

Onshore–offshore variations of copepod community in northern South China Sea

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Abstract Copepod communities in onshore and offshore waters show a gradient from primarily near shore to primarily oceanic species. Understanding the transition between these communities is fundamental to determining the range of coastal influence. Copepod communities in the northern South China Sea (nSCS) were studied based on samples collected by vertically towing a net in 10 February–6 March (winter) and 26 August–6 September (summer) of 2004. Calanoida species richness, total copepod abundance, Shannon–

Weaver diversity index, and onshore–offshore occurrence of dominant species showed obvious change from onshore to offshore waters. Although the offshore stations had lower abundance than the shelf stations, they had more species and larger diversity index. Abundance of some species (groups) with dominance index >5% (*Calanus sinicus*, *Euchaeta* spp., *Temora* spp., *Paracalanus parvus*, and *Subeucalanus subtenuis*) declined from onshore to offshore waters. Warm water species (*Pleuromamma abdominalis*, *P. gracilis*, and *P. robusta*) occurred in offshore waters in both cruises. Station (q-type) cluster analysis in winter and summer separated copepod community into onshore and offshore communities at ~40% level of similarity. The two communities were divided at the position of ~100-m isobath. In summer, *C. sinicus* occurred in the upwelling area east of Hainan Island, indicating the presence of an oversummering stock of this species.

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Introduction

Planktonic copepods are major members of zooplankton in biomass, abundance, and species number in marine pelagic ecosystems (de Puelles et al., 2003; Leandro et al., 2007). They graze on phytoplankton and microzooplankton (Sherr & Sherr, 2009). At the

same time, they are preyed by higher trophic levels such as fishes (Beaugrand et al., 2003). Therefore, copepods play pivotal roles in the transferring of energy from primary producers and microbial food web to the traditional food chain (diatom–copepod–fish) (Sherr & Sherr, 2009).

Coastal copepod communities are not isolated. They are inevitably influenced by the neighboring slope and basin waters. Understanding the transition between communities in onshore and offshore waters is fundamental to determine the range of coastal influence. Generally, the slope area is a transition zone between the coastal neritic system and the oceanic system. Onshore and offshore water is different in many aspects such as range of temperature, salinity, food type, and size and predator guilds (Mackas & Coyle, 2005). A species adapted to one environment might be unable to survive in another. Abundances of different species, therefore, follow a gradient from shelf to offshore waters. Copepod communities in onshore and offshore waters show a gradient from primarily near shore to primarily oceanic species. The abruptness of this gradient is a key feature of the ecology of coastal copepod communities and can be evaluated by station cluster analysis (Mackas, 1992; Kuipers et al., 1993; Lopes et al., 1999; Keister & Peterson, 2003; Morgan et al., 2003; Coyle & Pinchuk, 2005; Berasategui et al., 2006; Ramfos et al., 2006).

The South China Sea (SCS, Fig. 1A) is the largest semi-enclosed sea in the western tropical Pacific Ocean. In the northern South China Sea (nSCS, Fig. 1B), bottom topography is characterized by a steep continental slope between a shallow continental shelf (150–250 km width) in the northwest and a wide deep basin in the southeast. Surface current in this area is heavily influenced by East Asian Monsoon. In summer monsoon period (May–September), surface current is northeastward. In winter monsoon period (October to April next year), surface current is southwestward (Li, 2002). Summer upwelling along the coast of nSCS is a very common phenomenon. However, upwelling is not evenly distributed along the coast with strong upwelling east of Hainan Island (Li, 1990).

Data of planktonic copepods in nSCS is scarce and most of them are in the Pearl River estuary and waters with depth <200 m (Li et al., 2004, 2006; Tan et al., 2004). Copepods in the coastal area of nSCS

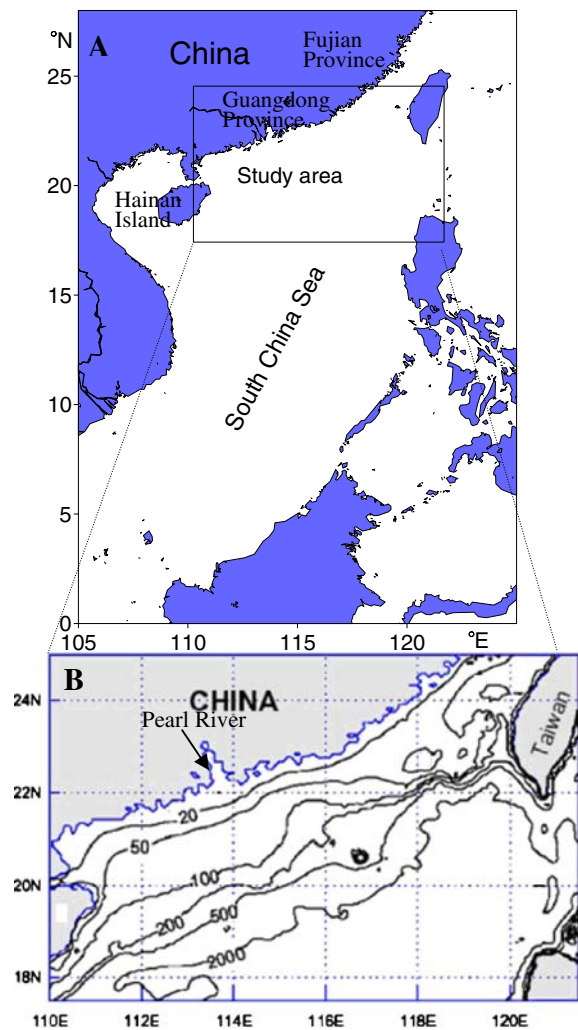


Fig. 1 Position (A) and isobath (B, adapted from Su (2004)) of northern South China Sea north of 18°N. Unit in isobath figure was meter

showed seasonal change and year to year variation. Generally, *Temora discaudata* and *Euchaeta concinna* dominated in spring. *Centropages furcatus* and *Undinula vulgaris* dominated in summer and autumn. *Canthocalanus pauper* and *E. concinna* dominated in winter (Li et al., 2006).

In this article, we study the gradient of planktonic copepod community from coastal area to slope and open ocean in nSCS. We hypothesized that, in the slope area of nSCS, copepod community will gradually change from coastal onshore community to offshore community as in other slope areas, and that the change in community structure would vary at different times of year.

Materials and methods

Station locations

Two cruises were carried out in nSCS in winter and summer, respectively, in 2004. The winter cruise was finished onboard R.V. *Yanping 2* during 10 February–6 March. Four transects (Fig. 2; A–D) was designed approximately perpendicular to the coastline. The summer cruise (26 August–6 September) was accomplished by R.V. *China Sea Guard 72* with two transects (Fig. 2; S1 and S2). Stations in transect D and S2 were the same stations with different names. Transect S1 was in the east of transect A. However, St. A9 and St. S1-1 was the same station in different cruise. Water depth (Table 1) increased from 17 m onshore (St. C7) to maximum 2,500 m (S1-10), i.e., the transects crossed coastal zone, continental shelf, slope, and open sea.

Hydrography and chlorophyll *a*

Remote-sensed AVHRR (advanced very high resolution radiometer) SST (sea surface temperature) data of local coverage with $1.1 \times 1.1 \text{ km}^2$ resolution were processed for the study area. Navigation and cloud detection techniques were applied in this study (Emery et al., 1986); cloud-free images were further processed to obtain the multi-channel SST data (Simpson & Humphrey, 1990; Kubota, 1994; Tang et al. 2004a, b).

The microwave scatterometer SeaWinds on QuikSCAT satellite measures surface wind speed over the oceans (Liu et al., 2000). On the basis of daily wind stress data, daily wind stress images were processed during the summer cruise.

In each station temperature and salinity as function of depth were obtained by lowering SBE-19 CTD instruments from surface to near the bottom. Water samples for chlorophyll *a* concentration (Chl *a*) measurement were collected at 0, 5, 10, 20, 30, 50, 100, and 200-m depth using Niskin bottles.

Water samples of 100–400 ml were filtered through GF/F glass-fiber filter for the determination of Chl *a*. The filters were kept at -20°C in a freezer until analyzing. The filters were extracted with 90% acetone at -20°C in a refrigerator without light for 24 h. Chl *a* was determined using Turner II fluorometer that was calibrated with pure chlorophyll *a* from Sigma.

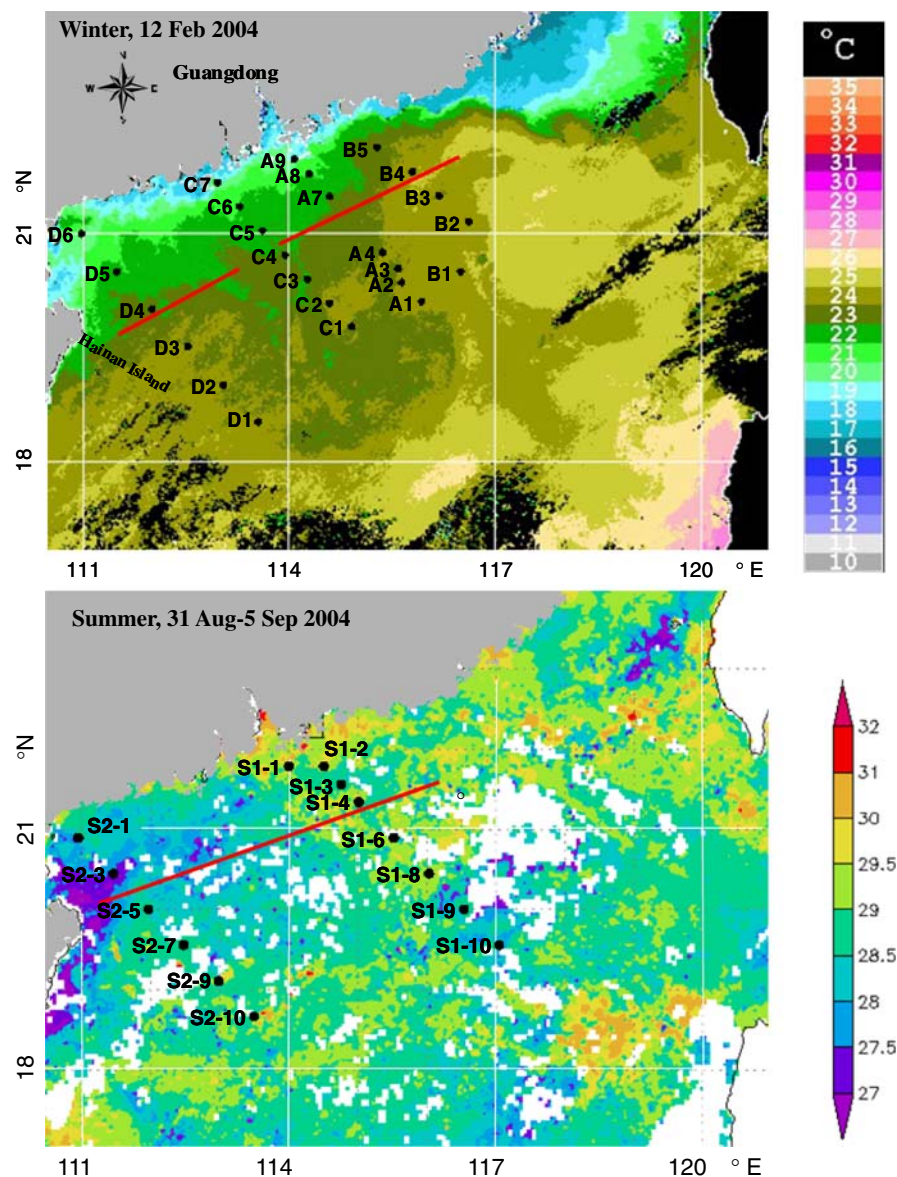
Copepod sample collection and data processing

In each station listed in Table 1 and Fig. 2, copepod samples were collected by conical plankton net (500- μm mesh size, 0.8-m mouth diameter, and 2.7 m total length) vertically towing from 2 m above bottom (from 200-m depth when water depth $>200 \text{ m}$) to the surface with a speed of 0.5 m s^{-1} . The samples in the cod end was poured into plastic bottles and fixed with formalin (final conc. 5%). Back in the laboratory, each sample was repeatedly divided with a Folsom splitter until subsample contained 300–500 copepod individuals. The subsamples were sorted and examined under stereomicroscope. Zooplankton groups of Chaetognatha, Alima larvae, Salps, Cladocera, Mysis, Amphipod, and copepods were counted. Copepod species was determined according to taxonomic references (Chen & Zhang, 1965; Chen et al., 1974). Species names were referred to Razouls et al. (2005–2008). Calanoid copepods were identified to species level while Cyclopoid copepods were identified to family level: Oithonidae, Oncaidae, Sapphirinidae, and Corycaidae. Individuals of copepodite stage were abundant and recorded as copepodites to genus: *Euchaeta* copepodite, *Candacia* copepodite, *Labidocera* copepodite, *Centropages* copepodite, and *Scolecithricella* copepodite. Other calanoid copepodite which could not be identified was labeled as calanoid copepodite. Abundance was derived from raw counts using subsample fraction, haul depth, and adopted as individuals per m^3 (ind./ m^3).

The characters of each station were examined in terms of calanoid species richness, dominant species, and Shannon–Weaver diversity index H' (Shannon & Weaver, 1963). The fraction (P_i) of i species abundance (N_i) in all species abundance (N) in all stations was calculated as $P_i = N_i/N$. The dominance index (Y) was calculated using the equation: $Y = P_i \times f_i$, where f_i was the occurring frequency of species i among all stations. Species with $Y > 2\%$ was defined as dominant species in each cruise (Xu & Chen, 1989). H' was calculated as $\sum_{i=1}^S (P_i) \log_2 P_i$, where S was total species number found in the cruise.

The dry weight (DW, μg) of each species was estimated according to the equation of Uye (1982): $\log DW = 3.13 \log L - 8.18$, where L was the prosome length (μm) of the species. Total dry weight

Fig. 2 Investigated stations and remote-sensed AVHRR SST images in winter (12 February, 2004) and summer (31 August–5 September 2004). The *solid line* showed the position where the copepod communities were divided into onshore and offshore communities by cluster analysis



of all the species in each station is calculated as the sum of dry weight of all the species appeared in that station.

Station (q-type) cluster analysis was performed according to Field et al. (1982) using group-average linkage based on the Bray–Curtis similarity matrix of root–root transformed original species abundance. The aim of the root–root transformation was to reduce the weights of abundant species. Species occurred in more than two stations were adopted. The software for cluster analysis was Primer 5 (Version 5.2.8).

Results

Satellite data and hydrograph

In February, SST was generally low in the nSCS, lower along the northern coastal water and higher in south part of nSCS. There was a cold water jet projecting from coast to the sea. A large cold eddy presented in the middle of nSCS (dark green color, 18–20°N, 114–116°E) (south of C1 station) on 12 February, 2004 (Fig. 2).

Table 1 Depth (*D*, m) of the stations (St.) in transects

St.	<i>D</i>	St.	<i>D</i>	St.	<i>D</i>	St.	<i>D</i>	St.	<i>D</i>	St.	<i>D</i>
A9	31	B5 ^a	50	C7	17	D6 ^a	24	S1-1 ^a	34	S2-1	27
A8	42	B4	95	C6	37	D5	58	S1-2	40	S2-3 ^a	53
A7	68	B3	150	C5	70	D4	89	S1-3	70	S2-5	94
A4	182	B2	324	C4	82	D3 ^a	152	S1-4	84	S2-7	160
A3	370	B1	790	C3	110	D2	231	S1-6	130	S2-9	150
A2 ^a	530			C2 ^a	182	D1 ^a	2,122	S1-8	1,000	S2-10	700
A1 ^a	1,100			C1	2,160			S1-9 ^a	1,100		
								S1-10	2,500		

^a Sampled at night (19:00 pm–6:00 am)

We could not find good daily SST image for summer due to cloud coverage. Therefore, we got one 6-day-average SST image during 31 August–5 September, 2004 (Fig. 2). This image showed strong cold water upwelling east of the Hainan Island. Southerly wind was observed on 31 August 2004 and westerly wind on 4 September, 2004.

The hydrograph of transects A–D and S1, S2 were depicted as in Fig. 3. Surface temperature, salinity, and Chl *a* in winter were 15.6–24.5°C, 31.18–34.77, and 0.1–1.8 µg/l, respectively. These values in summer were 27.5–30.1°C, 24.79–34.00, and 0.07–15.5 µg/l, respectively. From onshore to offshore, surface temperature and salinity increased while Chl *a* decreased. Vertically from surface to bottom (200 m when water depth >200 m), transect A and D were well mixed in onshore stations in terms of temperature, salinity, and Chl *a*. Other transects were well stratified in both offshore stations and onshore stations.

Copepod community

Totally 66 species belonging to Calanoida were identified in the two cruises, among them 58 in winter and 62 in summer. Calanoida species richness of each station ranged from 4 (St. D6) to 41 (St. S1-9), with larger values in the offshore side (Fig. 4).

Total copepod abundance (Fig. 4) was 11–398 ind./m³ in winter and 16–218 ind./m³ in summer. Total dry weight of all the copepods was 0.86–33.96 and 0.65–8.44 mg/m³ in winter and summer, respectively. Both total abundance and total dry weight was high in the onshore side. Shannon–Weaver diversity

index *H'* (Fig. 4) was 1.11–4.54 in winter and 2.78–4.85 in summer with high values in the offshore side.

Most of the species had low abundance. In winter, species with maximum abundance larger than 10 ind./m³ were *Calanus sinicus*, *Subeucalanus subtenuis*, *S. subcrassus*, *Paracalanus parvus*, *Clausocalanus furcatus*, *Euchaeta* copepodite, and *Temora stylifera*. Maximum abundance of *C. sinicus* was the highest (225 ind./m³) among all the species recorded. In summer, *C. sinicus*, *S. subtenuis*, *S. subcrassus*, *P. parvus*, *Clausocalanus pergens*, *Euchaeta* copepodite, *Temora turbinata*, *T. discaudata*, *T. stylifera*, and *Pleuromamma gracilis* had abundance larger than 10 ind./m³. Abundance of *T. turbinata* had the maximum abundance (72 ind./m³).

Although the copepod community was comprised of more than 60 species, the abundance variability of the community was due to abundance variability of very few species or copepodites. Dominant species (*Y* > 2%) in winter were *C. sinicus*, *P. parvus*, *Euchaeta* copepodite, *S. subcrassus*, *Clausocalanus arcuicornis*, and *C. furcatus*. In summer, the dominant species were *Canthocalanus pauper*, *Nannocalanus minor*, *S. subcrassus*, *P. parvus*, *T. turbinata*, *T. discaudata*, and *T. stylifera*. Total abundance of the dominant species was 50–96% (on average 76%) of total copepod abundance.

Some species with dominance index value *Y* > 5% were *C. sinicus* (winter 16.9%), *Euchaeta* copepodite (winter 11.1%, summer 11.1%), *T. turbinata* (summer 5.2%), *S. subtenuis* (winter 9.0%, summer 6.4%), and *P. parvus* (winter 11.9%, summer 5.1%). In order to study the spatial distribution of these species, we artificially combined *Euchaeta rimana*, *E. concinna*,

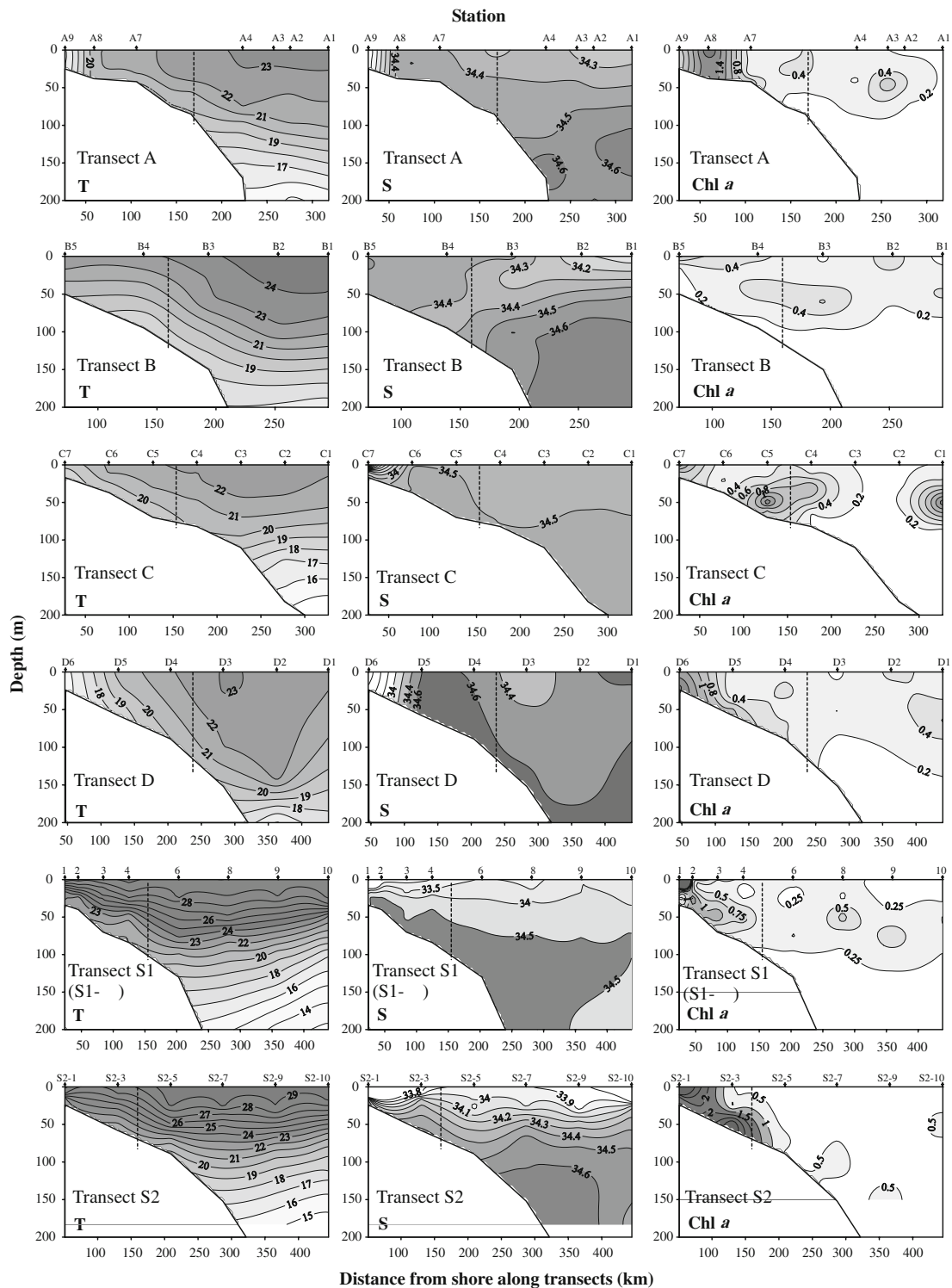


Fig. 3 Distribution of temperature (*T*, °C), salinity (*S*), and chlorophyll *a* concentration (*Chl a*, µg/l) along six transects. The vertical dashed lines in the figures showed the position

where the copepod communities were divided into onshore and offshore communities by cluster analysis

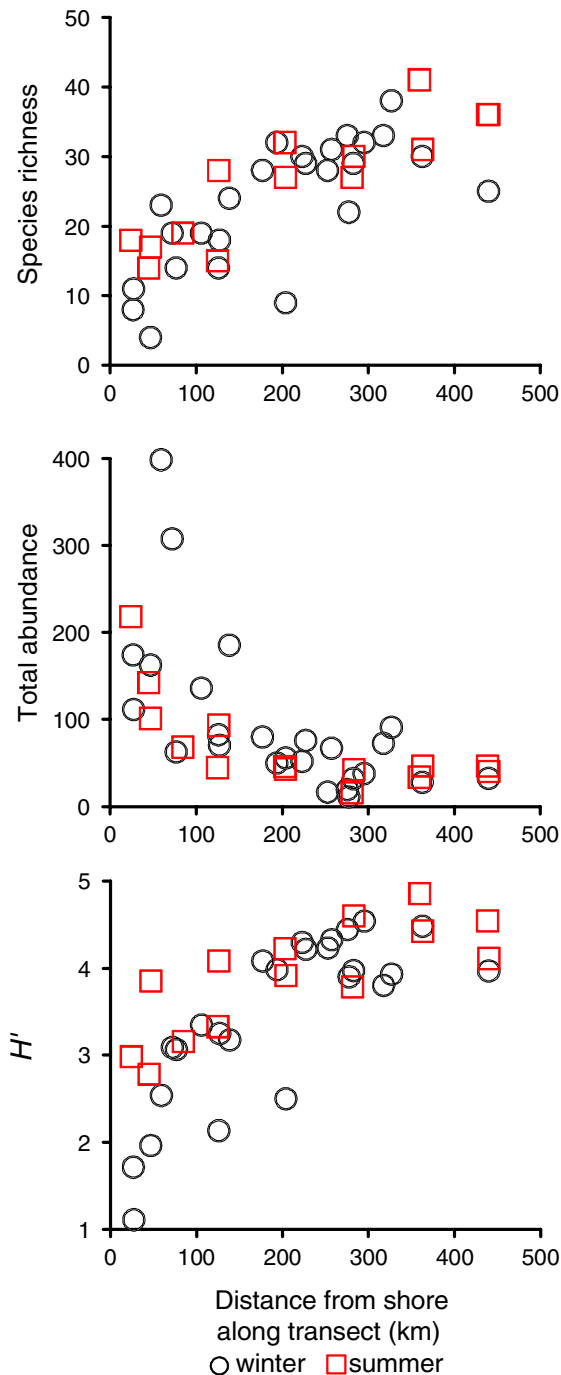


Fig. 4 Relationship between Calanoida species richness, total copepod abundance (ind./m³), Shannon–Weaver diversity index (H'), and distance from shore along transects

and their copepodite into group of *Euchaeta* spp. because the copepodite could not be identified into species. Similarly, *Temora trubinata*, *T. discaudata*,

T. stylifera were combined into *Temora* spp. because each of them had $Y > 2\%$ in summer. Abundance of *C. sinicus*, *Euchaeta* spp., *Temora* spp., *P. parvus*, and *S. subtenuis* declined from onshore to offshore area (Fig. 5). In the case of *P. parvus*, its abundance was high in St. C1. Similarly, *S. subtenuis* abundance was high in St. A1 (Fig. 5).

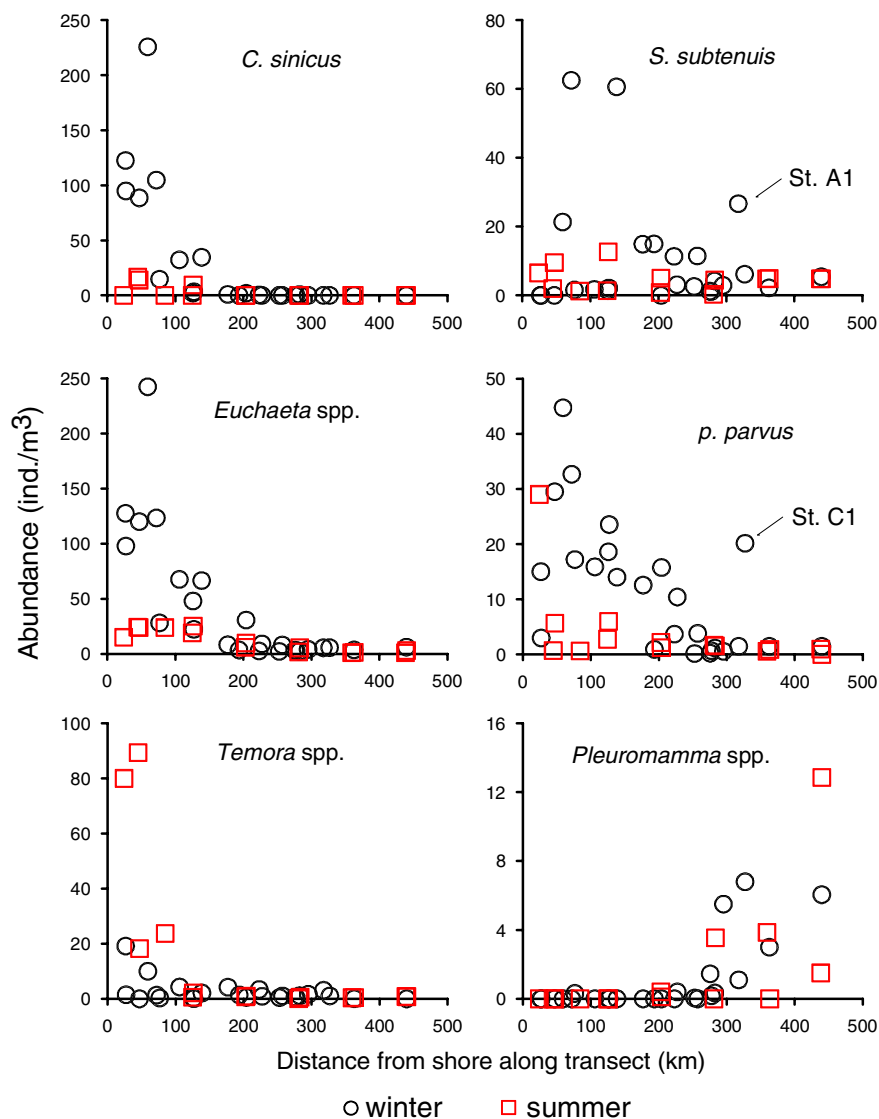
Although *P. gracilis* was not a dominant species in both winter and summer, this species was prominent because it was the only species which had maximum abundance >10 ind./m³ and only occurred in outermost stations. Similarly, we artificially combined the three species (*P. abdominalis*, *P. gracilis*, and *P. robusta*) in the genus *Pleuromamma* into a group of *Pleuromamma* spp. This group only occurred in the offshore deep stations of each transect (Fig. 5).

Abundance of the dominant species changed with seasons obviously. Some species had larger abundance in winter than in summer. For example, maximum abundance of *C. sinicus* was 225 ind./m³ in winter and 16 ind./m³ (St. S1-2) in summer, respectively. *C. sinicus* was also present in St. S2-1 (13.9 ind./m³) and St. S2-2 (9.4 ind./m³) in summer. Similarly, maximum abundance of *Euchaeta* spp. were 242 ind./m³ in winter and 25 ind./m³ in summer, respectively. Others had larger abundance in summer. *Temora turbinata* had maximum abundance of 7 ind./m³ in winter and 72 ind./m³ in summer (Fig. 5).

Classification dendrogram of stations separated the copepod community into onshore and offshore communities both in winter and summer at $\sim 40\%$ level of similarity (Fig. 6). The two communities were divided at ca. 100-m isobath (Fig. 2). Generally, onshore community had lower temperature, lower salinity, higher Chl *a*, lower Calanoida species richness, higher abundance, and lower diversity than offshore community in both winter and summer (Table 2). Both onshore and offshore communities had higher species richness, lower abundance, and higher diversity in summer than in winter (Table 2).

Dominant species in onshore and offshore communities in winter and summer were identified as in the whole community (Table 2). Dominant species in onshore community had higher Y ($>25\%$) in both summer and winter. Onshore community underwent seasonal succession with decrease in *C. sinicus* abundance and increase in *Temora* spp. abundance from winter to summer. Offshore community did not show obvious change between the two seasons. The

Fig. 5 Relationship between abundances of dominant species (groups) and distance from shore along transects



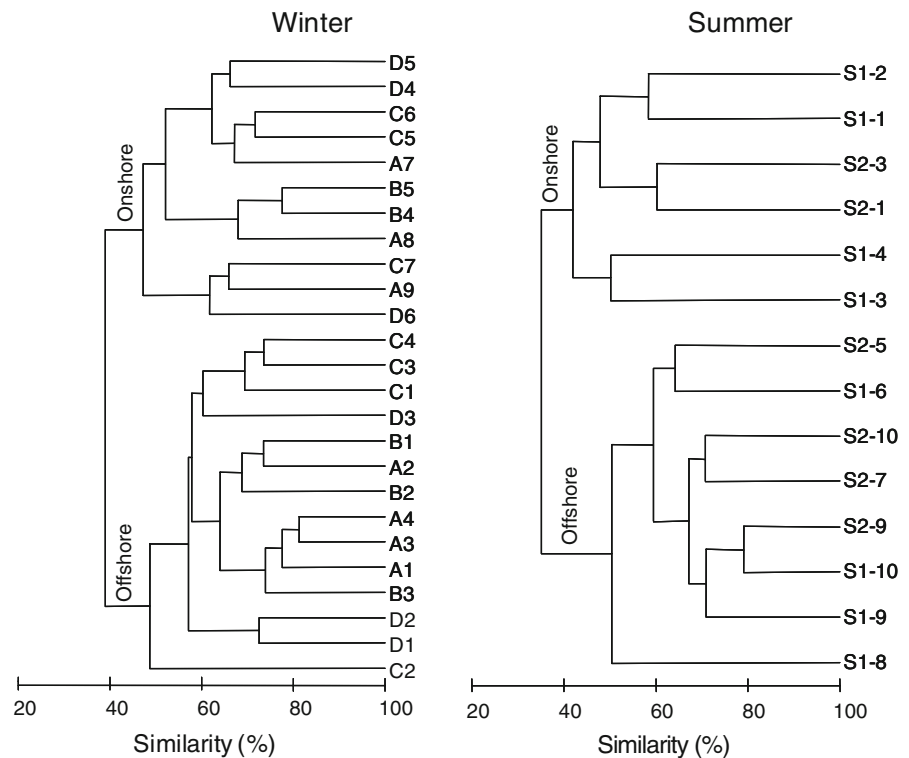
species dominance index among offshore stations in the two seasons identified nearly same dominant species (groups): *Euchaeta* spp., *Subeucalanus subtenuis*, *Cosmocalanus darwinii*, and *Nannocalanus minor*.

Discussion

In order to interpret and discuss the results of this study, limitation of the sampling method should be pointed out. Mesh size in this study was 500 μ m, which was too large for small size copepods to be fully

sampled. As a result, small copepods (<1 mm in length), which were generally the most important component of the zooplankton in the ocean (Turner, 2004), were not fully represented. Those small copepods include adults and copepodites of calanoid genera (such as *Paracalanus*, *Pseudocalanus*, *Acartia*, and *Clausocalanus*), cyclopoid genera (such as *Oithona*, *Oncaea*, and *Corycaeus*) and planktonic harpacticoids of the genus *Microsetella*. Caution should be taken concerning those species. However, some general characteristics of onshore and offshore copepod community variations could be identified in this study.

Fig. 6 Dendrogram result of station cluster analysis. Dendrogram of the sampling stations was based on root-root transformed species abundance using Bray–Curtis similarity matrix and weighted group-average linkage method



General characteristics of onshore and offshore copepod community variations

In our study, species richness decreased from shelf to offshore area. The result that the onshore communities were less diverse than the offshore communities agrees with Hebard (1966), Lee (1971), and Keister & Peterson (2003), who found that diversity tended to increase offshore in waters off Oregon, USA. This phenomenon has also been reported in slope waters off Mauritania (Kuipers et al., 1993), Brazil (Lopes et al., 1999) and Argentina waters outside Rio de la Plata River (Berasategui et al., 2006).

Total copepod abundances were generally higher on the shelf. This was consistent with that in Brazil (Lopes et al., 1999), Oregon (Morgan et al., 2003; Lamb & Peterson, 2005) and Ionian Sea, eastern Mediterranean (Ramfos et al., 2006) and northern California upwelling zone (Papastephanou et al., 2006). The higher abundance and biomass of the onshore community was attributed to the high productivity in onshore waters (Morgan et al., 2003). In this study, the Chl *a* was higher in the shelf stations (Fig. 3).

Copepod abundance and biodiversity in our study co-varied negatively: high abundance with low biodiversity on the shelf and vice versa in the offshore area. This phenomenon was also observed in northern California current ecosystem (Hooff & Peterson, 2006), where summer months resulted in increased copepod biomass and relatively few copepod species, whereas winter conditions were characterized by low biomass and high species richness.

Seasonal and spatial occurrence of dominant species with Y value $>5\%$

Calanus sinicus is a copepod with wide geographical distribution in the continental shelf waters of the northwest Pacific Ocean from Bohai Sea to coast of Vietnam. Far less information is available on the distribution pattern and seasonality of *C. sinicus* in the shelf waters of the South China Sea. Temperature is an important factor regulating the distribution of *C. sinicus* (Uye, 2000). The upper thermal limit for *C. sinicus* is 26–27°C (Wang et al., 2003). Temperatures $>23^{\circ}\text{C}$ are considered to be stressful to *C. sinicus* (Uye, 1988). *C. sinicus* was considered to

Table 2 Characteristics of onshore and offshore communities in winter and in summer

	T ($\pm SD$)	S ($\pm SD$)	Chl a ($\pm SD$)	SR ($\pm SD$)	A ($\pm SD$)	H' ($\pm SD$)	Dominant species (dominance index (Y) in onshore and offshore communities, respectively)
Winter							
Onshore, $n = 11$	20.3 (± 2.5)	34.02 (± 1.02)	0.72 (± 0.53)	14.8 (± 6.4)	158 (± 108)	2.53 (± 0.73)	<i>C. sinicus</i> (41.5%), <i>Euchaeta</i> spp. (13.1%), <i>S. subtenuis</i> (5.5%), and <i>P. parvus</i> (13.2%)
Offshore, $n = 14$	23.2 (± 0.7)	34.36 (± 0.19)	0.24 (± 0.11)	30.0 (± 3.8)	48 (± 26)	4.16 (± 0.23)	<i>E. subtenuis</i> (16.2%), <i>Euchaeta</i> spp. (8.5%), <i>Clausocalanus arcuicornis</i> (4.9%), <i>Cosmocalanus darwini</i> (4.3%), <i>C. furcatus</i> (3.4%), <i>Nannocalanus minor</i> (2.8%), and <i>R. nasutus</i> (2.2%)
Summer							
Onshore, $n = 6$	29.2 (± 1.1)	31.37 (± 3.56)	3.55 (± 6.06)	18.5 (± 5.0)	111 (± 61)	3.37 (± 0.50)	<i>Temora</i> spp. (26.8%), <i>Euchaeta</i> spp. (12.7%), <i>E. subcrassus</i> (9%), <i>P. parvus</i> (6.7%), <i>S. subtenuis</i> (5.0%), <i>C. sinicus</i> (3%), and <i>Canthocalanus pauper</i> (2.6%)
Offshore, $n = 8$	29.4 (± 0.1)	33.79 (± 0.19)	0.20 (± 0.07)	32.5 (± 4.8)	39 (± 10)	4.31 (± 0.36)	<i>E. subtenuis</i> (9.5%), <i>Euchaeta</i> spp. (9.3%), <i>N. minor</i> (8.3%), <i>Pleuromamma</i> spp. (4.1%), <i>C. darwini</i> (3.9%), <i>P. parvus</i> (2.5%), and <i>Neocalanus gracilis</i> (2.2%)

T surface temperature ($^{\circ}\text{C}$), S surface salinity, Chl a surface chlorophyll a concentration ($\mu\text{g/l}$), SR Calanoida species richness, A total copepod abundance (ind./m^3), H' Shannon–Weaver diversity index, SD standard deviation, n station number

be not endemic to Chinese shelf waters to the south of Fujian Province (Fig. 1), but was carried into nSCS by the cold China Coastal Current (CCC) which originated in the East China Sea (Hwang & Wong, 2005). The mass occurrence of this species in winter was consistent with previous reports. However, we found this species in late August and early September in one station near Hong Kong and two stations east of Hainan Island. Meanwhile, northeast monsoon did not begin in this period. SST data indicated a strong upwelling cold water east of Hainan Island, where *C. sinicus* appeared. Temperature in the upper waters of the upwelling area was $>23^{\circ}\text{C}$ (Fig. 3). Therefore, the upper layer was not a suitable habitat for this species to reside. It might stay below the thermocline where temperature was slightly lower than 23°C . Although stations outside of the upwelling had cold bottom waters ($<23^{\circ}\text{C}$), *C. sinicus* was not found in those stations. Therefore, the cold bottom water was not a source of *C. sinicus*. Thus, *C. sinicus* in the

nSCS was not caused by the CCC but rather an over-summering stock. The notion that *C. sinicus* was carried into nSCS by the CCC should be reconsidered.

There was very little knowledge about the seasonal and spatial distribution of *Euchaeta* spp. (*E. rimana* and *E. concinna*) and their relationship with environmental factors (Xu, 2006). In our study, abundance of *Euchaeta* spp. was higher in winter than in summer. This result was consistent with the data in East China Sea, where abundance of *E. concinna* was higher in autumn and winter than in summer (Xu, 2006).

Temora spp. was dominant in summer in our study and *T. turbinata* was more abundant than the other two species: *T. discaudata* and *T. stylifera*. *T. turbinata* was a widespread coastal species from tropical, subtropical, and temperate areas of the Indian Ocean, west Pacific, and Atlantic Oceans. There is a lower temperature limit to the survival of this species. For example, in the New Zealand region a temperature limit of about 15°C is apparent (Bradford, 1977).

In nSCS, very low abundance of *Temora* spp. in winter might be due to lower temperature stress.

Abundances of *C. sinicus*, *Euchaeta* spp., and *Temora* spp. showed obvious decreasing trend from onshore to offshore sites. These species might be sensitive to environmental change. However, other species might have good ability to adapt to different environments. *S. subtenuis* was an inhabitant of eutrophic oceanic waters (Fleminger, 1973). As a tropical oceanic species, it was extraordinary for *S. subtenuis* to occur in onshore stations as in transect B and S2. Wang & Zuo (2004) also found this species intruding northward into the Yellow Sea in winter along with the Yellow Sea Warm Current. Another species with good adaptive ability might be *P. parvus*. In winter, *P. parvus* was transported out to the sea as far as St. C1 while other coastal species diminished in the cold water jet.

Division of onshore and offshore copepod communities

Although zooplankton community in onshore and offshore waters showed a gradient from primarily near shore to primarily oceanic species, station cluster analysis identified separate onshore and offshore communities abruptly at the inner part of shelf break (depth of 100 m) in both winter and summer in this study. The zonation of onshore (shelf) and offshore/slope assemblages was a seasonal phenomenon in other sites. For example, groupings on the Gulf of Alaska were occasionally found in May 1999 and 2001, July 1998 and October 2000 (Coyle & Pinchuk, 2005). In offshore and coastal waters of the Ionian Sea (eastern Mediterranean), an ‘offshore’ and a ‘coastal’ copepod assemblage were defined in the surface layer (0–50 m) only during March (Ramfos et al., 2006). Keister & Peterson (2003) found that the zonation was found only in summer with upwelling condition off central Oregon coast.

The position where onshore and offshore communities could be divided might be related to fronts, which located most probably at or near the continental shelf break (Mackas & Coyle, 2005). In this study, the coastal current and oceanic water could be differentiated easily according to the sharp color changes in remote sensing sea surface temperature in winter (Fig. 2).

While the shelf community underwent seasonal succession, the offshore community did not show obvious change between the two seasons. This result was consistent with Keister & Peterson (2003), who studied the zooplankton zonation in Oregon coast (30–2,850 m depth). Their cluster analysis identified four primary groups (clusters) of stations based on similarities in zooplankton community structure. One of the groups was found in deep off-shelf waters in summer and at all stations in winter (“offshore summer/everywhere winter group”) during 1999 and 2000. The off-shelf community showed no change in summer and winter.

In summary, Calanoida species richness, total copepod abundance, Shannon–Weaver diversity index, and abundance of dominant species of planktonic copepod community in nSCS had abrupt onshore to offshore gradient both in winter and summer. Distinct onshore and offshore copepod communities were identified by station cluster analysis in both seasons. *C. sinicus* might have an over-summering stock.

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