Oceanologia (2016) 58, 124—134

Available online at www.sciencedirect.com

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ORIGINAL RESEARCH ARTICLE

# Scale-dependent environmental control of mesozooplankton community structure in three aquaculture subtropical bays of China☆

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Received 30 November 2014; accepted 9 November 2015
Available online 17 December 2015

**KEYWORDS**
Zooplankton;
Aquaculture;
Pollution effects;
Multivariate analysis;
Subtropical bays

**Summary** Most subtropical bays of China have been under heavy pollution since the late 1990s, mainly because of the rapid development of aquaculture and discharge of industrial and agricultural wastewater. Some projects were conducted to investigate the zooplankton community in these bays, but those studies were less focused on the relationship between spatial structure of mesozooplankton community and environmental variables in/among bays. The mesozooplankton community structures in relation to physical, chemical and biological variables were studied in three subtropical bays of China with seasons and different spatial scales during 2000 and 2002—2003. Data were collected on temperature (*T*), salinity (*S*), concentration of chlorophyll *a* (Chl *a*), pH, dissolved oxygen (DO), soluble reactive phosphate (SRP), dissolved inorganic nitrogen (DIN), chemical oxygen demand (COD), suspended particle material (SPM) and mesozooplankton taxonomic abundances. Correlation analysis showed that the main environmental factors correlated to the total abundance of mesozooplankton in these subtropical bays were Chl *a*, temperature, COD and SRP. Multivariate analysis indicated that DO, Chl *a* and temperature were the principal factors in influencing spatial differentiation of zooplankton

☆ This work was supported by the Global Change and Air-Sea Interaction Program (GASI-03-01-03-02), the China Ocean Mineral Resources Research and Development Association Program (DY125-11-E-03), National Natural Science Foundation of China (41406116), and Zhejiang Provincial Natural Science Foundation of China (LY12C03010).
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Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.

Production and hosting by Elsevier

http://dx.doi.org/10.1016/j.oceano.2015.11.002

community structure in the inter-bay scale. At the within-bay scale, the influencing factors were different among bays; the main factors were physical variables for Xiangshan Bay and Sanmen Bay, while chemical variables for Yueqing Bay, respectively. The results revealed that the environmental variables that affected spatial structure of mesozooplankton community were different at inter-bay scale and within-bay scales, and zooplankton community was more influenced by chemical (e.g. nutrients/ammonia) variables when under serious eutrophication condition, while it would be more influenced by physical variables (temperature/salinity) when under less eutrophic conditions.



## 1. Introduction

Mesozooplankton always play an important role in various marine environments (Karsenti et al., 2011), and constitute a significant link between phytoplankton, microzooplankton and higher trophic levels, including many kinds of commercially marine animals (Tait and Dipper, 1998). Therefore, the aquatic environment and profits of aquaculture are always heavily influenced by the mesozooplankton community (Ayón et al., 2008; Bianchi et al., 2003). In estuarine areas, the spatial and temporal variation of the mesozooplankton community are always driven by several main factors, such as salinity and hydrographic facts (Hwang et al., 2010b; Mouny and Dauvin, 2002). While in coastal bays, the variation is mainly affected by many more environmental variables, such as temperature, salinity, oxygen, chlorophyll *a* concentration and other chemical factors (Li et al., 2005; Ning et al., 2004; Roman et al., 1993; Uriarte and Villate, 2005). The relationship is much more variable, since there are only weak or absolutely no constant decisive environmental gradients in these bays (Liu et al., 2012; Sun et al., 2011). Considering such weak environmental gradients, the relationship between environment and the zooplankton community in weak-influx coastal bays, are quite similar to the condition of adjacent continental shelf, where the influencing factors of zooplankton communities are strong spatial-temporal variation (Hwang et al., 2010a; Li et al., 2011, 2013).

The Zhejiang Province is one of the most industrialized and densely populated regions of China. In this area, with the rapid development of aquaculture and the discharge of ever increasing amounts of industrial and agricultural wastewater, the coastal waters have been heavily polluted since the late 1990s. Along the coastline of Zhejiang Province, there are three bays which are dominated by aquaculture: Xiangshan Bay, Sanmen Bay and Yueqing Bay. In recent years, several projects were conducted to assess the extent to which the marine ecosystem was influenced by human activities, and the carrying capacity of these bays, mainly based on the water quality parameters and plankton community characteristics (Cai et al., 2013; Ning and Hu, 2005). The mesozooplankton communities of those bays were reported in several studies from 2003 (Table 1). However, several aspects were

**Table 1** Literatures reviewed about environmental variables which significantly affect the mesozooplankton community in these three bays.

| Location | Season | Biological variable | Related environmental variable | Literatures |
|---|---|---|---|---|
| Xiangshan Bay | Four seasons | – | – | Wang et al. (2003)* |
| | Four seasons | – | – | Wang et al. (2009)* |
| | Winter | – | – | Liu et al. (2004)* |
| | Winter | Biomass | SPM, TOC | Du et al. (2011)[1] |
| | | Abundance | *S* | |
| Yueqing Bay | Four seasons | Biomass | *T*, Chl *a* | Xu et al. (2012)[1] |
| | | Abundance | *T*, Chl *a*, PCD | |
| | Spring | Abundance | S | Liu et al. (2005)[2] |
| | Summer | Abundance | *S*, TIN, SRP | |
| Sanmen Bay | Summer | Abundance | TIN | Liu et al. (2006)[2] |
| | Winter | Abundance | Chl *a* | |
| | Spring | Abundance | *T*, *S*, Chl *a*, TIN, $SiO_3$, DO | Liu et al. (2012)[1] |
| | Summer | Abundance | pH, DO | |
| | Autumn | Abundance | *S*, $SiO_3$ | |
| | Winter | Abundance | COD | |
| | Four seasons | Abundance | *T*, *S*, Chl *a* | Xu et al. (2013)[3] |

Statistical method: [1]Correlation analysis; [2]Linear regression analysis; [3]Canonical correspondence analysis (CCA); *no statistical method used. When no statistical method was used in cited studies, the biological variable and environmental variable were not shown.
*Abbreviations*: SPM — suspended particle material; TOC — total organic carbon; TIN — total inorganic nitrogen; SRP — soluble reactive phosphate; DO — dissolved oxygen; COD — chemical oxygen demand; *T* — temperature; *S* — salinity; PCD — phytoplankton cell density.

ignored in previous works until now. First, as mentioned above, there was no strong and constant environmental gradient in these bays. Additionally, the relationship between the environment and zooplankton community was more complex and with markedly seasonal variation. Hence, the relationship should be analyzed separately for each season. If that relationship between an environmental variable and a biotic parameter was reversed among different seasons, a potential significant effect in a certain season was likely to be counterbalanced using a linear regression analysis for whole year's data. Second, most studies focused only on the relationship between environment and biomass/abundance, but ignored the influencing factors of spatial variation of zooplankton community structure, and the scale-dependent effect of these influencing factors. Third, simple correlation analysis, instead of ordination analysis or other multivariate statistics analyses were used. In such case, the relationship between environmental variables and zooplankton spatial community structure might be underestimated in previous works (Table 1) (Šmilauer and Lepš, 2014).

Nutrients are key factors in most pelagic ecosystems, which indirectly influence the community structure and size structure of phytoplankton, and then indirectly influence the abundance and community structure of zooplankton (Graneli et al., 1999; McQueen et al., 1989; Zhou et al., 2008). Pollution always results in extremely high nutrient conditions for marine ecosystems in coastal waters (Li and Daler, 2004), and may significantly influence the mesozooplankton community structure (Marcus, 2004; Uriarte and Villate, 2005). Eutrophication may affect mesozooplankton via several possible pathways: bottom-up trophic dynamics, a limitation of hypoxia/anoxia and a toxic effect of ammonia (Roman et al., 1993; Sullivan and Ritacco, 1985; Uye et al., 1999). However, the effect of eutrophication on mesozooplankton is more complicated in coastal waters (Chen et al., 2011; Marcus, 2004), because the mesozooplankton are also under the influences of changing predation pressure, variation of food quality and hydrological conditions.

All three bays were heavily affected by aquaculture, but the differences in geometry and the exchange rate with open waters influenced their environmental characters. Among those three bays, Yueqing Bay is one of eight most critically polluted bays in China, especially characterized by extremely high nitrogen concentration (Chen et al., 2010; EBCWC, 2003). The water quality of Sanmen Bay is slightly better than the others, mainly because of its capacious geometry and much higher exchange rate (Ning and Hu, 2005) (Fig. 1).

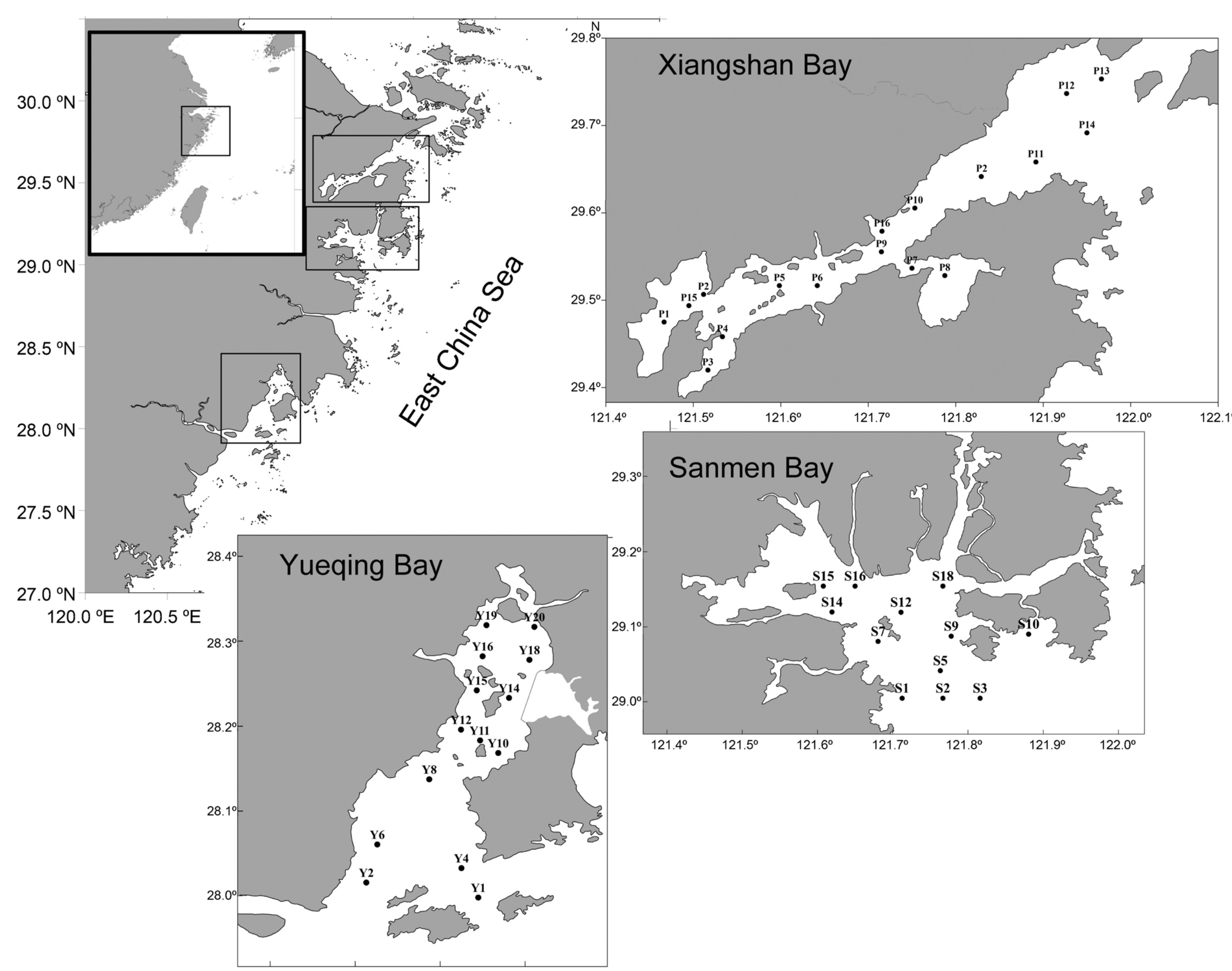


**Figure 1** Map of Xiangshan Bay, Sanmen Bay and Yueqing Bay (located on the coast of Zhejiang Province, China, 28.0°N–29.9°N), showing sampling stations in the present study.

On the other hand, higher water exchange rate with the open sea might depress the gradient of chemical variables from pollution and their residence time (Wang et al., 2011).

Based on the three bays' environmental differences and a common effect of eutrophication on mesozooplankton community, we hypothesized that the zooplankton community would be more influenced by chemical (e.g. nutrients/ammonia) and biological (e.g. Chl *a*) variables when under serious eutrophic conditions, while it would be more influenced by physical variables (temperature/salinity) when under less eutrophic conditions.

## 2. Material and methods

### 2.1. Study area

This study was conducted in three subtropical bays: Xiangshan Bay, Sanmen Bay and Yueqing Bay, along the coast of Zhejiang Province, China (28.0°N—29.9°N) (Fig. 1). All three bays are semi-enclosed (with various magnitude of openness), without strong freshwater influx and have been heavily influenced by aquaculture since the 1990s. Xiangshan Bay is about 563 $km^2$ in area, 10 m in mean depth and 40 m in maximum depth. Xiangshan Bay is relatively narrow and long, with about 50 km in total length and 9.5 km in mouth width. Sanmen Bay is about 540 $km^2$ in area, 9 m in mean depth and above 60 m in maximum depth. There are several branches deep into land, which creates over one hundred square kilometers shoal in the area. Its total length is about 42 km and with 22 km wide in mouth. Yueqing Bay is about 464 $km^2$ in area, approximately 10 m in mean depth and over a hundred meters in maximum depth. This bay is 42 km in length, 21 km in mouth wide and 4.5 km in minimum width.

### 2.2. Sampling procedure

Sampling was conducted during twelve short-period investigations (four seasons × three bays). For Xiangshan Bay, investigations were conducted at twenty sampling sites in January, April, July and October 2000. For Sanmen Bay and Yueqing Bay, investigations were conducted at twelve and fourteen sampling sites respectively, in August, November 2002, May and February 2003.

Zooplankton samples were collected by vertical tows (505 μm mesh size and 0.8 m in diameter, equipped with a HYDRO-BIOS flowmeter fixed in the mouth to measure the volume of water filtered) from near-bottom to surface. Net collections were fixed with 5% (v/v) buffered formaldehyde (with seawater) immediately. In laboratory, 5% to 25% fractions of total mesozooplankton sample were identified and counted according to the individual number (Chen et al., 1974; Zheng et al., 1984). Zooplankton abundance was expressed as ind. $m^{-3}$. The fundamental data of wet biomass and abundance of mesozooplankton community collected from those investigations had been published (Liu et al., 2005, 2006; Wang et al., 2003), thus most of those detailed data were not shown again in the present study. The raw data on abundance of each species in every station were analyzed in the present study. Absolutely rare species (a single occurrence for all sampling sites) were eliminated from correlation analysis and ordination analysis below, and they were not shown in the list of species (Appendix Table 1).

The physical environmental parameters, including salinity and temperature were recorded at 0.5 m under surface by a SYA 2-2 salinometer and thermometer. The water samples for nutrient analysis were collected at a depth of 0.5 m by Go-Flo bottles. Nitrate and nitrite were determined by the pink azo dye method and ammonia by the hypobromite oxidation-pink azo dye method; soluble reactive phosphorus was determined by the molybdenum blue method immediately after sampling (Parsons et al., 1984). The detection limits of $NO_3^-$, $NO_2^-$, $NH_4^+$, $PO_4^{3-}$ and $SiO_3^{2-}$ are 0.02 $\mu mol\ L^{-1}$, 0.05 $\mu mol\ L^{-1}$, 0.05 $\mu mol\ L^{-1}$, 0.03 $\mu mol\ L^{-1}$ and 0.07 $\mu mol\ L^{-1}$, respectively, for the present methods. The concentration of dissolved oxygen was measured using a direct spectrophotometry method (Pai et al., 1993). For the measurement of chlorophyll *a* (Chl *a*) concentration, a 500 mL water sample was gently filtered through a 0.22 μm cellulose filter and extracted in 90% acetone for 24 h in darkness and 4°C. The mean Chl *a* concentration was then determined fluorometrically (Turner Designs 10AU fluorometer) before and after acidification (Parsons et al., 1984). The concentration of suspended particle material (>0.45 μm) was only measured for Xiangshan Bay.

### 2.3. Data analysis

For the zooplankton abundance data and environmental data, we used unconstrained ordination, constrained ordination and correlation analysis to distinguish the main environmental variables which significantly affect the abundance of zooplankton and the zooplankton community structure, at different spatial scales and in different seasons. All analyses below were based on log-transformed abundance data and environmental data.

First, a Pearson correlation analysis was applied to find the relationship between abundance of zooplankton in three bays and environmental variables with seasons.

Second, the environmental variables which drive the heterogeneity of mesozooplankton community structure among the three subtropical bays in each season were distinguished. According to the methods by Šmilauer and Lepš (2014), DCA was used to find whether abundance data of zooplankton showed linear or unimodal responses to the underlying gradients in this region. For the data of spring, summer and autumn, the lengths of gradient were all less than 3, while the length of gradient was over 4 for the winter data. Thus, we conducted three redundancy analyses (RDA) for the spring, summer and autumn data, and a canonical correspondence analysis (CCA) for the data of winter. Explanatory environmental variables were chosen by the forward selection in RDA and CCA, and only those variables that significantly related to community structure according to Monte Carlo permutation tests ($p < 0.05$) were selected to be considered in RDAs and CCA, and to be shown in ordination diagrams. The variability explained for each environmental variable in CCA equals to λ value divided by total inertia.

Third, the environmental variables which affect the mesozooplankton community structure in each of the three subtropical bays in every season were distinguished. The model selection procedure was the same as above, and twelve separate RDAs were conducted. Also, only those variables that significantly influence community structure according to Monte Carlo permutation tests ($p < 0.05$) were selected to be considered in RDAs. In the present analysis, chemical variables included DIN, SRP, PH, COD, $NH_3$; biological variable included Chl *a*; physical variables included temperature and salinity.

The correlation analysis was performed using SPSS v19.0 (IBM Corp., Somers, NY, USA), and ordination analysis was performed using CANOCO v4.5 (Microcomputer Power, Ithaca, NY, USA).

## 3. Results

### 3.1. Environmental and biotic characteristic

Environmental data obtained during this study were given in Fig. 2 and Appendix Table I. Surface temperature showed an obvious seasonal variation in those three bays, by winter cooling and summer warming. Surface salinity was higher in spring/summer and lower in autumn/winter in Xiangshan Bay and Sanmen Bay, while lower in spring/summer and higher in autumn/winter in Yueqing Bay. The concentration of Chl *a* was significantly lower in Xiangshan Bay, compared to the other two, and also showed significant seasonal variations (Fig. 2).

Similar to the environmental variables, the abundance of mesozooplankton in the three bays also showed a temporal and spatial variation. In Xiangshan Bay, the seasonal peak appeared in spring, while for the other two bays, the abundance reached the highest level in summer (Fig. 3). Compared to the other two bays, the mesozooplankton abundance in Xiangshan Bay was significantly higher in spring and autumn (one-way ANOVA, $p = 0.002$, and $p = 0.006$, respectively), and in Sanmen Bay it was significantly higher in summer (one-way ANOVA, $p = 0.001$). In winter, the abundance in Yueqing Bay was lower, but not statistically significant (one-way ANOVA, $p = 0.075$). The mesozooplankton community structures were also quite different among the three bays. In Xiangshan Bay, *Centropages abdominalis* was

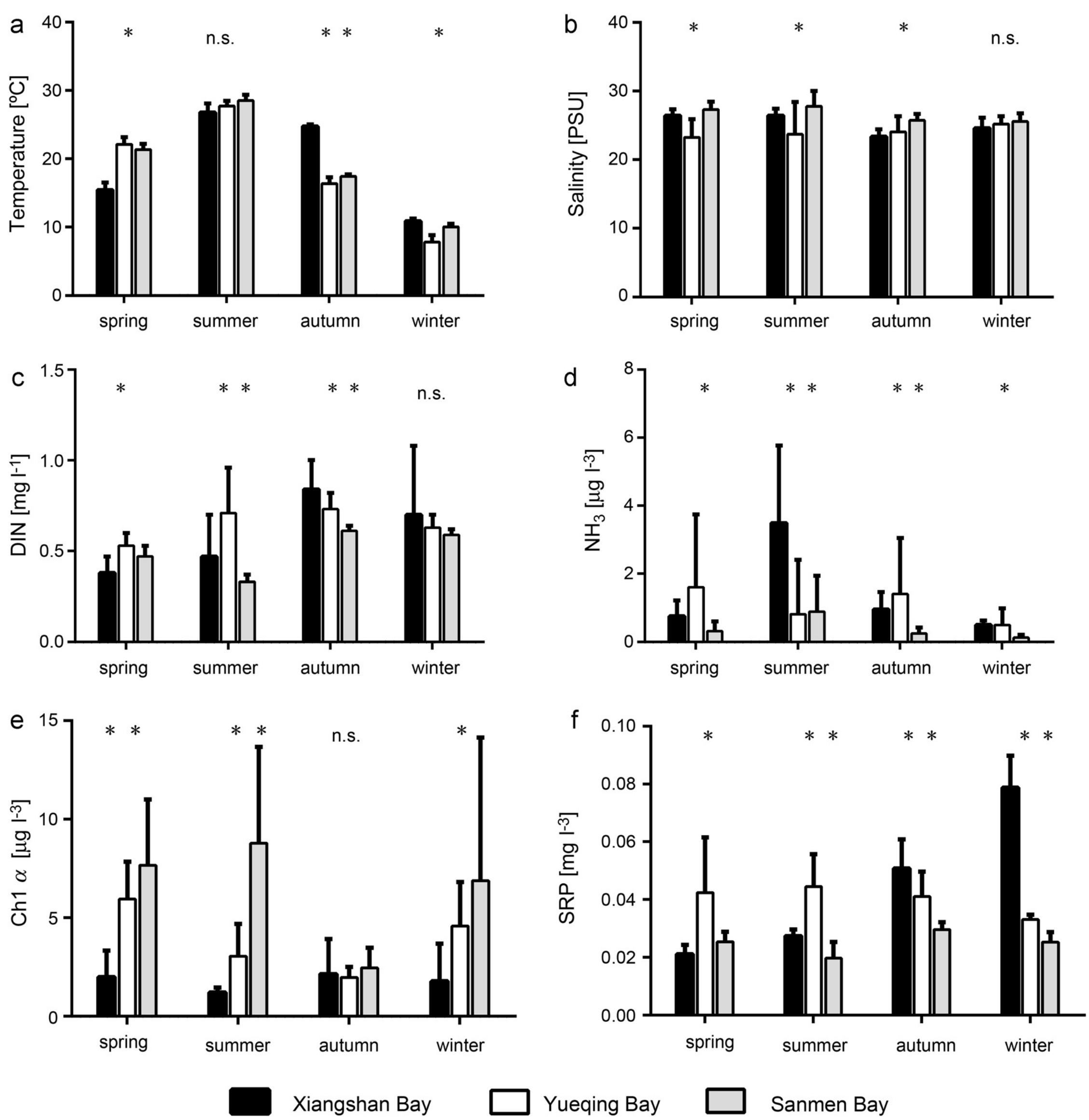


**Figure 2** Environmental variables of Xiangshan Bay, Sanmen Bay and Yueqing Bay ($^{*}p < 0.05$; $^{**}p < 0.01$).

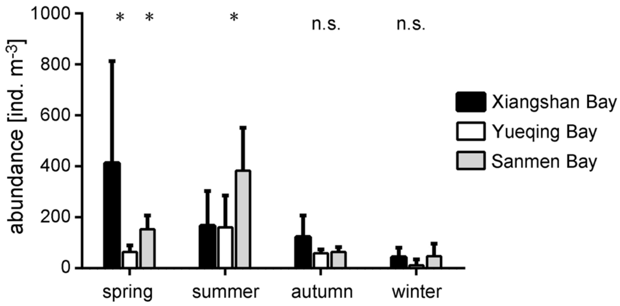


**Figure 3** Abundance of mesozooplankton community of Xiangshan Bay, Sanmen Bay and Yueqing Bay ($^{*}p < 0.05$; $^{**}p < 0.01$).

one dominant species in spring, summer and winter, especially with an extremely high relative abundance in spring. And *Acartia pacifica* only dominated in warm seasons. In Yueqing Bay, *Labidocera euchaeta* was always the dominant species all the year round, especially in warm seasons. In Sanmen Bay, two main dominant species were *Calanus sinicus* and *Acrocalanus gibber* (Table 2).

## 3.2. Environmental factors—zooplankton community relationships

### 3.2.1. Seasonal variation of environmental factors correlated to zooplankton abundance

Pearson correlation analysis indicated that environmental factors correlated to the abundance of mesozooplankton in these subtropical bays differed with seasons. In spring, it was positively related to DO and negatively related to temperature, COD and SRP. In summer, it was positively related to Chl *a*, temperature and COD, and negatively related to SPR. In autumn, it was positively related to temperature, and negatively related to Chl *a*. While in winter, it was positively related to Chl *a* and negatively related to salinity (Table 3).

**Table 3** Pearson correlation coefficients between abundance of mesozooplankton [ind. $m^{-3}$] and environmental variables in Xiangshan Bay, Yueqing Bay and Sanmen Bay in four seasons. The abbreviations of environmental variables were listed in Table 1.

| Variables | Abundance | | | |
|---|---|---|---|---|
| | Spring | Summer | Autumn | Winter |
| Chl *a* | n.s. | $0.666^{**}$ | $-0.333^{*}$ | $0.415^{**}$ |
| *T* | $-0.436^{**}$ | $0.376^{*}$ | $0.329^{*}$ | n.s. |
| DO | $0.512^{**}$ | n.s. | n.s. | n.s. |
| PH | n.s. | n.s. | n.s. | n.s. |
| *S* | n.s. | n.s. | n.s. | $-0.452^{**}$ |
| $NH_3$ | n.s. | n.s. | n.s. | n.s. |
| DIN | n.s. | n.s. | n.s. | n.s. |
| COD | $-0.468^{**}$ | $0.499^{**}$ | n.s. | n.s. |
| SRP | $-0.413^{**}$ | $-0.312^{**}$ | n.s. | n.s. |

*Note*: n.s. — $p > 0.05$; $^{*}$ $p < 0.05$; $^{**}$ $p < 0.01$.

### 3.2.2. Environmental factors affecting the spatial differentiation of zooplankton community structure

RDAs and CCA showed that environmental factors affecting the spatial differentiation of zooplankton community structure were significantly different with seasons ($p < 0.05$, Monte Carlo permutation tests) (Fig. 4). In spring, the differentiation between the community of Xiangshan Bay and the others was mainly explained by DO (28%) and temperature (3%), while the differentiation between the community of Yueqing Bay and Sanmen Bay was mainly driven by salinity (11%). In summer, the differentiation between the community of Sanmen Bay and the others was mainly explained by Chl *a* (16%) and salinity (7%), while there was no significant differentiation between the community of Xiangshan Bay and Yueqing Bay (Fig. 4). In autumn, the differentiation between the community of Xiangshan Bay and the others was mainly explained by temperature (25%). And the differentiation between the community of Yueqing Bay and Sanmen Bay

**Table 2** The dominant species of mesozooplankton community in Xiangshan Bay, Yueqing Bay and Sanmen Bay. The relative abundance of dominant species was given.

| Seasons | Dominant species | | |
|---|---|---|---|
| | Xiangshan Bay | Yueqing Bay | Sanmen Bay |
| Spring | *Centropages abdominalis* (76%) | Brachyura zoea larva (21%)<br>*Labidocera euchaeta* (14%)<br>*Zonosagitta bedoti* (12%) | *Calanus sinicus* (21%)<br>Brachyura zoea larva (11%) |
| Summer | Brachyura zoea larva (29%)<br>*Acartia pacifica* (17%)<br>*Centropages abdominalis* (11%) | *Labidocera euchaeta* (25%)<br>Brachyura zoea larva (14%) | *Acrocalanus gibber* (26%) |
| Autumn | *Paracalanus aculeatus* (20%)<br>*Acartia pacifica* (20%)<br>*Calanopia thompsoni* (11%) | *Labidocera euchaeta* (36%)<br>*Acrocalanus gibber* (18%)<br>*Acartia pacifica* (17%) | *Calanus sinicus* (20%)<br>*Acrocalanus gibber* (12%) |
| Winter | *Centropages abdominalis* (42%)<br>*Oikopleura dioica* (16%)<br>*Tortanus derjugini* (15%) | Gastropoda post larva (42%)<br>*Diastylis tricincta* (14%)<br>*Labidocera euchaeta* (9%) | *Centropages abdominalis* (33%)<br>*Tortanus derjugini* (17%)<br>*Diastylis tricincta* (16%) |

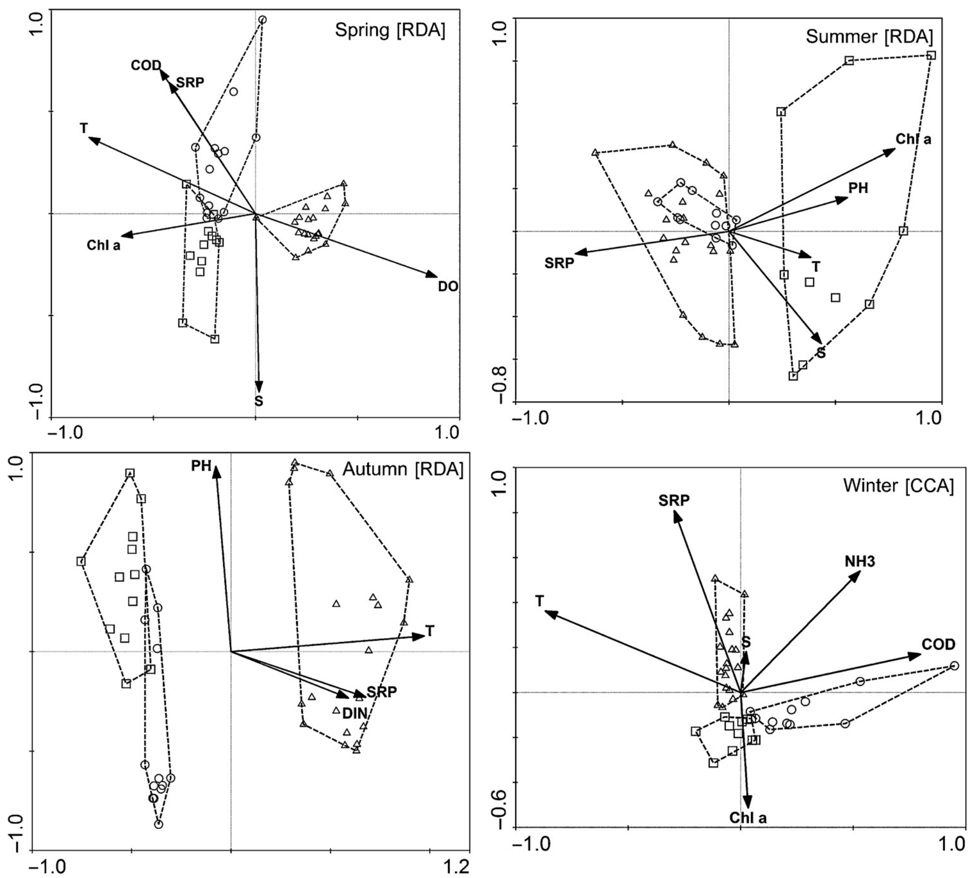


**Figure 4** RDA and CCA ordination diagrams of site scores in three bays and selected environmental variables (represented by arrows) in four seasons. Only the significantly explanatory environmental variables retained by a forward selection procedure ($p < 0.05$, Monte Carlo permutation test) are presented. The data from spring, summer and autumn were analyzed under RDA model, while the data from winter were analyzed under CCA model (see more details in Methods). Symbol: triangle — Xiangshan Bay; circle — Yueqing Bay; square — Sanmen Bay.

could be explained by pH (12%), though there was a considerable degree of overlap between them under this axis. Finally, in winter, temperature (12%) explained the differentiation between the community of Yueqing Bay and the others, while $NH_3$ (9%) and salinity (7%) could influence the differentiation between the community of Xiangshan Bay and Sanmen Bay (Table 4).

### 3.2.3. Environmental factors affecting the zooplankton community structure in each bay

RDA showed that zooplankton community structure was significantly related to several environmental variables, and it was quite variable with sites and seasons. Specifically, salinity, temperature and Chl *a* were always the main factors affecting the community structure in Xiangshan Bay (Table 5). For Sanmen Bay, the primary factors were always salinity and $NH_3$ in spring, summer and autumn, but SRP and temperature in winter (Table 6). Finally, the primary environmental factors were extraordinarily variable in Yueqing Bay, which were temperature in spring, DIN in summer, SRP, Chl *a* and DIN in autumn and COD in winter (Table 7). For the full year, physical variables were the dominant influencing factors for the zooplankton community structure in Xiangshan Bay and Sanmen Bay, while chemical variables were more dominant in Yueqing Bay (Table 8).

## 4. Discussion

Generally, we found that the environmental variables which affected the abundance and spatial differentiation of zooplankton community structure were significantly variable with seasons and with different spatial scales in these adjacent subtropical bays of China. Consistent with our hypothesis, the zooplankton community structure of Sanmen Bay, which has lower pollution rate than the two other bays, was most influenced by the physical variables; while that of Yueqing Bay, which is heavily polluted, was most influenced by the chemical variables. In Xiangshan Bay, which is moderately polluted, the zooplankton was again most influenced by physical variables.

Eutrophication may affect herbivorous zooplankton through providing more food directly by phytoplankton or indirectly by complex microbial food loop (Calbet and Landry, 1999; Jones and Flynn, 2005). The concentration of Chl *a* was always an important environmental gradient related to the level of primary productivity in coastal bays. Although Chl *a* was widely used as a biological indicator of eutrophication in some monitoring methods (Nixon, 1995), the present results indicated that it was not associated with nutrient concentration in these bays. As in other shallow turbid systems, the phytoplankton seems not to be nutrient-limited, but light

**Table 4** Ranking of environmental variables that significantly influenced the spatial differentiation of zooplankton community structure among three bays, based on Monte Carlo permutation test in redundancy analysis (RDA) (the data in spring, summer and autumn) and canonical correspondence analysis (CCA) (the data in winter) (499 samples, $p < 0.05$). The variability explained for each environmental variable in canonical correspondence analysis equals to λ value divided by total inertia. The abbreviations of environmental variables were listed in Table 1.

| Explanatory variable | Variability explained | *p*-value | *F*-value |
|---|---|---|---|
| **Spring (RDA)** | | | |
| DO | 0.28 | 0.002 | 16.93 |
| *S* | 0.11 | 0.002 | 7.8 |
| COD | 0.04 | 0.004 | 2.99 |
| SRP | 0.03 | 0.008 | 2.52 |
| Chl *a* | 0.03 | 0.024 | 2.08 |
| *T* | 0.03 | 0.028 | 2.1 |
| **Summer (RDA)** | | | |
| Chl *a* | 0.16 | 0.002 | 7.19 |
| *S* | 0.07 | 0.002 | 3.58 |
| PH | 0.05 | 0.01 | 2.63 |
| SRP | 0.05 | 0.006 | 2.75 |
| *T* | 0.04 | 0.04 | 2 |
| **Autumn (RDA)** | | | |
| *T* | 0.25 | 0.002 | 14.63 |
| PH | 0.12 | 0.002 | 8.12 |
| DIN | 0.04 | 0.008 | 2.66 |
| SRP | 0.03 | 0.012 | 2.2 |
| **Winter (CCA)** | | | |
| *T* | 0.12 | 0.002 | 5.12 |
| $NH_3$ | 0.09 | 0.002 | 4.05 |
| *S* | 0.07 | 0.002 | 3.68 |
| SRP | 0.04 | 0.006 | 2.07 |
| Chl *a* | 0.04 | 0.044 | 2.05 |
| COD | 0.03 | 0.022 | 1.86 |

**Table 5** Ranking of environmental variables that significantly influenced the community structure of mesozooplankton in Xiangshan Bay, based on Monte Carlo permutation test in redundancy analysis (RDA) (499 samples, $p < 0.05$).

| Explanatory variable | Variability explained | *p*-value | *F*-value |
|---|---|---|---|
| **Spring** | | | |
| *S* | 0.4 | 0.002 | 12.13 |
| Chl *a* | 0.13 | 0.002 | 4.71 |
| **Summer** | | | |
| *T* | 0.3 | 0.002 | 7.72 |
| Chl *a* | 0.14 | 0.002 | 4.3 |
| **Autumn** | | | |
| *S* | 0.28 | 0.002 | 7.15 |
| *T* | 0.18 | 0.002 | 5.51 |
| DIN | 0.07 | 0.012 | 2.36 |
| Chl *a* | 0.06 | 0.018 | 2.42 |
| **Winter** | | | |
| *S* | 0.37 | 0.002 | 10 |
| Chl *a* | 0.17 | 0.002 | 6.01 |
| $NH_3$ | 0.09 | 0.006 | 3.8 |
| PH | 0.07 | 0.01 | 2.86 |

**Table 6** Ranking of environmental variables that significantly influenced the community structure of mesozooplankton in Sanmen Bay, based on Monte Carlo permutation test in redundancy analysis (RDA) (499 samples, $p < 0.05$).

| Explanatory variable | Variability explained | *p*-value | *F*-value |
|---|---|---|---|
| **Spring** | | | |
| *S* | 0.23 | 0.002 | 3.05 |
| $NH_3$ | 0.23 | 0.002 | 3.78 |
| **Summer** | | | |
| *S* | 0.35 | 0.002 | 4.28 |
| **Autumn** | | | |
| *S* | 0.25 | 0.002 | 3.34 |
| **Winter** | | | |
| SRP | 0.39 | 0.002 | 5.81 |
| *T* | 0.19 | 0.002 | 3.69 |

availability is likely to be the limiting factor (e.g. Domingues et al., 2011; Guinder et al., 2009; Zhu et al., 2009). In the present result, the concentration of Chl *a* was not the dominant influencing factor of zooplankton community structure in all three bays. Similar phenomenon was also found in other eutrophic coastal waters (Chen et al., 2011; Uriarte and Villate, 2005). These results indicated that direct trophic link between phytoplankton and mesozooplankton was relatively weak in these bays.

Typically, due to hydrographic features and a gradient of nutrient or transparency along geometrical features, the concentration of Chl *a* often showed a decreasing gradient from inside to mouth in temperate and subtropical bays, such as Xiangshan Bay and Jiaozhou Bay in China (Li et al., 2005; Liu et al., 1997). However, this stable gradient was not observed in Yueqing Bay and Sanmen Bay (Chen et al., 2010 and the present study). Multivariate statistics analysis indicated that the concentration of Chl *a* was only able to explain the spatial pattern of zooplankton community in Xiangshan Bay, but not in Yueqing Bay and Sanmen Bay. There were two possible reasons: one, a high Chl *a* concentration meant redundant food for mesozooplankton, thus Chl *a* was a limiting factor for them no longer (Chen et al., 2011); two, other more dominant influencing factors existed, which outstripped the contribution of Chl *a* variation (Uriarte and Villate, 2005), such as DIN from extreme heavy pollution in Yueqing Bay.

Copepods always dominated mesozooplankton community in coastal waters (Chang et al., 2010; Liu et al., 2012), and they were generally considered to be relatively sensitive to poor water quality (Uriarte and Villate, 2005). Buttino (1994) reported that the viability and reproduction rate of *Acartia clausi* would be significantly depressed under a $NH_3$ concentration of 0.12 ppm. We were not aware of the sensitivity of local zooplankton community to $NH_3$, considering that $NH_3$ concentration in Buttino's report was approximately two

**Table 7** Ranking of environmental variables that significantly influenced the community structure of mesozooplankton in Yueqing Bay, based on Monte Carlo permutation test in redundancy analysis (RDA) (499 samples, $p < 0.05$).

| Explanatory variable | Variability explained | *p*-value | *F*-value |
|---|---|---|---|
| **Spring** | | | |
| *T* | 0.22 | 0.002 | 3.43 |
| **Summer** | | | |
| DIN | 0.4 | 0.002 | 6.06 |
| **Autumn** | | | |
| SPR | 0.39 | 0.002 | 7.05 |
| Chl *a* | 0.13 | 0.006 | 2.68 |
| DIN | 0.09 | 0.046 | 2.05 |
| **Winter** | | | |
| COD | 0.49 | 0.002 | 8.57 |

**Table 8** The total variability explained by chemical/biological/physical variables on zooplankton community structure of each bay in four seasons (chemical variables: DIN, SRP, PH, COD, $NH_3$; biological variable: Chl *a*; physical variables: temperature, salinity; based on Tables 5—7).

| | Variability explained | | |
|---|---|---|---|
| | Chemical variable | Biological variable | Physical variable |
| Xiangshan Bay | 0.23 | 0.5 | 1.53 |
| Sanmen Bay | 0.62 | 0 | 1.02 |
| Yueqing Bay | 1.37 | 0.13 | 0.22 |

orders of magnitude higher than those in the present study, thus the $NH_3$ concentration was likely to be the secondary factor in affecting the spatial structure of zooplankton community in the three bays.

The total abundance of mesozooplankton was not affected by DIN conditions in each season in our study, which was in accordance with other results in these three bays (Du et al., 2011; Xu et al., 2012, 2013), but it was negatively impacted by the SRP concentration in spring and summer. The exact mechanism of that relationship was unknown. Although all three bays exhibited eutrophic conditions, multivariate statistics analysis indicated that eutrophic conditions were the primary factor influencing the spatial structure of mesozooplankton community only in Yueqing Bay. The dominant species of the mesozooplankton communities were significantly different among the three bays, though the salinity and temperature were quite similar between Xiangshan Bay and Yueqing Bay. *L. euchaeta* is a common eurytopic and dominant species in the subtropical coast of China, distributed in a salinity range from 10 to 25 (Chen et al., 1995). A more recent study demonstrated that this species adapted to higher Chl *a* concentration and lower nutrient concentration in Hangzhou Bay (200 km north from Xiangshan Bay) (Sun et al., unpublished data). In summer and autumn, *L. euchaeta* was the first dominant species (the relative abundance is 25% and 36%, respectively) for the community in Yueqing Bay. Interestingly, RDA indicated that chemical variables also determined the spatial structure of community in these two seasons. A possible reason was that the lower nutrient condition for distribution area of *L. euchaeta* determined, to a great extent, the response of zooplankton community to DIN and SRP gradients in Yueqing Bay in summer and autumn. It also implied that the pelagic ecosystem of Yueqing Bay was under the most serious influence of pollution among the three bays.

Physical variables (temperature and salinity) were the main influencing factors for mesozooplankton community structure in Xiangshan Bay and Sanmen Bay. In contrast, chemical variables (DIN and SRP) were the main factors affecting community structure in Yueqing Bay during most of the year. These results indicated that salinity was usually still an important influencing factor for the mesozooplankton community structure of subtropical bays without strong freshwater influx and pollution, though it was no longer the only dominant factor, just as in typical estuary areas (Marques et al., 2006; Mouny and Dauvin, 2002). Moreover, this significant difference in influencing factors among different bays implied that the zooplankton community of Yueqing Bay was more heavily affected by pollution and aquaculture than Xiangshan Bay and Sanmen Bay.

## 5. Conclusions

The environmental variables influencing zooplankton community structure differed significantly with the seasons and spatial scales in subtropical bays of China which were heavily affected by pollution and aquaculture. DO, Chl *a* and temperature were the principal factors in affecting spatial differentiation of zooplankton community structure at the inter-bay scale. At within-bay scales, the influencing factors were different among adjacent bays: the main factors were physical variables for Xiangshan Bay and Sanmen Bay, while chemical variables for Yueqing Bay, respectively.

## Acknowledgements

We would like to thank Ping Xia for providing a high resolution map of the research area and Renée McDonald for her valuable corrections of the English. We also thank four anonymous reviewers for their kind comments and constructive advice.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.oceano.2015.11.002.

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