Plankton abundance, biovolume, and normalized biovolume size spectra in the northern slope of the South China Sea in autumn 2014 and summer 2015

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\begin{abstract}
Plankton abundance, biovolume and distribution in the northern slope of the South China Sea in summer 2015 and autumn 2014 were assessed by using flow cytometry and microscopy (FlowCAM) and ZooScan methods. Copepoda was the most dominant zooplankton in both seasons. \textit{Rhizosolenia} dominated the phytoplankton community in autumn. In summer, the dominant phytoplankton were \textit{Chaetoceros} and \textit{Thalassionema}. In autumn, the abundances of phytoplankton and zooplankton ranged from \(0.66 \times 10^3\) to \(7.83 \times 10^3\) ind. m\(^{-3}\) and \(0.34 \times 10^2\) to \(0.88 \times 10^3\) ind. m\(^{-3}\), respectively, whereas the biovolumes of phytoplankton and zooplankton ranged from 41.67 to 204.66 mm\(^3\) m\(^{-3}\) and 56.19-157.24 mm\(^3\) m\(^{-3}\), respectively. A wide range of normalized biovolume size spectra (NBSS), consisting of phytoplankton, mesozooplankton and macrozooplankton, were built, and the resulting NBSS slopes were flatter than the single zooplankton NBSS slope. The NBSS slopes were steeper in summer (mean \(\pm\) SE = \(-0.93 \pm 0.04\)) than in autumn (mean \(\pm\) SE = \(-0.69 \pm 0.05\)). Based on the biovolume (0.00024 mm\(^3\)–131.07 mm\(^3\)) of plankton in 19 size classes and the taxonomic groups in each size class, Bray-Curtis cluster analysis divided the plankton into five groups. The distributions of the five plankton groups coincided with changes in currents during autumn and summer. Groups A and B were distributed in a region with an anticyclonic and a cyclonic eddy, respectively. Group A was affected by SCSW (South China Sea Water) and KW (Kuroshio Water) and had a NBSS slope of nearly \(-1\). Group B was influenced by SCW, KW and SHW (Shelf Water), and the NBSS slope of group B showed a higher ecological transfer efficiency than that of group A. Group C and group D were influenced by westward currents. The sea surface temperature (SST) \((r = -0.52, P < 0.01)\), chlorophyll \(a\) concentration at the depth of the chlorophyll maximum (SMChl-\(a\)) \((r = -0.61, P < 0.01)\), and average chlorophyll \(a\) concentration (SACChl-a) \((r = -0.59, P < 0.01)\) were negatively correlated with the NBSS slope.
\end{abstract}

\section{Introduction}

Plankton are key factors in global biogeochemical cycles and important indicators of climate variability (Barton et al., 2013; Prowe et al., 2012; Edwards et al., 2013). Zooplankton link the primary producers (phytoplankton) with higher trophic levels (Banse, 1995; Wassmann et al., 2006). Both groups participate in energy fluxes, vertical particle fluxes, and biological pump processes in marine system (Buitenhuis et al., 2006; Körboe, 1998; Reynolds, 2001; Sanders and Wickham, 1993). Therefore, it is essential to study the characteristics of plankton to provide an understanding of the potential elemental and energy transfers within marine systems.

Body size is a well-established key plankton index (Bautista and Harris, 1992; Landry et al., 1985). Body size can reflect physiological and ecological activities such as metabolic processes and predator-prey relationships (Boudreau et al., 1991; Zhou and Hunteley, 1997). Size-based normalized biovolume size spectra (NBSS) are receiving increasing attention as an important alternative means for the study of plankton characteristics. Compared to time-consuming traditional approaches, NBSS characterize the energy fluxes and structures of plankton depending on size information in a simple and intuitive manner (Dickie et al., 1987; Platt and Denman, 1977; Quinones et al.,...
et al., 2016; Wang et al., 2016; Zhao et al., 2017; Gan et al., 2009). Most and is characterized by complex mesoscale physical processes (Leng et al., 2012). García-Comas et al., 2014 recently reported that in the East China Sea, no relationship between slope steepness and variations in slopes in different environments. In the coastal upwelling areas off Chile, the average NBSS slope of zooplankton was −1.18, with the mid-shelf showing the shallowest slope, and the inshore zone exhibiting a flatter slope, which was caused by an increase in the abundance of large organisms (> 3mm) (Manríquez et al., 2012). In the northeastern shelf of the South China Sea, the NBSS can distinguish physical processes, as the NBSS slope of the coastal upwelling area (~ 0.88) was shown to be steeper than that of the Pearl River plume (~ 0.759) (Zhou et al., 2015). The NBSS slope within an Arctic fjord was determined to be approximately −1 (Trudnowska et al., 2014). The relationship between NBSS parameters and environmental factors has also been examined. Furthermore, because of variations in slopes in different ecosystems, the factors that influence NBSS slopes might differ among regions (García-Comas et al., 2014; Manríquez et al., 2012). Garcia-Comas et al., 2014 recently reported that in the East China Sea, no relationship between slope steepness and the environment was observed. However, no study has examined the plankton NBSS and its relationship with environmental factors in the continental slope area of the South China Sea.

The South China Sea is the third largest marginal sea in the world and is characterized by complex mesoscale physical processes (Leng et al., 2016; Wang et al., 2016; Zhao et al., 2017; Gan et al., 2009). Most physical-biological coupling studies on the South China Sea have involved physical processes, phytoplankton stocks and primary production, and the results of these studies have indicated that mesoscale currents influence the distribution of phytoplankton, while cold eddies enhance phytoplankton growth (Ning et al., 2004; Tseng et al., 2005; Chen et al., 2007; Li et al., 2015; Dong et al., 2015). In addition, most studies of the NBSS have investigated individual functional groups (such as zooplankton or mesozooplankton), but the food chain in the marine system comprises several functional groups or trophic levels, and the interactions among these groups supports the marine ecological system. Thus, we built a wide range of biovolume spectra containing phytoplankton, mesozooplankton and macrozooplankton to evaluate the ecological status of plankton. In addition, establishing the NBSS in the Kuroshio Water (KW) and South China Sea Water (SCSW) of the continental slope area of the South China Sea were analyzed in terms of plankton abundance, biovolume and NBSS by using flow cytometry and microscopy (FlowCAM) and ZooScan. The relationship between plankton distributions and mesoscale currents, as well as that between environment factors and NBSS slopes, were analyzed.

2. Methods

2.1. Sampling

Sampling was conducted in autumn (October 2014) and summer (June 2015) on board R.V. Nanfeng in the northern slope of the South China Sea (Fig. 1, Table 1). Plankton samples were collected during the day or night using vertical tows with a microplankton net (opening area: 0.1m², mesh size: 0.077mm) for phytoplankton and a mesoplankton net (opening area: 0.2m², mesh size: 0.160mm) and macroplankton net (opening area: 0.5m², mesh size: 0.505mm) for zoo- plankton. Tows were from the bottom (depth: > 200m) or 200m (depth: > 200m) to the surface with a vertical speed of 0.4ms⁻¹. All samples were fixed in 5% formaldehyde and analyzed in the laboratory.

2.2. Environmental data collection

A SeaBird CTD (SeaBird Inc., USA) was used to record temperature and salinity. A CTD-Rosette (KC-Denmark Inc., Denmark) fitted with 10-L Niskin bottles collected water used for the determination of chlorophyll-a (Chl-a) concentrations. Chl-a was measured in samples collected at depths < 200m. When the bottom depth was < 200m, the deepest sampling depth was 5m above the sea bottom. A 200-μm mesh was used to remove zooplankton from the sample, after which the water was passed through 0.68μm Whatman GF/F membranes (Whatman Inc., England). The samples were preserved at −20°C for analysis using a Turner Designs fluorometer (Turner Designs Inc., USA).

2.3. Sample analysis

Two complementary techniques, namely, FlowCAM (Fluid Imaging Technologies Inc., USA) (Sieracki et al., 1998) and ZooScan (HYDROPTIC, France) (Gorsky et al., 2010), were used to determine plankton abundance. The samples from the microplankton net were analyzed by FlowCAM, mainly phytoplankton. And those from the mesoplankton and macroplankton nets were analyzed by ZooScan, respectively. Phytoplankton were counted and estimated using FlowCAM in an autotrigger mode. Prior to the estimations, a 5-mL aliquot of the water sample was filtered through 600-μm and 300-μm mesh nets, successively, and then diluted 4–8 times with distilled water. Samples within the size range of 77–300μm, as examined under a × objective lens, were pumped through a 3mm × 0.3mm cross-section chamber for 20min. Samples within the size range of 300–600μm were pumped through a 6mm × 0.6mm cross-section chamber for 20min. The organisms were assumed to be spherical, and the biovolume was calculated using the equivalent spherical diameter (ESD). Taxa information was obtained based on the South China Sea phytoplankton sample library of the FlowCAM system.

Zooplankton were estimated using the ZooScan system at a resolution of 4800 dpi. ZooScan is suitable for organisms ranging in size from 200μm to several centimeters, and there is no strict limitation on the number of individuals processed in each scan, but it is important to minimize the coincidence of overlapping animals on the optical surface. Thus, a fraction of each sample, usually between 1/2 and 1/64, was isolated with a splitter and analyzed with ZooScan hardware. Images were processed with ZooProcess (Gorsky et al., 2010) and classified by using Plankton Identifier software (Gasparini, 2007; Sun et al., 2011). ZooProcess will choose organisms larger than 300μm. All zooplankton were regarded as long ellipsoids. The length (here the major axis of the best fitting ellipse) and width (here the minor axis) of each organism were measured using ZooProcess, and their volumes were calculated using the following formula:

\[ V = \frac{4\pi}{3} \left( \frac{Major}{2} \right)^{2} \left( \frac{Minor}{2} \right) \]

The classification was conducted using the created set, which put similar visual appearances into a single folder. During the classification, the useful variables were length, width, area and volume, and the statistical algorithm was Spv 3 (C-svc RBF). After automatic classification using Plankton Identifier, correction of sorting was performed. Any incorrectly classified particles were moved to the correct folder.

2.4. Construction of NBSS

Before constructing the NBSS, all the organisms were picked out from the original FlowCAM- and ZooProcess-analyzed pictures, and all the detrital particles were discarded. Then, the phytoplankton and
Table 1
Sampling station information and hydrography parameters.

| Station | Location | Bottom depth (m) | Day/Night | Average temperature (°C) | Average salinity | Average Chl-a (mg·m\(^{-3}\)) |
|---------|----------|------------------|-----------|---------------------------|-----------------|-----------------------------|
|         | Latitude | Longitude        |           |                           |                 |                             |
| **Summer** |          |                  |           |                           |                 |                             |
| S01     | 20.35    | 114.24           | 123.00    | D                         | 23.50           | 34.28                        |
| S02     | 19.86    | 114.48           | 560.00    | N                         | 21.82           | 34.38                        |
| S03     | 19.42    | 114.79           | 1305.00   | D                         | 21.97           | 34.46                        |
| S04     | 18.93    | 115.08           | 3000.00   | N                         | 21.41           | 34.38                        |
| S05     | 19.14    | 115.64           | 3000.00   | N                         | 22.00           | 34.51                        |
| S06     | 19.63    | 115.32           | 2104.00   | N                         | 21.59           | 34.41                        |
| S07     | 20.10    | 115.05           | 480.00    | D                         | 21.28           | 34.39                        |
| S08     | 20.56    | 114.75           | 120.00    | N                         | 23.24           | 34.35                        |
| S09     | 20.80    | 115.27           | 190.00    | D                         | 24.49           | 34.26                        |
| S10     | 20.31    | 115.56           | 535.00    | N                         | 20.08           | 34.17                        |
| S11     | 19.79    | 115.87           | 1527.00   | D                         | 19.83           | 34.28                        |
| S12     | 19.43    | 116.20           | 1971.00   | D                         | 20.55           | 34.17                        |
| S13     | 19.67    | 116.71           | 2050.00   | N                         | 19.67           | 34.26                        |
| S14     | 20.35    | 116.46           | 975.00    | D                         | 19.60           | 34.39                        |
| S15     | 20.52    | 116.13           | 680.00    | N                         | 19.32           | 34.41                        |
| S16     | 20.99    | 115.73           | 225.00    | N                         | 19.37           | 34.44                        |
| **Autumn** |        |                  |           |                           |                 |                             |
| A01     | 20.35    | 114.23           | 120.00    | D                         | 26.40           | 34.17                        |
| A03     | 19.53    | 114.66           | 1250.00   | D                         | 22.48           | 34.37                        |
| A10     | 19.98    | 114.97           | 770.00    | D                         | 23.44           | 34.26                        |
| A12     | 20.55    | 114.71           | 110.00    | D                         | 21.12           | 34.41                        |
| A13     | 20.76    | 115.18           | 146.00    | N                         | 21.86           | 34.39                        |
| A22     | 21.00    | 115.75           | 214.00    | N                         | 24.47           | 34.43                        |
| A20     | 20.28    | 116.22           | 860.00    | D                         | 25.79           | 34.03                        |
| A06     | 19.14    | 115.64           | 2830.00   | N                         | 23.81           | 34.23                        |
| A05     | 18.86    | 115.10           | 3300.00   | D                         | 22.10           | 34.32                        |
| A08     | 19.54    | 115.38           | 2325.00   | D                         | 21.96           | 34.43                        |
| A15     | 20.02    | 115.70           | 1353.00   | D                         | 24.21           | 34.23                        |

Day/night means the sampling time of the station was in the daytime or nighttime.
zooplankton information (including the classification information, plankton length and volume and other particle parameters) was exported from the FlowCAM, ZooProcess and Plankton Identifier software.

Considering the discontinuity of sampling and the limitations of nets, for the construction of NBSS, we selected phytoplankton data with an ESD > 77 μm in the FlowCAM data, 300–505 μm in the mesoplankton fraction, and > 505 μm in the macroplankton portion (the mesoplankton samples and macroplankton samples were scanned by ZooScan separately). All biovolumes were grouped into 19 size classes from the minimum nominal size of 0.00024 mm$^3$ m$^{-3}$ to the maximum size 131 mm$^3$ m$^{-3}$. The nominal sizes were organized in a geometric 2n series (Sprules and Munawar, 1986; Thompson et al., 2013). With this delineation, the width of each size class (Δ w) comprised the lower limit of the nominal size (w). The normalized biomass ($\beta (B)$) in each size class was computed as follows (Platt and Denman, 1977):

$$\beta (B) = \frac{B(w, w + \Delta w)}{\Delta w}$$

where $B(w, w + \Delta w)$ is the total biomass in the size class $(w, w + \Delta w)$. The data for w and $\beta (B)$ were then plotted on a log-log axis, and the relationship was linear. This could be expressed as:

$$\log \beta (w) = b + a \log (w)$$

where a is the slope, and b is the intercept of the fitted line.

2.5. Cluster analysis

Cluster analysis was used to evaluate plankton spatial distributions. The NBSS slopes were used in the analysis. Bray-Curtis similarity distance was applied to analyze the similarities of different samples (Bray and Curtis, 1957). The similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method [unweighted pair group method using the arithmetic mean (UPGMA); Field et al., 1982] to group the samples. All analyses were conducted using SAS 9.2.

To clarify the relationship between environmental parameters (sea surface temperature and salinity, temperature and salinity at 200m or at the bottom of the stations when the depth was < 200m; average temperature and salinity; surface chlorophyll a concentration; chlorophyll a concentration at the depth of the Chl a maximum; and average chlorophyll a concentration) and plankton, redundancy analysis (RDA) was performed using CANOCO software.

2.6. Data analysis

Based on the results of the FlowCAM and ZooScan analyses, the taxonomic information of the plankton above 200m was analyzed, and the predominant plankton group indexes were calculated based on the species predominant indexes (Sun, 2001). The taxonomic information showed a maximum resolution at the genus level. The group predominant index (Y) was calculated as follows:

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

where N is the total number of plankton samples; i is the plankton taxonomic group; $n_i$ is the number of individuals in group i; and $f_i$ is the occurrence frequency of group i.

T-tests, one-way ANOVA, Wilcoxon test NparIway, and Kruskal-Wallis test with post hoc tests were applied to examine differences in the regression of NBSS parameters among groups. Pearson’s correlation analysis was performed to assess the relationship between NBSS slopes and environmental parameters. These analyses were conducted with SAS (version 9.2).

3. Results

3.1. Hydrography

The hydrographical parameters of the stations are shown in Table 1. In summer, the sea surface temperature (SST), the temperature at 200m (or the bottom when the depth was < 200m; SBT), and the mean temperature from 0 to 200m (SAT) ranged from 29.74 to 31.03°C, 12.59–20.05°C, and 19.32–24.49°C, respectively. The SBT and SAT distribution patterns were similar, in that high temperatures were observed near the continental shelf area, whereas low temperatures were detected east of the study area (stations S10–S16). The salinity at the surface (SSS), the salinity at 200m (or the bottom when the depth was < 200m; SBS), and the mean salinity from 0 to 200m (SAS) ranged from 31.45 to 34.01, 34.44–34.63, and 34.17–34.51, respectively. The SSS values in the western stations (stations S01–S09, 33.84 ± 0.09) were significantly higher than those in the eastern stations (stations S10–S16, 32.40 ± 0.86) (Wilcoxon test, P < 0.01). The surface chlorophyll a (SSChl-a) concentrations varied between 0.01 and 0.43 mg m$^{-3}$, and those in stations S09–S16 were higher than those in stations S01–S08. Chl-a concentrations at DCM (SMChl-a) were between 0.25 and 1.62 mg m$^{-3}$. The average concentration (SACHl-a) concentrations ranged from 0.07 to 0.48 mg m$^{-3}$. Station S08 showed the highest SMChl-a and SACHl-a concentrations.

In autumn, SST ranged from 26.85°C to 27.93°C. SBT varied considerably between 14.92°C to 22.01°C and decreased from nearshore to offshore. SAT was 21.12°C–26.39°C, and the distribution of SAT was similar to that of SBT. Salinity at < 200m showed a narrow range. SSS, SBS and SAS ranged from 33.50 to 34.41, 34.33–34.61, and 34.03–34.43, respectively. Furthermore, Chl-a concentrations during the summer (average concentration of 0.14 ± 0.10) were significantly higher than those in autumn (0.04 ± 0.03) (Wilcoxon test, P < 0.01). The surface chlorophyll a (SSChl-a) concentration ranged from 0.01 to 0.07 mg m$^{-3}$, and the highest concentration was observed at station A22. The highest Chl-a concentration (DCM) was observed between 50 and 100m. SMChl-a varied from 0.04 to 0.26 mg m$^{-3}$. SACHl-a was 0.01–0.11 mg m$^{-3}$, and SACHl-a decreased from northwest nearshore to offshore.

3.2. Plankton abundance and biovolume

3.2.1. Abundance and biovolume during summer

There were 39 groups of phytoplankton during summer, including 28 diatoms, 10 dinoflagellates, and 1 Cyanophyceae genus, with 71.79% consisting of diatoms (Table 2). The major phytoplankton groups were Chaetoceros, Rhizosolenia, Synedra, Thalassionema, Navicula, and Oscillatoria. Chaetoceros (Y = 0.290) and Thalassionema (Y = 0.286) accounted for 29.01% and 28.64% of the total phytoplankton abundance, respectively. A total of 16 zooplankton groups were identified, which consisted of copepoda, tunicate, gastropoda, and amphipoda (Table 3). Copepoda (Y = 0.692) accounted for 69.23% of all zooplankton.

The distribution patterns of phytoplankton and zooplankton in summer varied (Fig. 2a–d). Phytoplankton abundance ranged from 1.24 × 10$^3$ to 241.86 × 10$^3$ ind. m$^{-3}$, with an average abundance of 37.38 × 10$^3$ ind. m$^{-3}$. Zooplankton abundance ranged from 0.44 × 10$^3$ to 3.15 × 10$^3$ ind. m$^{-3}$, with an average abundance of 1.92 × 10$^3$ ind. m$^{-3}$. Phytoplankton and zooplankton biovolume varied from 363.98 mm$^3$ m$^{-3}$ and 13.69 mm$^3$ m$^{-3}$, respectively. Furthermore, the average phytoplankton and zooplankton biovolumes were 530.89 and 114.49 mm$^3$ m$^{-3}$, respectively. The area with the highest phytoplankton abundance showed low biovolume (Fig. 2a and b). The observed high phytoplankton abundance was mainly attributable to Rhizosolenia and Thalassionema (the percentages of these genera were 35.07% and 9.50% (Rhizosolenia) and 25.61% and 43.53% (Thalassionema) in stations S01 and S08, respectively). The observed high abundances and biovolume distributions of zooplankton were generally
zooplankton biovolume was 98.79 mm$^3$m$^{-3}$ and varied between 56.19 and 117.24 mm$^3$m$^{-3}$. Plankton biovolume exhibited different distribution patterns than plankton abundance. Phytoplankton biovolume decreased from the transects of the A13 and A15 stations to the northeast, whereas zooplankton biovolume decreased from onshore and offshore to the middle of the study area (Fig. 2f,h).

### 3.3. Plankton community

Based on the NBSS slope in the 19 size classes, the plankton during summer and autumn were classified into 5 groups (Fig. 3a). Each group contained 1 to 9 stations (Fig. 3c). The plankton collected during summer were divided into groups A and B. Plankton in stations S08–S16 constituted group A, whereas the other plankton were designated as group B. Plankton in station A01 were classified into group C. Group D1, which contained the rest of the stations during autumn, was then divided into 2 subgroups, namely, D1 and D2. Group D1 contained only the plankton at station A13, and Group D2 contained the plankton from the other stations.

The total abundances of the groups exhibited significant differences: group B showed the highest plankton abundance, followed by groups A, C, D2, and D1 (Table 6). Plankton in the 0.077–0.5 mm size class were predominant among all classes. In addition, abundance decreased with increasing size classes. The highest abundances of the 0.077–0.5, 0.5–1 and 1–2 mm size classes were observed in group B, and the 2–5 mm and > 5 mm size classes were detected in group C. The taxonomic composition differed among groups. *Rhizosolenia* was the most abundant phytoplankton in group A (35.97%), C (60.18%) and D2 (52.42%), while in group B and D1, the most abundant phytoplankton taxa were *Thalassiosira* (28.10%) and *Ceratium* (42.34%), respectively (Fig. 4a). For zooplankton composition, Copepoda was dominant in all five groups. In group B, Copepoda was the highest, with an abundance as high as 90.07% (Fig. 4b).

Different from the abundance distribution, the biovolume did not always decrease with increasing size classes (Table 6). The highest biovolume was observed in group B, which was due to the high biovolume in the 0.5–1 mm and 1–2 mm size classes; both phytoplankton and zooplankton were in the 0.5–1 mm size class, and group B had the most Copepoda in the 1–2 mm size class compared with other groups. Group C had the lowest biovolume, while the 2–5 mm size class of group C was the highest among the five groups, which was attributed to the high proportion of gelatinous zooplankton in this size class. The taxonomic composition of each size class in biovolume is exhibited in Fig. 5. The highest biovolume in size class 0.077–0.5 mm occurred in group A. In terms of taxonomic composition, *Rhizosolenia* also dominated in group A (31.76%), C (53.34%) and D2 (44.31%). In group B, *Oscillatoria* was the most abundant phytoplankton and accounted for 26.91% of the total plankton biovolume.

### Table 2

Information about phytoplankton in the northern slope of the South China Sea in summer.

| Groups        | Y   | Groups | Y   | Groups       | Y   | Groups       | Y   |
|---------------|-----|--------|-----|--------------|-----|--------------|-----|
| Amphipisolenia| 0.002| Dactylosolen| 0.009| Ornithocercus| 0.000| Stephanopyxis| 0.000|
| Asteromphalus | 0.000| Dinophysis| 0.000| Oscillatoria*| 0.061| Streptotheca| 0.000|
| Bacitracinum  | 0.016| Eucamptia| 0.000| Oxyrynchus| 0.000| Synedra*| 0.286|
| Bidulphus     | 0.000| Gessnerella| 0.000| Pinnularia| 0.003| Thalassiosira*| 0.045|
| Ceratium      | 0.012| Gymnura| 0.000| Planktonella| 0.003| Thaliacea| 0.000|
| Ceratocorys   | 0.003| Hemialas| 0.001| Proteropodium| 0.001| Trachyneis| 0.000|
| Chaetoceros*  | 0.290| Hyalectis| 0.000| Pyrocystis| 0.003| Navicula*| 0.026|
| Cladocumidum  | 0.005| Laidera| 0.000| Pyrophacus| 0.000| Nitzschia| 0.002|
| Corethron     | 0.002| Leptolydius| 0.000| Rhizosolenia*| 0.152| Noculica| 0.001|
| Coscinodiscus | 0.006| Lithophora| 0.000| Schroederella| 0.000|       |     |

Predominant taxa are indicated by *.

### Table 3

Information about zooplankton in the northern slope of the South China Sea in summer.

| Groups       | Y   | Groups     | Y   | Groups       | Y   | Groups     | Y   |
|--------------|-----|------------|-----|--------------|-----|------------|-----|
| Bivalve      | 0.000| Egg        | 0.006| Ostracoda    | 0.003| Timthinid  | 0.000|
| Chaetognatha | 0.013| Foraminifera| 0.003| Radiolaria   | 0.001| Tunicate* | 0.200|
| Cladocera    | 0.000| Gelatine   | 0.018| Euphausiacea| 0.005| Gastrotyp*| 0.036|
| Copepoda*    | 0.692| Echinodermata| 0.000| Fislarva     | 0.000| Amphipoda*| 0.020|

Predominant taxa are indicated by *.

### Similar (Fig. 2a–d) and were attributable to Copepoda.
Fig. 2. Horizontal distribution of plankton abundance and biovolume in the northern slope of the South China Sea: Phytoplankton abundance (a) in summer and (e) autumn; phytoplankton biovolume (b) in summer and (f) autumn; zooplankton abundance (c) in summer and (g) autumn; and zooplankton biovolume (d) in summer and (h).
Underestimated by the zooplankton whose ESD was not above 0.3mm and D2 were 28.11–33.80, 27.56–0.26 mg m⁻³. At the same time, the discontinued DCM: 0.55 mg m⁻³. The temperatures of the upper water (0–35m) of groups A, B, C, D1 and D2 were 28.11–30.71°C, 25.86–30.94°C, 27.81–27.82°C, 27.56–27.57°C, and 26.84–27.45°C, respectively, and the salinities were 33.80–33.97, 32.30–34.05, 33.89–33.90, 34.03–34.04, and 33.86–33.94. The water was identified as KW and SCSW, shown in Fig. 7 (Li et al., 2018). Furthermore, group B had the highest surface temperature and the lowest surface salinity of all groups, which was attributed to intrusions of Shelf Water (SHW) (Li et al., 2018). Group B had the highest Chl α concentrations (surface water: 0.21 mg m⁻³, DCM: 0.55 mg m⁻³ at a 50m), followed by group A (surface water: 0.07 mg m⁻³, DCM: 0.42 mg m⁻³ at 72m). The Chl α concentrations of groups C, D1, and D2 were similar, i.e., approximately 0.04 mg m⁻³ at the surface. The DCM of Group C was at 75m, with a concentration of 0.26 mg m⁻³. The influences of the hydrographic environment on the five groups are shown in Fig. 3b. RDA ordination diagram represented that SSChl a, SAT, SAS were the main factors affecting plankton community composition. SACChl-a, SBT, SMChl-a, SAT and SSChl-a showed an increasing correlation with the first axis. And SAS had strong correlation with the second axis. Besides, the main affecting environmental factors with group A, B and D2 were SAS, Chl a and SAT, respectively. SBT mainly affected group C and D1.

3.4. NBSS

Fig. 8 shows the mean NBSS for summer and autumn. All the NBSS slopes fit a linear relationship (P < 0.01). However, a marked “dome” can be seen on the X-axis at approximately 6–7, and this feature corresponds with the 0.25–0.31 mm ESD size class and consists of Oscillatoria, Thalassionema and Rhizosolenia in summer and Rhizosolenia in autumn. At the same time, the discontinued ‘dome’ was caused by the underestimated by the zooplankton whose ESD was not above 0.3 mm (Vandromme et al., 2012). NBSS slopes were significantly (Wilcoxon test, P < 0.01) steeper in the summer (mean ± SE = 0.93 ± 0.04, 1.09 to −0.61) than in autumn (mean ± SE = −0.69 ± 0.05, 0.76 to −0.50) due to the higher biovolume of small organisms in summer. Furthermore, the NBSS slopes of zooplankton were significantly (Wilcoxon test, P < 0.05) steeper during summer (mean ± SE = −1.03 ± 0.09, −1.00 to −0.46) than during autumn (mean ± SE = −0.91 ± 0.05, 0.99 to −0.63).

The NBSS of the five groups are shown in Fig. 9. The slopes varied among groups (Kruskal-Wallis test, p < 0.01). Group A showed the steepest NBSS slope (a = −0.99) due to the accumulation of Oscillatoria (22.6%) and Rhizosolenia (27.5%), thereby increasing the proportion of small plankton (0.077–0.5 mm size class, 81.53, followed by group B (a = −0.90), group C (a = −0.76), group D2 (a = −0.67), and group D1, which had the flattest slope (a = −0.61) because of the relatively low biovolume in the 0.5–1 mm size class. In this study, group A represented the region affected by SCSW and KW, and group B could represent the region influenced by SCSW, KW and SHW.

4. Discussion

4.1. Plankton abundance, biovolume and taxonomic groups

The abundance and biovolume of phytoplankton and zooplankton in the South China Sea in summer and autumn were calculated. The abundance of phytoplankton in summer and autumn (1.24×10⁵ to 241.86×10³ ind. m⁻³) and 0.66×10³ to 7.83×10³ ind. m⁻³) were similar to previously reported net-sampled abundances (60.2×10³ ind. m⁻³ and 21.2×10³ ind. m⁻³) (Dai et al., 2013; Gong et al., 2012). A previous study showed that the zooplankton abundances in summer and autumn in the northern part of the South China Sea were 0.32×10³ ind. m⁻³ and 0.14×10³ ind. m⁻³, respectively (Wang et al., 2014), and in summer in the northwest part of the South China Sea was 0.28×10³ ind. m⁻³ (Yin et al., 2007); these values were much lower than those in our study (1.92×10³ ind. m⁻³ and 0.47×10³ ind. m⁻³ in summer and autumn, respectively). This difference occurred because our study considered data from both medium and large plankton nets, while the previous studies each used only one type of net. The zooplankton biovolume values (114.49 mm³ m⁻³ in summer and 98.79 mm³ m⁻³ in autumn) were in the range of those for the Northwest Pacific Ocean (2.24–1007 mm³ m⁻³) reported by Sato et al. (2015).

In the phytoplankton community, diatoms were predominant and coexisted with dinoflagellates. Most phytoplankton species found in the South China Sea were widespread species (such as Chaetoceros, Synedra, Thalassionema, and Navicula), and a few were warm-water species (such as Rhizosolenia and Protoperidinium). This result agrees with reported phytoplankton compositions (Ning et al., 2004). As reported for the zooplankton community in the South China Sea (Wang et al., 2014; Yin et al., 2007; Zhou et al., 2015), Copepoda was predominant in both seasons, and the second most dominant taxa were tunicates in summer and Gastropoda in autumn. In contrast, Wang et al. (2014) and Zhou et al. (2015) found a high proportion of Cnidaria in zooplankton, especially in larger size classes, which was not observed in this study. This difference occurred because our sampling area was offshore, while theirs were nearshore or in the continental shelf.

4.2. Spatial and temporal variability

In the present study, the distributions of plankton groups that were clustered based on biovolume size spectra coincided with the currents in autumn and summer (Fig. 3c). Currents or mesoscale eddies...
influenced plankton distributions (Chen et al., 2003, 2007; Hirota and Hasegawa, 1999; Iguchi, 2004). According to the synchronized water mass analysis, hydrographical and circulation features were influenced by a cyclonic-anticyclonic eddy pair in summer (Fig. 3c), and there was cross-slope transport in the northern slope of the South China Sea in the upper 100m. In addition, the maximum velocity was observed in the intersection of two eddies (Chen et al., 2016). Thus, the biovolume and abundance of phytoplankton in groups A and B were the highest (the values were almost the same in the two groups, Table 6) among all groups due to the cross-slope transport with abundant nutrients. Groups A, B, C1, C2 and D were influenced by SCSW and KW. In addition, SHW also influenced group B (Chen et al., 2016; Li et al., 2018). Hirota and Hasegawa (1999) and Iguchi (2004) found that the zooplankton biomass in the Japan Sea was similar to that in the Kuroshio region. The zooplankton biovolume of the 5 groups in our study were in the range reported for the Japan Sea (135.1 ± 34.1 mm$^3$m$^{-3}$; Sato et al., 2015) and the Kuroshio extension (10.7 ± 7.5mm$^3$; Sato et al., 2015).

Group B was mainly distributed in the northeastern region of the study area, where a cyclonic eddy occurred. This group had the highest phytoplankton and zooplankton abundance and biovolume values.
The water was characterized by low salinity and high Chl a due to the SHW (Fig. 6). Previous studies have shown that cold eddies enhance primary nitrate-based new production and phytoplankton assemblages (Ning et al., 2004; Chen et al., 2007). The SHW brought significant amounts of nutrients into the South China Sea slope and provided a good growth environment for phytoplankton. It has been reported that in oligotrophic oceans (such as Kuroshio region), small-sized Copepoda are the predominant zooplankton (Nakata et al., 2001; Nakata and Koyama, 2003; Hsieh et al., 2004). As KW and SCSW were comprehensive water mass features of group B, which was in a region less oligotrophic than the Kuroshio region, the predominant zooplankton were middle-sized Copepoda, and organisms in the 1–2mm size class and accounted for 81.41% of all the Copepoda.

Groups A and B were sampled in summer, and the other groups were sampled in autumn. The synchronized water mass analysis showed that the study area was mainly

Table 6
Comparison of plankton abundance, biovolume, and slope (a) of NBSS (y = ax + b) of 5 plankton groups in the northern slope of the South China Sea.

| Parameter       | Group   | Kruskal-Wallis test | PLSD |
|-----------------|---------|---------------------|------|
| Abundance(inds. m⁻³) | A(7) | B(9) | C(1) | D1(1) | D2(9) |
| Total           | 24683.59 ± 35885.19 | 25253.00 ± 38123.08 | 6533.18 | 485.18 | 564.15 ± 160.45 | ** | A'B'C'D' D2b |
| phytoplankton   | 23982.08 | 24029.53 | 6028.86 | 417.40 | 514.48 | ** | A'B'C'D' D2b |
| zooplankton     | 701.51 | 1223.22 | 504.32 | 67.60 | 49.52 | NS | |
| 0.077–0.5mm     | 2486.45 ± 35818.67 | 2497.62 ± 37987.41 | 6488.70 | 387.58 | 474.42 ± 150.64 | ** | A'B'C'D' D2b |
| 0.5–1mm         | 170.74 ± 90.42 | 238.13 ± 169.18 | 25.28 | 56.53 | 58.90 ± 14.88 | ** | A'B'C'D' D2b |
| 1–2mm           | 23.69 ± 14.29 | 38.98 ± 17.88 | 14.4 | 38.40 | 27.24 ± 6.90 | NS | |
| >5mm            | 2.67 ± 1.91 | 4.26 ± 3.10 | 4.48 | 2.67 | 3.52 ± 1.82 | NS | |
| Biovolume(mm³ m⁻³) | Total | 612.04 ± 56.74 | 671.11 ± 62.90 | 150.47 | 296.87 | 205.2 ± 62.35 | ** | A'B'C'D' D2b |
| phytoplankton   | 528.90 | 532.44 | 41.67 | 203.89 | 106.97 | * | A'B'C'D' D2b |
| zooplankton     | 82.73 | 138.42 | 108.72 | 92.76 | 97.96 | NS | |
| 0.077–0.5mm     | 499.38 ± 61.67 | 492.36 ± 88.84 | 53.18 | 211.36 | 116.30 ± 44.99 | ** | A'B'C'D' D2b |
| 0.5–1mm         | 51.63 ± 8.53 | 78.05 ± 7.39 | 6.01 | 12.63 | 14.52 ± 4.69 | ** | A'B'C'D' D2b |
| 1–2mm           | 31.34 ± 18.82 | 55.99 ± 25.98 | 20.29 | 49.43 | 36.04 ± 9.63 | NS | |
| >5mm            | 2.97 ± 4.94 | 0.00 ± 0.00 | 23.55 | 0.00 | 5.46 ± 15.45 | NS | |
| NBSS Slope      | −0.98 ± 0.12 | −0.90 ± 0.13 | −0.82 | −0.61 | −0.67 ± 0.05 | ** | A'B'C'D' D2b |

Values are expressed as the mean ± SD. Differences among groups were tested by the Kruskal-Wallis test. **p < 0.01, *p < 0.05, NS: not significant. Numbers in parenthesis indicate the number of stations belonging to each group. Groups with different marks in the upper right corner are significantly different.
Fig. 5. Biovolume composition of plankton taxonomic groups in each size class for the 5 groups in the northern slope of the South China Sea.

Fig. 6. Vertical distribution of temperature, salinity, and chlorophyll a of the five groups in the northern slope of the South China Sea.
controlled by SCSW during autumn, and the proportions of SCSW and KW were similar in summer; thus, Oscillatoria was observed. The phytoplankton, in abundance and biovolume, ranked second in all five groups (Table 6). However, as group A was also affected by KW and SCSW, same as for group B, the zooplankton (in biovolume) were dominated by 1–2 mm size class Copepoda (77.33% of all Copepoda).

Groups C, D1 and D2 were sampled in autumn, when westward currents were identified as SCSW and KW in the study region (Fig. 3c). The influence of KW has been discussed above. In autumn, the lower temperature led to lower Chl-a and relatively low plankton abundance and biovolume values. Group C was observed at station A01, which was at the northwest region of the study area and ran straight into the mouth of the Pearl River Estuary; this region was mainly composed of SCW. Group C showed the highest number of phytoplankton (Fig. 2e) compared with other stations in autumn, which might be caused by the westward currents that transported more nutrients to the group.

4.3. NBSS

The NBSS slope of an equilibrium plankton system (Sheldon et al., 1972) and the steady oceanic ecosystem of the North Pacific Central Gyre (Rodríguez and Mullin, 1986) were −1. T-test analysis showed that the slopes in the present study were significantly different from −1 (autumn: P < 0.0001; summer: P < 0.0001), indicating that the plankton community in the South China Sea differed from that of a steady-state community, and there were significant seasonal and intergroup variabilities. In general, small plankton comprised the predominant group in the summer, which in turn resulted in steeper NBSS slopes compared to those observe during autumn. Furthermore, the slopes of groups B, C, D1 and D2 were shallower than −1, thereby indicating that the northern region of the South China Sea had high ecological transfer efficiency. The NBSS slope of group A (−0.99), which was affected by SCSW and KW, was very similar to that of a speculated steady-state community, while the NBSS slope of group B (−0.90) was flatter than −1, indicating a higher ecological transfer efficiency than group A, which occurred because in addition to SCSW and KW, SHW also affected the region and brought abundant nutrients. In this study, the zooplankton NBSS slopes (−1.03 ± 0.09 in summer, −0.91 ± 0.05 in autumn) were steeper than the plankton (including both phytoplankton and zooplankton) NBSS slopes (−0.93 ± 0.04 in summer, 0.69 ± 0.05 in autumn), which agrees with the generality that the slope of an individual function should be steeper than that of a whole aquatic community (Dickie et al., 1987; Kerr and Dickie, 2001).

Environmental factors could influence the distribution and availabilty of nutrients and the population dynamics of primary producers (Espinasse et al., 2014; García-Comas et al., 2014). All of these processes could impact the plankton structure and energy fluxes, thereby leading to different NBSS patterns. Temperature could influence the vertical migration of zooplankton, which in turn could lead to variations in ecological efficiencies (Liu, 2002). To test the relationship between slopes and environment parameters, we subjected the slopes of plankton (including both phytoplankton and zooplankton) NBSS slopes to a Pearson’s correlation analysis. The results showed that the slopes were negatively correlated with ST (r = −0.52, P < 0.01), MChl-a (r = −0.61, P < 0.01), and AChl-a (r = −0.59, P < 0.01) (Table 6). Chl-a and temperature were correlated with both NBSS slopes and plankton communities’ taxa compositions. García-Comas et al., 2014 reported that although there was a significant correlation between size diversity and Chl-a, NBSS slopes were not significantly correlated with any environmental variable. A study on the zooplankton and environmental conditions in a Chilean upwelling area (Manríquez et al., 2012) showed a correlation between slopes and Chl-a. Therefore, we inferred that the main factors affecting NBSS slopes change spatially. Over continental slopes, temperature and Chl-a concentrations influence plankton distributions (Marcolin et al., 2013). In a dynamic environment, such as the East China Sea (García-Comas et al., 2014), no correlation between the environment and NBSS slopes are observed. In upwelling areas, plankton distribution characteristics exhibit some relationship with Chl-a concentrations (Manríquez et al., 2012).

Some of the reported NBSS slopes of subtropical and tropical zooplankton are listed in Table 7. The slopes are associated with productivity, plankton structure, and nutrient conditions (Sprules and Munawar, 1986; Zhou, 2006; Zhou and Huntley, 1997; Zhou et al., 2009). The NBSS slope of the South China Sea during summer was similar to that of coastal regions such as Brazilian Continental Shelf coastal stations and the neighboring waters of Japan. On the other hand, the NBSS slope during autumn was similar to that of oceanic stations, Brazilian Continental Shelf oceanic stations, and Western Pacific group B. These differences might be due to the intrusion of SHW in the summer. The nutrients in the SHW might influence the plankton, particularly by enhancing phytoplankton growth on the continental slope.
Fig. 9. Mean plankton NBSS of the 5 groups in the northern slope of the South China Sea.

Table 7
Comparison of the slopes (a) of NBSS (y = ax + b) (biovolume units) of the zooplankton communities of subtropical regions.

| Location/region                      | Size range (mm) | Slope     | References                  |
|--------------------------------------|-----------------|-----------|-----------------------------|
| Brazilian Continental Shelf (coastal stations and Abrolhos Bank) | 0.25–8          | –1.01     | Marcolin et al. (2013)      |
| Brazilian Continental Shelf (oceanic stations) | 0.25–8          | –0.91     | Marcolin et al. (2013)      |
| Western Pacific                       | 0.31–20         | –0.92–0.85| Dai et al. (2016)           |
| The neighboring waters of Japan       | 0.25–5          | –1.13 (–1.24––0.90) | Sato et al. (2015)          |
| California Bight                      | 0.05–8.0        | –2.30     | Napp et al. (1993)          |
| South China Sea                       | 0.16–4          | –0.82 (–0.91–0.67) | Zhou et al. (2015)          |
| East China Sea                        | 0.2–15          | –0.83 (–0.97–0.73) | García-Comas et al., 2014  |
| Tasman Sea                            | 0.11–3.3        | –0.69 (–0.78–0.59) | Baird et al. (2008)        |
| South China Sea (summer)              | 0.31–6.3        | –1.03     | This study                  |
| South China Sea (autumn)              | 0.24–6.3        | –0.91     | This study                  |
| South China (affected by SCSW and KW) | 0.31–6.3        | –0.99     | This study                  |
| South China (affected by SCSW, KW and SHW) | 0.31–6.3       | –0.90     | This study                  |
5. Conclusions

Significantly higher phytoplankton and zooplankton abundances were observed in summer than in autumn. In autumn, *Rhizosolenia* and *Copepoda* were the dominant phytoplankton and zooplankton species while in summer, the dominant phytoplankton consisted of *Chaetoceros* and *Thalasiosira*. The plankton community in the South China Sea differed from that of a steady-state community, and there were significant seasonal and intergroup variabilities. In general, small plankton were the predominant group in the summer, which in turn resulted in steeper NBSS slopes than those observed during autumn.

The distribution of plankton was coupled with the geographic process of mesoscale currents. The NBSS can distinguish different water masses, and the NBSS slopes of the SCSW and KW regions (~ 0.99) were steeper than those of the ECSW, KW and SHW regions (~ 0.90). NBSS slopes could be used as an effective indicator of ecological transfer efficiency among different plankton groups. Zooplankton NBSS slopes were steeper than the plankton (including both phytoplankton and zooplankton) NBSS slopes. In the northern slope of the South China Sea, the temperature and Chl a concentrations largely influenced various plankton indices.

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