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Research papers

# Distribution and abundance of thaliaceans in the northwest continental shelf of South China Sea, with response to environmental factors driven by monsoon

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ABSTRACT

The distribution and abundance of thaliaceans were studied in relation to physical and biological variables during summer and winter in the northwest continental shelf of South China Sea. Based on the topography and water mass of the surveyed region, it was divided into three subregions: region I (onshore waters of the east Leizhou Peninsula), region II (onshore waters of the east and southeast Hainan Island) and region III (offshore waters from Leizhou Peninsula to Hainan Island). During summer due to a strong southwest monsoon, a cold eddy and coastal upwelling dominated in regions I and II, respectively, whereas the onshore and offshore waters were vertically mixed during winter due to a strong northeast monsoon. A total of 18 thaliacean species (including 3 subspecies) were collected. The mean species richness was higher in summer compared to winter, with the occurrence of higher values during summer and winter at region II and region III, respectively. The average thaliacean abundance is also higher in summer than in winter, with higher values at region I in summer and no significant difference among three subregions in winter. *Doliolum denticulatum* and *Thalia democratica* were the dominant species during summer and winter. The results suggested that the seasonal and spatial distribution of thaliacean richness was considered to be the result of physical factors such as temperature and ocean current in summer and winter. Spatial distribution of thaliacean abundance was affected by chlorophyll *a* concentration increased by the occurrence of coastal upwelling and cold eddy in summer. Southwest and northeast monsoons are shown to play an important role in shaping the distribution of species richness and abundance of thaliaceans in the northwest continental shelf of South China Sea.



## 1. Introduction

Thaliaceans (including three orders of doliolids, pyrosomes and salps) are large pelagic gelatinous zooplankton and widespread in the world's oceans (Thompson, 1948). They have complex life cycles with obligatory alternation of sexual and asexual generations (Bone, 1998), and are adapted to respond quickly to physical and biological dynamics (Paffenhöfer and Lee, 1987; Deibel and Paffenhöfer, 2009). They are receiving an increasing attention recently due to their ecological, evolutionary and biogeochemical importance (Boero et al., 2008). Although most thaliacean species occur in the open ocean, a few of them are generally abundant and are aggregated mainly on tropical and subtropical continental shelves (Deibel, 1985, 1998; Paffenhöfer and Lee, 1987; Paffenhöfer et al., 1995; Deibel and Paffenhöfer, 2009).

Temperature, food, and ocean currents are generally considered to be the major factors influencing on the distribution of epipelagic animals both spatially and temporally. Thaliacea tend to congregate in the areas of high abundances of nano- and ultraplankton (Nakamura, 1998; Cristian and Madin, 2004). In the current California region, studies show that thaliacean distribution is correlated positively with phytoplankton and negatively with crustacean herbivores (Berner and Reid, 1961; Silver, 1975; Blackburn, 1979). Most doliolids and salps appear to be abundant close to the increasing concentrations of chlorophyll *a* (Chl *a*) in the northern part of the Levantine Sea (Weikert and Godeaux, 2008), in the Japan Sea (Iguchi and Kidokoro, 2006) and in the northern Arabian Sea (Naqvi et al., 2002). Thaliceans occur regularly in upwelling waters, rich in nutrients and phytoplankton and are transported by the Florida Current with the result of southerly winds from the South Atlantic Bight (Deibel, 1985; Paffenhöfer and Lee, 1987; Paffenhöfer et al., 1995; Deibel and Paffenhöfer, 2009). However, limited information is available on thaliacean distribution in the western tropical Pacific Ocean.

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The South China Sea (SCS) is the largest semi-enclosed sea in the western tropical Pacific Ocean. In the northern SCS, bottom topography is characterized by a steep continental slope between a shallow continental shelf (width from 150 to 250 km) in the northwest and a wide deep basin in the southeast (Sun, 2008). The climate in the SCS is dominated by the East Asian monsoon system (Su, 2004). In the winter the northeast (NE) monsoon prevails, and in summer the winds reverse their directions to the southwest (SW). The direction of surface current and the occurrence of upwelling in the north SCS are controlled by both topography and monsoon.

Detailed studies on the taxonomy of thaliaceans in the China seas are available(Chen, 1978; Hou, 1984; Hu, 1985; Huang, 2008); however, the quantitative information concerns the environmental factors forced by monsoon that regulate the distribution of thaliaceans in the South China Sea (SCS) is less. Tew and Lo (2005) reported the abundances of thaliaceans (*Doliolum denticulatum*, *Thalia democratica*) at different stages were correlated with temperature and salinity in the Taiwan Strait. Lin and Lin (2006) reported that 23 species (including 6 subspecies) were found and their abundances were positively correlated with Chl *a* concentration in the central SCS. However, the water circulation made thaliaceans aggregating with the high abundance of 2.4 ind. $m^{-3}$ during autumn with low primary production in the central SCS.

The goal of this study is to reveal species composition and abundance distribution of thaliaceans in the northwest continental shelf of SCS, and discuss the influence of environmental factors driven by SW and NE monsoons on their distribution and assemblage. We hypothesized that in the northwest continental shelf of SCS, the distribution of thaliaceans would vary spatially between SW and NE monsoon.

## 2. Material and methods

### 2.1. Study area

The surveyed region is located in the northwest continental shelf of SCS (17°17.10′–21°25.62′N,109°28.74′–113°13.26′E), including coastal waters of the east Leizhou Peninsula and the continental shelf from the east mouth of Qiongzhou Strait to the east and southeast Hainan Island (Fig. 1). The topography of the eastern Leizhou Peninsula is relatively regular with a depth less than 200 m. The isobaths are parallel with the coastline in the east Leizhou Peninsula, but to the continental slope with the maximum depth of 1900 m (Fig. 2, station H7 with the depth of 1980 m) in the east and southeast of Hainan Island. The climate in

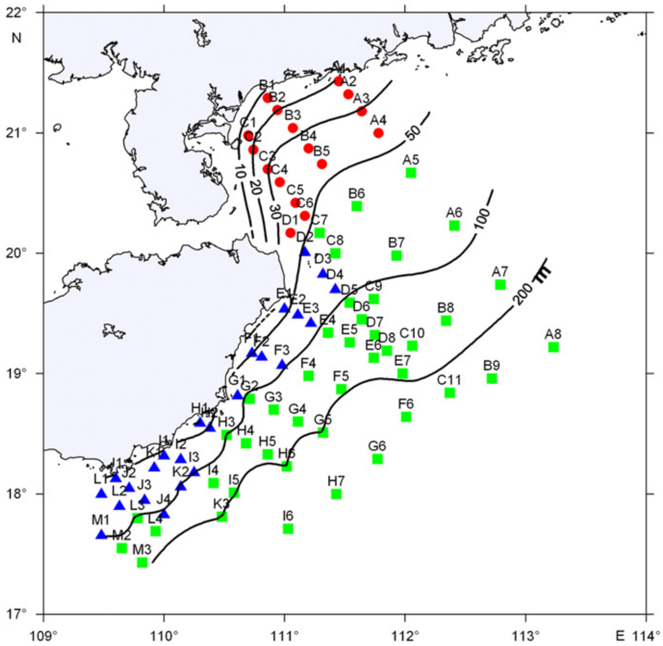


**Fig. 2.** Sampling stations. The red circle represented sampling stations in the east inshore waters of Leizhou Peninsula (region I); the blue triangle represented sampling stations in the east and southeast inshore waters of Hainan Island (region II) and the green rectangle represented the offshore waters from Leizhou Peninsula to Hainan Island (region III)—represented the depth contour. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

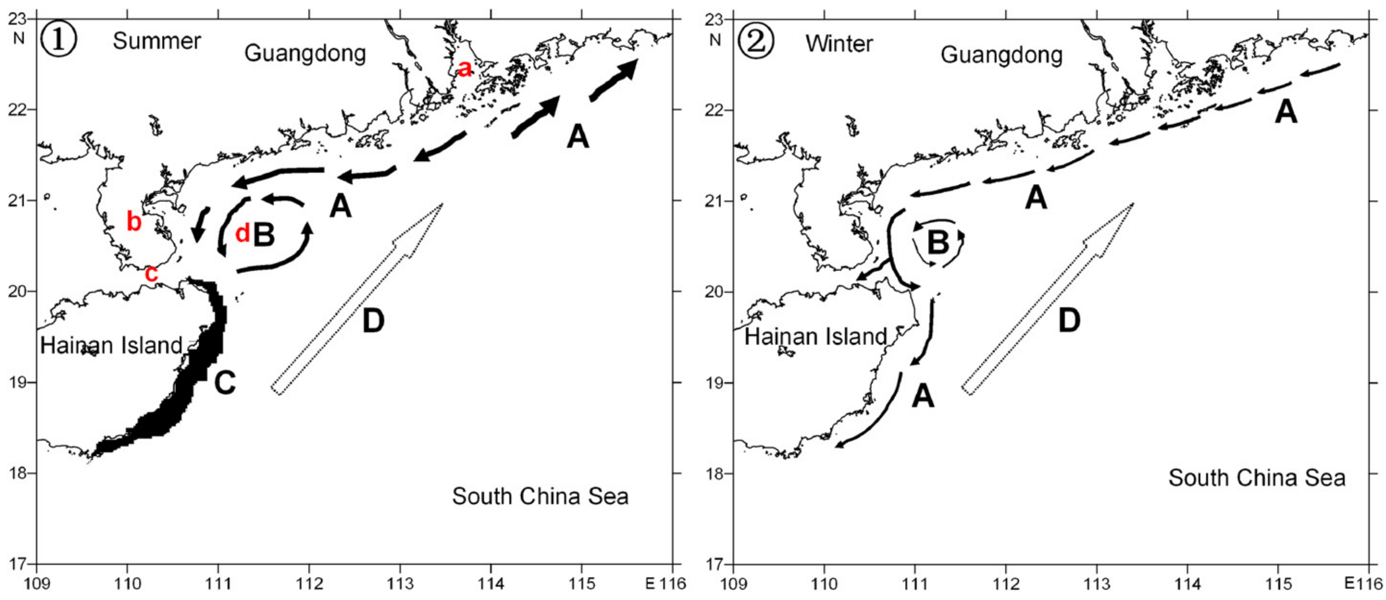


**Fig. 1.** Maps showing the schematic of ocean currents. A, B and D represented Guangdong Coastal Current, cyclonic circulation and South China Sea Warm Current, respectively, in Fig. 1① and ②, C represented coastal upwelling at the east and southeast of Hainan Island in Fig. 1①. The length of B diameter represented the intensity of cyclonic circulation and the black represent the width of coastal upwelling. a, b, c and d represented the Pearl River Estuary, Leizhou Peninsula, Qiongzhou Strait and Guangzhou Bay, respectively. (Source from Li et al. (2010).)

the investigated area is dominated by tropical and subtropical East Asia monsoon. Seasons prevail in the NE monsoon from October to March or April next year and convert to SW monsoon from June to August.

The current system of the investigated region is controlled by Guangdong Coastal Current, the cyclonic circulation (cold eddy), coastal upwelling and South China Sea Warm Current (Fig. 1① and ②). The path and direction of Guangdong Coastal Current are under the influence of the East Asia Monsoon and Pearl River runoff. It generally flows southwestward during winter when NE monsoon prevails, while it turns northeastward during summer when SW dominates (Fig. 1①A and ②A). But it still flows southwestward around the eastern coast of Leizhou Peninsula as a result of a large number of Pearl River discharge pressure during summer (Guan and Chen, 1964; Huang et al., 1992; Yang et al., 2003). The current flows northeastward impacted by SW monsoon in the eastern side of Guangzhou Bay, whereas in the western side of Guangzhou Bay it flows southwestward; therefore, the two reverse current directions cause the formation of a local cyclonic circulation, which is located between 20°20′–21°10′N and 110°50′–112°00′E (Fig. 1①B and ②B). The cyclonic circulation exists throughout the year, and its intensity is determined by the monsoonal strength (Huang et al., 1992; Yang et al., 2003; Guan and Yuan, 2006). A coastal upwelling will appear in the east onshore waters of Hainan Island driven by strong SW monsoon and topography (Han et al., 1990; Wu and Li, 2003; Jing et al., 2009; Su and Pohlmann, 2009), whose center is located between 18°30′–20°30′N and 110°–111°30′E, and shallow from 30 m water depth and 10 km offshore (Fig. 1①C). It starts in April, is strongest from June to August, weakens in September and disappears after October. South China Sea Warm Current (SCSWC) is a consistent northeastward current straddling over the shelf-break region (Guan and Chen, 1964; Guan, 1998; Chiang et al., 2008; Wang et al., 2010). During the summer monsoon it spreads over most parts of the shelf outside the coastal current zone, while under the strong northeasterly winter monsoon it persists around the shelf-break area (Fig. 1①D and ②D).

### 2.2. Sampling

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 northwest continental shelf of SCS, respectively. Zooplankton was sampled by vertical tow net from 1 m above the bottom (depth <200 m) or from 200 m (depth >200 m) to the surface using plankton nets of 505 μm mesh size (diameter mouth: 50 or 80 cm) at 82 stations (Fig. 2). The net mouth was fitted with a flowmeter to determine the volume of filtered water during each tow (unit: $m^3$). Trawl winch speed was about 1 m $s^{-1}$. The samples collected were immediately fixed in 5% formalin.

Temperature and salinity were measured on board at each station using a SeaBird CTD probe from surface to near bottom. Water samples for the measurement of Chl *a* concentration were collected using 5 L Niskin bottle at the depths of 0, 10, 30 m and near the bottom layers if the station depth was below 50 m, or from 0, 10, 30, 50, 75, 100, 150 and 200 m if it was above 200 m.

### 2.3. Laboratory procedures

The zooplankton samples were examined and counted individually, and thaliaceans were separately analyzed. Thaliaceans in each sample were identified to their species level when possible and counted under a low-power microscope based on taxonomy references (Thompson, 1948; Yamaji, 1977; Chen, 1978; Hou, 1984; Hu, 1985). Individuals at different generation stages (phorozooid and gonozooid in dodiolids, solitary and aggregate in salps) were combined. All densities of water column were presented as number of individuals per cubic meter (unit: ind. $m^{-3}$).

For the determination of Chl *a* concentration, a 500 mL water sample was gently filtered through a 0.70 μm cellulose filter and extracted with 90% acetone for 24 h in darkness. The mean of water column Chl *a* concentration (unit: mg $m^{-3}$) was then determined fluorimetrically (Turner designs 10 AU fluorometer) before and after acidification (Parsons et al., 1984).

### 2.4. Data analyses

Based on the topography and water mass of the surveyed region, it was divided into three subregions: regions I (onshore waters of the east Leizhou Peninsula), II (onshore waters of the east Hainan Island) and III (offshore waters from the east Leizhou Peninsula to Hainan Island). Region I was controlled by the Coastal Fresh Water Mass and the Near Shore Mixed Water Mass, with a depth less than 50 m (including 16 stations). Region II was controlled by the Surface Water Mass of SCS, with a depth greater than 100 m (including 24 stations). The water mass of region II was also influenced by coastal upwelling in summer. Region III was controlled by the Surface Water Mass of SCS throughout the year (including 42 stations) (Li et al., 2002).

Independent samples *T* test was conducted to examine the significant differences between summer and winter seasons for environmental and biological parameters. A one-way ANOVA (least significant difference or LSD) was used for analyzing the differences of physical and biological parameters among three subregions. Pearson correlation analysis was applied to find the distribution of thaliaceans in relation to environmental variables. Surface temperature and salinity were analyzed using the 0.5 m layer data with the exception of water column Chl *a* concentration.

## 3. Results

### 3.1. Summer-winter variation of environmental factors and spatial distribution

#### 3.1.1. Horizontal distribution of temperature, salinity and Chl a concentration

The value was higher in summer than in winter for surface temperature ($t$=22.96, $P<0.001$) and salinity ($t$=3.02, $P<0.01$). The mean surface temperature was 28.62 °C (±1.53 °C) and 22.95 °C (±1.54) °C in summer and winter, ranging from 23.71 to 30.74 and 18.77 to 25.27 °C, respectively. The mean surface salinity was 33.99 (±0.26) and 33.72 (±0.56) in summer and winter with a range from 32.67 to 34.28 and 31.51 to 34.60, respectively. The distribution of surface temperature was uneven with lower temperature (<27 °C) observed in east onshore waters between Leizhou Peninsula and Hainan Island and higher temperature (>30 °C) was observed in the offshore waters from the east of Leizhou Peninsula to Hainan Island during summer (Fig. 3a). The surface temperature increased from north to south and from onshore to offshore waters in winter (Fig. 3b). Temperature at region III was shown to be significantly higher than at regions I and II during both summer ($F$=19.10; $P<0.001$) and winter ($F$=147.63; $P<0.001$) (Fig. 4A). The distribution of surface salinity increased from onshore to offshore waters and its isobar with 33 approached to the coastline of Leizhou Peninsula closer in summer than in winter (Fig. 3c and d). Salinity at region I was significantly lower than that at region II and III ($P<0.01$) and

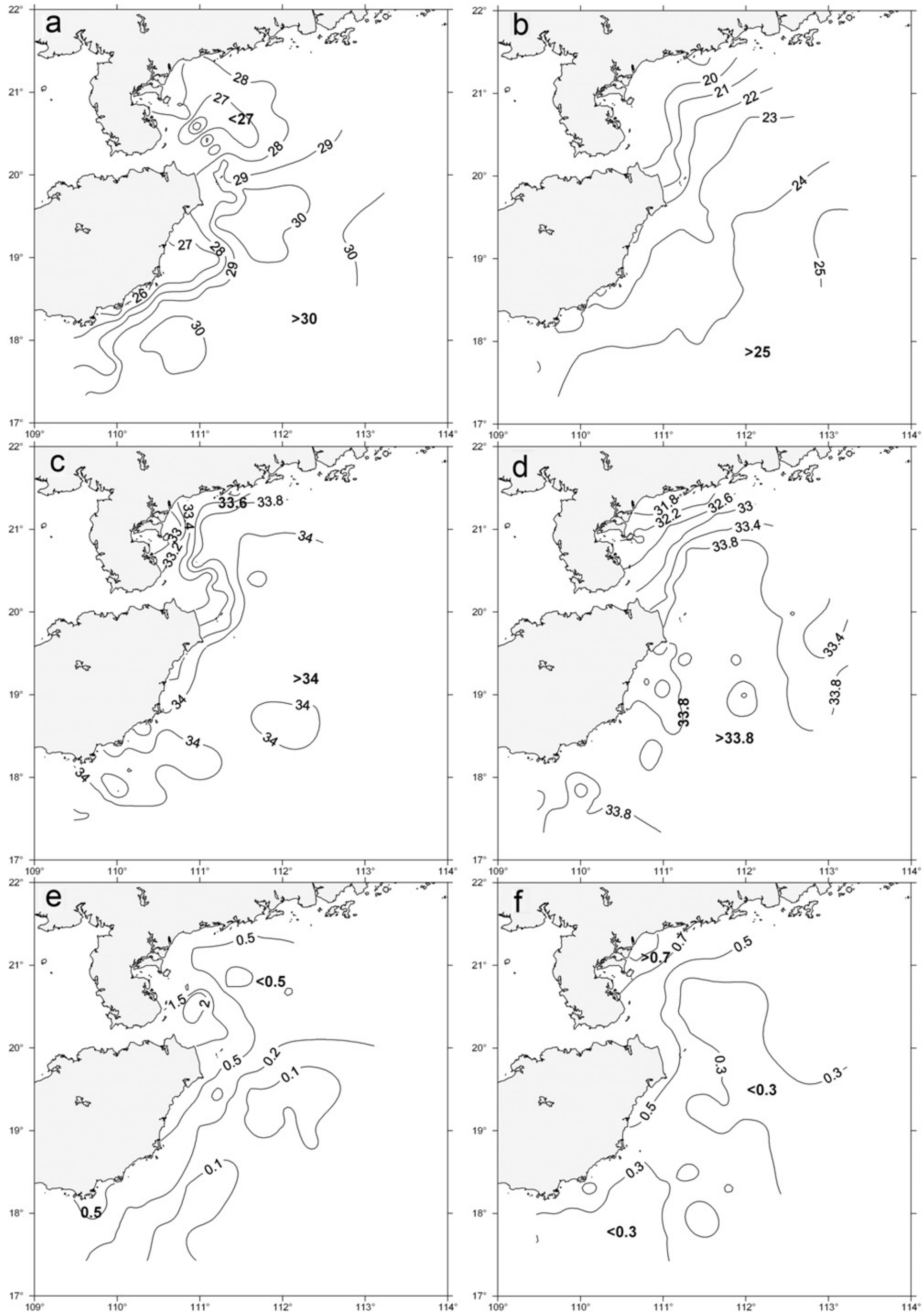


**Fig. 3.** Horizontal distribution of surface temperature (°C), surface salinity and chlorophyll *a* concentration in the northwest continental shelf of SCS ((a) summer-temperature; (b) winter-temperature; (c) summer-salinity; (d) winter-salinity; (e) summer-Chl *a*; (f) winter-Chl *a*).

there was no significant difference between region II and III during both summer and winter (Fig. 4B).

The values of Chl *a* were not significantly different from summer to winter ($t=0.74$, $P=0.46$); however, it was shown to be significantly different among three regions ($P<0.01$) (Fig. 4C). The mean Chl *a* value was 0.41 ($\pm 0.49$) and 0.37 ($\pm 0.17$) mg $m^{-3}$ with a range from 0.03 to 3.25 and 0.12 to 0.94 mg $m^{-3}$ during summer and winter, respectively. The distribution of Chl *a* decreased generally from onshore to offshore waters irrespective of summer or winter (Fig. 3e and f). However, it appeared especially with a maximum value of 3.25 mg $m^{-3}$ at station C4 between the Guangzhou Bay and the east mouth of Qiongzhou Strait and also high in the southeast onshore waters of Hainan Island in summer (Fig. 3f).

### 3.1.2. Vertical distribution of temperature, salinity and Chl a concentration

Transect C is located in the east of Leizhou Peninsula and its temperature, salinity and Chl *a* are shown in Fig. 5. The isopleths of temperature and salinity elevated from the bottom to the surface in summer (Fig. 5a and c). The vertical distribution of temperature and salinity was found to be evenly distributed in the onshore waters during winter (Fig. 5b and d). The Chl *a* occurred with higher

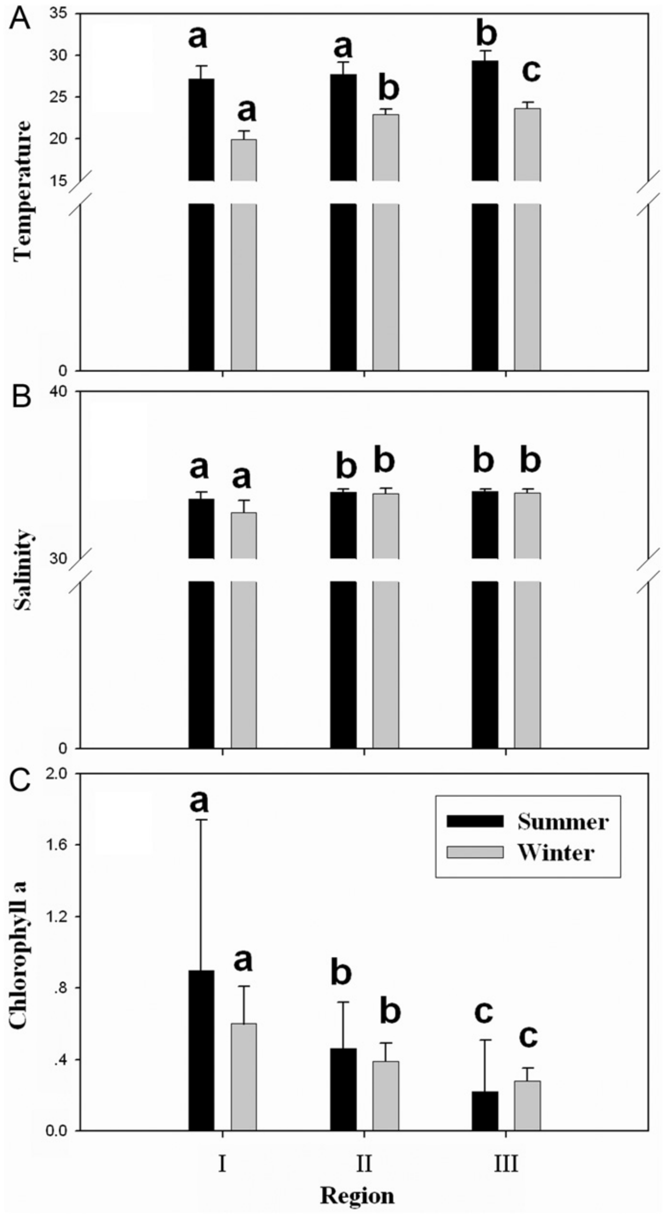


**Fig. 4.** Variations of the mean surface temperature (A), salinity (B) and Chl *a* (C) at region I, II and III in summer and winter. Error bars represent SD. Columns denoted by different letters are significantly different from each other (ANOVA, $P<0.05$).

concentration from 50 to 10 m layer in the onshore waters in summer and mixed well in winter (Fig. 5e and f).

### 3.2. Summer-winter variation of thaliacean community and spatial distribution

#### 3.2.1. Variation of species composition and spatial distribution

A total of 18 species (including 3 subspecies, *Cyclosalpa pinnata polae*, *Thialia democratica orientalis* and *T. d. echinata*) of thaliaceans belonging to 12 genera and 3 families were identified (Table 1). Species richness was significantly higher in summer than in winter ($t=4.45$, $P<0.01$). The mean species richness was 3.2 ($\pm$1.1) and 2.2 ($\pm$1.7) with a range from 1 to 6 in summer and from 0 to 5 in winter. Thaliacean species preferred to habit in steep continental shelf around the inshore and offshore waters of Hainan Island (Fig. 6a and b). The species occurred at region II with higher richness than at region I and III during summer, while it presented at region III with higher values than that of region I and III during winter (Fig. 7A). Pearson correlation analysis indicated that the spatial distribution of species richness was positively correlated to temperature and salinity at regions I and III in winter (Table 2).

#### 3.2.2. Variation of thaliacean abundance and spatial distribution

Thaliacean abundance was significantly higher in summer than in winter ($t=3.69$, $P<0.01$), with the former 5 times more than the latter (Table 1). The region of high values was recorded in the east mouth of Qiongzhou Strait and the east onshore waters of Leizhou Peninsula with a maximum value at station D1 (175 ind. $m^{-3}$) in summer (Fig. 6c). Moreover, the high abundance was also observed in the east and southeast onshore waters of Hainan Island during both summer and winter (Fig. 6c and d). The thaliacean abundance was obviously higher at region I than at regions II and III in summer ($F=9.67$, $P<0.01$), but there was no significant difference among three regions in winter (Fig. 7B). Pearson correlation analysis indicated that temperature had a negative effect on thaliacean distribution regionally, and their regional distribution was positively correlated to salinity and Chl *a* (Table 2).

#### 3.2.3. Variation of dominant species and spatial distribution

*Doliolum denticulatum* and *Thalia democratica* dominated in summer and winter according to their abundance (Table 1). The abundance was significantly higher in summer than in winter for *D. denticulatum* ($t=2.66$, $P<0.01$) and *T. democratica* ($t=4.62$, $P<0.01$). The high values of *D. denticulatum* abundance ($>100$ ind. $m^{-3}$) appeared with in the onshore waters such as around Guangzhou Bay, the east mouth of Qiongzhou Strait and the east and southeast of Hainan Island in summer, and concentrated mainly in the onshore and offshore waters of Hainan Island during winter (Fig. 8a and b). *T. democratica* was generally more abundant in the onshore waters than in the offshore waters in summer, but occurred occasionally in the offshore waters in winter (Fig. 8c and d). The abundance of *D. denticulatum* was significantly higher at region I compared to both region II and III during summer ($F=5.24$, $P<0.01$), and it was similarly higher at region II than the other two regions during winter ($F=4.46$, $P<0.05$) (Fig. 9A). The abundance of *T. democratica* was shown to be significantly lower at region III than at regions I and II in summer ($F=6.18$, $P<0.01$) and no significant differences were observed during winter (Fig. 9B).

## 4. Discussion

The present study is aimed to understand the influence of environmental factors driven by SW and NE monsoon on the distribution of thaliaceans in the northwest continental shelf of SCS. It was found that the distribution of thaliacean species and abundance varied seasonally and regionally. One of the limitations in the sampling methodology is that a vertical stratified sampling was not carried out. Therefore some important information on the vertical distribution of thaliaceans is ignored. The sampling with vertical stratification is widely used in other studies (Deibel, 1985; Paffenhöfer and Lee, 1987; Paffenhöfer et al., 1995; Tow and Lo, 2005; Weikert and Godeaux, 2008).

### 4.1. Influence of monsoon on the distribution of thaliacean species

A total of 18 species of thaliacean species were collected from the northwest continental shelf of SCS, which accounted about 50% of total thaliacean species in China seas with 34 species (Huang, 2008; Liu, 2008). The total number of species richness is

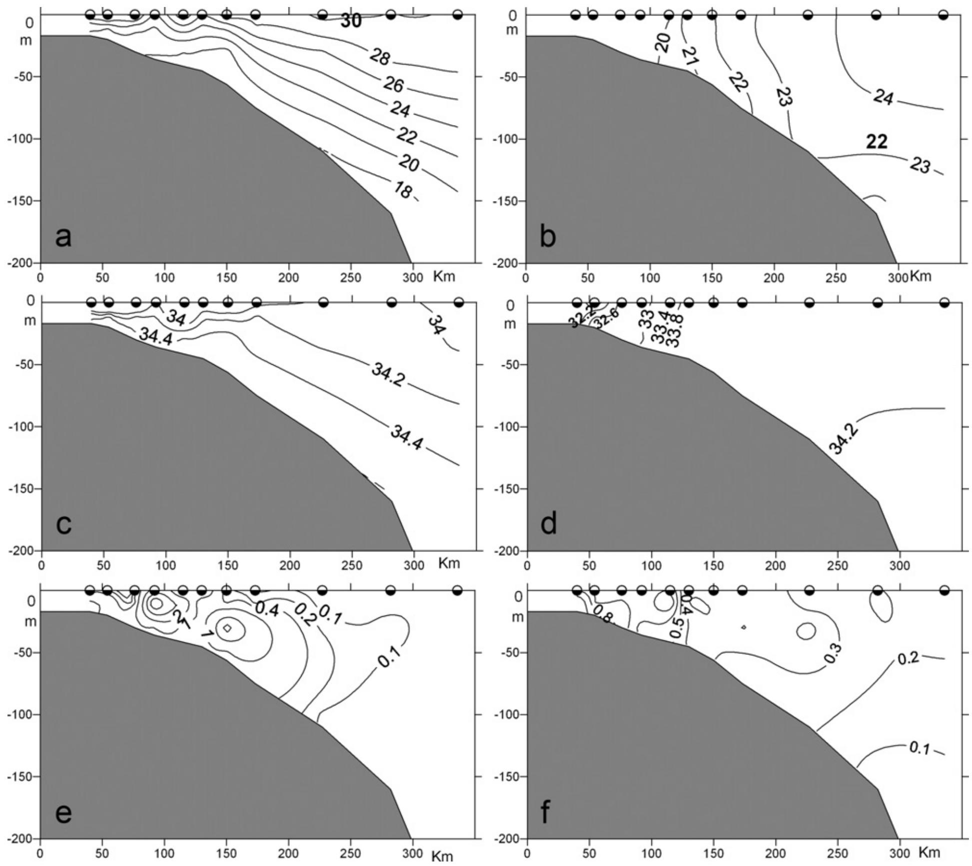


**Fig. 5.** Vertical distribution of temperature (°C) and salinity and chlorophyll *a* concentration at transect C ((a) summer-temperature; (b) winter-temperature; (c) summer-salinity; (d) winter-salinity; (e) summer-Chl *a*; (f) winter-Chl *a*).

**Table 1**
Species composition and abundance (ind. $m^{-3}$) of thaliaceans in the northwest continental shelf of SCS.

| Species | Summer | | | Winter | | |
|---|---|---|---|---|---|---|
| | Mean ± SD | Range | % | Mean ± SD | Range | % |
| *Cyclosalpa affinis* (Chamisso,1819) | 0.00 ± 0.01 | 0–0.06 | 0.01 | 0.00 ± 0.00 | 0–0.01 | 0.02 |
| *Cyclosalpa floridana* (Apstein,1894) | 0.02 ± 0.16 | 0–1.42 | 0.15 | / | / | / |
| *Cyclosalpa pinnata* (Forskål, 1775) | 0.69 ± 5.81 | 0–52.63 | 5.83 | 0.07 ± 0.36 | 0–3.14 | 3.37 |
| *Doliolum denticulatum* (Quoy et gaimard,1834) | 8.32 ± 20.42 | 0–169.09 | 70.63 | 1.82 ± 3.67 | 0–21.80 | 87.39 |
| *Dolioletta gegenbauri* (Uljanin, 1884) | 1.28 ± 3.24 | 0–18.15 | 10.82 | 0.04 ± 0.21 | 0–1.82 | 1.92 |
| *Iasia zonaria* (Pallas,1774) | / | / | / | 0.02 ± 0.09 | 0–0.67 | 1.08 |
| *Ihlea punctata* (Forskål, 1775) | 0.01 ± 0.03 | 0–0.20 | 0.06 | 0.05 ± 0.09 | 0–0.33 | 2.19 |
| *Pegea confoederata* (Forskål, 1775) | 0.00 ± 0.00 | 0–0.04 | 0.00 | / | / | / |
| *Pyrosoma atlanticum* Péron, 1804 | 0.02 ± 0.07 | 0–0.42 | 0.19 | 0.01 ± 0.03 | 0–0.20 | 0.35 |
| *Ritteriella amboinensis* (Apstein,1904) | 0.01 ± 0.05 | 0–0.46 | 0.05 | 0.00 ± 0.02 | 0–0.21 | 0.15 |
| *Ritteriella picteti* (Apstein,1904) | / | / | / | 0.00 ± 0.02 | 0–0.14 | 0.09 |
| *Salpa maxima* Forskål, 1775 | / | / | / | 0.01 ± 0.05 | 0–0.32 | 0.36 |
| *Thalia democratica* (Forskål, 1775) | 1.37 ± 2.59 | 0–12.89 | 11.65 | 0.05 ± 0.17 | 0–1.20 | 2.44 |
| *Traustedtia multitentaculata* (Quoy et gaimard,1834) | 0.07 ± 0.26 | 0–1.85 | 0.56 | 0.01 ± 0.08 | 0–0.07 | 0.64 |
| *Weelia cylindrica* (Cuvier,1804) | 0.01 ± 0.04 | 0–0.37 | 0.05 | / | / | / |
| | 11.78 ± 23.47 | 0.13–175.15 | 100 | 2.08 ± 3.88 | 0–21.80 | 100 |

*Note*: "/" represents not occurrence; "%" represents *i* species abundance account for total abundance.

obviously higher in the northwest continental shelf of SCS than in the Bohai Sea (Bi et al., 2000) and the Yellow Sea (Section of plankton group, 1964; Chen, 1978; Zuo et al., 2005), where only 2 and 6 species were discovered, respectively, and is similar to that of the East China Sea (Xu and Lin, 2007), the Taiwan Strait (Zhang et al., 2003a, 2003b; Tew and Lo, 2005), but lower than in the central and southern regions of SCS (Chen, 2003; Lin and Lin, 2006) where more than 20 species were found. The species number increased from the north to southern coasts of China seas. The sea surface temperature in the coast of China seas also increased from the Bohai Sea to the SCS during the same season based on the latitude division and solar radiation (Guan and Chen, 1964; Sun, 2008). Therefore temperature might play an important role in the distribution of thaliacean species. Our results suggest that the distribution of thaliacean species was positively related to temperature during winter (Table 2). Thaliaceans are widespread in the world's oceans, with a preference for tropical and warm temperate waters (Thompson, 1948; Deibel, 1998). The range of surface temperatures in the surveyed area in summer is suitable for thaliaceans survival and not a limitation factor.

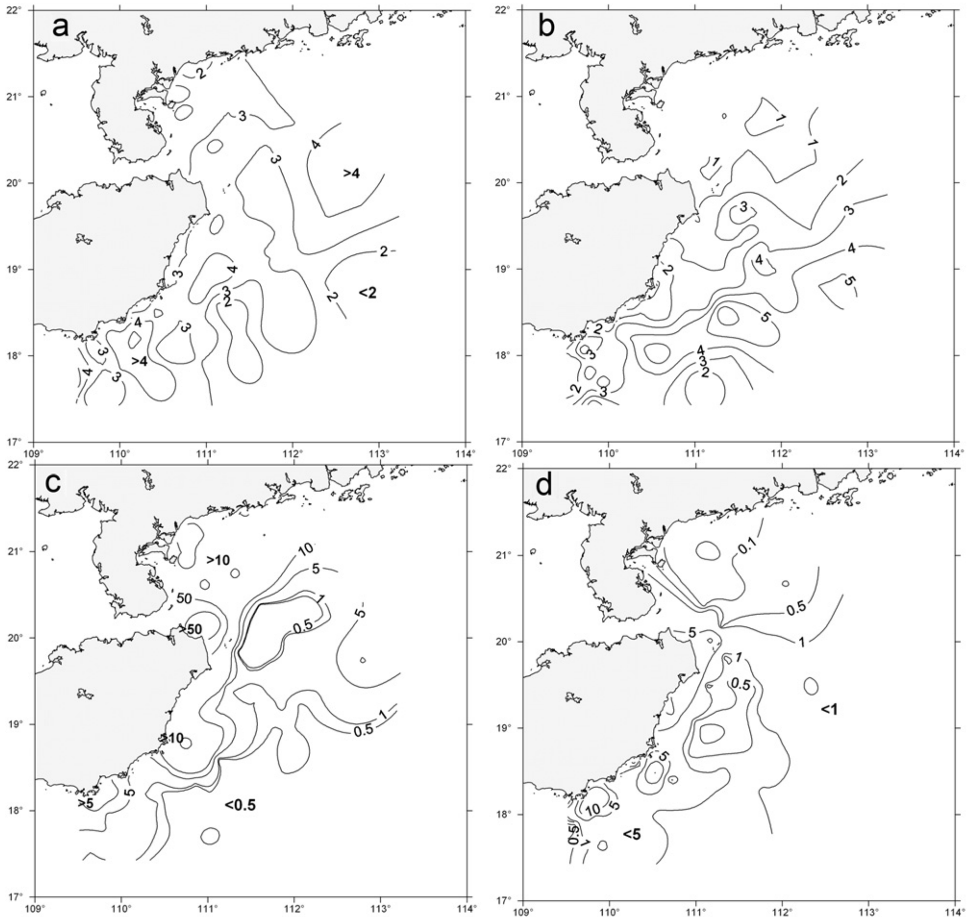


**Fig. 6.** Distribution of species richness and abundance of thaliaceans in the northwest continental shelf of SCS ((a) summer-richness; (b) winter-richness; (c) summer-abundance; (d) winter-abundance).

However in winter, the temperature differences are significant among three regions increasing from north to south and onshore to offshore waters (Figs. 3b and 4A), and the species number is obviously higher at region III compared to regions I and II (Figs. 6b and 7A). The total number of thaliacean species did not show seasonal variations with each of the 13 species were present during both summer and winter, but the mean species richness is significantly higher during summer than winter.

The distribution of thaliacean species was not only influenced by temperature crucially, but also affected by ocean current. The SCSWC originates from the offshore area east of the Hainan Island, flows over the shelf/slope region, passes through the Taiwan Strait and finally enters the East China Sea throughout the year (Guan and Chen, 1964). It spreads over onshore and offshore waters of Hainan Island in summer and persists around the shelf-break areas in winter with the higher temperature than the surrounding waters (Wang et al., 2010). Our results showed that the high values of thaliacean species were located at region II in summer, while at region III in winter (Fig. 7A). The water mass of region I is influenced by Guangdong Coastal Current and controlled by Coastal Fresh Water Mass and the Near Shore Mixed Water Mass (Li et al., 2002). It is also affected by a cold eddy throughout the year, so that the low temperature and salinity waters dominate compared to that of regions II and III. A one-way ANONA analysis indicated that the number of species at region I was significantly lower than at region II in summer and at region III in winter (Fig. 7A). The occurrence of thaliacean species might be due to the active SCSWC and the negative Guangdong Coastal Current effects. The distribution of thaliacean species in the East China Sea and Taiwan Strait was also changed with seasonal temperature and ocean current (Zhang et al., 2003a, 2003b; Tew and Lo, 2005; Xu et al. 2007).

It is necessary to be noted that some species occur seasonally and regionally in the surveyed region. Three species of *Cyclosalpa floridana*, *Pegea confoederata* and *Weelia cylindrica* occurred only in summer, and their distribution was mainly from the east and southeast onshore and offshore waters of Hainan Island. *Iasia zonaria*, *Ritteriella amboinensis* and *Salpa maxima* appeared only in winter around the onshore and offshore waters of Hainan Island (Table 1). *I. zonaria* was distributed in the onshore and offshore waters of Hainan Island with a mean of 0.02 ind. $m^{-3}$ and did not occur in the onshore and offshore waters of Leizhou Peninsula in winter.

### 4.2. Influence of monsoon on the distribution of thaliacean abundance

The abundance of thaliaceans is significantly higher in summer than in the winter in the northwest continental shelf of SCS, which is in accordance with the findings of the East China Sea (Xu et al., 2007) and the Taiwan Strait (Zhang et al., 2003a), but contrary to the observations in the central SCS, which had high thaliacean abundance in winter than in summer (Lin and Lin, 2006). The occurrence of high thaliacean abundance in the East China Sea is observed during the spring with the value of 8.13 ind. $m^{-3}$ (Xu et al., 2007), and during autumn in the center of SCS with the value of 2.37 ind. $m^{-3}$ (Lin and Lin, 2006). In this study, that the observations indicate that thaliacean abundance

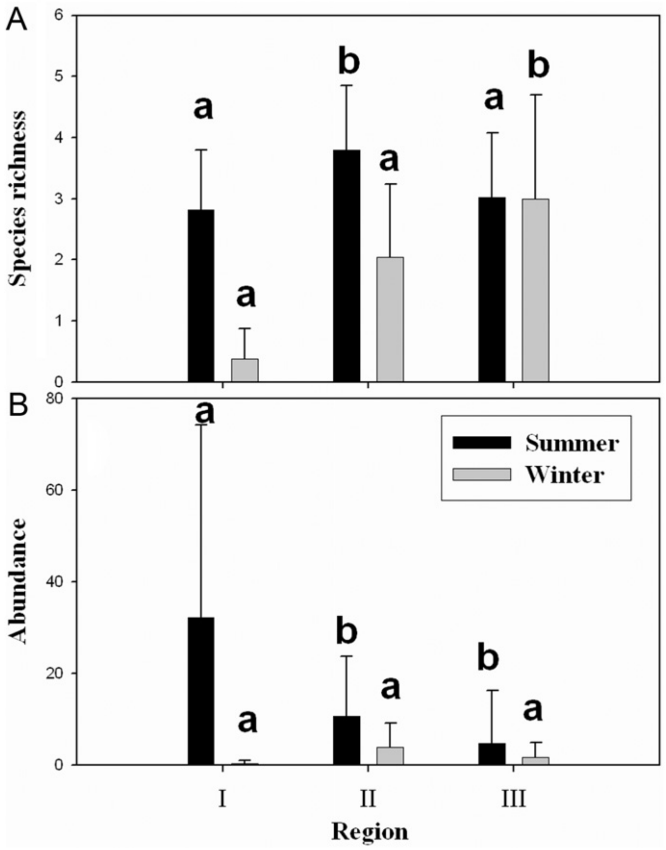


**Fig. 7.** Variations of the mean species richness (A) and abundance (B) of thaliaceans at region I, II and III in summer and winter. Error bars represent SD. Columns denoted by different letters are significantly different from each other (ANOVA, $P<0.05$).

**Table 2**
Correlation coefficients between species richness and abundance of thaliaceans and environmental factors among three regions in summer and winter.

| Season | Variables | Temperature | Salinity | Chl *a* |
|---|---|---|---|---|
| Summer | I-Richness | N.S. | N.S. | / |
| | II-Richness | N.S. | N.S. | / |
| | III-Richness | N.S. | N.S. | / |
| Winter | I-Richness | 0.837** | 0.666** | / |
| | II-Richness | N.S. | N.S. | / |
| | III-Richness | 0.453** | N.S. | / |
| Summer | I-Abundance | N.S. | N.S. | N.S. |
| | II-Abundance | N.S. | N.S. | 0.646** |
| | III-Abundance | −0.577** | N.S. | N.S. |
| Winter | I-Abundance | N.S. | 0.532* | N.S. |
| | II-Abundance | −0.412* | N.S. | N.S. |
| | III-Abundance | N.S. | N.S. | N.S. |

*Note:* N.S: $P>0.05$;
"/" Represented not correlation.
* $P<0.05$.
** $P<0.01$.

during summer with the value of 11.78 ind. m$^{-3}$ in the northwest continental shelf of SCS (Table 1), which could be due to the influence of different environmental conditions. The increase in the abundance of thaliaceans in spring is caused by the intrusion of Kuroshio warm current in the East China Sea (Xu et al., 2007), and the water circulation pattern is the main reason for high abundance in autumn in the center of SCS (Lin and Lin, 2006). However, the presence of coastal upwelling and cold eddy driven by SW monsoon is one of the most important physical processes in the investigated area of northern SCS.

Generally, surface temperature is higher in the onshore waters than offshore waters in the SCS during summer when SW monsoon prevails. However, it is observed that low temperature and high saline waters that exist in the onshore surface waters along the coasts from Leizhou Peninsula to the east and southeast of Hainan Island, and the temperatures are significantly lower at both regions I and II than at region III in summer (Figs. 3a, c and 4A). The appearance of abnormally low temperature and high salinity in the surface waters during summer suggests that an occurrence of an upwelling event, which had been confirmed by Jing et al. (2009) in both climatological remote sensing SST image and field data. The centers of cold water at the surface always show a strong patchiness in the east of Qiongzhou Strait (Su and Pohlmann, 2009). It was found that the center of cold surface waters was in the east onshore waters of Leizhou Peninsula and the inshore waters of Hainan Island (Fig. 3a), while the region of high Chl *a* concentration and high abundances of thaliaceans were recorded in the east mouth of Qiongzhou Strait and the east and southeast onshore waters of Hainan Island (Figs. 3e and 6c). The abundance of thaliaceans at region II is positively correlated to Chl *a* concentration (Table 2). The above results suggest that the increasing Chl *a* concentration is the main reason for the increased thaliacean abundance. However, at region I, the relationship between Chl *a* and thaliacean abundance is not correlated though both are present higher values than the other two regions (Table 2, Figs. 4C and 7B). We consider it as the stations with high Chl *a* and thaliaceans are not correspondingly overlapped, such as the former with a maximum value of Chl *a* (3.3 mg m$^{-3}$) at station C4 and the latter at station D1 (175 ind m$^{-3}$) (Figs. 3e and 6c). The maximum abundance of thaliaceans is recorded before the low temperature region between cold eddy in the east onshore waters of Leizhou Peninsula and coastal upwelling from the east shore waters of Hainan Island.

The influence of cold eddy and coastal upwelling on the distribution of thaliacean abundance is attributed to the high Chl *a* concentration. Thaliacea have complex life cycles with the alternation of sexual and asexual generations (Bone, 1998), and asexual reproduction results in thaliaceans being able to respond quickly to the favorable conditions of physical and phytoplankton dynamics (Deibel, 1985; Paffenhöfer and Lee, 1987; Paffenhöfer et al., 1995). As a consequence, thaliaceans are generally assembled in the region with high Chl *a*. *Dolioletta gegenbauri* was the most dominant species in Zhejiang coastal upwelling system and its abundance increased significantly in the shore areas (He et al., 1988). The positive influence of Chl *a* concentration on thaliacean abundance increased was also observed in the California current region (Berner and Reid, 1961; Silver, 1975; Blackburn, 1979), the northern part of Levantine Sea (Weikert and Godeaux, 2008), the Taiwan Strait (Tow and Lo, 2005; Zhang et al., 2003a) and the center of SCS (Lin and Lin, 2006). The occurrence of thaliacean abundance is located in the region with high phytoplankton production induced by the cold eddy and coastal upwelling during summer (Figs. 1, a, e and 6c). This is similar to that of northwestern Spain (Huskin et al., 2003) and the South Atlantic Bight (Deibel, 1985; Paffenhöfer and Lee, 1987; Paffenhöfer et al., 1995; Deibel and Paffenhöfer, 2009).

The patches of neritic salps and doliolids could be predictable and occur at various places in the world with the environmental condition of shallow continental shelf, upwelling waters and favorable winds (Deibel and Paffenhöfer, 2009), and the bloom of *Dolioletta gegenbauri* is explained on the shelf of the South Atlantic Bight (Deibel, 1985; Paffenhöfer et al., 1984, 1995; Paffenhöfer and Lee, 1987; Deibel and Paffenhöfer, 2009). In this

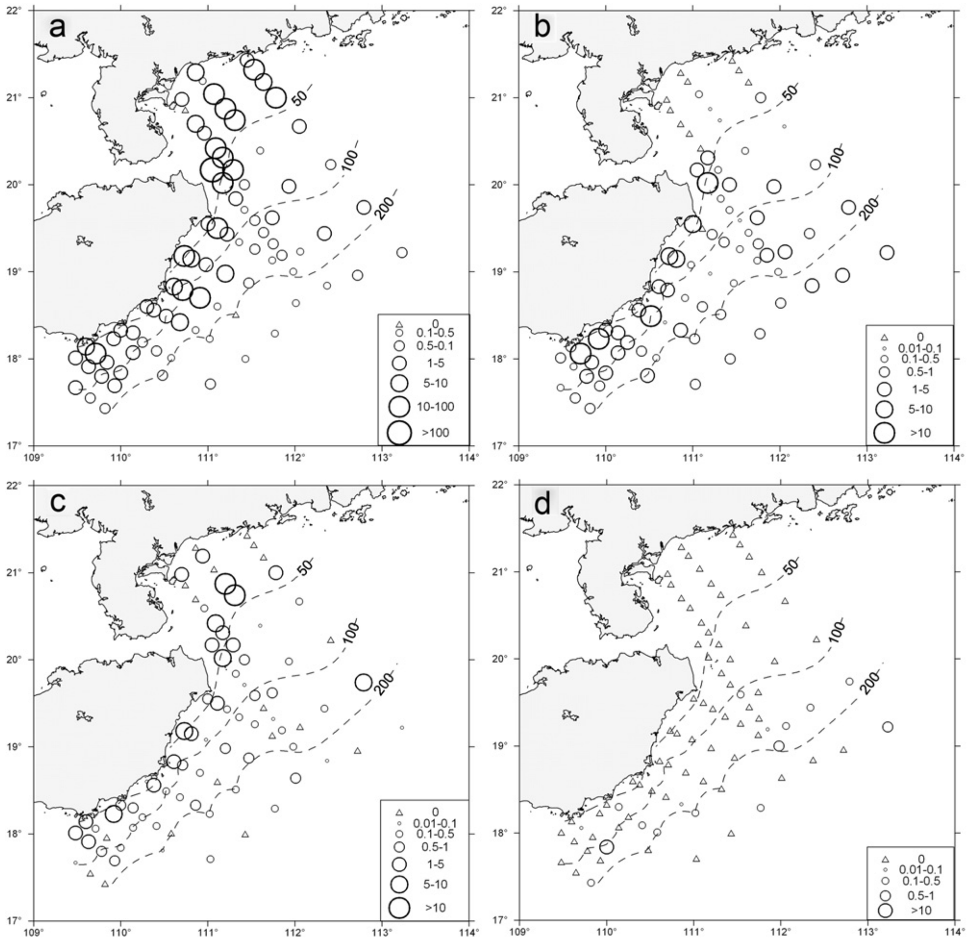


**Fig. 8.** Distribution of dominant species abundance in the northwest continental shelf of SCS ((a) summer—*D. denticulatum*; (b) winter—*D. denticulatum*; (c) summer—*T. democratica*; (d) winter—*T. democratica*).

study, the patches of thaliaceans resulted from the increased Chl *a* concentrtion forced by the cold eddy and coastal upwelling driven by both monsoon and topography, which is very similar to that in the South Atlantic Bight. In contrast to the dominance of *D. gegenbauri* in the South Atlantic Bight, *D. denticulatum* is the most dominant species in the northwest continental shelf of SCS (Table 1).

*D. denticulatum*, described as a neritic speices, inhabits the subtropical anticyclonic gyres and the area between in the Pacific Ocean (Berner and Reid, 1961). It has been found in abundance in various tropical and subtropical coastal waters, such as in the Australian waters (Thompson, 1948), the west coast of California (Berner and Reid, 1961), the Kuroshio (Yamaji, 1977), the southwest Taiwan coastal water (Tew and Lo, 2005) and the SCS (Yang et al., 1979; Lin and Lin, 2006). *D. denticulatum* is adapted to respond rapidly to the increased Chl *a* concentration at region I during summer, but retreated to region II and III during winter (Figs. 8a, b and 9A). The water depth in the east mouth of Qiongzhou Strait is less than 50 m, along with high Chl *a* concentration from 50 to 10 m might increase the abundance of *D. denticulatum* with the preference to the upper 50 m of the water column (Berner and Reid, 1961). In contrast with *D. denticulatum*, *T. democratica* occurred in slightly warmer waters (Fig. 8a–d) and distributed sporadically around the offshore waters in small numbers during winter, but could reach to the onshore waters with increased abundance in summer. The migration from offshore to onshore waters may be brought by the upwelling waters.

Under the influence of northeasterly monsoon during the winter cruise, onshore and offshore waters are vertically mixed well (Fig. 5b, d and f). The distribution of temperature, salinity and Chl *a* was characterized gradually from onshore to offshore waters (Fig. 3b, d and f). There is no significant difference from thaliacean abundance in spite of significant variance in the Chl *a* among three regions.

## 5. Conclusion

Our results suggest the value of temperature, salinity and the species richness and abundance of thalianceans in summer is significantly different from that in winter, and the regional distribution of temperature, salinity, Chl *a* and the species richness and abundance of thalianceans varies among all the three regions under this study. The environmental conditions of the three regions are controlled by different water masses during summer and winter. The seasonal and regional fluctuations of thaliaceans and environmental factors may be the consequence of the monsoon influence, in which seasonal fluctuations of coastal currents and temperature are in contrast to each other. The presence of coastal upwelling and cold eddy creates an area with high Chl *a* concentration that is favorable and conducive to the development of thaliacean patches. Future studies would investigate the vertical distribution of between SW and NE monsoons in the northwest continental shelf of SCS.

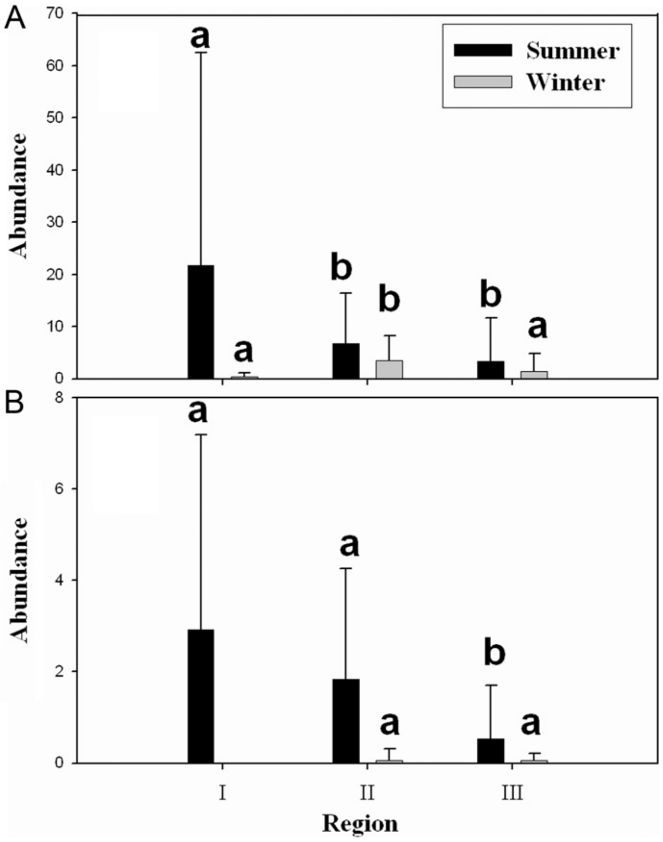


**Fig. 9.** Variations of the mean abundance of *D. denticulatum* (A) and *T. democratica* (B) at region I, II and III in summer and winter. Error bars represent SD. Columns denoted by different letters are significantly different from each other (ANOVA, $P < 0.05$).

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