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Species diversity patterns of marine plankton and benthos in Chinese bays: Baseline prior to large-scale development

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ABSTRACT

More than 28,000 marine species have been recorded in China, which accounts for approximately 10% of all marine organisms in the world and plays a potentially important role in protecting global marine biodiversity. However, knowledge of marine biodiversity patterns in China is limited, and in particular, no comparative diversity analysis has been carried out for Chinese bays. In this study, national-scale species diversity patterns of coastal bays were examined on the basis of investigations for approximately 81 bays throughout the entire Chinese coastline in the 1980s and the early 1990s, revealing the baseline of diversity patterns prior to large-scale development. Diversity patterns found for coastal bays in China in this study include the following: (1) species richness of benthic macrofauna was larger than that of phytoplankton or zooplankton; (2) spatially, species richness in the subtropical zone was significantly greater than that in the temperate zone; (3) species richness and bay area were significantly correlated and followed power law relationships; and (4) there were significantly positive correlations of species richness among phytoplankton, zooplankton, and benthic macrofauna. The species diversity patterns of marine benthos and plankton for coastal bays in China, in some ways, coincided with general terrestrial patterns. This is the first study to examine national-scale species diversity patterns of coastal bays in China. The findings provide new insights to conservation biology in the marine environment and also are fundamental for future studies of biodiversity and the impact of development on biodiversity.

Keywords. marine species diversity, diversity pattern, cross-taxon congruence, species-area relationship

1. Introduction

Significant reduction and loss of marine biodiversity has been recognized as a common issue globally (Upton 1992; Worm et al. 2006; Schipper et al. 2008), with the highest losses in coastal waters as a consequence of massive population and intensive development in coastal zones (Beatley 1991; Angel 1993; Gray 1997). The China Seas with a total area

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of 4.73 million km², an important part of the western Pacific Ocean, span 38 latitudinal zones consisting of the Bohai Sea, Yellow Sea, East China Sea, and South China Sea from north to south (Chen 1997). Abundant biodiversity in the China Seas, where more than 28,000 marine species have so far been recorded (Huang and Lin 2012), accounts for approximately 11% of global marine organisms and has been recognized as being globally significant (Huang 2008; Liu 2008, 2011; Huang and Lin 2012). On the other hand, marine biodiversity in China has been continually subjected to enormous threats from natural and anthropogenic stresses, predominantly as a result of large-scale development since the 1990s. This has aroused growing concern with respect to biodiversity conservation and has generated a large number of status investigations. Thus, the current status of marine biodiversity in China has been well documented. However, knowledge of a baseline prior to recent intensive disturbance is limited. Earlier baselines are invaluable, particularly for coastal bays because these are likely to already have nearby cities and to attract much larger populations as a result of increased development following major economic changes.

Diversity patterns have been commonly observed and well studied for a long time, and numerous studies have paid attention to latitudinal gradients (e.g., Stevens 1989; Willig, Kaufman, and Stevens 2003; Hillebrand 2004), species-area relationships (e.g., MacArthur and Wilson 1967; Martin 1981; Tjørve 2003), the relationship of species diversity across different taxonomic groups (e.g., Wolters, Bengtsson, and Zaitsev 2006; Qian 2007; Heino 2010), and bathymetric depth gradients (e.g., Rex and Etter 2010). Although these patterns of marine biodiversity have been described for some marine biotas, knowledge of marine diversity in this respect is relatively limited and lags far behind that of terrestrial studies (Rex et al. 2005; Rex and Etter 2010).

Latitudinal gradients are well-known and the oldest ecogeographic patterns in ecology. Species richness generally increases from polar areas to the tropics, and the pattern seems to hold true for many terrestrial and marine taxonomic groups (e.g., Sanders 1968; Astorga et al. 2003; Rombouts et al. 2009; Rex and Etter 2010). This trend has been reported for a wide range of marine biotas, such as deep-sea isopods, gastropods, and bivalves in the North Atlantic (Rex et al. 1993); gastropods in the western Atlantic and eastern Pacific Oceans (Roy et al. 1998); tuna and billfish in the global open oceans (Worm et al. 2005); infauna and epifauna in the northeastern Pacific shelf (Roy, Jablonski, and Valentine 2000); echinoderms in the China Seas (Liao and Xiao 2011); and epifaunal invertebrates (Witman, Etter, and Smith 2004) and copepods at a global scale (Rombouts et al. 2009). Moreover, 198 published biodiversity patterns suggested a high generality of this trend in the marine realm (Hillebrand 2004). Nevertheless, not all marine groups follow this pattern, and considerable debate remains (Roy, Jablonski, and Valentine 2000; Kerswell 2006; Rombouts et al. 2009). For instance, the global distribution of diversity of nematodes in shallow water has not shown a clear latitudinal trend (Mokievsky and Azovsky 2002).

Cross-taxon congruence refers to the spatial congruence of species diversity across the different taxonomic groups (Toranza and Arim 2010). A growing number of studies have been conducted to examine this pattern in the terrestrial world, especially among birds,

vascular plants, butterflies, ants, vertebrates, and mammals (Gaston 2000; Vessby et al. 2002; Worm et al. 2005; Wolters, Bengtsson, and Zaitsev 2006; Qian 2007; Heino 2010; Toranza and Arim 2010). However, cross-taxon congruence in marine ecosystems has rarely been documented, and the generality of such congruence is still controversial and ambiguous, although a few studies have shown significant cross-taxon congruence of biodiversity (Irigoien, Huisman, and Harris 2004; Dolan 2005; Worm et al. 2005; Karakassis et al. 2006). For example, significant relationships were found between tuna or billfish diversity and zooplankton diversity (Worm et al. 2005), but other results have not shown strong correlations (Irigoien, Huisman, and Harris 2004).

Species-area relationship is a common phenomenon representing one of the earliest quantitative models in biogeography (Neigel 2003). It is generally accepted that the species number tends to increase with area size (MacArthur and Wilson 1967). This pattern has been used to estimate species richness, predict species loss, and also provide a useful tool for reserve design (May and Stumpf 2000; Thomas et al. 2004; Polgar 2009). Several models have been developed and applied to describe this pattern (Tjørve 2003; Dengler 2009); the most widely used among these are the power functions (Arrhenius 1921; Rosenzweig 1995; Scheiner 2003). In the marine environment, power function relationships of species-area have been documented in some cases, such as coral reef fish along the Israeli coast of the Gulf of Aqaba at the Red Sea (Belmaker et al. 2007).

Diversity patterns have been described for some marine biotas at both global and regional scales (Irigoien, Huisman, and Harris 2004; Worm et al. 2005; Barton et al. 2010; Tittensor et al. 2010). Knowledge in this respect is very limited in China, and no comparative diversity analysis has been carried out for coastal bays at the national scale. In this study, diversity patterns of plankton and benthic macrofauna were examined for coastal bays in China, including general latitudinal difference, cross-taxon congruence, and species-area relationships. This is a historical baseline based on the investigation for approximately 81 bays along the entire Chinese coastline in the 1980s and the early 1990s. The aim of this study is to provide a national-scale baseline of marine biodiversity prior to large-scale development in China, which is fundamental for future studies on biodiversity investigation, assessment, and management and also adds essential knowledge for both global and national marine biodiversity conservation and restoration.

2. Material and methods

a. Data acquisition

The data were extracted from a series of *Records of Bays in China* (Editorial Committee for Records of Bays in China 1991a, 1991b, 1992, 1993a, 1993b, 1993c, 1993d, 1994, 1997, 1998, 1999a, 1999b), which reported the results of a series of coastal and marine investigations for approximately 81 bays implemented in the 1980s and the early 1990s along the entire Chinese coastline. These bays were delineated into three climatic zones: temperate (40 bays), subtropical (31 bays), and tropical (10 bays) zones. There were 40

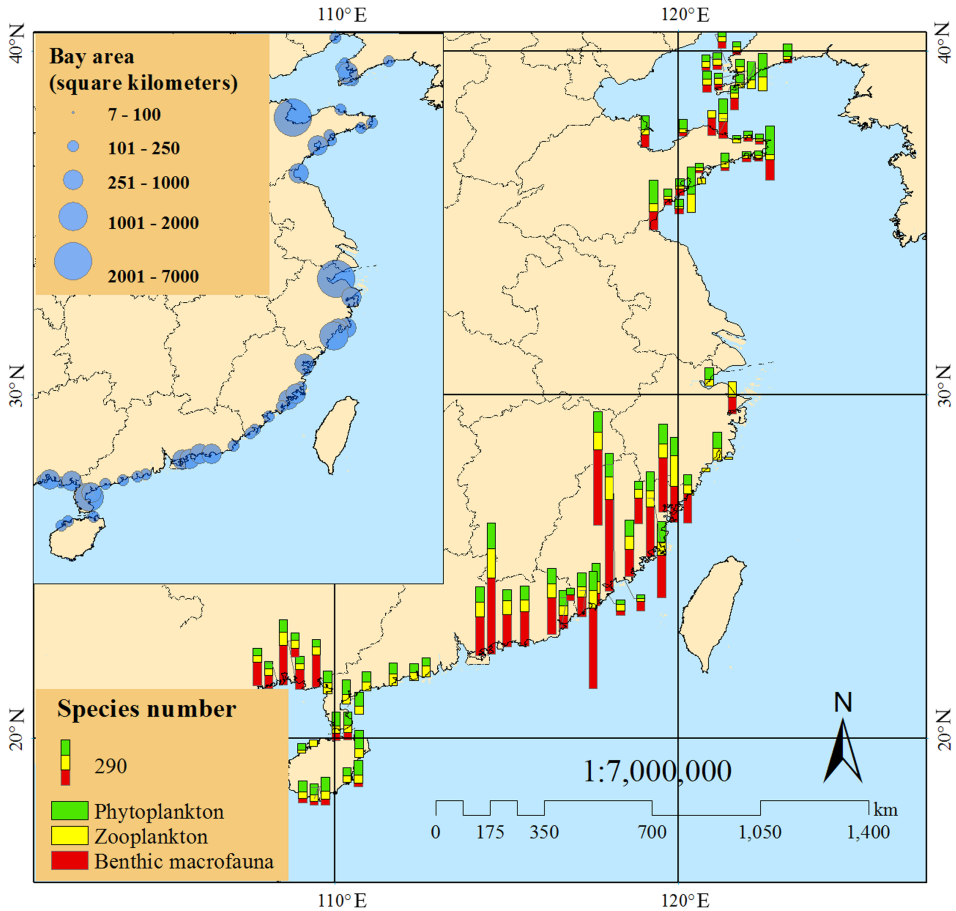


Figure 1. Species richness distributions of marine plankton and benthos in Chinese bays. Green represents species richness of phytoplankton, yellow represents species richness of zooplankton, red represents species richness of benthic macrofauna, and lack of color indicates unavailable data for a taxonomic group.

bays in the temperate climate zone from Jinzhou Bay in Liaoning Province to Haizhou Bay in Shandong Province, 31 bays in the subtropical zone from Hangzhou Bay in Zhejiang Province to Leizhou Bay in Guangxi Province, and 10 bays in the tropical zone in Hainan Province (Fig. 1). The bay areas ranged from 10 km² to 7,000 km². Sampling methods were consistent for all bays according to the “Comprehensive Investigation Protocol on Coastal Zone and Resources in China” (EGCIPCZRC 1986). In brief, plankton sampling was conducted using plankton nets with a mesh size of 0.077 mm for phytoplankton and 0.505 mm for zooplankton. Benthic macrofauna samples were collected using a grab sampler and were processed by sieving through a 0.5 mm mesh sieve.

In this study, an extensive database of species richness (i.e., the number of species in a given area) was compiled across three taxonomic groups (i.e., phytoplankton, zooplankton, and benthic macrofauna). Not all bays had complete information for all three taxonomic groups. The data on species richness were available for phytoplankton in 74 bays, zooplankton in 80 bays, and macrofauna in 57 bays. These data provided important baseline information prior to considerable disturbance.

b. Statistical analyses

Student's *t*-test was implemented with SPSS version 17.0 (SPSS Inc.) to test the climatic difference of species richness by log-transformed data of species richness. In addition, for each climatic zone, a box plot was made to visualize the distribution of species richness. The box plot conveyed a series of statistical information, including minimum and maximum rank values, median, and upper and lower quartiles. In the mainland of China, most of the bays were in the temperate and subtropical climate categories, whereas there were only 10 tropical bays in our study. Therefore, the latitudinal difference in species richness was compared between temperate and subtropical zones, considering that the sample size and the latitudinal extension of tropical bays were much smaller than that of the other two climate zones.

Frequency distribution histograms were generated (SPSS 17.0) to test the rough difference of species richness among different taxonomic groups, combined with descriptive statistics. To assess the cross-taxon congruence, both Pearson's correlation tests and Spearman's rank order tests were applied using SigmaPlot version 10.0 (Systat Software Inc.) to check the correlations of species richness between any two taxonomic groups. In addition, the relationships between different taxonomic groups were determined by simple linear regression analysis after the species richness data were logarithmically transformed.

The power function, linearized by logarithmic transformations, was performed with SigmaPlot 10.0 to examine the species-area relationship: $\log S = z \log A + c$ (Arrhenius 1921; Rosenzweig 1995; Scheiner 2003), where S represents species richness for each taxonomic group, A is bay area, and c and z are parameters (coefficients) estimated from the data in this study. The area of the bays in this study varied greatly from 10 km² to 7,000 km²; however, the large majority of bays (~98%) fell approximately between 10 km² and 2,000 km², and only two bays were large in size, namely Hangzhou Bay (~5,000 km²) and Laizhou Bay (~7,000 km²). Therefore, the statistical analysis for species-area relationship was done with these two large bays excluded.

3. Results

The distribution of species richness in bays along the Chinese coast is shown in Figure 1. Student's *t*-test results showed that the species richness was significantly higher in the subtropics than that in the temperate zone for all three taxonomic groups ($P = 0.001$ for phytoplankton, $P < 0.001$ for zooplankton, and $P < 0.001$ for benthic macrofauna). In

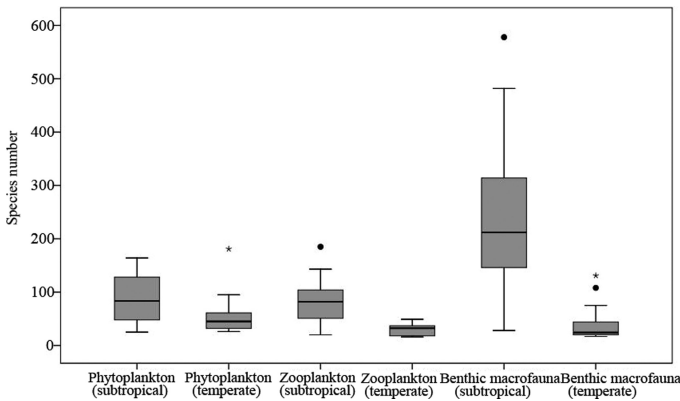


Figure 2. Box plots of species richness in subtropical and temperate zones in Chinese bays. The outliers in the box are also identified as greater than 1.5 or 3.0 times of the interquartile range, respectively.

Table 1. Descriptive statistical value of different climatic zones (without exceptional values).

Taxonomic groups	Climatic zones	Minimum range value	Maximum range value	Upper quartile	Lower quartile	Median
Phytoplankton	Temperate	25	151	59.5	29	46
	Subtropical	25	164	109.5	52	83.5
Zooplankton	Temperate	14	55	37	19.75	33
	Subtropical	12	143	84	47.75	67
Benthic macrofauna	Temperate	17	116	44	21	29
	Subtropical	28	482	242	85	177

addition, similar results were also demonstrated in box plots and corresponding statistical values (Fig. 2, Table 1).

The general distribution of species richness varied among different taxonomic groups (Figs. 1 and 3): (1) the species richness of phytoplankton ranged from 25 to 181, with a mean of approximately 75, and the species richness in 77.03% of bays was less than 100; (2) the species richness of zooplankton ranged from 20 to 192, with a mean of approximately 55, and the species richness in 91.25% of bays was less than 100; (3) the species richness of benthic macrofauna ranged from 17 to 578, with a mean of approximately 127, and the species richness in 56.14% of bays was less than 100.

In terms of cross-taxon congruence, correlation analysis indicated that the correlation between zooplankton and benthic macrofauna was significant ($P < 0.001$), and the coefficient values (R) were 0.82 for Pearson correlation and 0.81 for Spearman's rank correlation analysis. Similar results were found between phytoplankton and zooplankton, and the R

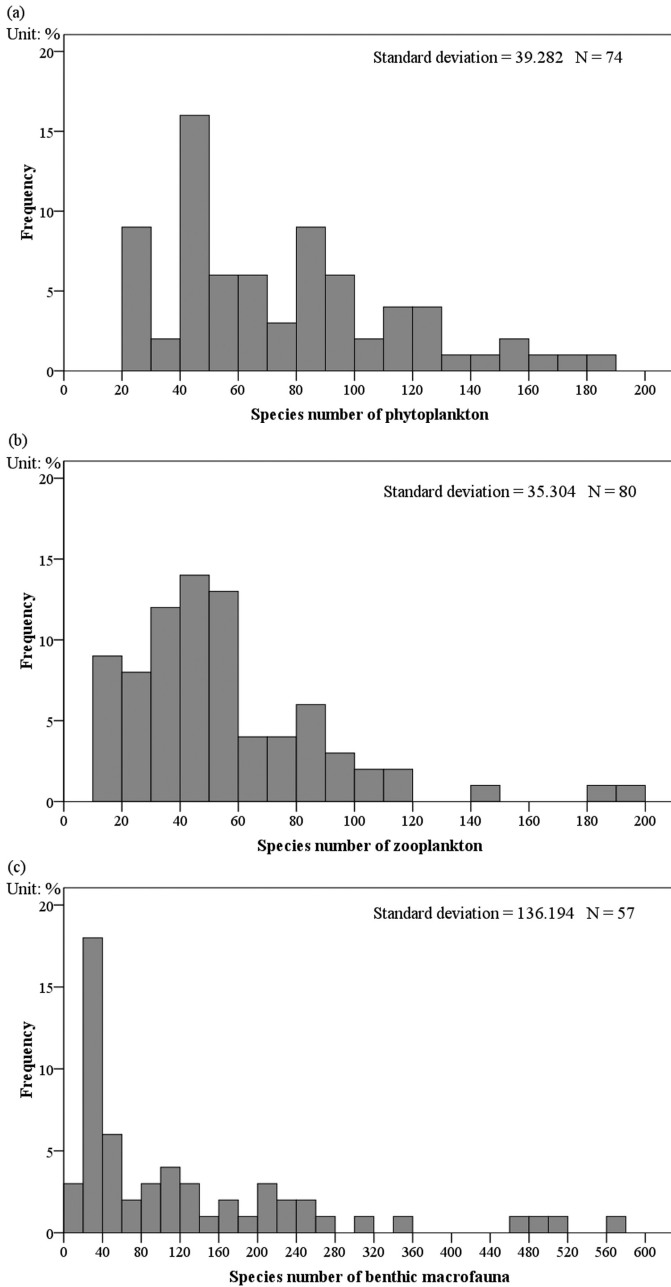


Figure 3. Frequency distribution histogram of species richness: (a) phytoplankton, (b) zooplankton, and (c) benthic macrofauna.

values were 0.70 and 0.76 ($P < 0.001$), respectively. The correlation between phytoplankton and benthic macrofauna was also significant ($P < 0.001$), with R values of 0.68 for the two analyses. In addition, a linear regression test also showed the positive relationship of species richness between any two of the three different taxonomic groups (Fig. 4).

For species-area relationship, regression correlation analysis indicated that significant correlations were found between bay area and species richness of each taxonomic group ($P < 0.001$). The correlation values were 0.64, 0.47, and 0.48 for benthic macrofauna, phytoplankton, and zooplankton, respectively. Moreover, regression analysis showed that species richness and bay area followed the classical power model (Fig. 5).

4. Discussion

Previous studies have reported latitudinal gradients of marine biodiversity distribution and have shown that species richness generally increases from polar to tropical areas (e.g., Hillebrand 2004). The present study also demonstrated a clear latitudinal variation in species richness of marine biota in Chinese bays and that the richness was significantly higher in the subtropical zone than the temperate zone, irrespective of the taxonomic group (Figs. 1 and 2). These results were also consistent with a nationwide pattern of marine species richness in which marine species richness increases gradually from the temperate Yellow Sea in the north to the tropical South China Sea (Huang 1994; Huang 2008; Liu 2008).

Similar to the general pattern documented on a global scale that marine biodiversity in the benthic system is higher than in the pelagic system (Gray 1997), the species richness of benthic macrofauna recorded in this study was larger than that of phytoplankton or zooplankton (Figs. 1 and 2). Although a number of published studies have indicated that species richness is typically weakly correlated ($R < 0.7$) among different taxonomic groups (Heino 2010), the correlation analysis in this study showed significant positive correlations of species richness between different taxonomic groups ($0.62 \leq R \leq 0.82$, $P < 0.001$; Fig. 4). Our results indicate a strong congruence of species richness between different taxonomic groups. Similar patterns for other terrestrial and marine biota have also been commonly demonstrated (Gaston 2000; Worm et al. 2005; Qian and Kissling 2010). This congruence pattern may be attributed to the similar responses of biota to common environmental conditions (Heino 2002; Schouten et al. 2009; Toranza and Arim 2010).

The present study shows that the strengths of correlation vary among different pair-wise taxonomic groups. The strongest degree of congruence was found between zooplankton and benthic macrofauna. Species richness of phytoplankton (as producers) showed stronger correlations with zooplankton (as primary consumers) than with benthic macrofauna (higher-level consumers). Likewise, species richness of benthic macrofauna was better correlated with zooplankton than phytoplankton. These results suggest that taxonomic groups with coterminous trophic level in the food chain have stronger congruence than indirectly linked

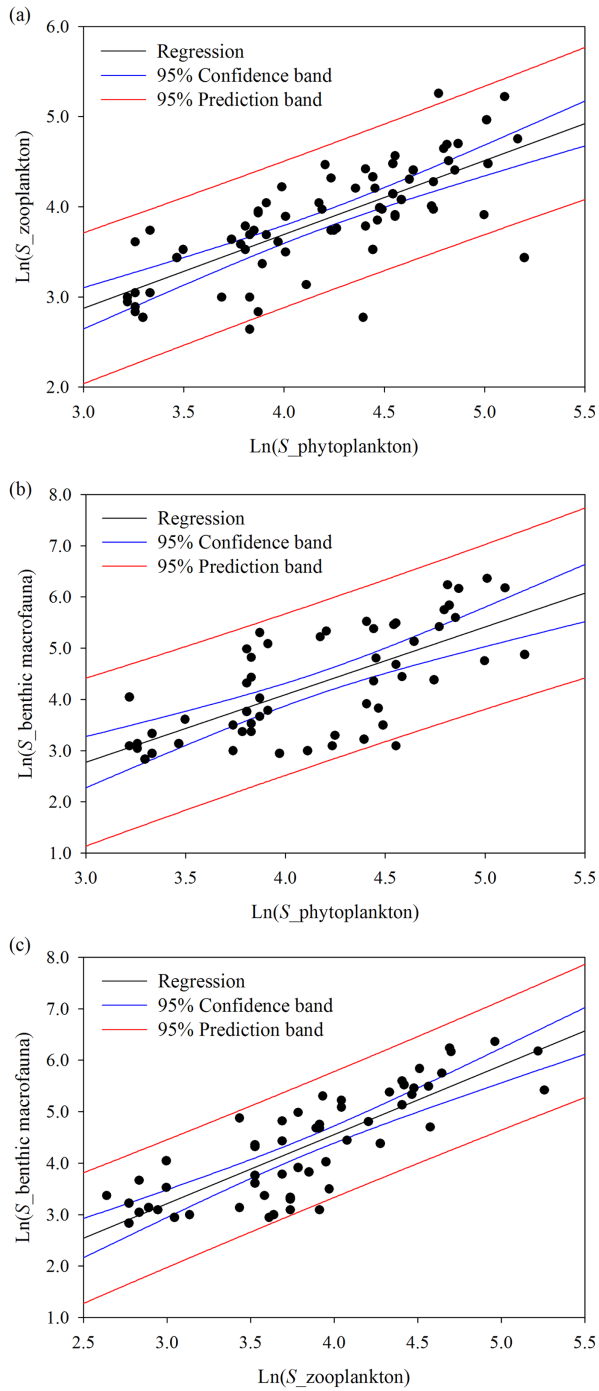


Figure 4. Linear regression of species richness between different taxonomic groups. (a) Phytoplankton and zooplankton: $\ln(S_{\text{zooplankton}}) = 0.415 + 0.820 \times \ln(S_{\text{phytoplankton}})$, $R = 0.74$, $F_{1,71} = 86.38$, $P < 0.001$, $N = 73$. (b) Phytoplankton and benthic macrofauna: $\ln(S_{\text{benthic}}) = -548.11 + 162.31 \times \ln(S_{\text{phytoplankton}})$, $R = 0.64$, $F_{1,53} = 36.90$, $P < 0.001$, $N = 55$. (c) Zooplankton and benthic macrofauna: $\ln(S_{\text{benthic}}) = -0.810 + 1.341 \times \ln(S_{\text{zooplankton}})$, $R = 0.82$, $F_{1,54} = 110.24$, $P < 0.001$, $N = 56$.

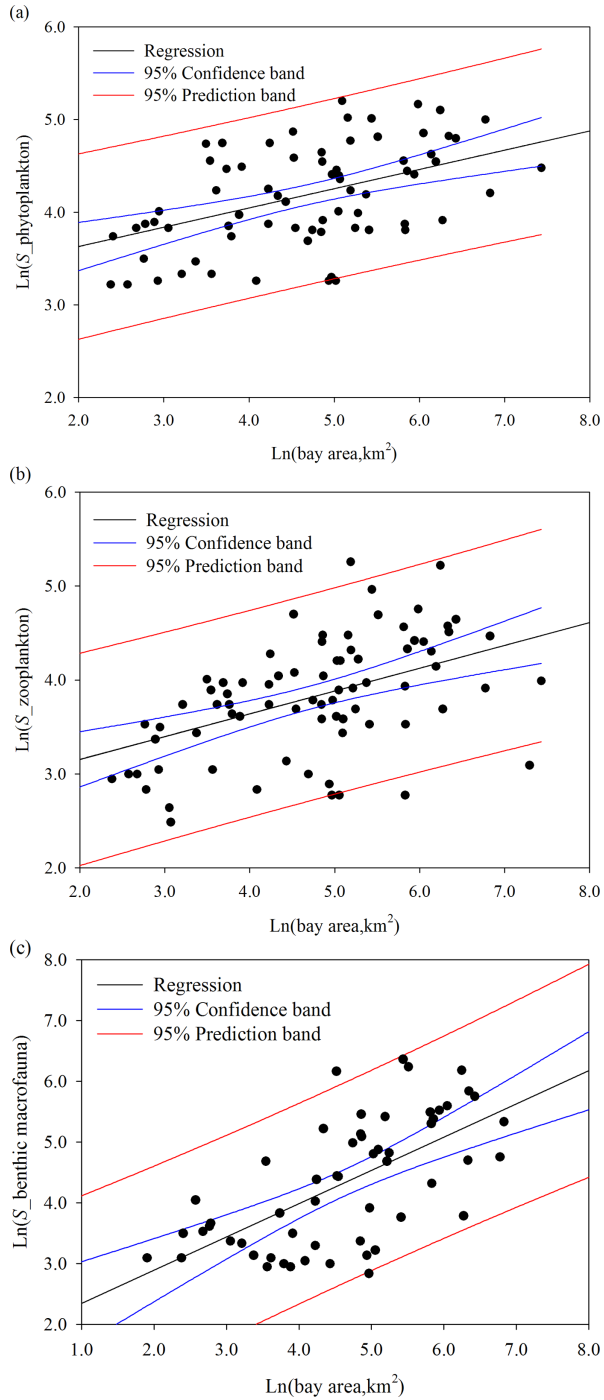


Figure 5. Power functions of species-area relationship for different taxonomic groups in Chinese bays in which the variables were measured in log units. S is species richness, A is bay area, and c and z are coefficients. (a) Phytoplankton: $\ln(S_{\text{phytoplankton}}) = 3.212 + 0.208 \ln A$, $R = 0.47$, $F_{1,70} = 19.88$, $P < 0.001$, $N = 72$. (b) Zooplankton: $\ln(S_{\text{zooplankton}}) = 2.669 + 0.243 \ln A$, $R = 0.48$, $P < 0.001$, $N = 78$. (c) Benthic macrofauna: $\ln(S_{\text{benthic macrofauna}}) = 1.797 + 0.547 \ln A$, $R = 0.64$, $P < 0.001$, $N = 56$.

groups. Similar results were also found in terrestrial ecosystems where primary consumers show stronger association with plants than higher-level consumers (Hutchinson 1959).

Cross-taxon congruence in diversity is important to the selection of indicator groups for biodiversity surveys and conservation planning (Gladstone 2002; Heino 2010). Compared with terrestrial studies, selecting indicator groups is more important in the marine environment because marine surveys are more difficult as a result of the cost of investigation, relatively limited knowledge of marine processes, and a lack of professional talent in marine species identification. In this study, strong and significant correlations ($0.62 \leq R \leq 0.82$, $P < 0.001$) were found among phytoplankton, zooplankton, and benthic macrofauna. The findings presented here might be applied to select indicator groups for biodiversity monitoring, assessment, and conservation planning in marine areas. However, different spatial scales might lead to differences in the extent of congruence; generally, congruence patterns are clear on broad scale, whereas patterns are much more ambiguous in small regions (Lund and Rahbek 2002; Qian and Kissling 2010; Fattorini, Dennis, and Cook 2012). Thus, although strong cross-taxon congruence was found on the national scale in this study, this congruence pattern might not be applicable to regional or other smaller scales.

For each taxonomic group, the results showed that species richness was positively and significantly correlated with bay area, following a classical power relationship. This significant relationship can be expected from the equilibrium theory of island biogeography (MacArthur and Wilson 1967), an empirical theory proposed to account for the effect of island area on species richness (Lomolino 2000). This study indicated that the empirical regression was also applicable; however, the strengths of species-area correlations of Chinese bays ($0.47 \leq R \leq 0.64$, $P < 0.001$) were less significant than previously reported studies (Diamond and Mayr 1976; Triantis et al. 2008). This is likely due to the bays' peninsula characteristics. Following the island biogeography theory, the analogy is reversed for coastal bays in this study, where a bay is an island of water surrounded by land. However, a bay is more like a peninsula that is not a completely insular island ecosystem because of access to the ocean.

Among the three taxonomic groups, benthic macrofauna had higher a correlation value ($R = 0.64$, $P < 0.001$) between species richness and bay area than phytoplankton ($R = 0.47$, $P < 0.001$) and zooplankton ($R = 0.48$, $P < 0.001$). This finding indicated the greater effect of bay surface area on the species richness of benthos than that of plankton. In addition, z values in the power law model, which indicate the strength of the increase in species richness with bay area, also varied among taxonomic groups. The z values for phytoplankton (0.21) and zooplankton (0.24) fell in the range reported by previous studies (0.20–0.40) (Connor and McCoy 1979; Connor, McCoy, and Cosby 1983), whereas the z value for benthic macrofauna was much higher (0.55). This further confirmed the assumption that the z value should increase with trophic rank (Holt et al. 1999). These findings might be explained by the difference in habitat characteristics among taxonomic groups. Plankton

are carried by ocean currents and are more mobile in water bodies (with three-dimensional distributions). However, benthic macrofauna in sedimentary environments are less affected by oceanic transportation and would exchange less with the open sea; this stability is more similar to the situation of the island habitat.

In conclusion, this study recorded a clear latitudinal gradient of species richness in Chinese bays, with higher richness in the subtropical zone than the temperate zone, and species richness increased with bay area following a power law function. This study also found clear cross-taxon congruence among phytoplankton, zooplankton, and benthic macrofauna. In addition, differences were found between benthos and plankton. Benthic macrofauna had much higher species richness than phytoplankton and zooplankton and also showed stronger correlation with bay area, indicating that bay size had a greater effect on the species richness of benthos than that of plankton.

The global decline of biodiversity highlights the need to understand biodiversity patterns and identify the effect of anthropogenic disturbances on biodiversity. This study provides a baseline of marine biodiversity patterns prior to large-scale development. However, knowledge of the response of biodiversity patterns to anthropogenic disturbance is still limited. Further studies would focus on the changes in biodiversity with coastal economic development. In addition, the combination of ecological and environmental management strategies and policies is worth further study to enhance the protection and restoration of Chinese coastal biodiversity.

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