chaetognaths on the north west continental shelf of the South China Sea during three seasons.

	Summer		Winter		Spring	
Species	Occurrence (%)	Density (ind. m^{-3})	Occurrence (%)	Density (ind. m^{-3})	Occurrence (%)	Density (ind. m^{-3})
Aidanosagitta bedfordii	2.44	<0.1	1.22	<0.1	1.22	<0.1
Aidanosagitta bipunctata	12.20	0.1 ± 5.8	3.66	<0.1	14.63	0.9 ± 5.0
Aidanosagitta delicata	7.32	1.2 ± 0.3	6.10	<0.1	6.10	<0.1
Aidanosagitta johorensis	2.44	0.1 ± 2.9	6.10	<0.1	7.32	<0.1
Aidanosagitta neglecta	28.05	0.5 ± 0.2	42.68	1.8 ± 4.4	4.88	<0.1
Aidanosagitta regularis	75.62	2.1 ± 4.1	85.37	3.1 ± 2.8	70.73	0.9 ± 1.1
Decipisagitta decipiens	—	—	—	—	1.22	<0.1
Ferosagitta ferox	73.17	1.1 ± 4.7	84.15	0.8 ± 0.8	91.46	1.8 ± 4.0
Ferosagitta robusta	19.52	<0.1	21.95	0.1 ± 0.2	21.95	0.1 ± 0.2
Flaccisagitta enflata	100	25.7 ± 0.3	100	13.6 ± 8.0	96.34	29.2 ± 86.2
Flaccisagitta hexaptera	18.29	<0.1	9.76	<0.1	19.51	<0.1
Krohnitta pacifica	67.07	1.1 ± 12.5	73.17	1.2 ± 2.0	24.39	0.1 ± 0.3
Krohnitta subtilis	25.61	0.1 ± 0.0	2.44	<0.1	15.85	<0.1
Mesosagitta minima	87.80	6.9 ± 10.9	32.93	0.3 ± 0.5	57.32	2.5 ± 6.1
Pseudosagitta lyra	13.41	0.1 ± 0.9	1.22	<0.1	29.27	1.5 ± 6.9
Pterosagitta draco	75.61	1.3 ± 1.2	68.29	1.1 ± 1.4	54.88	0.8 ± 2.0
Serratosagitta pacifica	84.15	3.3 ± 5.0	82.93	9.3 ± 8.4	92.68	8.4 ± 8.7
Zonosagitta bedoti	31.71	1.6 ± 0.3	32.93	0.6 ± 1.4	29.27	0.7 ± 1.7
Zonosagitta pulchra	10.98	<0.1	48.78	0.3 ± 0.8	10.98	<0.1
Larvae	87.80	8.6 ± 0.2	87.80	4.6 ± 8.3	37.80	1.9 ± 6.6

—, no occurrence. Occurrence = frequency of occurrence/82 (the station number).

ecological characteristics of chaetognaths were different among the regions. Warm water coastal species like *Zonosagitta bedoti, Aidanosagitta neglecta* and *A. delicata* were important species in terms of abundance throughout Region I. Low temperature and low salinity were the limiting factors for the oceanic warm-water species (Table 2). In addition, *Serratosagitta pacifica*, *Mesosagitta minima*, *Pterosagitta draco*, *Flaccisagitta hexaptera*, *Pseudosagitta lyra* and *Krohnitta subtilis* were oceanic warm water species that were recognized as offshore water indicator species. Warm water euryhaline species (*F. enflata*, *A. regularis*, *Ferosagitta ferox*) occurred in all three regions.

Distribution of species richness

The number of species was higher in Region III than in Region II; Region I had the lowest in all three seasons (Figure 5A). Species richness was higher in summer than in winter; species richness was lowest in all three regions in spring. Region III in summer had the highest number of species (10) while Region I in spring had the lowest species richness (4). Noteworthy is the detection of *Zonosagitta nagae* when using plankton nets of 505 μm mesh size (mouth diameter: 0.5 m) in summer in Region I.

The seasonal variation of species richness was rather remarkable ($F = 21.395$, $P < 0.001$) (Figure 5A). There were clear differences in species richness among the three regions in summer ($F = 34.912$, $P < 0.001$), spring ($F = 43.853$, $P < 0.001$) and winter ($F = 29.221$, $P < 0.001$). There were significant differences between seasons in the distribution pattern of the species richness ($F = 9.921$, $P < 0.001$). Species richness was positively correlated with temperature and salinity (Table 2). Overall, Region III supported significantly more chaetognath species richness than Regions I and II ($P < 0.01$).

Distribution of species abundance

The average chaetognath abundances were 54.0 ±44.5, 36.8 ±16.7 and 48.9 ±95.5 ind. m^{-3} in summer, winter and spring, respectively. The abundance of chaetognaths was obviously higher in inshore waters than offshore waters during all three seasons (Figure 4D–F). During summer, there was an area of high abundance (>100 ind. m^{-3}) in the eastern

Table 2. Correlations between biological indices of chaetognaths and environmental factors in the South China Sea.

	Summer			Winter			Spring		
Variables	Temperature	Salinity	Copepod abundance	Temperature	Salinity	Copepod abundance	Temperature	Salinity	Copepod abundance
Richness	0.470**	0.426**	−0.599**	0.625**	0.590**	−0.191$^{n.s.}$	0.622**	0.267*	−0.391**
Density	−0.158$^{n.s.}$	−0.549**	0.776**	−0.196$^{n.s.}$	0.022$^{n.s.}$	0.407*	−0.496**	−0.727**	0.590*
Flaccisagitta enflata	−0.247*	−0.558**	0.751**	−0.369**	−0.231*	0.451**	−0.510**	−0.727**	0.545**
Serratosagitta pacifica	0.316**	0.173$^{n.s.}$	−0.220*	0.425**	0.393**	−0.121$^{n.s.}$	0.206$^{n.s.}$	0.169$^{n.s.}$	0.150$^{n.s.}$

$^{n.s.}P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$.

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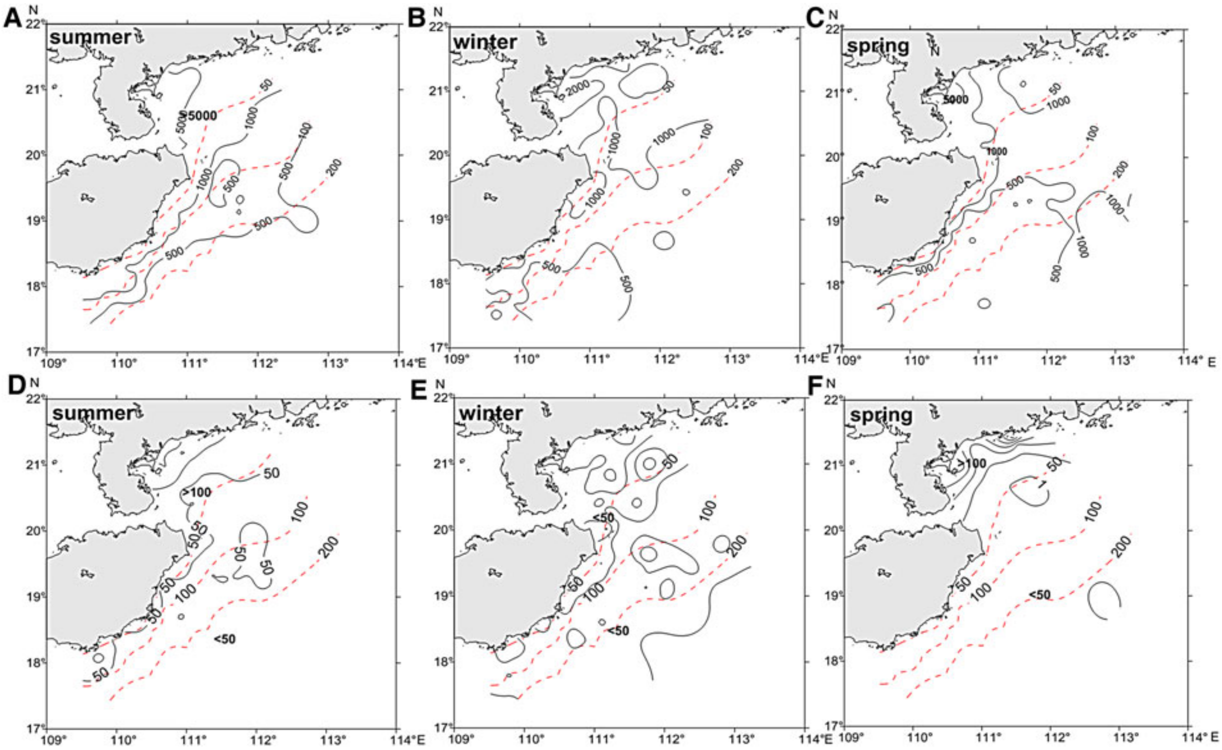

Fig. 4. Distribution of copepod abundance (upper row) (ind. m^{-3}) and chaetognath abundance (lower row) (ind. m^{-3}) on the north-west continental shelf of the South China Sea.

coastal water of the Leizhou Peninsula. At water depths of 0–50 m their abundance was higher than 50 ind. m^{-3}, while fewer than 50 ind. m^{-3} were detected at depths greater than 50 m (Figure 4D). A high abundance area (>50 ind. m^{-3}) in winter was located in the east mouth of Qiongzhou Strait and the eastern coastal waters of Leizhou Peninsula. The abundance during the spring peaked in the eastern coastal waters of Leizhou Peninsula (>100 ind. m^{-3}; Figure 4F). The lowest abundance was found in the eastern offshore water of the Leizhou Peninsula and some patches south-east of Hainan Island in winter (Figure 4E). The differences in densities among the seasons were less marked and not statistically significant ($F = 1.694$, $P = 0.186$). Chaetognaths abundance was significantly correlated with copepod abundance at the level of 0.01 in all three seasons (Table 2).

Dominant species

Flaccisagitta enflata had the highest dominance of the species overall during all cruises. *Flaccisagitta enflata* determined the horizontal distribution of chaetognaths (Table 3). *Serratosagitta pacifica* also was a dominant species in all three seasons. In addition, *Mesosagitta minima* and *Ferosagitta ferox* were present in fair numbers in spring and summer, while *Aidanosagitta regularis* and *Pterosagitta draco* were quite abundant in summer and winter, respectively (Table 3).

Flaccisagitta enflata was the most dominant species, with mean densities of 25.7 (±0.3), 13.6 (±8.0) and 29.2 (±86.2) ind. m^{-3}, which represented 47.63%, 36.88% and 59.73% of the total chaetognath abundances in summer, winter and spring, respectively. *Flaccisagitta enflata* displayed no clear seasonal pattern of occurrence, although populations were denser during summer and spring than in winter (Figure 5C). Similar patterns of distribution of *F. enflata* were found in summer and spring: (1) the abundance peaked (as high as 100 ind. m^{-3}) in the east coastal waters of the Leizhou Peninsula; (2) their abundance was around 50 ind. m^{-3} where depths were less than 50 m; and (3) low densities ranged from 5 to 10 ind. m^{-3} in both Regions II and III. During spring, a low abundance was found in the eastern water of the Leizhou Peninsula where water depth is 50 m. The abundances were generally low (about 10 ind. m^{-3}) in winter. The abundance of *F. enflata* was obviously higher in inshore waters than offshore waters in summer

Table 3. Dominance and percentage of total abundance of dominant species of chaetognaths during three seasons in the South China Sea.

Season	Species	Dominance	Percentage (%)
Summer	*Flaccisagitta enflata*	0.476	47.63
	Larvae	0.140	15.96
	Mesosagitta minima	0.112	12.81
	Serratosagitta pacifica	0.051	6.02
	Aidanosagitta regularis	0.029	3.87
Winter	*F. enflata*	0.369	36.88
	S. pacifica	0.209	25.22
	Larvae	0.110	12.56
	A. regularis	0.073	8.55
	Krohnitta pacifica	0.024	3.35
	Aidanosagitta neglecta	0.021	4.97
	Pterosagitta draco	0.021	3.06
Spring	*F. enflata*	0.575	59.73
	S. pacifica	0.159	17.16
	Ferosagitta ferox	0.034	3.71
	M. minima	0.029	5.05

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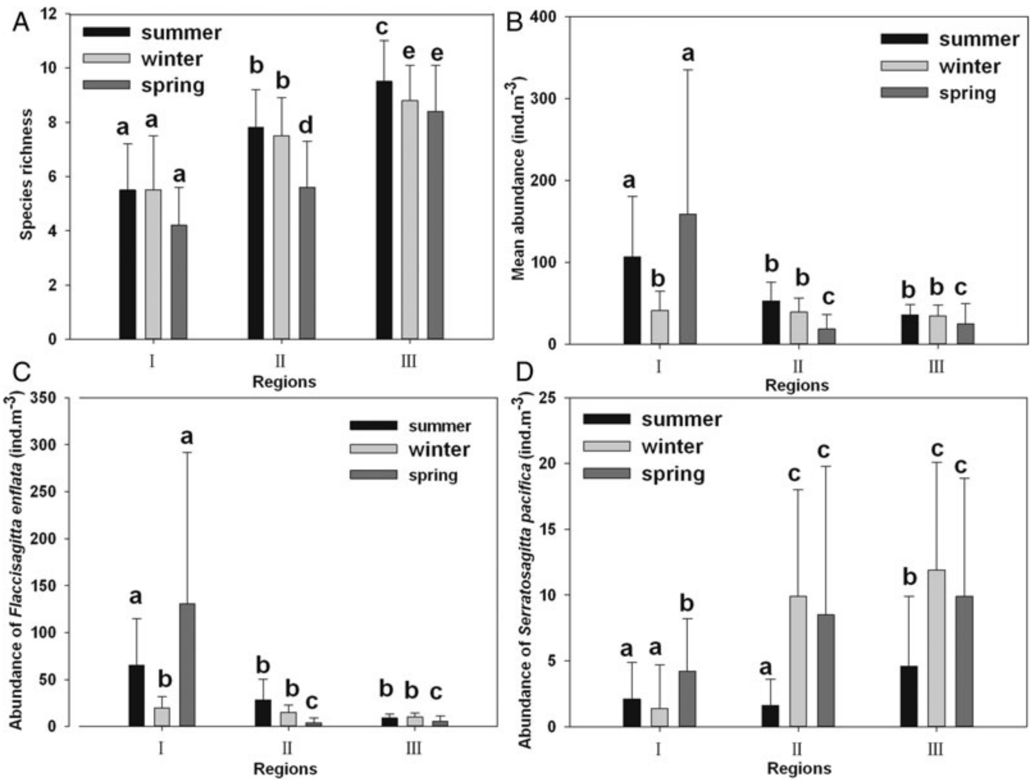

Fig. 5. Variations of species richness and abundance of chaetognaths at three sub-regions of the South China Sea in three seasons: (A) mean species richness; (B) mean total chaetognath abundance; (C) *Flaccisagitta enflata* abundance; (D) *Serratosagitta pacifica* abundance. Error bars represent SD. Columns denoted by different letters are significantly different from each other (ANOVA, $P < 0.05$).

and spring ($P < 0.001$), while it showed no difference in winter between inshore waters and offshore waters ($P > 0.05$). Abundances of *F. enflata* were negatively correlated with temperature ($P < 0.05$) and salinity ($P < 0.01$) (Table 2).

Serratosagitta pacifica was second to *F. enflata* in terms of relative abundance with densities of 3.3 ± 5.0, 9.3 ± 8.4 and 8.4 ± 8.7 ind. m^{-3} in summer, winter and spring, respectively. *S. pacifica* displayed obvious seasonal occurrence ($P < 0.001$). It showed different patterns from *F. enflata* in horizontal distribution: abundance in winter was higher offshore, but inshore during summer. During spring, the abundance increased with distance from the coast, from 5 ind. m^{-3} where the depth was 50 m, to 10 ind. m^{-3} where the depth was 200 m. Their abundance during summer was higher in Region III than in the other two regions ($P < 0.01$), but abundances did not differ significantly among the three regions in winter ($P > 0.05$) (Figure 5D). In the spring, Region II had the highest abundance of *S. pacifica* ($P < 0.01$) (Figure 5D). *S. pacifica* is a very close relative of *F. enflata* that more or less replaces it in winter. *S. pacifica* showed no clear relationships with environmental or biological factors (Table 2).

DISCUSSION

Influence of environmental factors on species distribution

Most species detected in the study prefer warm water (Dai, 1995; Lin *et al.*, 2010). The species richness of chaetognaths was markedly higher in the tropical and sub-tropical waters of the SCS and the East China Sea than in the temperate waters of the Bohai Sea and the Yellow Sea. The numbers of species recorded in the Bohai Sea, the Yellow Sea and the East China Sea were 4, 14 and 31, respectively. The SCS, with 38 species, had the highest species richness (Xiao, 2004).

Environmental parameters play an important role in the dynamics of plankton communities. Different hydrographic conditions affected the distribution patterns of the various species of chaetognaths. Due to the combined effects of the Guangdong coastal current (GCC), inshore mixing water masses and the cold eddy, Region I has characteristics of low temperature and low salinity. The south-west monsoon and bottom topography can cause intense upwelling in Region II, which lasts from April to October. Therefore, a higher density of copepods was found in Region II in summer and spring (April). In contrast, the offshore waters are controlled by surface water of the SCS and affected by the SCS warm current, which is stronger in winter due to the north-east monsoon. So the offshore waters have characteristics of high temperature and high salinity (Wang *et al.*, 2010) and the number of dominant species was higher in winter than summer and spring (Table 3). Table 2 shows that species richness was positively correlated with temperature and salinity. The effect of the SCS warm current on the species richness of thaliaceans is in agreement with this result (Li *et al.*, 2011).

During the summer cruise we sampled *Zonosagitta nagae* when using plankton nets of 505 μm mesh size (mouth diameter: 0.5 m). *Zonosagitta nagae* was often found in temperate coastal waters throughout the Yellow Sea and the East China Sea (Lin, 1982). In the East China Sea, it occurs in high abundances, second to that of *F. enflata* (Xu & Chen, 2005). The occurrence of *Z. nagae* may indicate the presence of lasting

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intensification of the Pearl River dilute waters in summer, which enhanced the GCC in the west of Guangdong Province. Therefore, the chaetognaths probably were transported from higher latitude. Temperature was a major factor influencing the distribution range of *Z. nagae*, which was restricted to summer and is probably related to the existence of the cold vortex. Therefore it can be regarded as a cold eddy indicator in the sampled region.

Influence of environmental factors on abundance distribution

The density of chaetognaths of the north-west continental shelf of the SCS was not only higher than reported for other areas in China's seas (Dai, 1989, 1995; Zhang & Chen, 1991; Du *et al.*, 2003, 2004; Xu *et al.*, 2004), but also greater than other regions in the world: 5.6–74.9 ind. m^{-3} from 0–25 m in the Sargasso Sea in the tropical Atlantic (Pierrot-Bults & Nair, 2010), 6.9–9.8 ind. m^{-3} in the Algerian Basin of the western Mediterranean Sea (Riandey *et al.*, 2005) and 2.6–17.3 ind. m^{-3} in the Australian sector of the Southern Ocean (Makoto, 1989). The marine mesozooplankton on the north-west continental shelf of the SCS is dominated by copepods. The abundance of copepods was about two to three times higher in inshore waters than in offshore waters. The high abundance of chaetognaths on the north-west continental shelf of the SCS may result from favourable food conditions for herbivorous copepods, which are preyed on by chaetognaths (Ramírez-Ávila & Álvarez-Cadena, 1999).

The combined effects of the cold eddy, upwelling and the appropriate temperature and salinity in spring and summer produced a high food supply in Region I which was closely followed by high densities of chaetognaths (Figure 4). The abundances of chaetognaths and copepods were significantly correlated (Table 2). Differences of abundance among the three regions in winter were less clear due to the north-east monsoon. In addition, upwelling still occurred to the east of Hainan Island in summer. High primary production and secondary production supported high densities of chaetognaths, which were distributed in patches (Figure 4).

Influence of environmental factors on dominant species

Flaccisagitta enflata and *Serratosagitta pacifica* were the two most abundant species during summer, winter and spring, and showed no seasonal variation in the stable conditions. *Flaccisagitta enflata* is an epiplanktonic, temperate and warm water species (Alvariño, 1965; Andréu, 1992) with a wide distribution in the Indian, Atlantic and Pacifica Oceans (Pierrot-Bults & Nair, 1991), and found over relatively broad temperature and salinity ranges (Xiao, 2004). *Flaccisagitta enflata* is also the most abundant species in this study and also one of the most abundant species in the Bohai Sea, the Yellow Sea and the East China Sea (Du *et al.*, 2003). Changes in the distribution and abundance of *F. enflata* have very important effects on distribution of total chaetognaths (Du *et al.*, 2003). A 505 μm mesh size plankton net (mouth diameter: 0.5 m) yielded higher abundances (14.1 ind. m^{-3}) of *F. enflata* in the surveyed region than reports for other areas in China's seas. For example, the abundance of *F. enflata* was 3.58 ind. m^{-3} in the Beibu Gulf (Sun, 1989), 11.67 ind. m^{-3} in the Taiwan Strait (Dai, 1989), with seasonal average abundances of 3.98, 5.52, 4.46 ind. m^{-3} in the Nansha Islands (Lin *et al.*, 2010). In addition, the density is also higher than reported in other regions: 1–7 ind. m^{-3} recorded in the neritic region of the Agulhas Current (Stone, 1969), 13–33 ind. m^{-3} recorded in the North Atlantic (Baier and Purcell, 1997) and 17–31 ind. m^{-3} recorded in the Indian Ocean (Øreslan, 2000).

In our study, chaetognath abundance in Region I (>50 ind. m^{-3}) was higher than in the other two regions because of its lower temperature, low salinity and more abundant food. The abundance of *F. enflata* was negatively correlated with temperature and salinity, but positively correlated with copepod abundance. *Flaccisagitta enflata* occurred where the waters or currents meet (Hong *et al.*, 1991), indicating interactions between coastal and offshore waters. During the summer, Region I experiences the confluence of a large volume of Pearl River discharge, a strong GCC and offshore water—another reason why *F. enflata* abundance is higher in Region I than in other regions. In contrast, there were no clear differences between regions in winter because decreased Pearl River discharge rates result in SCS warm current dominance in all three regions.

Serratosagitta pacifica occurs in relatively wide temperature ranges and high salinity. Its high abundance is mainly limited by salinity (Sun, 1989). *Serratosagitta pacifica* is generally regarded as a good indicator of offshore water in inshore regions. Intense coastal water plus upwelling caused low abundance of this species in inshore water in summer, except for a small patch on the east mouth of the Qiongzhou Strait. Its abundance was highest in winter and related to the weak coastal water and upwelling in winter. *Serratosagitta pacifica* abundance was higher in the other areas, except for a small part of Region I, where abundances ranged from 5 to 10 ind. m^{-3}. At the same time, high abundances in winter also testified to the strengthening of the SCS warm current. *Serratosagitta pacifica's* distribution is closely related to the warm current and can be regarded as an indicator species of Kuroshio water offshore in the East China Sea and Taiwan Strait (Xiao, 2004).

Aidanosagitta neglecta is a neritic or distant neritic Indo-Pacific species and is usually associated with warm water masses (Tse *et al.*, 2007). In this study, higher abundances of *A. neglecta* were recorded during the winter. This contrasts with the view of Tse *et al.* (2007) that *A. neglecta* was positively correlated with temperature. On the other hand, it can be a good indicator of the enhanced influence of the SCS warm current in winter. In addition, oceanic warm water species, such as *Mesosagitta minima*, *Pterosagitta draco*, *Flaccisagitta hexaptera*, *Pseudosagitta lyra* and *Krohnitta subtilis* can also be indicators of the SCS warm current.

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REFERENCES

Alvariño A. (1965) Chaetognaths. *Oceanography and Marine Biology: an Annual Review* 3, 115–194.

Andréu P. (1992) Vertical migration of three coastal species of chaetognaths in the western Mediterranean Sea. *Scientia Marina* 56, 367–372.

Baier C.T. and Purcell J.E. (1997) Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Marine Ecology Progress Series* 146, 43–53.

Bieri R. (1959) The distribution of the planktonic Chaetognatha in the Pacific and their relationship to the water masses. *Limnology and Oceanography* 4, 1–28.

Bieri R. (1991) Systematics of the Chaetognatha. In Bone Q., Kapp H and Pierrot-Bults A.C. (eds) *The biology of chaetognaths*. Oxford: Oxford University Press, pp. 122–136.

Bohata K. and Koppelmann R. (2013) Chaetognatha of the Namibian Upwelling Region: taxonomy, distribution and trophic position. *PLOS ONE* 8, 1–14.

Boltovskoy D. (1981) *Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino*. Mar del Plata, Argentina: INIDEP, 936 pp.

Bone Q., Kapp H. and Pierrot-Bults A.C. (1991) Introduction and relationship of the group. In Bone Q., Kapp H. and Pierrot-Bults A.C. (eds) *The biology of chaetognaths*. Oxford: Oxford University Press, pp. 1–4.

Casanova J.P. (1986) Quatre nouveaux chaetognathes atlantiques abyssaux (genre Heterokrohnia): description, remarques éthologiques et biogéographiques. *Oceanologica Acta* 9, 469–477.

Cheney J. (1985) Spatial and temporal abundance patterns of oceanic chaetognaths in the western North Atlantic. Vertical distribution and migrations. *Deep-Sea Research* 32, 1061–1075.

Dai Y. (1989) Study on ecology of chaetognaths in western Taiwan Strait. *Acta Oceanologica Sinica* 11, 486–492. [In Chinese.]

Dai Y. (1995) A study on the species diversity of chaetognaths in China seas. *Chinese Biodiversity* 3, 69–73. [In Chinese, with English summary.]

Du F., Li C. and Jia X. (2003) Species composition and quantity distribution of Chaetognatha in Beibu Bay in autumn and winter. *Journal of Fishery Sciences of China* 10, 235–241. [In Chinese, with English summary.]

Du F., Li C. and Jia X. (2004) Species composition and community structure of Chaetognatha in Beibu Bay. *Journal of Fishery Sciences of China* 11, 59–64 (in Chinese, with English summary).

Duró A. and Saiz E. (2000) Distribution and trophic ecology of chaetognaths in the western Mediterranean in relation to an inshore–offshore gradient. *Journal of Plankton Research* 2, 339–361.

Feigenbaum D.L. and Maris R.C. (1984) Feeding in the Chaetognatha. *Oceanography and Marine Biology: an Annual Review* 22, 343–392.

Gibbons M.J. (1992) Diel feeding and vertical migration of *Sagitta serratodentata* Krohn tasmanica Thomson (Chaetognatha) in the southern Benguela. *Journal of Plankton Research* 14, 249–259.

Guan B. (1998) A review of study on the South China Sea Warm Current. *Oceanologia et Limnologia Sinica* 29, 322–329. [In Chinese, with English summary.]

Hong H., Qiu S., Ruan W. and Hong G. (1991) *Minnan–Taiwan bank fishing ground upwelling ecosystem study*. Beijing: Science Press. [In Chinese.]

Huang Q., Wang W., Li Y., Li Z. and Mao M. (1992) General situations of the current and eddy in the South China Sea. *Advance in Earth Sciences* 7, 1–9. [In Chinese, with English summary.]

Jing Z., Qi Y., Hua Z. and Zhang H. (2009) Numerical study on the summer upwelling system in the northern continental shelf of the South China Sea. *Continental Shelf Research* 29, 467–478.

Kimmerer W.J. (1984). Selective predation and its impact on prey of *Sagitta enflata* (Chaetognatha). *Marine Ecology Progress Series* 15, 55–62.

Kruse S., Bathmann U. and Brey T. (2009) Meso- and bathypelagic distribution and abundance of chaetognaths in the Atlantic sector of the Southern Ocean. *Polar Biology* 32, 1359–1376.

Li K., Yin J., Huang L., Lian S., Zhang J. and Liu C. (2010) Monsoon-forced distribution and assemblages of appendicularians in the north-western coastal waters of South China Sea. *Estuarine, Coastal and Shelf Science* 89, 145–153.

Li K., Yin J., Huang L., Zhang J., Lian S. and Liu C. (2011) Distribution and abundance of thaliaceans in the north-west continental shelf of South China Sea, with response to environmental factors driven by monsoon. *Continental Shelf Research* 9, 979–989.

Li L. (2002) Advance in observational studies of upper layer circulations of the South China Sea. *Journal of Oceanography in Taiwan Strait* 21: 114–125. [In Chinese, with English summary.]

Lin Q., Yin J., Huang L. and Zhang G., Li K. (2010) Quantity distribution of chaetognaths in response to the change of monsoon in the upper waters around the Nansha Islands. *Acta Oceanologica Sinica* 32, 100–109. [In Chinese, with English summary.]

Lin Y. (1982) Distribution of Chaetognatha in the shelf areas of the East China Sea, *Studia Marina Sinica* 19, 51–63. [In Chinese, with English summary.]

Liu R. (2008) *Checklist of marine biota of china seas*. Beijing: Science Press. [In Chinese].

Marlétaz F., Martin E., Perez Y., Papillon D., Caubit X., J. Lowe C., Freeman B., Fasano L., Dossat C., Wincker P., Weissenbach J. and Le Parco Y. (2006) Chaetognath phylogenomics: a protostome with deuterostome-like development. *Current Biology* 16, 577–578.

Mulkana M.S. and Mcilwain T.D. (1973) The seasonal occurrence and abundance of Chaetognatha in Mississippi Sound. *Gulf Research Report* 4, 264–271.

Øresland V. (2000) Diel feeding of the chaetognath *Sagitta enflata* in the Zanzibar Channel, western Indian Ocean. *Marine Ecology Progress Series* 193, 117–123.

Pierrot-Bults A.C. (2008) A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. *Deep-Sea Research II: Topical Studies in Oceanography* 55, 137–141.

Pierrot-Bults A.C. and Nair V.R. (1991) Distribution patterns in Chaetognatha. In Bone Q., Kapp H. and Pierrot-Bults A.C. (eds) *The biology of chaetognaths*. Oxford University Press, Oxford, pp. 86–116.

Pierrot-Bults A.C. and Nair V.R. (2010) Horizontal and vertical distribution of Chaetognatha in the upper 1000 m of the western Sargasso Sea and the Central and South-east Atlantic Horizontal and vertical distribution of Chaetognatha in the upper 1000 m of the western Sargasso Sea and the Central and South-east Atlantic. *Deep-Sea Research II: Topical Studies in Oceanography* 57, 2189–2198.

Ramírez-Ávila Y. and Álvarez-Cadena J.N. (1999) Chaetognath species composition from a coral reef lagoon in the Mexican Caribbean Sea. *Revista de Biología Tropical* 47 (Supplement 1), 157–163.

Reeve M.R. (1970) The biology of chaetognatha I. Quantitative aspects of growth and egg production in *Sagitta hispida*. In Steele J.H. (ed.) *Marine food chains*. Berkeley, CA: Oliver & Boyd and University of California Press, pp. 168–189.

Riandey V., Champalbert G., Carlotti F., Taupier-Letage I. and Thibault-Botha D. (2005) Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. *Deep Sea Research Part I: Oceanographic Research Papers* 11, 2029–2048.

Russell F.S. (1935) On the value of certain plankton animals as indicators of water-movements in the English Channel and North Sea. *Journal of the Marine Biological Association of the United Kingdom* 20, 309–332.

Russell F.S. (1936) Observations on the distribution of plankton animal indicators made on Col. E. T. Peel's Yacht 'St. George' in the Mouth of the English Channel, July, 1935. *Journal of the Marine Biological Association of the United Kingdom* 20, 507–552.

Russell F.S. (1937) The seasonal abundance of the pelagic young of teleostean fishes in the Plymouth area. Part. IV. The year 1936, with notes on the conditions as shown by the occurrence of plankton indicators. *Journal of the Marine Biological Association of the United Kingdom* 21, 679–686.

Shannon L.V. and Pillar S.C. (1986) The Benguela ecosystem. Part III. *Plankton. Oceanography and Marine Biology: an Annual Review* 24, 65–170.

Stone J.H. (1969) The Chaetognatha community of the Agulhas Current: its structure and related properties. *Ecological Monographs* 39, 433–463.

Su J. (2004) Overview of the South China Sea circulation and its influence on the coastal physical oceanography outside the Pearl River Estuary. *Continental Shelf Research* 24, 1745–1760.

Su J. and Pohlmann T. (2009) Wind and topography influence on an upwelling system at the eastern Hainan coast. *Journal of Geophysical Research* 114, C06017.

Sun Y. (1989) A preliminary analysis on the composition and quantity of Chaetognath at the coast of Guangxi. *Tropic Oceanology* 8, 39–45. [In Chinese, with English summary.]

Terazaki M. (1989) Distribution of chaetognaths in the Australian sector of the Southern Ocean during the Biomass Sibex Cruise (KH-83-4). *Polar Biology* 2, 51–60.

Tse P., Hui S. and Wong C. (2007) Species composition and seasonal abundance of Chaetognatha in the subtropical coastal waters of Hong Kong. *Estuarine, Coastal and Shelf Science* 73, 290–298.

Tokioka T. (1965) The taxonomical outline of chaetognaths. *Publications of the Seto Marine Biological Laboratory* 12, 335–357.

Ulloa R., Palma S. and Silva N. (2000) Bathymetric distribution of chaetognaths and their association with water masses off the coast of Valparaíso, Chile. *Deep-Sea Research I* 47, 2009–2027.

Wang D., Hong B. and Xu H. (2010) Numerical investigation on propulsion of the counter-wind current in the northern South China Sea in winter. *Deep-Sea Research* 157, 1206–1221.

Xiao Y. (2004) *Fauna Sinica Invertebrata. Volume 38. Chaetognatha Sagittoidea*. Beijing: Science Press. [In Chinese.]

Xu Z. and Chen Y. (1989) Aggregated intensity of dominant species of zooplankton in autumn in the East China Sea and Yellow Sea. *Journal of Ecology* 8, 13–15.

Xu Z. and Chen Y. (2005) Relationships between dominant species of Chaetognatha and environmental factors in the East China Sea, *Journal of Fishery Sciences of China* 12, 76–82. [In Chinese, with English summary.]

Xu Z., Dai Y. and Chen Y. (2004) Study on species composition and diversity of Chaetognatha in the East China Sea. *Journal of Shanghai Fisheries University* 13, 304–309. [In Chinese, with English summary.]

and

Zhang G. and Chen Q. (1991) Chaetognaths in the waters around the Nansha Islands during the periods of spring and summer. In *Collected papers on marine biology study of Nansha Islands and their adjacent sea areas (II)*. Beijing: Ocean Press, pp. 102–122. [In Chinese].

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