Connectivity of nekton assemblages along artificial reefs and adjacent waters in Haizhou Bay

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Abstract:
The successful construction of marine protected areas (MPAs) in temperate waters largely depends on our understanding of the distribution and coexistence of organisms with varying habitat preferences, which helps us to better understand the community patterns mediated by connectivity in coastal areas. This study was conducted to examine the connectivity of nekton assemblages in artificial reefs and adjacent waters, which included five habitats: the artificial reef area (AR), aquaculture area (AA), natural area (NA), estuary area (EA) and comprehensive effect area (CEA), in Haizhou Bay in October 2020. Analysis of variance (ANOVA) showed that there were significant differences in the characteristics and abundances of nekton in each habitat ($P<0.05$). Approximately 38.2% of the individuals were found in at least three habitats, and very few species were present in only a single habitat. Several highly abundant nekton species were selected according to the kernel density estimates (KDEs), and their body lengths varied gradationally among habitats, potentially indicating migration and diffusion during their life history. The results showed that artificial reefs and adjacent waters in Haizhou Bay are related by similar nekton assemblages and ontogenetic variation. Finally, this study has implications for the conservation and monitoring of nekton assemblages in artificial reefs and adjacent waters, highlighting that the principle of connectivity should be taken into consideration in the design of MPAs and MPA networks that can be applied in different stages of implementation and in different combinations of scenarios.

Key words: connectivity, nekton, artificial reef, adjacent sea area, Haizhou Bay

1 Introduction

The global trends of continuous processes associated with human activities and coastal development, such as overfishing, habitat destruction and marine environmental pollution, have led to the general degradation of the entire coastal ecosystem, which has imposed tremendous pressure on estuaries, harbors, gulfs and nearshore regions (Walker et al., 2014; Dance et al., 2015; Cordova et al., 2018; Reis et al., 2019). Over the years, artificial reefs have been constructed as human-made structures to increase environmental quality and species abundance in marine ecosystems for coastal ecological restoration (Seaman and Sprague 1991; Anne et al. 2015; Folpp et al. 2020) by creating suitable habitats and places for many marine organisms to grow, reproduce, forage and hide (Sherman et al., 2002). At present, ecological principles combining the planning, design and operation of artificial reefs have been extensively investigated in many coastal areas (Whitmarsh et al. 2008; Walker et al. 2014; Anne et al. 2015; Folpp
et al. 2020). Given that artificial reefs aim to retard marine habitat degradation, protect endangered species and restore biodiversity, artificial reefs are regarded as conservation and enhancement tools for marine environments and habitat recovery (Dafforn et al., 2015; Becker et al., 2017).

Habitat connectivity provides an important perspective for further study of coastal ecosystems (Dance et al., 2015; Diana et al., 2018). It includes two mechanisms: movements of nekton in different stages of life history (Flitcroft et al., 2018) and transport and exchange of nutrients (fundamental elements such as C, N, P, and S) (Garcia et al., 2017; Laske et al., 2019), which play an important role in maintaining population structures and regulating ecological processes. Most ecological studies on habitat connections and distribution patterns of marine nekton focus on a limited number of species or habitat types (Reis et al., 2019); thus, obtaining accurate and different information on related species and habitats in various types of ecosystems seems to be a major challenge.

Haizhou Bay, located in Lianyungang City, Jiangsu Province, is one of the important fishing grounds in the Yellow Sea of China (Wang, 1993). Because of numerous human activities, such as overfishing, port construction and waterway transportation, since the 1980s, the habitat environment and fishery resources in Haizhou Bay have been vastly and adversely affected, resulting in the fragmentation of habitats and the destruction of ecosystem structure (Zhang et al., 2006; Zhang et al., 2013). Since 2002, the local government has begun to build marine protected areas (MPAs) dominated by artificial reefs for ecological restoration and resource conservation in Haizhou Bay (Zhang et al., 2006; Wu et al., 2012). The construction of artificial reefs affects aquatic biodiversity and food web ecology by affecting the flow of water, sediments and organisms (Clark et al. 1999; Sherman et al. 2002). These processes in turn affect the community structure and ecological pattern in adjacent waters and finally alter the connectivity between habitats (Keller et al. 2017; Reeds et al. 2018). However, the impacts of artificial reefs on marine ecosystems and communities in adjacent waters, as well as ontogenetic changes and utilization patterns of reef nekton, are largely unknown, especially in temperate seas (Diana et al. 2018).
To support the sustainable socioeconomic development of MPAs, therefore, it is necessary to thoroughly explore the relationship between biodiversity and connectivity in artificial reefs and adjacent waters.

In this study, we aim to (1) analyze the nekton assemblages and connectivity in artificial reefs and adjacent waters in Haizhou Bay, (2) preliminarily explore the influence of artificial reefs on the distribution pattern of nekton resources in adjacent waters, and (3) identify ontogenetic shifts in nekton-habitat association patterns. Our research will help better understand the connectivity of communities between different habitats in temperate waters and provide a more scientific basis and improve specific planning for improving the strategy, fishery management and construction of MPAs and MPA networks in temperate coastal habitats in China.

2 Material and methods

2.1 Study area

Haizhou Bay, located west of the coast of Lianyungang city, Jiangsu Province, north of the Qingdao Fishing Ground, and south of the Lysi Fishing Ground, is mainly composed of sandy and muddy habitats and represents an open bay with an area of approximately 877 km² (Wang 1993). The climate and hydrology of Haizhou Bay are greatly influenced by the mainland, and most fishing areas are controlled by coastal currents (Luo et al. 2009). The tidal current in Haizhou Bay is mainly rotating flow, with a velocity of 0.4-0.65 m/s (Xie et al. 2007). The environmental and fishery resource surveys presented in this study were conducted in the coastal waters of Haizhou Bay in autumn 2020.

2.2 Defining habitat types

According to the available geographical coordinate data sets in the study area (34°49.20-34°55.00N, 119°16.167-119°59.50E), five major investigation areas ranging from the Linhong Estuary to the artificial reef area were set, including the estuary area (EA), the most polluted area and featuring a coarse sand substrate; the aquaculture area (AA), an area mainly used for culturing shellfish and algae; the artificial reef area (AR), a protected area consisting of a series of reefs on the sea bottom; the natural area (NA),
an area that has not been overly impacted by humans; and the comprehensive effect area (CEA), an area in which several habitats co-occur. The distribution of the sampling sites is shown in Figure 1.

To determine how the nekton utilized the habitat, the species were divided into the following nine habitat groups: (1) AR species, which were present only in the artificial reef area; (2) AA species, which were present in only the aquaculture area; (3) EA species, which were present only in the estuary area; (4) NA species, which were present only in the natural area; (5) AR-AA-EA species, which were present in the artificial reef area, aquaculture area and estuary area; (6) AR-EA-NA species, which were present in the artificial reef area, estuary area and natural area; (7) AR-AA-NA species, which were present in the artificial reef area, aquaculture area and natural area; (8) AA-NA-EA species, which were present in the artificial reef area, natural area and estuary area; (9) AR-AA-EA-NA species, which were present in all four habitats (as a comparison area, CEA was not included in the statistics) (Nakamura and Sano 2004).

Figure 1. Study area and sampling site
AR, CEA, AA, EA and NA represent the artificial reef area, comprehensive effect area, aquaculture area, estuary area and natural area, respectively.

2.3 Sample collection

Environmental data were recorded by a CTD (conductivity, temperature, and depth) measuring system, sediment was collected using a sediment sampler, and nekton were sampled by a single ship with a wing single capsule bottom trawl (15/4×8 m, mesh size: 1×1 cm) at each site. The fishery investigation was conducted for approximately 30
minutes. Because a large number of reefs or culture nets and cages are commonly present at the bottom of AR and AA, we could only sample around these habitats (see the solid box of the study area in Figure 1). After identification, the samples were packed into 100×150 cm PVC bags with fresh ice for preservation. The collection, treatment and analysis of samples were in accordance with the relevant provisions of the Marine Survey Code (General Administration of Quality Supervision, 2007). The basic biological indicators (weight and length) and numbers of all samples were recorded in the onshore laboratory (the total length of each sample was accurate to 0.1 cm). All nekton were identified to the lowest possible classification level (http://www.fishbase.org).

2.4 Statical analysis

The larval to adult ratio and species abundance in each habitat were calculated to evaluate the relationship between the use of different habitat types and nekton size. All nekton were identified at the family level, and the numbers were counted. One-way analysis of variance (ANOVA) was used to determine the differences in the number of individuals and species and to analyze the differences in different body lengths of nekton in each habitat. The similarity of nekton assemblages among different habitats was calculated using continuous trawl data. To evaluate the distribution of species in different habitats, samples were clustered based on Bray-Curtis similarity, and the results were visualized by nonmetric multidimensional scale analysis (NMDS). Nonparametric multivariate analysis of variance (NPMANOVA; α=0.05) was used to analyze the differences in nekton community composition in different habitats. To verify the ontogenetic variation in the fish-habitat associations of a selection of species, kernel density estimates (KDEs) were run by body length frequency data from each habitat type. All statistical analyses were run in R software (Ver. 4.0.3).

3 Results

3.1 Characteristics of environment

The characteristics of the environment in the study area of Haizhou Bay are illustrated in Figure 2. The depth ranged from EA (4.40±2.91 m) to RA (12.56±2.63 m),
and the mean salinity ($23.76\pm6.63$) reflected the gradient from near the shore (EA: $13.59\pm1.56$) to far from shore (NA: $30.87\pm0.09$). The particle size of sediments changed from EA ($16.86 \ \mu m$) to NA ($62.52\pm6.70 \ \mu m$), which reflected the distribution of waters and sediments in Haizhou Bay. The mean temperature was $19.54\pm0.39^\circ C$ and gradually increased from EA ($18.47\pm0.04^\circ C$) to AR ($19.75\pm0.13^\circ C$). The mean dissolved oxygen levels were stable along this horizontal gradient ($8.10\pm0.35 \ \text{mg/l}$). At the habitat level, the mean salinity, temperature and dissolved oxygen levels could represent the coastal environment in Haizhou Bay.

![Figure 2. The depth, temperature and salinity distribution of the study area in Haizhou Bay](image)

3.2 Nekton community characteristics

A total of 10,234 individuals were collected from five habitats, including 68 species belonging to 42 families (Appendix 1). A total of 2867 individuals belonging to 21 families and 35 species were collected in AR, 3213 individuals from 29 families and 39 species were collected in AA, and 2664 animals belonging to 22 families and 39 species were collected in CEA. In contrast, there were fewer species found in EA (1263 animals belonging to 13 species in 8 families) and NA (227 animals belonging to 20 species in 15 families) (Figure 3, Appendix 1).

The predominant species in AR were Gobiidae (4 species, 12.1%, represented by *Chaeturichthys stigmatis*), followed by Penaeidae (5 species, 15.1%, represented by *Trachypenaeus curvirostris*). The most dominant species of AA was Clupeidae (2 species, 5.1%), represented by the species *Sardinella zunas*. The species in NA were mainly composed of Gobiidae (2 species, 10%), Portunidae (1 species, 5%) and Penaeidae (2 species, 15%), and those in EA were composed of Portunidae (2 species, 16.7%), *Portunus trituberculatus* and *Charybdis japonica*. The dominant family of CEA was Penaeidae (1 species, 2.6%). In terms of the number of individuals, Gobiidae
was the dominant family of RA, accounting for 26.6% of all species, followed by Penaeidae, which accounted for 21.8% of all species. Clupeidae was the main family in AA, accounting for approximately 41.6%, and Gobiidae was the main family in NA, accounting for 25.6%. The most important family in EA was Portunidae, accounting for 77.6%. *Oratosquilla oratoria* of Penaeidae was the dominant species in CEA, accounting for approximately 30% (Figure 4, Appendix 1).

The results of one-way ANOVA showed that the mean numbers of individuals of fish, shrimp, crab, shellfish, and cephalopods were significantly different between NA and AR and between CEA and AA ($P<0.05$). The mean number of individuals in AR, CEA and AA was significantly higher than that in NA ($P<0.05$).

Figure 3. Species and mean numbers of individuals of fish, shrimp, crab, shellfish, and cephalopods in the five habitats

Figure 4. Species and mean numbers of individuals of different families in the five habitats

3.3 Nekton assemblage and utilization of different habitats

Nearly all species were widely distributed in the five habitats, with the majority using two, three, or four habitats at the same time, but only Gobiidae, Squillidae, Cynoglossidae, Sciaenidae, Penaeidae and Portunidae were found living in all five
habitats, among which *C. Stigmatias*, *O. Oratoria* and *P. Trituberculatus* had the largest numbers (Appendix 1). There were 18 specific species that appeared to use a single habitat, including 10 species of Platycephalidae and Pholidae in AR, Apogonidae in NA and Mugilidae and Paguridae in AA.

Univariate PERMANOVA results showed that the species abundances of the five marine habitats were significantly different (*P*<0.05) (Table 1). Analysis of each habitat separately revealed that there were significant differences in species abundance between the two groups of five habitats (*P*<0.05) (Table 2). The community structure of the five habitats was inconsistent not only at the overall level but also among each of the habitats.

Table 1. Univariate PERMANOVA results for the overall interaction of species abundances of species in the five habitats

| Group | Df  | Sums of squares | Mean squares | F. Model | Variation (R^2) | P (>F) |
|-------|-----|----------------|--------------|----------|----------------|--------|
| site  | 4   | 5.5804         | 1.3951       | 8.5139   | 0.6300         | 0.001  |
| Residuals | 20 | 3.2772         | 0.1639       |          | 0.3700         |        |
| Total  | 24  | 8.8577         |              |          |                |        |

Note: R^2 is the variance contribution; the higher the R^2 value is, the higher the explanation degree of abundance between different habitats. The same below in Table 2.

Table 2. Univariate PERMANOVA results of pound-by-pair interactions of the species abundances of species in the five habitats

| Group | Df | Sums of squares | Mean squares | F. Model | Variation (R^2) | Pr (>F) |
|-------|----|----------------|--------------|----------|----------------|---------|
| AR/NA | 1  | 1.1685         | 1.1685       | 5.5307   | 0.4088         | 0.008   |
| AR/CEA| 1  | 0.9411         | 0.9411       | 5.7191   | 0.4169         | 0.009   |
| AR/AA | 1  | 1.1030         | 1.1030       | 4.43213  | 0.3565         | 0.009   |
| AR/EA | 1  | 1.2615         | 1.2615       | 10.4299  | 0.5659         | 0.01    |
| NA/CEA| 1  | 1.5579         | 1.5579       | 10.2601  | 0.5619         | 0.007   |
| NA/AA | 1  | 1.3624         | 1.3624       | 5.7695   | 0.4190         | 0.012   |
| NA/EA | 1  | 1.8698         | 1.8698       | 17.2758  | 0.6834         | 0.008   |
| CEA/AA| 1  | 1.4096         | 1.4096       | 7.4413   | 0.4819         | 0.009   |
| CEA/EA| 1  | 1.6588         | 1.6588       | 26.9704  | 0.7712         | 0.007   |
| AA/EA | 1  | 1.6184         | 1.6184       | 11.0992  | 0.5811         | 0.01    |

The results of clustering analysis were visualized by nonmetric multidimensional scale analysis (Figure 5). According to NMDS, habitat arrangement in the multivariate space clearly revealed a separation along the NMDS 1 axis, which clearly showed that AA and NA were located on the left and right sides of the central axis, respectively. AA has the largest shaded area, and EA has the smallest, suggesting that the possible range
of species abundance changes in the five habitats was AA>AR>NA>CEA>EA (Figure 5). The shaded range of CEA overlaps with those of AR, EA and AA but not that of NA, which proves that CEA was a transitional area among several other habitats. However, the shaded range of NA overlaps with that of AA and AR, indicating that there was a potential relationship between species composition among these three habitats. EA, similar to NA, hardly overlaps with other habitats except for CEA, indicating that the marine nekton assemblages in these two habitats form an isolated group with little overlap with other habitats. NA overlaps with habitats other than EA, which may explain why nekton assemblages in natural waters exist in other habitats.

Figure 5. Visualization of the nonmetric multidimensional scale (NMDS) results for the composition of the nekton assemblages sampled by trawling in the different marine habitat types of Haizhou Bay. The stress function value (0.1635<0.2) shows the rationality of the ranking model. Different colored shaded areas represent the different habitat types, and the points indicate each sampling site. The size of the shaded area reflects the species abundance, and the degree of overlap of shaded areas represents the degree of difference in species abundance between habitats.

3.4 Length and size classes of nekton

According to the KDEs of nekton with different body lengths, the three fish with the highest abundance (A. C. stigmatias, B. Amblychaeturichthys hexanema, and C. Collichthys lucidus), and the top three most abundant shrimp and crabs (D. O. oratoria, E. T. curvirostris, and F. P. trituberculatus) were selected, and their body length distribution in different habitats is described in Figure 6. There were significant differences in the body length distributions of the six species in the five habitats.
The maximum and minimum lengths of *C. stigmatias* appeared in AA (22.4 cm) and CEA (7.1 cm), and those of *A. hexanema* appeared in NA (7.0 cm) and AR (14.8 cm), respectively. The mean lengths of *C. lucidus* were 14.63±1.64 cm, 10.65±0.94 cm, 11.28±1.85 cm, 12.1±0.43 cm and 14.3±0.85 cm in AR, NA, CEA, AA, and EA, respectively. These results indicated that *C. lucidus* has a strong ability to shift among habitats and a wide distribution in different habitats. The body length of *C. lucidus* was larger in EA and AR than in the other habitats, possibly because the cross-habitat shifts of *C. lucidus* led to some potential connectivity between RA and EA. The maximum sizes of *O. oratoria* and *P. trituberculatus* were 15.6 cm and 18.6 cm in CEA, and the minimum sizes were 4.8 cm and 3.5 cm in AR and NA. The maximum and minimum sizes of *T. curvirostris* were 11.4 cm and 4.7 cm in CEA. These results could indicate some possible individual shifts between habitats.
Figure 6. Kernel density analysis for the different size classes of six abundant nekton species with multihabitat associations in Haizhou Bay. The upper and lower limits of the box indicate the 1st and 3rd quantiles, respectively, and the inner line of the box indicates the average of the data distribution. (A. C. stigmatias, B. A. hexanema, C. C. lucidus, D. O. oratoria, E. T. curvirostris, F. P. trituberculatus)

4 Discussion

Understanding the relationships between habitats for baseline establishment is an important part of ecosystem approaches in fishery management, biodiversity conservation and spatial planning in coastal areas (Olds et al. 2016; Liao et al. 2017). In the past, the study of nekton resources in Haizhou Bay focused only on artificial reef areas and contrasting areas (Zhang et al. 2006; Sun et al. 2006; Su et al. 2015), which is not scientific or reasonable. The contrasting areas include CEA, AA, NA and other habitats, and AA is subdivided into a shellfish culturing area, an algae culturing area and so on. Therefore, the contrasting areas previously surveyed may represent combinations of any of these habitats, thereby greatly affecting the evaluation of the effect of artificial reefs on MPAs and the results of fishery resource analysis. In addition, comparing the distribution of nekton resources in a single habitat cannot explain the intrinsic connection of habitats (Diana et al. 2018). Therefore, based on the principle of ecological connectivity, the study area of Haizhou Bay is clearly divided into five habitats through sampling data over the years, which is conducive to the study of the potential relationship between the characteristics of nekton resources and the interaction of population structure in the artificial reefs and adjacent waters.
EA is a major source of nutrient transport to the ocean and represents an important transition region in which energy from land and sea mixes, and this area is dominated by a variety of nekton communities (Pasquaud et al. 2008; Emily et al. 2017). However, we did not observe a high level of species abundance in EA, which may be related to EA being subjected to the strongest interference by humans (Li et al. 2011). Furthermore, the water level of EA fluctuates due to the intermittent influence of tides, which may lead to different nekton assemblages (Reis et al. 2019). AA presents a unique nekton assemblage with a variety of benthic shellfish and snails that other habitats do not include, which could explain the remarkable effect of the high benthic abundance in AA. The current of Haizhou Bay includes a branch of the Yellow Sea Warm Current and the coastal current, which flows from northeast to southwest (Sun et al. 2003). Therefore, the high species abundance in CEA is expected as it is a gathering place of AA, RA and NA habitats. Artificial reefs are an effective way to increase habitats and populations of fish species (Folpp et al. 2020); thus, we assume that AR is a mosaic that connects other habitats. Since artificial reefs were placed in habitats, the abundance of nekton has showed an increasing trend over time (Wang et al. 2017), similar to results from most temperate seas (Lowry et al. 2014; Smith et al. 2016; Folpp et al. 2020). The mean abundance of nekton in AR was higher than that in the other habitats except for CEA, and it featured a relatively unique nekton assemblage (Figure 2). In addition, AR includes almost all species present in the other habitats except for species specific to EA, AA, and NA, especially benthic mollusks of AA, and this pattern reflects the good effect produced by artificial reefs over many years. In the present study, 14.3%-29% of families and 26.1%-50.3% of individual species were found in at least three habitats, and very few species utilized a single habitat (Table 3). Most nekton use a variety of habitats, suggesting that they may migrate and emigrate between habitats and demonstrating connectivity between the nekton assemblages of artificial reefs and the nekton assemblages in adjacent waters.

| Habitat group | All Family/% | Individuals/% |
|---------------|--------------|---------------|
| AR            | 4.8          | 0.02          |
| AA            | 23.8         | 1.1           |

Table 3. Percentage contribution of all family members and individuals of each habitat group.
In the present study, strong links were also identified between the size-related nekton assemblages and the distribution of habitats in artificial reefs and adjacent waters. Little fluctuation in the body length of Gobiidae was found between habitats, which may be related to its weak swimming ability and settlement behavior after reaching adulthood (Han et al. 2013). The body size of *P. trituberculatus*, with strong swimming ability, also showed little variation in this study. The reason is that *P. trituberculatus* is active in coastal waters but not in offshore regions, such as AR and NA (Song et al. 1989). Moreover, EA is also the discharge area of *P. trituberculatus* in Haizhou Bay, which verifies the view in this study. In total, the body length of each nekton gradually increases from EA to RA, not only indicating that EA is a breeding ground for most fish, shrimp and crabs but also reflecting the ontogenesis of some marine nekton in terms of the use of different habitats. The body length gradient of *C. lucidus* and *O. oratoria* in different habitats indicates strong cross-habitat shifts, and a larger length of *C. lucidus* appears in both AR and EA, which suggests that artificial reefs increase fish abundance by attracting fish (Lowry et al. 2014). Our findings support the conclusion that in this coastal region, many nekton, such as *C. lucidus* and *O. oratoria*, undergo migration and diffusion from estuarine habitats to artificial reefs in Haizhou Bay with increasing size during their life history. This finding reveals the connectivity between artificial reefs and adjacent waters.

According to the characteristics of the species and environment in temperate seas, it is worth considering selecting the appropriate netting gear during the survey. The coastal waters of the Yellow Sea where Haizhou Bay is located are mainly dominated by muddy and sandy habitats, in which the underwater visibility is low, making it difficult to study the nekton communities by means of diving or snorkeling (Dorenbosch et al. 2007; Wang et al. 2011). Moreover, the current velocity is relatively

|       | NA  | 2.4 | 0.03 |
|-------|-----|-----|------|
|       | EA  | 0   | 0    |
|       | AR/AA/EA | 19 | 49.3 |
|       | AR/EA/NA | 14.3 | 38.3 |
|       | AR/AA/NA | 16.7 | 26.1 |
|       | AA/EA/NA | 19 | 41.5 |
|       | AR/AA/EA/NA | 14.3 | 50.3 |
high, and the methods of underwater visual surveys, such as baited remote underwater video systems (BRUVs), are very limited (Reis et al. 2019). Therefore, trawl and gill nets are more commonly used for sampling in this region. However, trawling is the fishing method with the greatest harm to fisheries and marine environments (Yang 1997). In the future, habitat connectivity could be assessed by combining trawling and gill net methods. In addition, it remains unclear whether some migratory species use a variety of habitats to complete their life cycle at different stages of their life histories or whether they simply exhibit cross-habitat behavior. It may be necessary to combine otolith microelement (Thais et al. 2020) or environmental DNA (eDNA) (Yamanaka et al., 2016) techniques for further in-depth analysis.

5 Conclusion

The connectivity of artificial reefs and adjacent waters in temperate seas is largely unknown. In this study, a mesoscale survey of nekton communities associated with artificial reefs and adjacent waters in Haizhou Bay was conducted for the first time and describes the characteristics of the rich diversity of nekton in the coastal ecosystem of Haizhou Bay. We found evidence to support habitat connectivity between artificial reefs and adjacent waters in Haizhou Bay. In addition to describing some nekton assemblages and multihabitat associations, the results also emphasize the ontogenetic variation in some nekton and the influence of specific habitats on their life history. We can infer that artificial reefs and adjacent habitats are connected via the movement of organisms and individual shifts. In the past, research on the relationship between nekton communities and habitats in Haizhou Bay was not deep enough. In the future, the principles of connectivity should be taken into account, and artificial reefs should be considered a key component of broader coastal habitat mosaics when designing MPAs and MPA networks that can be applied at different stages of implementation and in different combinations of scenarios.

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Data Availability statement

The data that support the findings of this study are available from the corresponding author [Shuo Zhang], upon reasonable request.

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Appendix 1. The number of individuals in the artificial reef area (AR), comprehensive effect area (CEA), aquaculture area (AA), estuary area (EA) and natural area (NA) in Haizhou Bay

| Species                          | Family       | AR  | CEA | AA  | EA  | NA  |
|----------------------------------|--------------|-----|-----|-----|-----|-----|
| *Amblychaeturichthys hexanema*   | Gobiidae     | 35  | 0   | 2   | 112 | 65  |
| *Coilia mystus*                  | Engraulidae  | 0   | 0   | 1   | 0   | 0   |
| *Lateolabrax japonicus*         | Percichthyidae | 4   | 0   | 0   | 0   | 0   |
| *Largehead hairtail*            | Trichiuridae | 0   | 7   | 0   | 0   | 2   |
| *Larimichthys polyactis*        | Sciaenidae   | 33  | 1   | 1   | 35  | 10  |
| *Konosirus punctatus*           | Clupeidae    | 0   | 0   | 3   | 0   | 2   |
| *Conger myriaster*              | Congridae    | 4   | 0   | 1   | 0   | 3   |
| *Enedrias fangi*                | Pholidae     | 0   | 0   | 0   | 0   | 0   |
| *Engraulis japonicus*           | Engraulidae  | 0   | 0   | 0   | 0   | 1   |
| *Leiognathus rivalatus*         | Leiognathidae| 0   | 0   | 0   | 0   | 2   |
| *Collichthys lucidus*           | Sciaenidae   | 32  | 6   | 3   | 38  | 93  |
| *Syngnathussp*                  | Sygnathidae  | 0   | 0   | 5   | 0   | 0   |
| *Cynoglossus joyneri*           | Cynoglossidae| 31  | 2   | 7   | 13  | 12  |
| *Odontamblyopus rubicundus*     | Gobiidae     | 9   | 1   | 10  | 0   | 87  |
| *Pennahia argentata*            | Sciaenidae   | 16  | 0   | 5   | 6   | 17  |
| *Rhynchoconger ectenurus*       | Congridae    | 0   | 0   | 0   | 0   | 3   |
| *Johnius belangerii*            | Sciaenidae   | 6   | 0   | 0   | 0   | 8   |
| *Symechogobius hasta*           | Gobiidae     | 0   | 0   | 1   | 0   | 138 |
| *Chaeturichthys stigmatias*    | Gobiidae     | 453 | 57  | 41  | 0   | 345 |
| *Apogon lineatus*               | Apogonidae   | 0   | 3   | 0   | 0   | 0   |
| *Scomberomorus niphonus*        | Scombridae   | 0   | 0   | 0   | 0   | 1   |
| *Paralichthys olivaceus*        | Paralichthyidae | 1   | 0   | 1   | 0   | 0   |
| *Thryssa kammalensis*           | Engraulidae  | 0   | 0   | 102 | 0   | 17  |
| *Pampus argenteus*              | Stromateidae | 0   | 1   | 1   | 0   | 0   |
| *Cryptocentrus filifer*         | Gobiidae     | 0   | 0   | 0   | 0   | 2   |
| *Sardinella zunas*              | Clupeidae    | 0   | 0   | 1340| 0   | 0   |
| *Repomucenus olidus*            | Callionymidae| 13  | 1   | 0   | 0   | 0   |
| *Tridentiger barbatus*           | Gobiidae     | 239 | 0   | 0   | 10  | 11  |
| *Platycephalus indicus*         | Platycephalidae | 1   | 0   | 0   | 0   | 0   |
| *Mugilsoiny Basilewsky*         | Mugilidae    | 0   | 0   | 20  | 0   | 0   |
| *Mugil cephalus*                | Mugilidae    | 0   | 0   | 18  | 0   | 0   |
| Animal Group | Species Name               | Family            | Count 1 | Count 2 | Count 3 | Count 4 | Count 5 |
|-------------|---------------------------|-------------------|---------|---------|---------|---------|---------|
| Shrimp      | *Ilisha elongata*         | Pristigasteridae  | 0       | 0       | 310     | 0       | 22      |
| Shrimp      | *Nibea albiflora*         | Sciaenidae        | 0       | 0       | 0       | 0       | 1       |
| Shrimp      | *Setipinna tenuifilis*    | Engraulidae       | 3       | 1       | 0       | 0       | 2       |
| Shrimp      | *Harpadon nehereus*       | Synodontidae      | 0       | 0       | 0       | 0       | 1       |
| Shrimp      | *Oratosquilla oratoria*   | Squillidae        | 621     | 10      | 213     | 44      | 798     |
| Shrimp      | *Trachypena curvostris*   | Penaeidae         | 509     | 16      | 151     | 0       | 308     |
| Shrimp      | *Alpheus japonicus*       | Alpheidae         | 50      | 12      | 64      | 0       | 189     |
| Shrimp      | *Parapenaeopsis tenella*  | Penaeidae         | 100     | 16      | 2       | 0       | 36      |
| Shrimp      | *Penaeus penicillatus*    | Penaeidae         | 2       | 0       | 0       | 2       | 1       |
| Shrimp      | *Fenneropenaeus chinensis* | Penaeidae       | 2       | 2       | 0       | 0       | 0       |
| Shrimp      | *Parapenaeopsis hardwickii* | Penaeidae    | 3       | 0       | 0       | 0       | 0       |
| Shrimp      | *Alpheus distinguendus*   | Alpheidae         | 166     | 5       | 0       | 0       | 61      |
| Shrimp      | *Exopalaemon carinicauda* | Palaemonidae      | 30      | 9       | 10      | 15      | 0       |
| Shrimp      | *Metapenaeopsis dalei*    | Penaeidae         | 10      | 0       | 0       | 0       | 0       |
| Shrimp      | *Penaeus semisulcatus*    | Penaeidae         | 0       | 0       | 0       | 1       | 0       |
| Crab        | *Charybdis japonica*      | Portunidae        | 265     | 0       | 179     | 14      | 24      |
| Crab        | *Portunus trituberculatus*| Portunidae        | 142     | 55      | 610     | 966     | 343     |
| Crab        | *Heikea japonica*         | Dorippidae        | 3       | 0       | 4       | 7       | 2       |
| Crab        | *Matuta planipes*         | Calappidae        | 0       | 0       | 0       | 0       | 1       |
| Crab        | *Eucrate crenata*         | Goneplacoidea     | 0       | 0       | 2       | 0       | 0       |
| Crab        | *Paguridae*               | Paguridae         | 0       | 0       | 50      | 0       | 0       |
| Crab        | *Pyrhila pisum*           | Leucosiidae       | 0       | 0       | 2       | 0       | 0       |
| Cephalopods | *Octopus variabilis*      | Octopodidae       | 1       | 0       | 0       | 0       | 4       |
| Cephalopods | *Octopusoecellatus*       | Octopodidae       | 0       | 0       | 1       | 0       | 0       |
| Cephalopods | *Loligo beka*             | Loliginidae       | 76      | 15      | 0       | 0       | 49      |
| Cephalopods | *Sepiella maindroni*      | Sepiidae          | 1       | 0       | 0       | 0       | 0       |
| Cephalopods | *cuttloefish*             | Sepiidae          | 0       | 0       | 7       | 0       | 0       |
| Shellfish   | *Rapana venosa*           | Muricidae          | 2       | 0       | 4       | 0       | 0       |
| Shellfish   | *Mactra antiquata*        | Mactridae          | 0       | 0       | 0       | 0       | 1       |
| Shellfish   | *Scapharca subcrenata*    | Arcidae           | 0       | 0       | 27      | 0       | 1       |
| Shellfish   | *Solen grandis*           | Solenidae         | 0       | 0       | 1       | 0       | 0       |
| Shellfish   | *Mytilus coruscus*        | Mytilidae         | 0       | 0       | 1       | 0       | 0       |
| Shellfish   | *Glossaulax didyma*       | Naticidae         | 0       | 0       | 11      | 0       | 0       |
| Shellfish   | *ostrea gigas unub*       | Ostreidae         | 0       | 0       | 1       | 0       | 0       |
| Shellfish   | *Echinoderm*              |                    |         |         |         |         |         |
| Echinoderms | *Asterias amurensi*       | Benthopeccintidae  | 2       | 0       | 0       | 0       | 1       |
| Echinoderms | *Tamaria sp*              | Benthopeccintidae  | 1       | 0       | 3       | 0       | 0       |
| Echinoderms | *Echinoidea*             | Echinoidea        | 0       | 0       | 5       | 0       | 0       |
Figures

Figure 1

Study area and sampling site. AR, CEA, AA, EA and NA represent the artificial reef area, comprehensive effect area, aquaculture area, estuary area and natural area, respectively. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

The depth, temperature and salinity distribution of the study area in Haizhou Bay.
Figure 3

Species and mean numbers of individuals of fish, shrimp, crab, shellfish, and cephalopods in the five habitats.

Figure 4

Species and mean numbers of individuals of different families in the five habitats.
Figure 5

Visualization of the nonmetric multidimensional scale (NMDS) results for the composition of the nekton assemblages sampled by trawling in the different marine habitat types of Haizhou Bay. The stress function value (0.1635 < 0.2) shows the rationality of the ranking model. Different colored shaded areas represent the different habitat types, and the points indicate each sampling site. The size of the shaded area reflects the species abundance, and the degree of overlap of shaded areas represents the degree of difference in species abundance between habitats.
Figure 6

Kernel density analysis for the different size classes of six abundant nekton species with 251 multihabitat associations in Haizhou Bay. The upper and lower limits of the box indicate the 1st and 3rd quantiles, respectively, and the inner line of the box indicates the average of the data distribution. (A. C. stigmatias, B. A. hexanema, C. C. lucidus, D. O. oratoria, E. T. curvirostris, F. P. 254 trituberculatus)
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