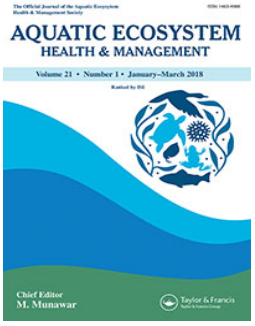

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Community structure and biovolume size spectra of mesozooplankton in the Pearl River estuary

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The Pearl River estuary is the second largest estuary in China. This study reported the species composition and size structure of mesozooplankton in the upper and lower Pearl River estuary in the dry and wet seasons. The normalized biovolume size spectrum of mesozooplankton was constructed to analyze the trophic structure of the community. Copepods were the numerically predominant mesozooplankton group at all sampling stations. However, when converted into biovolume, medusae were dominant in the upper estuary in the dry season and Chaetognatha were dominant in the lower estuary in the wet season. There were apparent seasonal and spatial variations in the normalized biovolume size spectrum characteristics in the Pearl River estuary. In the dry season, the average fitted regression line of the normalized biovolume size spectrum had a slope of −1.02 in the upper estuary and −0.88 in the lower estuary. In the wet season, the average fitted regression line of the normalized biovolume size spectrum had a slope of −0.32 in the lower estuary, and no significant regression of the normalized biovolume size spectrum was found in the upper estuary. It is suggested that the mesozooplankton community was unstable in the upper estuary due to the strong freshwater perturbation in the wet season. The size diversity and normalized biovolume size spectrum slope indicated that the strength of top-down control and trophic efficiency was highest in the lower estuary in the wet season.

Keywords: zooplankton, pelagic ecosystem, size diversity, seasonal variation

Introduction

Aquatic foodwebs are strongly size structured with larger predators eating smaller prey (Sheldon et al., 1972). Body size constrains prey-predator interactions and physiology, which is related to the ecological role of the organisms, particularly in the pelagic environment. In general, predation and nutrient contents control the biomass and size structure of the zooplankton (Masson et al., 2004). On the other hand, body size is a fundamental determinant of energy flow, species diversity and population densities (Peters and Wassenberg, 1983; Woodward et al., 2005), and has been widely recognized as a key factor in the analysis of community structure and trophic interactions in

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plankton foodwebs (Brucet et al., 2006; Ye et al., 2013). The size distribution of the planktonic community can be used to compare the trophic structure, ecosystem function, and response to perturbations (Martin et al., 2006; Ye et al., 2013; Ma et al., 2014), which is especially useful in species-rich ecosystems with complex trophic pathways (Polis and Strong, 1996).

Biomass size spectrum theory had been widely used in the analysis of pelagic foodweb structure. It has been proven that biomass in aquatic ecosystem is roughly uniformly distributed over logarithmic size classes (Sheldon et al., 1972; Zhou, 2006). Biomass can be used to examine the general energetic characteristics of foodwebs even though some details can be lost (Martin et al., 2006). In aquatic ecosystems, the biomass of plankton is usually calculated from the biovolume (Sun and Liu, 2003). The efficiency of biomass transfer to larger organisms can be indicated by the slope of the biovolume size spectrum (Gaedke, 1993; Dai et al., 2016). The slope of the normalized biovolume size spectrum (NBSS) should be about -1 if the pelagic community is close to a steady state (Quiñones et al., 2003; Zhou, 2006; Sato et al., 2015). Ma et al. (2014) indicated that the steeper slope of the NBSS usually suggested the more human-induced perturbations in a subtropical bay. When a community has more trophic levels, the slope of its biovolume size spectrum should become flatter because there is more biomass in the community (Zhou, 2006). Trudnowska et al. (2014) suggested that the flat slopes of size spectra pointed to long food chains in the outer part of a glacial Arctic fjord. The NBSS has been applied to various aquatic ecosystems for examining the trophic dynamics and potential human impacts, such as lakes (Sprules and Munawar, 1986), reservoirs (Ho et al., 2013), oceanic domains (Zhou et al., 2009; Basedow et al., 2010; Dai et al., 2016), bays (Ma et al., 2014) and estuaries (Lam-Hoai et al., 2006). With the development of automated identification techniques for zooplankton (e.g. Video Plankton Recorder and ZooScan), the analysis of the biomass size spectrum has become increasingly popular in the study of pelagic ecosystems (Marcolin et al., 2013; Sato et al., 2015; Dai et al., 2016).

Estuaries are usually characterized by a large biological richness and extremely high productivity, with the plankton community generally being radically different between the dry and wet seasons (Lam-Hoai et al., 2006). The Pearl River estuary (PRE) is the second largest estuary in China, and is located on the northern shelf of the South China Sea (Harrison et al., 2008). The Pearl River stretches for 2,214 km and drains an area of 452,000 km^2 (Zhao, 1990). Its annual average discharge is 10,524 m^3 s^{-1}, with a substantial seasonal variation. About 80% of the total river discharge occurs in the wet season (April to September), while the remaining 20% occurs in the dry season (October to March) (Zhao, 1990). As a result, the biotic and abiotic environments display significant seasonal variations in the PRE (Harrison et al., 2008). Salinity is one of the most important environmental factors affecting zooplankton abundance and species richness in this estuary (Tan et al., 2004; Li et al., 2006). Most studies of zooplankton in estuaries are limited to the species composition and spatial distribution. Only a few biological studies have compared ecosystem structure and function in the different regions of PRE and between the dry and wet seasons (see the review in Harrison et al., 2008). The size structure and the ecological function of zooplankton have not been studied extensively in this estuary. No information on mesozooplankton size structure is available for the PRE.

In this study, the mesozooplankton species composition, abundance, biovolume, size structure, and NBSS were examined in the upper and lower region of PRE in dry and wet seasons. The purpose of this study was to examine the spatial and seasonal variations of mesozooplankton size structure and trophic efficiency in the PRE.

Materials and methods

In this study, 22 stations were sampled to study the environmental conditions of the PRE during 1–3 December 2011 (dry season) and 25–28 June 2012 (wet season). Eight stations were chosen to analyze the community and size structure of mesozooplankton: upper estuary (S3, S4, S5 and S6) and lower estuary (S18, S19, S20, and S22) (Figure 1). Because of bad weather conditions, mesozooplankton samples were not collected at S20 in the wet season. Temperature and salinity were measured in situ using a YSI 6600 multi-probe sensor (Yellow Springs Instrument Co., Yellow Springs, OH, USA). Chlorophyll *a* (Chl *a*) was determined by

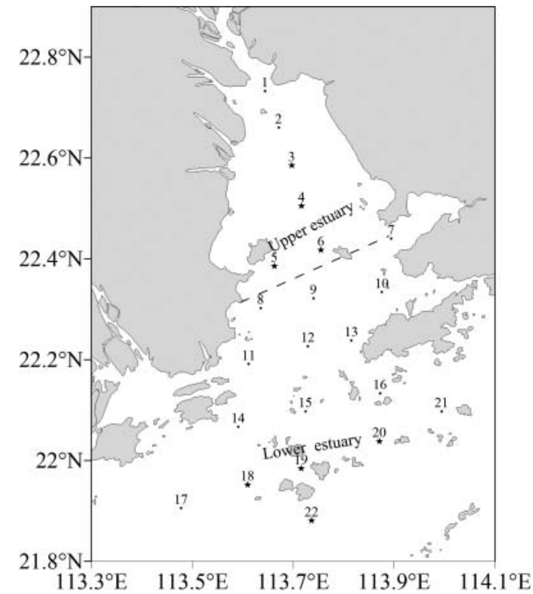

Figure 1. Map of the Pearl River estuary (PRE) and location of the sampling sites. S3, S4, S5 and S6 were chosen to represent the upper estuary, while S18, S19, S20 and S22 were chosen to represent the lower estuary.

90% acetone extraction and with fluorometric analysis. Mesozooplankton were collected with vertical net hauls (conical plankton net, 0.5 m diameter, length 2 m, and mesh size 169 μm) from the bottom to the surface retrieved at 0.5 m s^{-1}. The filtered water volume was measured with a calibrated flowmeter. The samples were fixed in borax-buffered formaldehyde to a final concentration of 4% and stored in the dark until further analysis in the laboratory. Zooplankton samples were identified to type, genus, and species when possible and counted using a microscope at 40 × magnification. When the densities were too high, sub-samples were taken and at least 100 individuals in each sub-sample were counted. Mesozooplankton belonging to the same category or group usually have a similar body shape. The individual biovolume was calculated by the analogous geometric models according to its body shape, such as the copepods was considered as ellipsoid, and the chaetognaths was considered as cylinder (Ma et al., 2014). Because the body size of one species may span several size classes in different life stages, we separated some species into specific size classes for the precise estimation of the biovolume distribution along the size class. For example, the species of copepods were counted according to their prosome length at an interval of 0.25 mm from <0.5 mm to a maximum of 2.5 mm, and the species of chaetognaths were counted according to the body length at an interval of 1.25 mm from <1.25 mm to a maximum of 15 mm. Through this counting method, one species can be classified into different size classes during the analysis of size structure and size diversity.

The NBSS calculation and plotting methods were established according to Sprules and Munawar (1986) and García et al. (2014). The NBSS was built by arranging the organisms in size-classes with increasing widths, following a geometric 2^n series. The biovolume (mm^3 m^{-3}) of a size class was divided by the width of the size class to build a normalized size spectrum: $Log_2(A_i/\Delta V) = a\log_2 V_i + b$, A_i is the total biovolume (mm^3 m^{-3}) in the size class, V_i is the maximum individual biovolume (mm^3) in one size class, ΔV is the size interval of size class ($\Delta V = Vi - V(i-1)$, $Vi = 2V(i-1)$, $V1 = 5 \times 10^{-8}$ mm^3), and a and b are constants. In this NBSS equation, the intercept b can indicate the productivity, the slope a can reflect the energy transfer efficiency along foodwebs in the ecosystem, and the regression coefficient (R^2) can indicate the stability of the ecosystem (Sprules and Munawar, 1986; Boudreau et al., 1991; Martin et al., 2006; Sourisseau and Carlotti, 2006). Size classes with zero biovolume were not considered when computing the NBSS linear regression. Because the abundance of minimum and maximum size classes was greatly influenced by the mesh of the plankton net (García et al., 2014), data for these size classes were neglected for all regressions.

The taxonomic diversity (H') of the zooplankton community was calculated using the numerical abundance of each identified taxon according to the Shannon-Weaver index (H') (Shannon and Weaver, 1949), $H' = -\sum_{i=1}^{S} Pi \log_2 Pi$, where P_i is the proportion of species i in relation to its total abundance. The calculation of size diversity ($H'S$) is similar to that of the taxonomic diversity (Vandromme et al., 2012; García-Comas et al., 2014), and was computed using the biovolume of the 12 size classes used in the NBSS, while P_i is the proportion of size class i in relation to total biovolume. The species dominance index (Y) was calculated as follows: $Y = \frac{ni}{N}fi$, where f_i is the frequency of occurrence of species i, n_i is the abundance of species i, N is the total abundance of all species. The dominant species (or groups) were defined when the dominance index Y was ≥ 0.02 (Xu and Chen, 1989). The significances of the temporal and spatial differences were evaluated using one-way ANOVA. Statistical analysis was performed using the software SPSS 17.0.

Results

Temperature, salinity, and chlorophyll in the Pearl River estuary

Surface water temperature was significantly higher in the wet season (Figure 2). The average temperature in surface waters was 22.5°C and 28.8°C in the dry and wet season, respectively. The spatial variation of surface water temperature was not significant in the PRE. However, spatial and seasonal variability of salinity was evident, which gradually increased from northwest to southeast and displayed a significant decline in the wet season because of the high river discharge (Figure 2). In the dry season, the surface average salinity was 18.6 and 34.2 in the upper and lower estuary, respectively. In the wet season, the estuarine waters were mainly dominated by freshwater, with a surface average salinity of 0.5 in the upper estuary and 8.3 in the lower estuary. The Chl *a* concentration was significantly higher in the wet season, when the peak value (20.3 μg l^{-1}) was recorded from the lower station S22.

Species composition and the abundance of mesozooplankton

The number of mesozooplankton species or groups in the upper and lower estuary was 22 and 28 in December, and 18 and 33 in June, respectively. The difference in species composition between the upper and lower estuary was great in the wet season (Table 1). *Paracalanus parvus* and

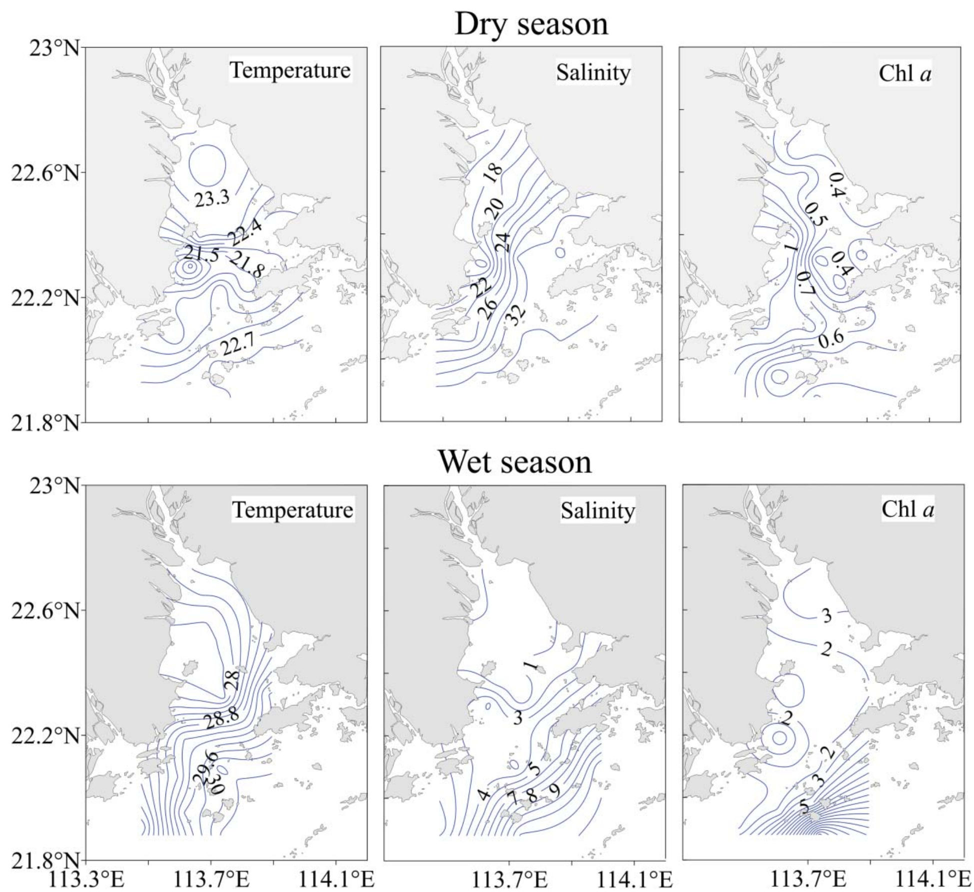

Figure 2. The distribution of temperature, salinity, and Chl *a* in the surface waters during the dry and wet seasons of the Pearl River estuary (PRE).

Oithona tenuis were the most important species in both the upper and lower parts of the PRE in the dry season. *Acartiella sinensis* was the dominant species in the upper estuary in both the dry and wet season; however, it was not recorded in the lower estuary. In general, there were more dominant species in the lower estuary, especially in the wet season. During the wet season, there were only three dominant species in the upper estuary, but there were ten dominant species in the lower estuary (Table 1). Some species were only identified in a specific region or season. For example, *Microsetella norvegica* was only found in the lower estuary in the dry season, and *Lucifer* sp. were only recorded in the lower estuary in the wet season.

There were great differences in the abundance and biovolume composition of mesozooplankton in this study (Figure 3). In terms of abundance, the mesozooplankton communities were primarily dominated by copepods, pelagic tunicates, planktonic larva and decapods. Copepods were predominant, making an average contribution to the total density in the upper and lower estuary of 86.9 and 94.5% in the dry season, and 75.9 and 64.1% in the wet season, respectively. When converted into biovolume, the mesozooplankton communities were primarily dominated by copepods, medusa, and Chaetognatha. Copepods accounted for 16.7 and 55.8% of the total biovolume in the dry season, and 76.5 and 9% in the wet season in the upper and lower estuaries, respectively. Medusae (mainly *Pleurobrachia globosa*) accounted for 80.5% of the total biovolume in the upper estuary in the dry season. Chaetognatha (mainly *Sagitta*

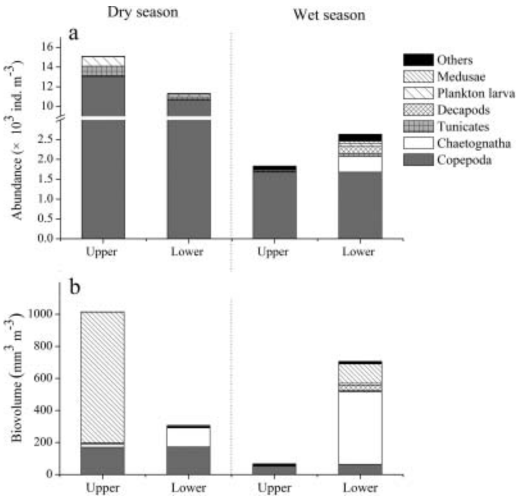

Figure 3. Abundance ($\times 10^3$ ind. m^{-3}) and biovolume (mm^3 m^{-3}) of mesozooplankton in the upper and lower estuaries in the dry and wet seasons.

Table 1. The abundance ($\times$ 10^3 ind. m^{-3}) of dominant species (dominance index $Y > 0.02$) in the upper and lower estuary in the dry and wet seasons. "–": $Y < 0.02$ or not found.

		Upper estuary				Lower estuary			
		Abundance		Dominance		Abundance		Dominance	
Groups	**Species**	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Copepoda	*Acartia* spp.	–	0.12	–	0.03	–	0.23	–	0.07
	Acartia spinicauda	–	–	–	–	–	0.13	–	0.03
	Acartiella sinensis	1.93	1.33	0.10	0.73	–	–	–	–
	Canthocalanus pauper	–	–	–	–	0.92	0.16	0.06	0.04
	Corycaeus spp.	–	–	–	–	0.69	–	0.06	–
	Oithona tenuis	2.31	–	0.16	–	1.48	–	0.13	–
	Paracalanus parvus	5.28	–	0.37	–	6.62	0.61	0.59	0.20
	Pseudodiaptomus poplesia	–	0.15	–	0.04	–	–	–	–
	Pavocalanus crassirostris	2.35	–	0.04	–	–	0.19	–	0.04
	Subeucalanus subcrassus	–	–	–	–	0.23	–	0.02	–
	Temora turbinata	–	–	–	–	–	0.23	–	0.08
Plankton larva	Nauplii	0.87	–	0.06	–	–	–	–	–
	Mysidacea larva	–	–	–	–	–	0.09	–	0.03
Tunicates	*Oikopleura dioica*	–	–	–	–	–	0.48	–	0.16
Chaetognatha	*Sagitta enflata*	–	–	–	–	–	0.29	–	0.09
	Sagitta betodi	–	–	–	–	–	0.10	–	0.02

enflata) accounted for 63.9% of the total biovolume in the lower estuary in the wet season.

Both the abundance and biovolume of total mesozooplankton were higher in the upper estuary than that in the lower estuary in the dry season (Figure 3). In the dry season, the average abundance of total mesozooplankton was 15.1×10^3 and 11.3×10^3 ind. m^{-3} in the upper and lower estuary; and the average biovolume of total mesozooplankton was 1015 and 307 mm^3 m^{-3} in the upper and lower estuaries, respectively. In the wet season, the abundance and biovolume of total mesozooplankton were all higher in the lower estuary. The average total mesozooplankton biovolume were 560 mm^3 m^{-3} in the lower estuary and 70 mm^3 m^{-3} in the upper estuary.

Size distribution and normalized biovolume size spectrum of mesozooplankton

The zooplankton individual biovolume ranged from 0.8×10^{-3} (nauplii) to 54.8 mm^3 (*Pleurobrachia globosa*) in the PRE, with a corresponding size class ranging from -10.25 to 6.75. The individual biovolume varied substantially even within the same species. Small size classes were generally composed of copepods. *Subeucalanus subcrassus* was the largest copepod species, with a biovolume ranging from 8.7×10^{-3} to 0.6 mm^3. Medusae and Chaetognatha, the large-size groups, were primarily dominant in classes larger than 1.7 in the lower estuary both in the dry and wet seasons (Figure 4). Because of the huge biovolume of *P. globosa*, there was a significantly high biovolume in the largest size class in the upper estuary during the dry season. Chaetognatha was the most important group for the total biovolume in the lower estuary of the wet season, which occurred from a size class of -6.25 to 3.75, with the biovolume ranging from 9.7×10^{-3} mm^3 to 10 mm^3. In the lower estuary, the mesozooplankton biovolume was usually dispersed over a wider size class.

The NBSS curves were plotted according to the size classes and the normalized biovolume, and the corresponding parameters were listed in Table 2. Most of the linear regressions of the NBSS were significant ($p < 0.05$) in the dry season. The NBSS had a relatively low regression coefficient in the wet season. In the upper estuary, none of the regressions were significant in the wet season, with very low value of R^2. In contrast, all of the regressions were significant in the lower estuary in the dry season, with high R^2 values ranging from 0.6 to 0.87. The slope and intercept

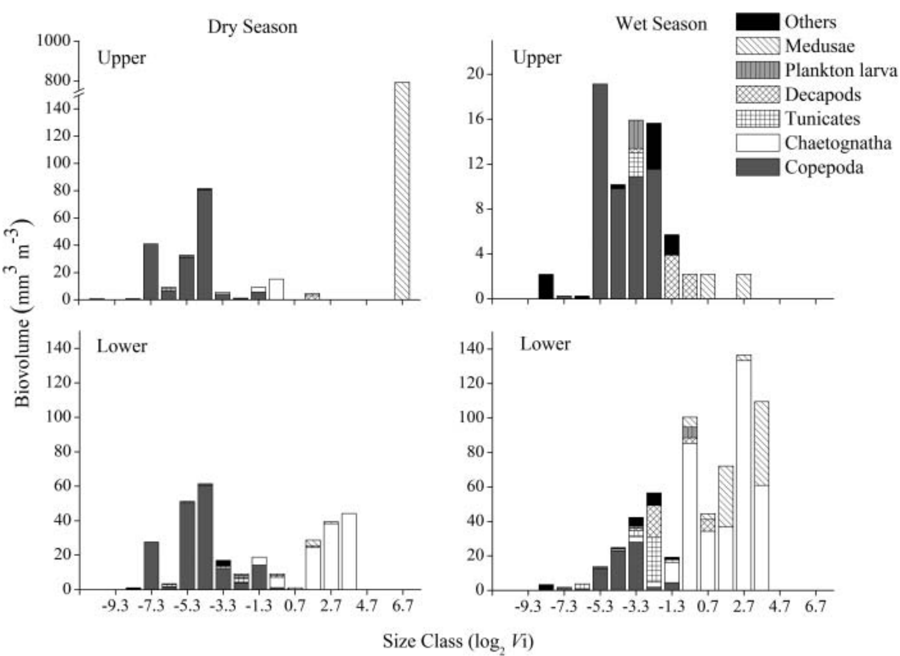

Figure 4. Biomass size distribution of mesozooplanton in the upper and lower estuaries in the dry and wet seasons.

Table 2. The normalized biovolume size spectrum (NBSS) parameters of mesozooplankton in the upper and lower estuaries in the dry and wet seasons.

		Dry season				Wet season			
		Slope	Intercept	R^2	p	Slope	Intercept	R^2	P
Upper	S3	−1.267	2.678	0.707	0.018	−0.124	6.844	0.023	0.748
	S4	−1.202	2.950	0.580	0.238	−0.019	8.819	0.000	0.975
	S5	−1.622	0.283	0.931	0.008	−0.329	2.889	0.565	0.085
	S6	−0.589	4.936	0.510	0.046	−0.307	5.652	0.097	0.689
Lower	S18	−0.797	4.733	0.595	0.009	−0.326	7.248	0.510	0.031
	S19	−0.896	4.927	0.865	<0.001	−0.347	6.555	0.444	0.050
	S20	−0.895	3.635	0.649	0.009	–	–	–	–
	S22	−1.108	3.307	0.822	0.001	−0.366	7.171	0.773	<0.001

of the NBSS were similar between the upper and lower estuaries, but were significantly different between the dry and wet seasons. On average, the NBSS regression lines for mesozooplankton were steeper in the dry season (Figure 5). In the dry season, the average fitted regression line of the NBSS had a slope of −1.02 in the upper estuary and −0.88 in the lower estuary. In the wet season, the average fitted line of the NBSS had a slope of −0.32 in the lower estuary, but no significant regression of the NBSS was found in the upper estuary. The steepest slope (−1.62) of the NBSS was found at site S5 in the upper estuary in the dry season. Comparing all the samples, the NBSS slopes were significantly steeper in the dry season than in the wet season (paired t-test, $p < 0.001$).

Taxonomic diversity and size diversity

Taxonomic and size diversity displayed a similar tendency, except in the upper estuary in the dry season (Figure 6). In the dry season, the average values of H' were 2.07 and 1.97 in the upper and lower estuaries, while the average values of $H'S$ were 1.57 and 1.74 in the upper and lower

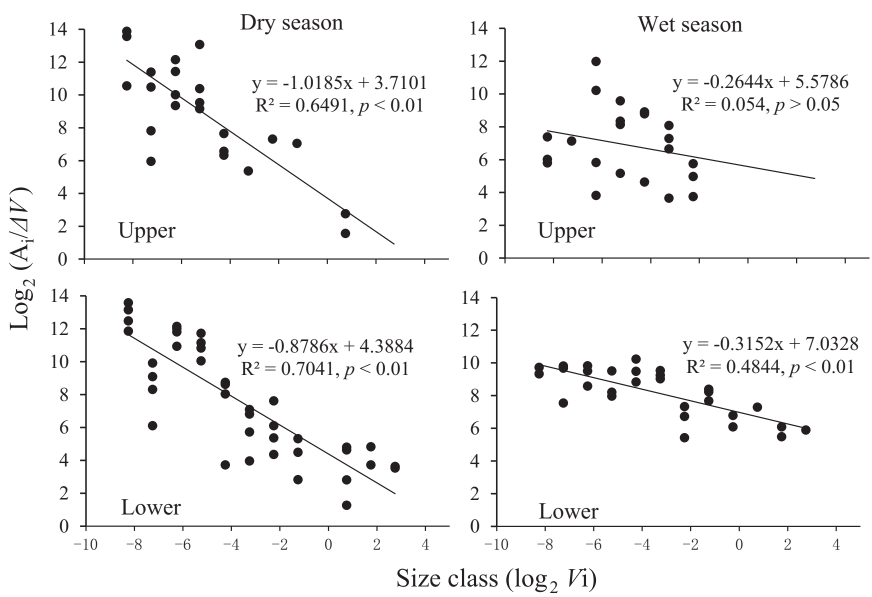

Figure 5. Mean normalized biovolume size spectrum of mesozooplankton in the upper and lower estuaries in the dry and wet seasons.

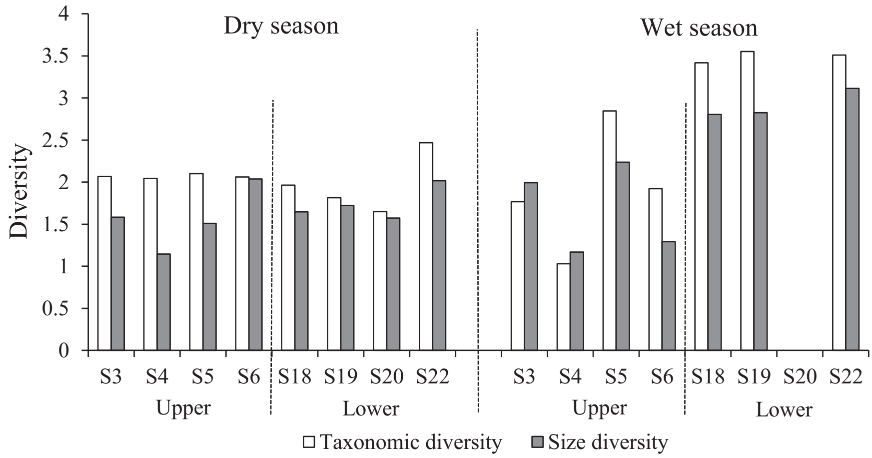

Figure 6. Taxonomic and size diversity of mesozooplankton in the upper and lower estuaries in the dry and wet seasons.

estuaries, respectively. The taxonomic and size diversities were significantly higher in the lower estuary in the wet season (ANOVA, $p < 0.05$). The average values of H' were 1.89 and 3.49 in the upper and lower estuaries, while the average values of $H'S$ were 1.67 and 2.91 in the upper and lower estuaries, respectively. In the wet season, taxonomic diversity was significantly correlated with the slope, intercept, and R^2 of NBSS ($p < 0.05$), while size diversity was significantly correlated with the value of R^2 ($p < 0.05$).

Discussions

Species and size structure of the mesozooplankton community in the Pearl River estuary

Many previous studies have indicated that copepods are the most important group in the oceanic planktonic ecosystem (Tan et al., 2004; Li et al., 2006). In this study, our results also showed that the total abundance of mesozooplankton was mainly contributed by copepods in both the upper/lower estuaries and dry/wet seasons. However, when converted into biovolume, copepods only contributed 17% of the total biovolume in the upper estuary and 9% in the lower estuary. Because of the large size of Chaetognatha and medusae, these groups were important contributors to the total biovolume even when their numerical abundance was low in the PRE. Medusae accounted for less than 0.2% of the total mesozooplankton density in the upper estuary during the dry season. However, they accounted for more than 80% of the total biovolume of mesozooplankton. Some studies have indicated that density statistics are inadequate for the measurement of plankton stock and might underestimate the contribution of large species that are present at a low density (Hillebrand et al., 1999; Ma et al., 2014). From the biovolume analysis, our results showed that Chaetognatha were also important in the pelagic foodweb, accounting for 64% of the total zooplankton biovolume in the lower estuary in the wet season. It is well-known that these gelatinous organisms frequently dominate the biovolume, but not the biomass when converted to dry weight or carbon (Harris et al., 2000). However, according to the rule of larger predators eating smaller prey in aquatic ecosystem (Sheldon et al., 1972), biovolume is still more appropriate than density when analyzing the trophic interactions in planktonic foodwebs. In previous studies in the PRE where density was used for analysis (Tan et al., 2004; Li et al., 2006), the ecological importance of Chaetognatha may be underestimated in the planktonic community.

Because individual zooplankton usually consume prey with a smaller body size, size diversity can indicate trophic niche segregation among different sizes in the pelagic foodweb (Brucet et al., 2006). Some studies have suggested that an increasing zooplankton size diversity would enhance the strength of top-down controls on phytoplankton through diet niche partitioning (Ye et al., 2013). Badosa et al. (2007) reported that some functional aspects of the community structure might be better reflected by size diversity than species diversity. In the present study, the species and size diversity displayed a similar tendency, except in the upper estuary in the dry season. In the dry season, the species diversity did not display obvious differences (range from 2.04 to 2.10) between the sample stations of the upper estuary, but the size diversity had a significantly lower value of 1.15 at S4. Comparing the biovolume size distribution, we found that the large size class was generally absent at S4 and the regression of the NBSS was not significant. These results suggested that size diversity might be more useful for indicating the variation of the functional structure of the planktonic community. In addition, species and size diversity were highest in the lower estuary in the wet season, suggesting a distinctly higher diversity in species composition and trophic interaction.

Ecological indication of normalized biovolume size spectrum parameters

This is the first study to report the size distribution and biovolume size spectra of zooplankton in the PRE. Information regarding spatial and temporal changes in the mesozooplankton NBSS is extremely valuable for evaluating the structure of the marine ecosystem (Zhou et al., 2013; García-Comas et al., 2014). The regression coefficient (R^2) should be the most important factor when evaluating the structure and function of an ecosystem using size spectrum theory. In the PRE, the low R^2 value of NBSS in our results suggests the stability of the mesozooplankton trophic structure was low in the wet season. In the upper estuary, due to the low biomass and size diversity, all the NBSS regressions were not significant for the four sampling stations in the wet season. In contrast, all the NBSS regressions were highly significant in the lower estuary in the dry season. A low R^2 value for the NBSS may indicate the community is unstructured or in a non-equilibrium state according to the view of trophic structure (Boudreau et al., 1991). Our results suggested that the trophic structure of planktonic mesozooplankton was more stable in the dry season than in the wet season; and more stable in the lower estuary than in the upper estuary.

Variations in ecosystem productivity can be well reflected in the NBSS (Sprules and Munawar, 1986; Basedow et al., 2010). Higher intercepts and steeper slopes usually reflect higher productivity, while flatter slopes and the presence of more biomass in larger particles indicate a more important contribution from large organisms and higher energy transfer efficiencies (Marcolin et al., 2013; Dai et al., 2016). In this study, because of the poor correlation of the NBSS, it was not appropriate to discuss the ecological significance of the mesozooplankton NBSS in the upper estuary in the wet season. However, the regressions of the NBSS were generally significant in the dry season and in the lower estuary in the wet season. Our results showed a clear difference in the NBSS of mesozooplankton between the dry and wet season in PRE. Especially in the lower part of the PRE, the slopes of NBSS were significantly flatter and the intercepts of NBSS were higher in the wet season than in the dry season. The high intercepts of the NBSS indicated a high productivity in the lower estuary in the wet season, which was consistent with the accompanying high total mesozooplankton biovolume and total Chl *a* concentration. In general, the NBSS of mesozooplankton suggested that the productivity and energy transfer efficiency were highest in the lower estuary in the wet season. In addition, the slope of the NBSS regression line can also be used as an index of the bottom-up or top-down control of the marine ecosystem (Zhou et al., 2006; Ye et al., 2013). The relatively steeper size spectrum slopes and lower size diversity of the zooplankton community might suggest a weaker strength of the top-down control (Ye et al., 2013). Through in situ gut evacuation experiments, Tan et al. (2004) indicated that the zooplankton in the PRE had a strong effect on the phytoplankton standing stocks in the wet season and a minor impact on the phytoplankton standing stocks in the dry season. This is consistent with our results. In this study, the steeper slope of the NBSS and lower size diversity suggested a weak top-down control of mesozooplankton on phytoplankton in the dry season in the PRE.

Conclusions

Results of this study suggested that biovolume is a useful parameter for the analysis of trophic interactions in a planktonic foodwebs. Size diversity was more sensitive for determining the variation of trophic structure in a planktonic community. In the PRE, the characteristics of the

NBSS were significantly different between the dry and wet seasons, with the slope of the regression line being steeper in the dry season than in the wet season. It was concluded that the productivity and trophic efficiency were higher in the lower estuary in the wet season.

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