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# Functional diversity and secondary production of macrofaunal assemblages can provide insights of biodiversity-ecosystem function relationships

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## Abstract

**Background** Semi-enclosed bays are important links in the material cycle and energy flow between terrestrial and marine ecosystems. They are also areas of intense human activities and heavily influenced by such activities as aquaculture, industrial and agricultural wastewater discharge. The rate of biodiversity loss and changes in ecosystems have prompted research into the relationship between species diversity and ecosystem functioning. Studies have shown that application of functional diversity indices is useful for assessing the status of ecosystem functioning. We quantitatively sampled macrofauna in a semi-enclosed bay in four seasons and analyzed the relationship between species, functional diversity and secondary production, biomass and feeding functional groups of macrofauna.

**Results** The annual secondary production was 325.01 kJ $m^{-2}$ $year^{-1}$. Detritivorous, carnivorous and planktophagous feeders were the main functional groups of macrofauna. Differences in the spatial–temporal distribution of functional groups were influenced by *Ruditapes philippinarum* and *Hemileucon bidentatus*. Functional richness had significant negative correlations with macrofaunal biomass and secondary production. Functional divergence, functional dispersion and Rao's quadratic entropy had highly significant negative correlations with macrofaunal biomass and secondary production.

**Conclusion** The results showed that high overlap of ecological niches can increase competition for habitat resources, leading to a decline in biomass and secondary production. In addition, aquaculture could promote the use of habitat resources to some extent, while it could increase competition for ecosystem resources (including habitat resources, atmospheric resources, water resources, etc.). Functional diversity is a good indicator for the ecosystem functioning and the competition status for habitat resources, which can provide insights into the current state of ecosystem function.

**Keywords** Semi-enclosed bay, Species diversity, Ecosystem functioning, Secondary production, Feeding functional groups, Functional diversity

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## Background

The ecological consequences of species diversity loss have aroused great concern in recent decades [1]. Human impact on the environment has not only led to a general decline in species diversity, but also to unpredictable functional changes [1]. Numerous studies demonstrated, both experimentally and theoretically, that local diversity (α diversity) loss impaired the functioning and stability of ecosystems [2–4]. Studies in recent decades have shown that biodiversity effects on ecosystems are (a) real and large, (b) often caused by complementarity; and (c) occur in many terrestrial, freshwater, and marine ecosystems [3]. With the expansion of research, ecosystem functional importance is becoming more and more obvious.

In the world's oceans, benthic habitats and the role of organisms living in marine sediments are important for ecosystem functioning. Macrofauna occur globally at all water depths and are important as consumers and in the energy flow and material cycling [5], including an important role in the nitrogen cycle of coastal marine ecosystems [6]. Research on macrofaunal ecosystem functioning began in the 1990s, and was primarily used to study specific biological characteristics and functions of specific macrofauna [7]. Early studies often used biomass or secondary production as the proxy for ecosystem functioning. The secondary production of marine macrofaunal communities refers to the increase in biomass or energy of macrofauna in the studied area by growth and reproduction in a unit of time, which is the result of ecosystem metabolism and can be used as a monitoring index for the stability of ecosystems [8]. However, it was not until 2000s that the study of ecosystem functioning of macrofauna began to cover a wider range of concepts, including the environmental relevance and the biological characteristics of species [9]. Early studies of classification by different biological traits involved feeding functional groups (FGs), which are permanent or temporary assemblages of species with similar trophic functions in an ecosystem [10, 11]. Studies have shown that functional diversity (FD) is the most relevant measure for interpreting the relationship between biodiversity and ecosystem functioning [12, 13], and for reliably predicting the rate of ecosystem processes. Functional diversity is defined as the range of variation in functional characteristics among species within a community [14], and a key question is how functional traits differ in response to environmental disturbances. The study of functional diversity can help to understand the interspecific species coexistence and niche overlap, explore the use of resources within the ecosystem, and further analyze the current state of ecosystem functioning. Functional diversity indices have mainly been applied to studies of terrestrial plant ecosystems, and reports on marine benthic ecosystems are limited [15, 16].

Semi-enclosed bays are the direct recipients of land-based sources of pollution such as heavy metals and organic pollutants and among the most important areas for economic development and aquaculture [17–19]. The ecosystem health of semi-enclosed bays is particularly relevant to economic growth and social progress at both regional and larger scales [20]. Due to their position at the sediment–water interface and their relatively long and sedentary life, macrofauna have been considered to be potentially powerful indicators in the assessment of marine ecosystem health [21, 22]. The weak mobility and a limited range of activities make them susceptible to environmental changes, thus more accurately reflecting the long-term macro-changes in the ecosystems [23, 24]. Currently, studies on macrofaunal impact assessment and environmental health focuses more on taxonomic aspects of community structure and the development of biological indices [25–28].

Jiaozhou Bay, located on the southern coast of the Shandong Peninsula in China, is a semi-enclosed natural bay of the Yellow Sea. The Bay area is a highly urbanized complex ecosystem, with several surface runoffs in the north and surrounded by important clam-farming activity. Over the last few years, the rate of biodiversity loss and changes in ecosystems have motivated research towards understanding the relationship between Biodiversity and Ecosystem Functioning [29]. Currently, Assessment of marine ecosystem health using macrofaunal functional diversity and the feeding functional group in Jiaozhou Bay is lacking. In this study, we synthesized species diversity and secondary production in Jiaozhou Bay, as well as feeding functional groups and functional diversity measured on the four cruises. The primary objectives of this study were (i) to explore the utilization of habitat resources by macrofauna and evaluate the ecosystem functioning of the Bay, (ii) to study the effects of aquaculture on abundance of *Ruditapes philippinarum*, which in turn affects the use of habitat resources and secondary production in a semi-enclosed bay, (iii) by analyzing the relationship between functional diversity and secondary production, to understand interspecific coexistence and ecological niche complementarity, and further to analyze the important aspects of biodiversity impact on ecosystems.

## Materials and methods

### Study area

In this study, four cruises of quantitative sampling of macrofauna in Jiaozhou Bay were undertaken in February, May, August and November of 2014, representing winter, spring, summer and autumn, respectively. The distribution of sites is shown in Fig. 1. All the four cruises had 14 evenly distributed sites, covering most of the Bay.

Among them, site J2 was close to the *Ruditapes philippinarum* farm. Due to the weather condition, in the spring and autumn cruises, samples at site J6 were not collected successfully and only 13 sites were sampled.

## Field sampling and laboratory process

Undisturbed sediment samples were collected using a 0.05 $m^{-2}$ box-corer. The sediment was screened with a 0.5 mm mesh size sieve, and all the retained biological samples and residues were transferred to sample bottles and stored by adding 75% ethanol. Surface sediments (0–5 cm) were also collected for the analysis and determination of environmental factors at each site, including chlorophyll *a* (Chl-*a*) and phaeophorbide (Pha), water content ($W_{H2O}$), organic matter (OM) and the grain size, which were labelled and stored frozen at − 20 °C. Latitudes and longitudes were recorded by a shipboard GPS system, and environmental factors, i.e. water temperature (T), salinity (S) and water depth (D) were measured with a CTD probe (911 Plus, Sea-Bird, USA). For OM and $W_{H2}O$, the $K_2Cr_2O_7$–$H_2SO_4$ oxidization method was used. To evaluate Chl-*a* and Pha contents, samples were treated for 24 h with 90% acetone before being tested using fluorescence spectrophotometry (Trilogy, Turner, USA). Meanwhile, the grain size was measured by a laser diffraction particle size analyzer (MASTERSIZER 3000 Laser Particle Sizer, MASTERSIZER, UK).

The biological samples were stained with 1‰ Rose Bengal sodium salt for 24 h, then sorted and identified to species level with a stereo microscope (NSZ-608T, Nanjing Jiangnan Novel Optics Company, China). The wet weights of all the macrofauna were measured using an electronic balance (GL2004B, Shanghai Yoke Instrument Company, China) with a sensitivity of 0.0001 g.

## Data analysis

### Species diversity

Based on the abundance of macrofauna, the biodiversity indices for each site in Jiaozhou Bay were calculated using PRIMER 6.0, including the species richness index (*d*), the species evenness index (*J'*) and the Shannon–wiener index (*H'*).

$$d = (S - 1)/\log_2 N$$

$$J' = H'/\log_2 S$$

$$H' = -\sum_{i=1}^{s} P_i \log_2 P_i$$

where $P_i$ is the proportion of the abundance of species *i*; *N* is the abundance of all species; *S* is the number of macrofaunal species of each site.

### Secondary production

A multi-parameter artificial neural net-work (ANN) model was used to estimate somatic secondary production [30] in this study. The ANN model consisted of 20 input nodes, two hidden nodes (H), and one output node, i.e., log(P/B) [30]. The conversion factors for the different taxa are shown in Additional file 1: Table S1 [31, 32]. The network was parameterized as follows:

$$\log(P/B) = a_0 + a_1 * H_1 + a_2 * H_2$$

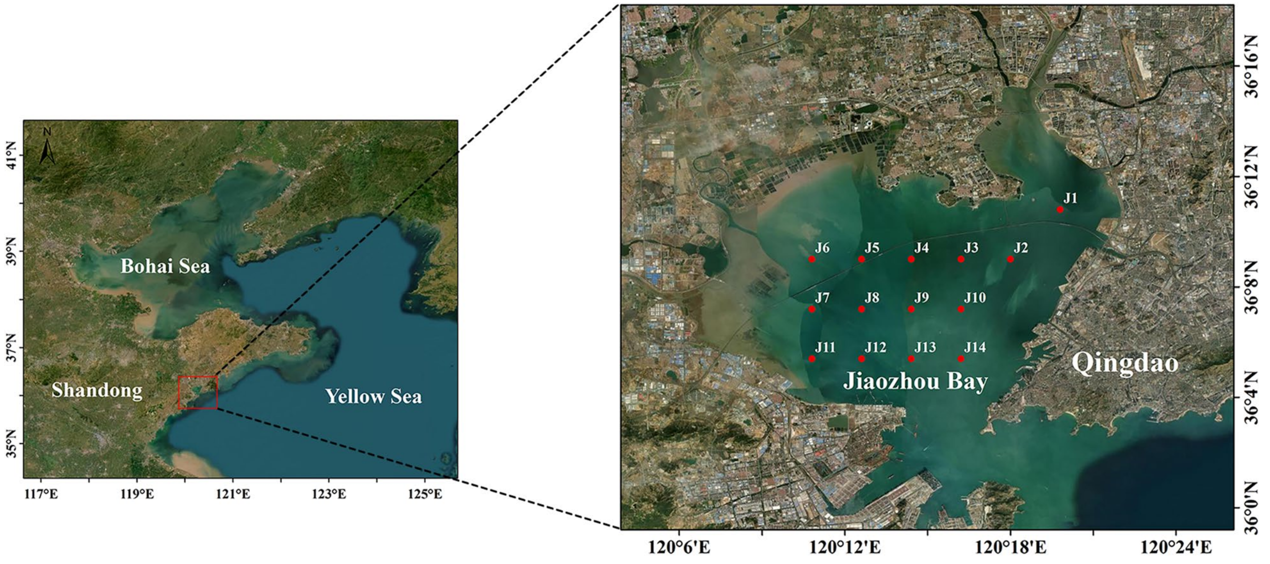

**Fig. 1** Sampling sites of macrofauna in Jiaozhou Bay, China

### *Feeding functional groups and feeding evenness index*

Information on functional groups of macrofauna in the study area was obtained mainly from published literature, as well as from internationally available online professional databases (BIOTIC, at http://www.marlin.ac.uk/biotic/). The macrofauna was divided into five functional group types based on feeding habits [33, 34]. Planktophagous group (Pl): animals filter feeding on organic particles or tiny plankton. Phytophagous group (Ph): animals feeding on vascular plants and seaweeds. Carnivorous group (C): animals feeding on meiofauna and larvae. Omnivorous group (O): animals feeding on other organisms, degraded leaves, small bivalves and crustaceans. Detritivorous group (D): animals feeding on organic detritus and sediment.

Based on the Shannon–Wiener index ($H'$) and the evenness index, Gamito and Furtado [35] proposed the feeding evenness index ($j_{FD}$) of macrofauna, and calculated by the following formula:

$$H'_{FD} = -\sum_{i=1}^{n} (P_i \log_2 P_i)$$

$$j_{FD} = \frac{H'_{FD}}{\log_2 n}$$

where $P_i$ is the percentage of the abundance of group $i$; $n$ is the number of functional groups.

The ecosystem health state (EHS) was determined from the identical ratio intervals following the methods of Gamito et al. [36], Peng and Li [37] and Cai et al. [38]: the values of the feeding evenness index greater than 0.80 corresponded to undisturbed and a high EHS; values between 0.80 and 0.60 indicate slightly disturbed and a good EHS; values 0.40–0.60 indicate moderately disturbed and a moderate EHS; values 0.20–0.40 indicate poorly disturbed and a poor EHS; and evenness values less than or equal to 0.20 signal badly disturbed and a bad EHS.

### *Functional diversity*

*Biological traits* Biological traits are the adaptations to the environmental factors, developed over evolutionary time, that are specific to specific habitat [39]. Based on the biological traits summarized by Lam-Gordillo et al. [29], seven categories were selected for analysis in this paper, as detailed in Additional file 1: Table S2.

The biological traits in macrofauna were determined by consulting numerous published books and articles as well as bioinformatics websites (e.g. BIOTIC, WoRMS www.marinespecies.org, etc.) and by consulting professional experts in various taxa for some undocumented traits of the species, using the genus level.

*Functional diversity indices calculation* Functional metrics in this study include functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). Functional richness is the amount of niche space filled by species in the community [40]. Low functional richness indicates that some of the resources potentially available to the community are unused, which will reduce production [41]. Functional evenness is the evenness of abundance distribution in filled niche space, and when it is low it means that the resource is unused or overused [40]. And functional evenness can be seen as an indicator of production, stability and resistance to invasion [40]. Functional divergence is the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community. High functional divergence indicates a high degree of niche differentiation, and thus low resource competition [40]. Functional dispersion is a more intuitive index, which is the multivariate analogue of the weighted mean absolute deviation; this makes it unaffected by species richness by construction, functional dispersion indicates the mean distance in multidimensional trait space of individual species to the centroid of all species [42].

The functional richness (FRic) calculation formula is as follows [40]:

$$FR_{ic} = \frac{SF_{ic}}{R_c}$$

where $SF_{ic}$ is the ecological niche space occupied by species within site $i$, $R_c$ is the absolute value range of the trait $c$.

The functional evenness (FEve) calculation formula is as follows [43]:

$$FE_{ve} = \frac{\sum_{i=1}^{s-1} cmin\left(PEW_i \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

where $S$ is species richness, $PEW_i$ is the locally weighted uniformity of species $i$.

The functional divergence (FDiv) calculation formula is as follows [40]:

$$FD_{iv} = \frac{2}{\pi}\arctan[5 \times \sum_{i=1}^{N} [(lnC_i - \overline{lnx})^2 \times A_i]]$$

where $C_i$ is the value of the functional trait of item $i$, $\overline{lnx}$ is the weighted average of the natural pairs of species characteristic values, $A_i$ is the relative abundance of the functional trait of item $i$.

The functional dispersion (FDis) calculation formula is as follows [42]:

$$\boldsymbol{c} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j}$$

$$FD_{is} = \frac{\sum a_j z_j}{\sum a_j}$$

where $c$ is the weighted centre of mass in i-dimensional space, $x_{ij}$ is the property of trait $i$ of species $j$, $a_j$ is the abundance of species $j$, $z_j$ is the distance from species $j$ to the centre of mass $c$.

The Rao's quadratic entropy (RaoQ) calculation formula is as follows [44]:

$$RaoQ = \sum_{i=1}^{s-1} \sum_{j=1+i}^{s} d_{ij} p_i p_i$$

where $d_{ij}$ is the difference between species $i$ and species $j$, $p_i$ is the relative abundance of species.

The functional diversity indices calculation for macrofauna was done in the R (4.0.3), loading the "FD" [45] installation package.

## Results

### Species diversity

The number of macrofaunal species ranged from 67 to 120, with the highest value occurring at site J10 in the eastern part of the bay and the lowest value at site J6 in the northwestern part of the bay, with a mean value of 92. Species richness index ranged from 9.32 to 14.79, with the highest and lowest values appearing at the same site as the number of macrofaunal species, with an average of 11.78. Species evenness index ranged from 0.46 to 0.76, with the highest values occurring at site J8 and J9 in the middle of the bay and the lowest at site J2 in the northeast of the bay, with an average of 0.69. Shannon–wiener index ranged from 2.14 to 3.61, with the highest values occurring at site J10 in the eastern part of the bay and the lowest values at site J2 in the northeastern part of the bay, with a mean value of 3.11. The species diversity of macrofauna at each site in Jiaozhou Bay is detailed in Table 1.

**Table 1** Average species diversity indices of macrofaunal assemblages in Jiaozhou Bay

| Site | *S* | *d* | *J′* | *H′*($\log_e$) |
|---|---|---|---|---|
| J1 | 84 | 11.00 | 0.68 | 3.03 |
| J2 | 107 | 12.59 | 0.46 | 2.14 |
| J3 | 91 | 11.49 | 0.65 | 2.95 |
| J4 | 92 | 11.95 | 0.70 | 3.18 |
| J5 | 77 | 10.29 | 0.68 | 2.96 |
| J6 | 67 | 9.32 | 0.73 | 3.05 |
| J7 | 86 | 11.08 | 0.68 | 3.02 |
| J8 | 107 | 14.29 | 0.76 | 3.56 |
| J9 | 97 | 12.22 | 0.76 | 3.46 |
| J10 | 120 | 14.79 | 0.75 | 3.61 |
| J11 | 96 | 11.80 | 0.70 | 3.19 |
| J12 | 82 | 10.11 | 0.67 | 2.96 |
| J13 | 88 | 11.58 | 0.72 | 3.22 |
| J14 | 95 | 12.42 | 0.71 | 3.25 |

*S* the number of macrofaunal species, *d* species richness index, *J′* species evenness index, *H′* Shannon–wiener index

### Secondary production

The average annual secondary production in Jiaozhou Bay measured in this study was 325.01 kJ m$^{-2}$ year$^{-1}$, and the spatial distribution pattern is shown in Fig. 2a. Among the 14 sites, the highest secondary production value was at site J2 in the northeastern part of the bay with 1636.27 kJ m$^{-2}$ year$^{-1}$, followed by Site J8 in the central part of the bay with a value of 470.11 kJ m$^{-2}$ year$^{-1}$. The lowest value of secondary production was at site J14 in the southeastern part with 36.06 kJ m$^{-2}$ year$^{-1}$, followed by site J12 in south-central bay with 50.79 kJ m$^{-2}$ year$^{-1}$. The results showed a trend of gradually decreasing production around site J2 as the center.

The average annual secondary production of *Ruditapes philippinarum* was 205.58 kJ m$^{-2}$ year$^{-1}$, accounting for 63.25% of the total macrofaunal secondary production (Fig. 2b). Among the 14 sites, the highest secondary production value was at site J2 in the north-east with 1563.57 kJ m$^{-2}$ year$^{-1}$. The lowest value was at sites J9, J10, J12 and J13 in the central and southern bay, where the secondary production was 0, with no *Ruditapes philippinarum* collected. The spatial distribution pattern of the secondary production of *Ruditapes philippinarum* was generally the same as that of the total secondary production.

In addition, with the exception of *Ruditapes philippinarum*, the average annual secondary production of other macrofauna was 119.43 kJ m$^{-2}$ year$^{-1}$. Among the 14 sites, the highest secondary production was at sites J8 in the middle of the bay and J10 in the eastern part of the bay, with 428.28 kJ m$^{-2}$ year$^{-1}$ and 370.46 kJ m$^{-2}$ year$^{-1}$, respectively. And the lowest of secondary production was at sites J5 in the north-western and J14 in the south-eastern, with 23.95 kJ m$^{-2}$ year$^{-1}$ and 35.01 kJ m$^{-2}$ year$^{-1}$, respectively (Fig. 2c).

### Feeding functional groups

A total of 249 species (excluding undetermined species) of macrofauna were collected in four cruises in Jiaozhou Bay. The largest functional group was detritivorous group with 83 species (33.33%), followed by carnivorous group with 82 species (32.93%), planktophagous group with

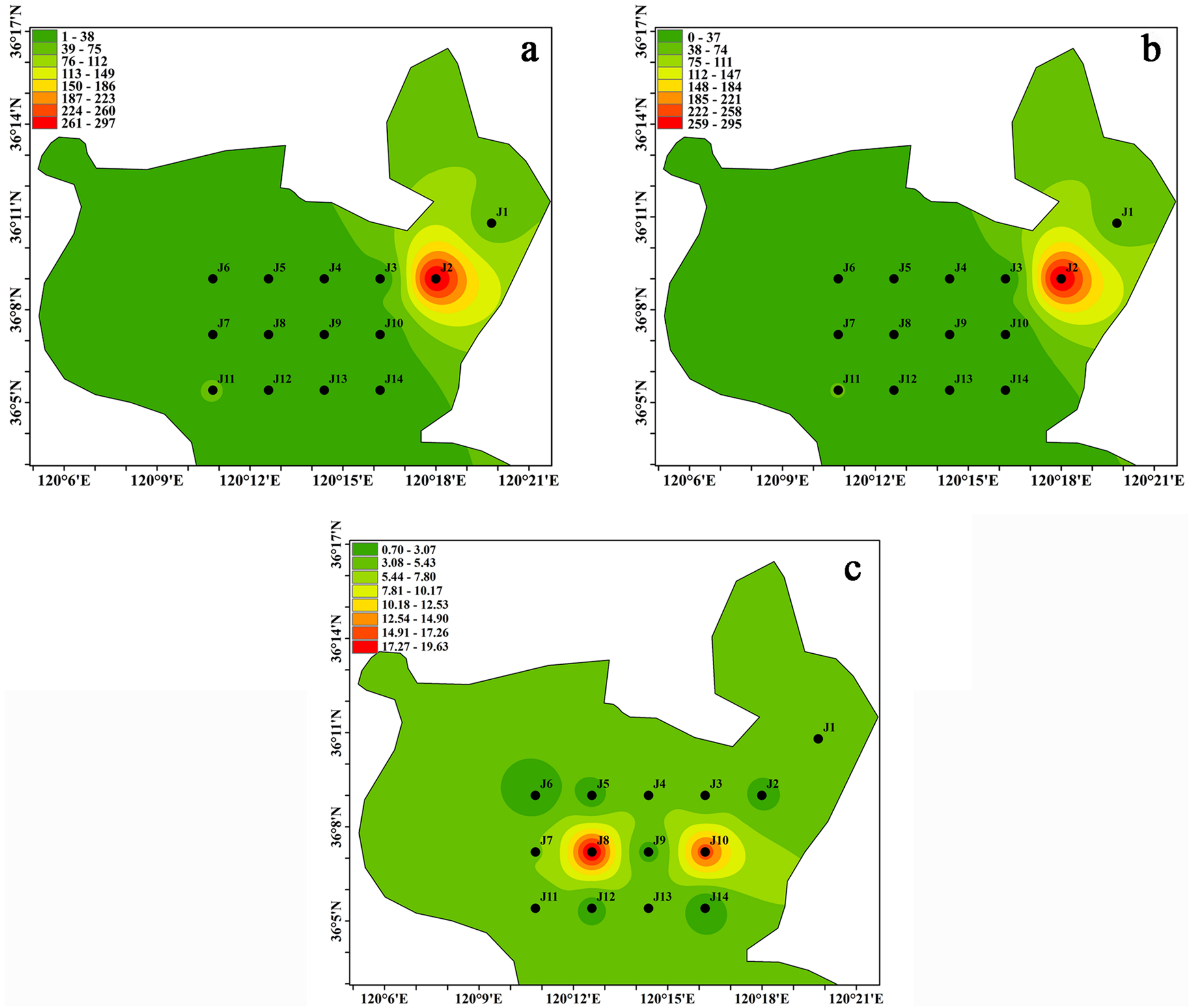

**Fig. 2** Spatial distribution patterns of secondary production of macrofauna in Jiaozhou Bay, China. **a** total macrofauna; **b** *Ruditapes philippinarum*; **c** macrofauna without *Ruditapes philippinarum*; Unit: kJ m$^{-2}$ year$^{-1}$

64 species (25.70%), omnivorous group with 16 species (6.43%) and phytophagous group with 4 species (1.61%).

### *The spatial distribution of the feeding function groups*

The abundance of functional groups on the four cruises, and their distribution are shown in Fig. 3a. The average abundance and relative abundance of detritivorous group were significantly higher than those of other feeding functional groups, its dominance being particularly obvious. Excluding the site J2 in the north-east of the Bay, where *Ruditapes philippinarum* dominates, the sum of the abundances of carnivorous group and detritivorous group accounted for more than half of the total abundance at other sites. The order of average feeding functional groups abundance was as follows: Detritivorous group (1106.07 ind. m$^{-2}$) > Carnivorous group (582.32 ind. m$^{-2}$) > Planktophagous group (453.75 ind. m$^{-2}$) > Omnivorous group (227.50 ind. m$^{-2}$) > Phytophagous group (3.13 ind. m$^{-2}$). The order of relative abundance of the feeding functional groups was in the same order as the abundance, with Detritivorous group (48.37%) > Carnivorous group (25.41%) > Planktophagous group (15.82%) > Omnivorous group (10.24%) > Phytophagous group (0.16%).

The spatial distribution of the abundance of feeding functional groups was dominated by detritivorous group and carnivorous group, except for J2 where planktophagous group dominated, with no significant differences in spatial distribution. There was no obvious spatial

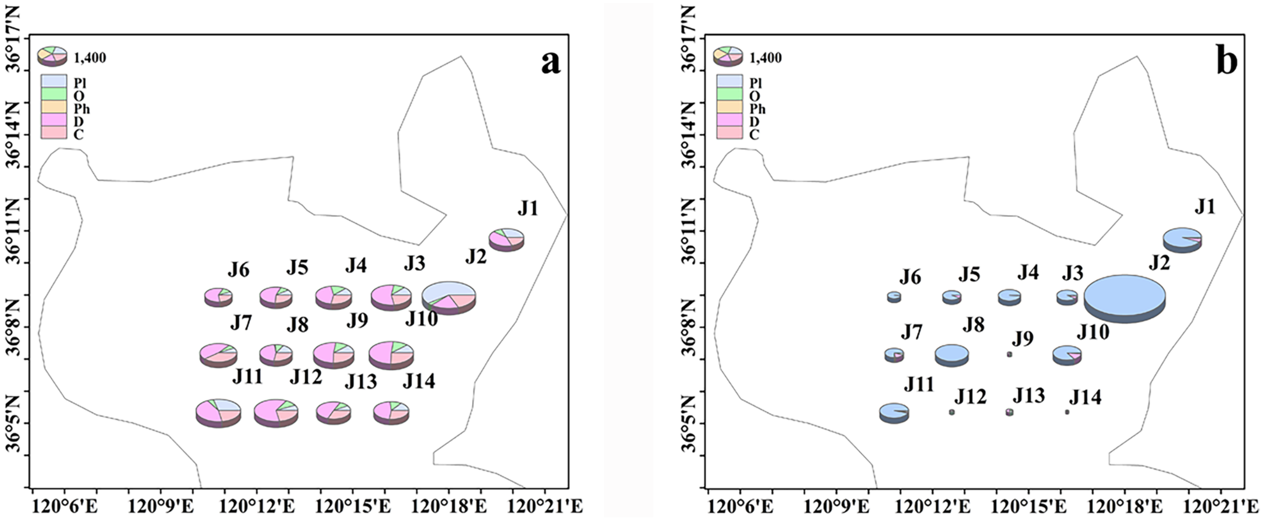

**Fig. 3** Spatial distribution patterns of functional groups of macrofaunal assemblages in Jiaozhou Bay, China. *Pl* Planktophagous group, *Ph* Phytophagous group, *C* Carnivorous group, *O* Omnivorous group, *D* Detritivorous group, Unit: abundance (ind. $m^{-2}$) and biomass (g $m^{-2}$)

difference in the distribution of biomass, and planktophagous group was the main group.

The highest value of the feeding evenness index appeared in site J14 in the south-eastern part of the bay. The lowest value of 0.66 was at site J2 in the north-eastern part of the bay (Table 2). Based on the ecosystem health state [36, 38] determined from the same rate intervals, the environmental assessment of the entire survey area was undisturbed-slightly disturbed.

### *Temporal distribution of feeding functional groups*

The number of species in macrofaunal functional groups of macrobenthos in four seasons, summer (161) > fall (143) > spring (140) > winter (99) (Table 3). Except for summer, the detritivorous group had the largest number among all the functional groups. The number of species belonging to the phytophagous group was the lowest in all four cruises, and this group was completely absent in winter. In terms of total macrofaunal abundance, autumn (3288.21 ind. $m^{-2}$) > summer (2708.21 ind. $m^{-2}$) > spring (2296.43 ind. $m^{-2}$) > winter (1198.21 ind. $m^{-2}$). In the four cruises, the highest abundance belonged to detritivorous group and the lowest belonged to phytophagous group. In terms of total macrofaunal biomass, autumn (756.03 g $m^{-2}$) > summer (572.09 g $m^{-2}$) > spring (487.44 g $m^{-2}$) > winter (164.61 g $m^{-2}$). Among the four cruises, planktophagous group had the highest biomass.

**Table 2** Results of the feeding evenness index ($j_{FD}$) of macrofauna and its environmental quality assessment in Jiaozhou Bay

| Site | $j_{FD}$ | Environmental quality |
|---|---|---|
| J1 | 0.79 | Slightly disturbed |
| J2 | 0.66 | Slightly disturbed |
| J3 | 0.71 | Slightly disturbed |
| J4 | 0.80 | Slightly disturbed |
| J5 | 0.69 | Slightly disturbed |
| J6 | 0.76 | Slightly disturbed |
| J7 | 0.67 | Slightly disturbed |
| J8 | 0.80 | Undisturbed |
| J9 | 0.85 | Undisturbed |
| J10 | 0.74 | Slightly disturbed |
| J11 | 0.88 | Undisturbed |
| J12 | 0.72 | Slightly disturbed |
| J13 | 0.70 | Slightly disturbed |
| J14 | 0.90 | Undisturbed |

Badly disturbed: $j_{FD} < 0.20$; Poorly disturbed: $0.20 < j_{FD} < 0.40$; moderately disturbed: $0.40 < j_{FD} < 0.60$; slightly disturbed: $0.60 < j_{FD} < 0.80$; undisturbed: $j_{FD} > 0.80$

## Functional diversity

### *The spatial distribution of functional diversity*

The distribution patterns of annual mean functional diversity indices of macrofauna at the 14 sites are shown in Fig. 4. Functional richness varied from 126.88 to 6954.81 with a mean of 1844.51. Functional evenness varied from 0.31 to 0.43 with a mean of 0.38. Functional divergence varied from 0.68 to 0.87 with a mean of 0.80. Functional dispersion varied from 2.80 to 4.74 with a mean of 4.24. Rao's quadratic entropy varied from 10.91 to 24.46 with a mean of 20.82. The trend of functional richness was higher in the northeast than in the south-west in the Bay. The trend in functional evenness was

**Table 3** Seasonal changes in the number of species, abundance, biomass of the macrofauna in Jiaozhou Bay

| Cruise | Categories | D | C | Pl | O | Ph |
|---|---|---|---|---|---|---|
| Winter | The number of species | 38 | 28 | 22 | 11 | 0 |
| | Abundance (ind. $m^{-2}$) | 481.79 | 448.93 | 162.86 | 104.64 | 0 |
| | Biomass (g $m^{-2}$) | 5.15 | 3.89 | 154.91 | 0.65 | 0 |
| Spring | The number of species | 58 | 45 | 24 | 11 | 2 |
| | Abundance (ind. $m^{-2}$) | 1159.64 | 528.57 | 469.29 | 137.50 | 1.43 |
| | Biomass (g $m^{-2}$) | 16.31 | 4.24 | 464.81 | 2.08 | 0.00 |
| Summer | The number of species | 51 | 58 | 41 | 10 | 1 |
| | Abundance (ind. $m^{-2}$) | 1323.21 | 610.71 | 560.00 | 211.07 | 3.21 |
| | Biomass (g $m^{-2}$) | 16.32 | 6.16 | 546.98 | 0.70 | 1.93 |
| Autumn | The number of species | 53 | 40 | 36 | 11 | 3 |
| | Abundance (ind. $m^{-2}$) | 1459.64 | 741.07 | 622.86 | 456.79 | 7.86 |
| | Biomass (g $m^{-2}$) | 17.01 | 8.92 | 728.85 | 1.00 | 0.24 |

*D* Detritivorous group, *C* Carnivorous group, *Pl* Planktophagous group, *O* Omnivorous group, *Ph* Phytophagous group

higher in the western and north-eastern parts of the bay, decreasing towards the central and southern parts. The trend in functional divergence was increasing from the northeast to the southwest. Site J2 had the lowest value of functional dispersion, which was located in the north-east of the bay, and the values increased around this site, with the highest value in the south-west of the Bay. Rao's quadratic entropy and functional dispersion were highly consistent in the entire bay.

#### Temporal distribution of functional diversity

*Functional richness* The temporal distribution pattern of functional richness (Fric) was summer > autumn > spring > winter, as shown in Additional file 1: Fig. S1. In winter, FRic ranged from 0 to 20.34 with a mean of 3.72, and it tended to increase from the west to the east of the bay. In spring, it ranged from 0 to 104.80 with a mean of 14.07, and it tended to decrease from the northeast to other regions. In summer, it ranged from 0 to 1976.90 with a mean of 519.45, and it tended to increase from the west to the east. In autumn, it ranged from 2.02–634.44 with a mean of 90.50, and it tended to increase from the center to the surrounding area, peaking at Site J2.

*Functional evenness* The temporal distribution pattern of functional evenness (FEve) was winter (0.50) > summer (0.48) > spring (0.46) > autumn (0.44), as shown in Additional file 1: Fig. S2. In terms of the ranges of FEve, winner, spring, summer and spring were 0.45–0.64, 0.33–0.53, 0.35–0.59 and 0.32–0.53, respectively. Overall, FEve was relatively medium in spring, and the lower area of FEve in summer, autumn and winter gradually moved northwards and expanded from the south. In particularly, FEve was relatively high in the north-east throughout the year.

*Functional divergence* The temporal distribution pattern of functional divergence (FDiv) was spring (0.84) > summer (0.82) > winter (0.79) > autumn (0.78), as detailed in Additional file 1: Fig. S3. In terms of the ranges of FDiv, winner, spring, summer and spring were 0.67–0.90, 0.69–0.94, 0.69–0.92 and 0.67–0.81, respectively. Excluding winter, FDiv had a tendency to increase from the north-east to the southwest. The south-west had relatively high FDiv values in all the four cruises.

*Functional dispersion* The temporal distribution pattern of functional dispersion (FDis) was summer (4.37) > spring (4.14) > winter (4.10) > autumn (3.73), as shown in Additional file 1: Fig. S4. In terms of the ranges of FDis, winner, spring, summer and spring were 3.64–4.74, 2.39–4.93, 1.63–5.05 and 3.08–4.29, respectively. Overall, distribution of FDis was relatively medium in spring. And the low value area for FDis was an increasing trend from the north to the south in summer, autumn and winter. Among them, the FDis was relatively high in the south-west throughout the year.

*Rao's quadratic entropy* The temporal distribution pattern of Rao's quadratic entropy (RaoQ) was summer (22.63) > spring (21.49) > winter (18.94) > autumn (16.74), as detailed in Additional file 1: Fig. S5. In terms of the ranges of RaoQ, winner, spring, summer and spring were 15.08–24.17, 11.82–29.67, 5.02–28.81 and 11.72–20.98, respectively. The RaoQ was high in the east and low in the west in spring. The lower areas of RaoQ in summer, autumn and winter were a tendency to move the north to the south.

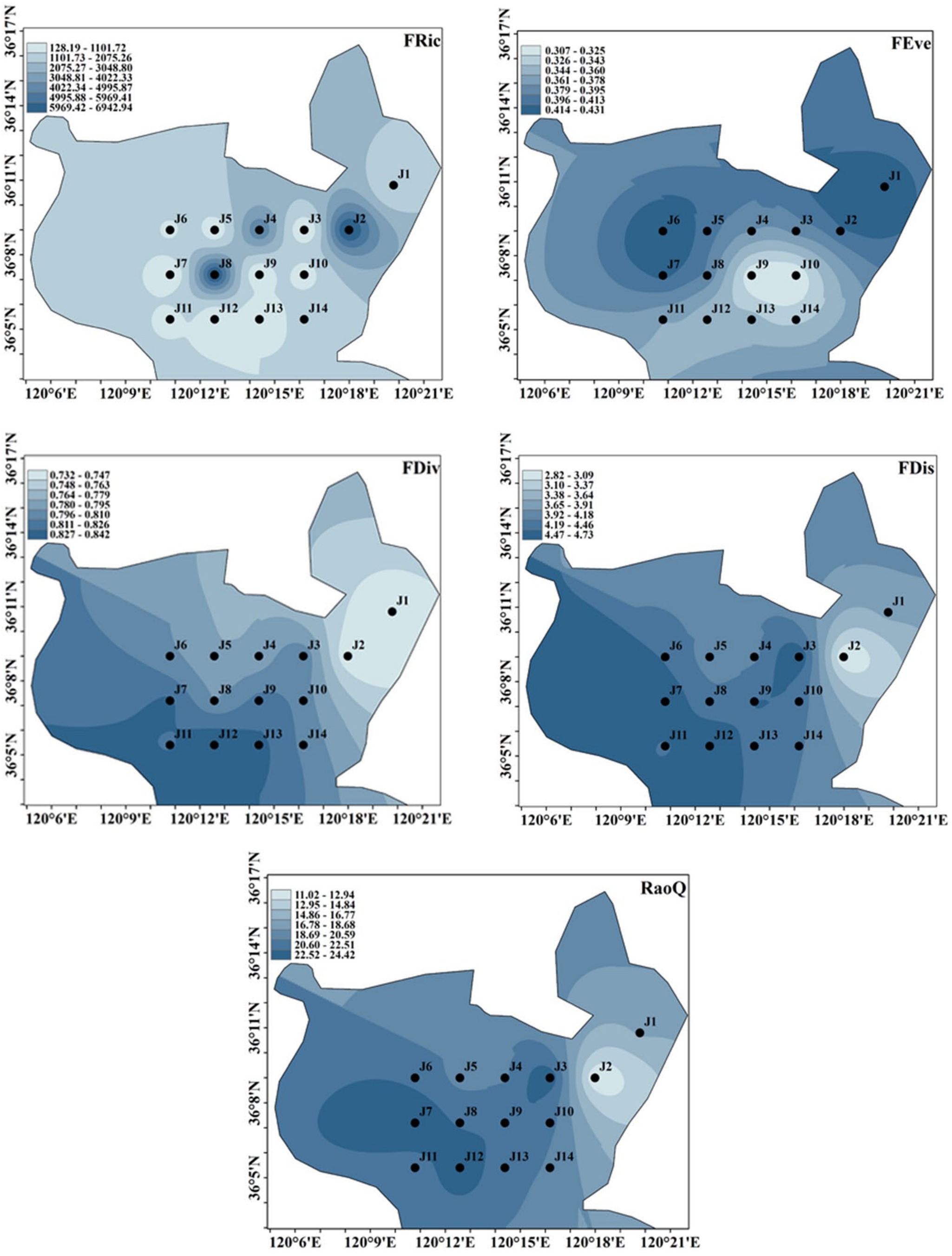

**Fig. 4** Functional diversity distribution of macrofauna in Jiaozhou Bay. *FRic* functional richness, *FEve* functional evenness, *FDiv* functional divergence, *FDis* functional dispersion, *RaoQ* Rao's quadratic entropy.

## Correlation analysis

Pearson correlation analysis (Table 4 and Fig. 5) showed that abundance and biomass of *Ruditapes philippinarum* had highly significant positive correlations with secondary production ($P<0.01$), and they were significantly positively correlated with functional richness ($P<0.05$). They also had highly significant negative correlations with the species evenness index, Shannon–Wiener index, functional divergence, functional dispersion, and Rao's quadratic entropy ($P<0.01$). Total biomass had highly significant positive correlations with secondary production, and functional richness, and it also had highly significant negative correlations with species evenness index, Shannon–Wiener index, functional divergence, functional dispersion, and Rao's quadratic

**Table 4** Pearson correlation analysis of species diversity, ecosystem functioning and environmental factors in Jiaozhou Bay

| | The abundance of *Ruditapes philippinarum* | The biomass of *Ruditapes philippinarum* | Secondary production | $j_{FD}$ | FRic | FEve | FDiv | FDis | RaoQ |
|---|---|---|---|---|---|---|---|---|---|
| S | 0.299 | 0.277 | 0.438 | 0.136 | 0.440 | − 0.518 | − 0.219 | − 0.272 | − 0.245 |
| *d* | 0.130 | 0.115 | 0.306 | 0.224 | 0.465 | − 0.481 | − 0.226 | − 0.198 | − 0.147 |
| *J′* | − 0.901** | − 0.908** | − 0.647* | 0.522 | − 0.386 | − 0.405 | 0.451 | 0.693$^{**}$ | 0.716$^{**}$ |
| *H′* | − 0.796** | − 0.810** | − 0.785** | 0.550$^{*}$ | − 0.254 | − 0.549$^{*}$ | 0.387 | 0.604$^{*}$ | 0.634$^{*}$ |
| Water depth | − 0.352 | − 0.360 | − 0.413 | 0.223 | − 0.278 | − 0.712$^{**}$ | 0.433 | 0.293 | 0.254 |
| Bottom water salinity | 0.024 | 0.009 | 0.024 | − 0.036 | 0.206 | − 0.005 | 0.228 | 0.152 | 0.149 |
| T | − 0.136 | − 0.105 | − 0.108 | − 0.213 | 0.139 | 0.139 | 0.139 | 0.139 | 0.139 |
| pH | − 0.165 | − 0.163 | − 0.066 | − 0.029 | − 0.030 | 0.070 | − 0.073 | 0.064 | 0.091 |
| Chl-*a* | 0.214 | 0.228 | 0.172 | 0.453 | 0.117 | 0.224 | − 0.377 | − 0.332 | − 0.377 |
| Pha | 0.032 | 0.011 | 0.113 | 0.247 | 0.033 | 0.255 | 0.072 | 0.156 | 0.141 |
| Organic matter | − 0.218 | − 0.226 | − 0.291 | 0.021 | − 0.343 | 0.323 | 0.306 | 0.343 | 0.375 |
| Median diameter | 0.126 | 0.142 | 0.183 | − 0.133 | − 0.004 | 0.192 | − 0.113 | − 0.093 | − 0.137 |
| Silty clay content | − 0.162 | − 0.187 | − 0.194 | 0.240 | 0.022 | − 0.224 | 0.068 | 0.101 | 0.139 |
| Secondary production | 0.954** | 0.953** | 1 | − 0.289 | 0.720** | 0.319 | − 0.741** | − 0.849** | − 0.834** |
| $j_{FD}$ | − 0.312 | − 0.350 | − 0.289 | 1 | − 0.021 | − 0.381 | − 0.027 | 0.166 | 0.140 |
| FRic | 0.575* | 0.591* | 0.720** | − 0.021 | 1 | 0.276 | − 0.725$^{**}$ | − 0.644$^{*}$ | − 0.550$^{*}$ |
| FEve | 0.328 | 0.355 | 0.319 | − 0.381 | 0.276 | 1 | − 0.427 | − 0.334 | − 0.291 |
| FDiv | − 0.674** | − 0.694** | − 0.741** | − 0.027 | − 0.725$^{**}$ | − 0.427 | 1 | 0.921$^{**}$ | 0.881$^{**}$ |
| FDis | − 0.855** | − 0.875** | − 0.849** | 0.166 | − 0.644$^{*}$ | − 0.334 | 0.921$^{**}$ | 1 | 0.988$^{**}$ |
| RaoQ | − 0.864** | − 0.879** | − 0.834** | 0.140 | − 0.550$^{*}$ | − 0.291 | 0.881$^{**}$ | 0.988$^{**}$ | 1 |

*FRic* functional richness, *FEve* functional evenness, *FDiv* functional divergence, *FDis* functional dispersion, *RaoQ* Rao's quadratic entropy, *S* is the number of macrofaunal species of each site, *d* species richness index, *J′* species evenness index, *H′* Shannon–Wiener index, $j_{FD}$ the feeding evenness index

** Means correlation is significant at the 0.01 level

* Means correlation is significant at the 0.05 level

entropy ($P<0.01$). Functional richness had highly significant negative correlations with functional divergence ($P<0.01$), and it also had significant negative correlations with functional dispersion and Rao's quadratic entropy ($P<0.05$). Functional richness had highly significant negative correlations with functional divergence ($P<0.01$), and it also had significant negative correlations with functional dispersion and Rao's quadratic entropy ($P<0.05$). Functional evenness had highly significant negative correlations with water depth ($P<0.01$), and it also had significant negative correlations with Shannon–Wiener index ($P<0.05$). Functional divergence, functional dispersion, and Rao's quadratic entropy were highly significantly positively correlated ($P<0.01$). Both functional dispersion and Rao's quadratic entropy had highly significant positive correlations with species evenness index ($P<0.01$), and they were also significantly positively correlated with Shannon–Wiener index ($P<0.05$).

## Discussion

### Secondary production in relation to species diversity and functional diversity

The present study showed that secondary production had highly significant negative correlations with species evenness index and Shannon–Wiener index. High-yielding ecosystems in nature tend to have low species diversity [46]. *Ruditapes philippinarum* was the main contributor to the secondary production of this study, and the presence of large numbers of *Ruditapes philippinarum* reduces species diversity. Li et al. [47] proposed a unimodal relationship between holistic biodiversity and ecosystem functioning, and excessive biodiversity was detrimental to ecosystem functioning. However, secondary production was highly significantly positively correlated with biomass ($P<0.01$). This was the same as the findings of Quan et al. [48] and Li et al. [49]. Neither total biomass nor secondary production were significantly correlated with any environmental factors. Low values of functional richness indicate that some of the resources (alpha niches) potentially available to the community are unoccupied, which will reduce secondary production [41]. In this study, secondary production was significantly positively correlated with FRic, which was consistent with the above hypothesis. Lower values of functional divergence, functional dispersion and Rao's quadratic entropy indicate high overlapping of ecological niche

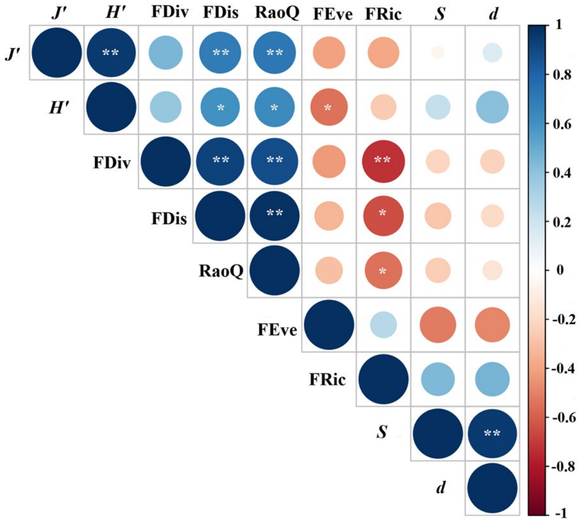

**Fig. 5** Results of Pearson correlation analysis of species diversity and functional diversity in Jiaozhou Bay, China. **means correlation is significant at the 0.01 level; *means correlation is significant at the 0.05 level; *FRic* functional richness, *FEve* functional evenness, *FDiv* functional divergence, *FDis* functional dispersion, *RaoQ* Rao's quadratic entropy, *S* is the number of macrofaunal species of each site, *d* species richness index, *J′* Species evenness index, *H′* Shannon–Wiener index

and highly prevalent resource competition for animals, which can lead to the decrease in secondary production [40].

The present study found that secondary production was significantly higher in northeastern of Jiaozhou Bay than those in other areas. This may be due to the presence of several rivers discharging into the sea in the northern part of Jiaozhou Bay, which could provide abundant terrestrial nutrients for nearshore marine organisms. In addition, the north-east of the bay was a marine-farmed area of the shellfish *Ruditapes philippinarum*. Resource changes in *Ruditapes philippinarum* were one of the main factors contributing to changes in secondary production [50].

### Feeding functional groups in relation to species diversity and functional diversity

Macrofauna constitutes the main connection between organic matter, nutrient sources and higher trophic level organisms in the food web of offshore ecosystems, while it is sensitive to external stress, thus effectively indicating the health of ecosystems [51]. Owing to the spatial and temporal variability of macrofaunal communities, it is relatively difficult to assess ecosystem condition using only their biodiversity, and the use of functional groups improves predictability [52]. Our results indicated that there was a little difference in the spatial distribution of abundance of the 5 functional groups, with differences in biomass mainly due to the uneven distribution of *Ruditapes philippinarum*. Spring, summer and autumn were significantly higher in abundance and biomass than winter. Jiaozhou Bay comprises semi-enclosed warm temperate waters and resident species generally have long life cycles, and it is assumed that this results in little variation in functional groups over time and space. The crustacean *Hemileucon bidentatus* had high abundance in this study which belonged to the detritivorous group, which contributed to the dominance of the detritivorous group in the study area. The biomass of the planktophagous group had high dominance mainly due to the large number of *Ruditapes philippinarum* in the study area.

In this study, the detritivorous group, carnivorous group and planktophagous group functional groups contained more species, accounting for 91.97% of the total number of species. This is similar to the conclusion of studies in the subtidal zone of other Chinese marine areas [37, 53, 54]. Few species of the phytophagous group occurred in each cruise, and were completely absent in the winter cruise, so this group was extremely scarce throughout Jiaozhou Bay. The type and cover of vegetation and the level of primary production directly affect the distribution of nutrient sources and food structure, and consequently the distribution of macrofaunal functional groups [55]. The type of substrate sediments in Jiaozhou Bay is dominated by clay powder sand and powdered clay [56, 57], resulting in a lack of plants such as algae, explaining the paucity of species of the phytophagous group.

### Species diversity in relation to functional diversity

Functional diversity reflects overall differences in functional traits, reflecting their response to environmental disturbances [16]. Studies have shown that functional trait composition is important for studying macrofaunal ecosystem functions and community composition [58, 59]. The loss or increase of species with certain functional traits may have a significant impact on specific ecosystem processes, while the loss or increase of other species may have a small impact on specific ecosystem processes, but different processes may be affected by different species and functional groups [60].

This study showed that there was significant spatial variation and temporal variation in the functional diversity of macrofauna in Jiaozhou Bay. Spatial differences may be due to water depth, resource utilization, biological traits composition, etc. Studies showed that water depth affected the distribution of macrofauna [61]. The reason of temporal variation was presumed to be that temperature played a decisive role in the distribution of macrofauna. Scholars showed that macrofauna in tropical rivers were higher in species, abundance and biomass than in temperate rivers, while temperate rivers were higher than cold temperate rivers and cold zones [62]. Temperature affected the growth and development of macrofauna. Generally, as the temperature rises, the metabolism of macrofauna is accelerated, and the growth and development of macrofauna are also accelerated [63].

### Impact of bottom aquaculture

With the aquaculture industry further expanding, intensifying and diversifying during the past decades, it is widely accepted that aquaculture is very important in meeting the increasing world demands for high-quality protein [64]. Research has shown that, because of their natural characteristics, bivalves, as important species in the ecosystem, have the ability to affect the surrounding environment in both negative and positive ways [65]. Based on the study of [66], it was learned that although the abundance and biomass of *Ruditapes philippinarum* were relatively high in this study, it still cannot be considered as a keystone species. Jiaozhou Bay is an important breeding base for *Ruditapes philippinarum*. Based on the results of the correlation analysis, we conclude that the presence of abundant *Ruditapes philippinarum* reduces the species diversity of the macrofauna. The abundance and biomass of *Ruditapes philippinarum* had significantly positive correlations with functional richness, which could suggest that farming had contributed to some extent to the use of the resource. And the abundance and biomass of *Ruditapes philippinarum* had highly significantly negative correlations with functional divergence, functional dispersion and Rao's quadratic entropy ($P<0.01$), so the dominance of *Ruditapes philippinarum* resulted in a high degree of overlapping ecological niches and increasing of resource competition.

## Conclusions

This paper explored the relationships between ecosystem function factors in Jiaozhou Bay based on year-round sampling of macrofauna in semi-enclosed bays. Species diversity had significantly negative correlations with biomass and secondary production, which validates the general conclusion that high-yielding ecosystems in nature tended to have low species diversity (Fig. 6). Species diversity showed significant positive correlations with the feeding evenness index, functional dispersion and Rao's quadratic entropy ($P<0.05$). High species diversity resulted in a less disturbed ecosystem and provided the ecosystem with a wider range of biological traits, increasing the degree of complementation of ecological niches. Functional richness had significant positive correlations with total biomass and secondary production. And functional divergence, functional dispersion and Rao's quadratic entropy had highly significant negative correlations with total biomass and secondary production. It suggests that high overlapping of ecological niches can increase competition for habitat resources, leading to a decline in biomass and secondary production. In addition, aquaculture could promote the use of habitat resources to some extent, while it could increase competition for ecosystem resources. This study shows that functional diversity is a good indicator of the ecosystem functioning and resource competition.

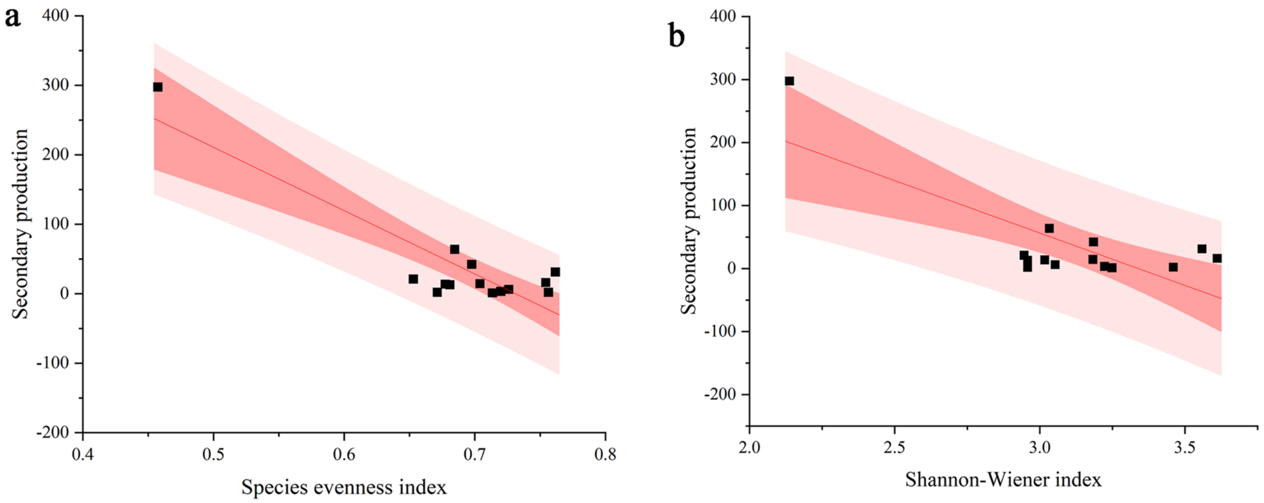

**Fig. 6** Results of Pearson correlation analysis between secondary production and species diversity in Jiaozhou Bay, China. **a** Species evenness index; **b** Shannon–Wiener index

### Abbreviations

| | |
|---|---|
| FGs | Functional groups |
| FD | Functional diversity |
| Chl-*a* | Chlorophyll *a* |
| Pha | Phaeophorbide |
| $W_{H2O}$ | Water content |
| OM | Organic matter |
| T | Water temperature |
| S | Salinity |
| D | Water depth |
| *d* | Species richness index |
| *J′* | Species evenness index |
| *H′* | Shannon–Wiener index |
| ANN | Artificial neural net-work |
| Pl | Planktophagous group |
| Ph | Phytophagous group |
| C | Carnivorous group |
| O | Omnivorous group |
| D | Detritivorous group |
| $j_{FD}$ | The feeding evenness index |
| EHS | The ecosystem health state |
| Fric | Functional richness |
| FEve | Functional evenness |
| FDiv | Functional divergence |
| FDis | Functional dispersion |
| RaoQ | Rao's quadratic entropy |

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-024-00889-7.

**Additional file 1: Table S1.** Conversion factors of the biomass and energy for macrofauna. **Table S2.** Biological traits of macrofauna used in the calculation of functional diversity. **Table S3.** Biological trait assignation of macrofaunal eight dominant species in Jiaozhou Bay, China. **Figure S1.** Temporal variation in functional richness of macrofaunal assemblages in Jiaozhou Bay, China. **a** Winter **b** Spring **c** Summer **d** Autumn. **Figure S2.** Temporal variation in functional evenness of macrofaunal assemblages in Jiaozhou Bay, China. **a** Winter **b** Spring **c** Summer **d** Autumn. **Figure S3.** Temporal variation in functional divergence of macrofaunal assemblages in Jiaozhou Bay, China. **a** Winter **b** Spring **c** Summer **d** Autumn. **Figure S4.** Temporal variation in functional dispersion of macrofaunal assemblages in Jiaozhou Bay, China. **a** Winter **b** Spring **c** Summer **d** Autumn. **Figure S5.** Temporal variation in Rao's quadratic entropy of macrofaunal assemblages in Jiaozhou Bay, China. **a** Winter **b** Spring **c** Summer **d** Autumn.

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### Author contributions

ZW: methodology, software, formal analysis, data curation, writing—original draft. JX: methodology, software, formal analysis, data curation, writing—original draft. ZDX: methodology, investigation, data curation, writing—review and editing. XSL: conceptualization resources, writing—review and editing, supervision, funding acquisition.

### Data availability

No datasets were generated or analysed during the current study.

## Declarations

### Competing interests

The authors declare no competing interests.

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