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Variation in the attached community structure and function of artificial habitats during ecological succession: A case study of the artificial reef area in Bailong Pearl Bay, China

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With the continuous development of ports, ship transportation, resource extraction and artificial habitat deployment, an increasing number of artificial structures have created new usable spaces for marine organisms, and the biological communities living on their surfaces have undergone ecological succession. However, related studies have ignored ecological functions, interspecific relationships, and stability in different successional stages. Based on traditional taxonomy, this study applied functional diversity, niche overlap and niche breadth indexes to compare the attached organisms on artificial reefs (ARs) with different construction times in Bailong Pearl Bay, Fangchenggang City, Guangxi Zhuang Autonomous Region, China. The change trends of richness, habitat resource supply, resource utilization degree and efficiency, and interspecific relationships during the succession process were analysed. The results indicated that richness increased with functional diversity. While the number of species increased, the attached organisms showed different functional characteristics, and the number of species with identical traits decreased. The attached community in the later stage of development had a higher degree of utilization of ecological space, more comprehensive and efficient utilization of effective resources, a stronger degree of complementarity of organismal niches, and weaker interspecific competition. In the early stage of the developmental process, the attached community was affected by more environmental factors and had very significant correlations with those factors. The combination of the niche overlap index and the niche breadth index indicated that the resource supply supporting the survival and development of the attached organisms on the ARs with earlier construction times may be greater. The decrease in the number of

biomarkers, the similarity of biomarkers belonging to the same family, and the similarity of dominance alternation all indicated that during the process of long-term development and community succession, the organisms attached to the various parts of the ARs tended to become more similar.

KEYWORDS

attached community, artificial reefs, biodiversity, functional diversity, ecological niche, Bailong Pearl Bay

1 Introduction

Ecological succession is defined in general as the perturbation of a specific area leading to changes in the habitat and community, occurring either naturally or by human action (Vaz-Pinto et al., 2014; Uribe et al., 2015; Herbert et al., 2017). Odum (1971) comprehensively summarized the change trends of structural and functional characteristics during ecosystem development, including community energetics, community structure, life history, nutrient cycling, selection pressure, and homeostasis. Through comparisons of the ecosystem development period and mature period, it was found that the ecosystem succession process tends to become more complex in structure, with increased species diversity, better functions and greater stability. A number of studies on the succession process of terrestrial ecosystems have confirmed the above conclusions. For example, in an investigation of the secondary succession of subtropical forests in China, it was found that the vegetation richness in the middle and late successional stages was significantly higher than that in the early successional stage, and bacterial community diversity showed an upwards trend from early to mid-late succession (Shang et al., 2021). The prokaryotic and fungal community compositions in the soil changed greatly in the early stage but tended to be consistent in the later stage (Liu et al., 2021). The vegetation characteristics of different successional stages on the Loess Plateau are consistent with farmland, grassland, shrub forest, pioneer forest and climax communities. While soil enzyme activity increased with the secondary succession process, soil organic carbon, soil total nitrogen, water-organic carbon, and soil available and nitrate concentrations also showed an upwards trend (Wu et al., 2020). In addition, the succession process of terrestrial ecosystems was accompanied by a transition from r-strategists to K-strategists (Zhou et al., 2017), and the degree of group differentiation also increased with the succession process (Hahn et al., 2016).

Compared with land, the ocean has remained chemically and biologically stable for a long time, but with the continuous development of ports, ship transportation, resource extraction and artificial habitat deployment, an increasing number of

artificial structures have created new usable space for marine organisms, and the biological community inhabiting their surface appears to have experienced ecological succession (Vicente et al., 2021). The sessile, attached or free-living organisms that inhabit the surface of objects in the marine environment are called marine attached organisms (Lin et al., 2020). Research from the perspective of marine economic development regards attached organisms as fouling organisms, focuses on the mechanism of biological pollution, and aims to derive effective strategies for preventing and controlling biological pollution on specific surfaces in the marine environment (Iljin et al., 2013; Yen et al., 2013; Tao et al., 2021). However, from the perspective of ecological research, marine attached organisms are an important part of the marine ecosystem. The attached community not only provides a food source for organisms at high trophic levels (Lin et al., 2018) but also increases microspatial complexity (Jaubet et al., 2013; Lavender et al., 2017), providing shelter and breeding sites for a variety of swimming organisms (Machado et al., 2019) and allowing them to colonize and grow (Antoniadou et al., 2010; Birdsey et al., 2012). Studies on the succession trend of attached communities in specific sea areas usually use hanging boards of different materials as biological attachment bases, such as PVC boards (Lezzi et al., 2018; Vicente et al., 2021), ceramic boards (Uribe et al., 2015), acrylic boards (Abed et al., 2019), and silicate concrete boards (Zhan et al., 2021). For artificial structures actually deployed in seawater, visual and photographic methods are usually used to identify, record and analyse the attached organisms (Fariñas-Franco and Roberts, 2014; Higgins et al., 2019; Toledo et al., 2020). Parameters such as dominant species, biomass, coverage rate and traditional taxonomic diversity indexes (Shannon index, richness index, evenness index, etc.) are commonly used as indicators to measure differences in the attached community between different successional stages. Vicente et al. (2021) found that structures formed by sessile organisms tended to become more complex with succession, leading to increases in abundance and biomass and changes in the composition of associated free-living communities. Abed et al. (2019) investigated the attached community on acrylic boards in the coastal waters of the

Sultanate of Oman in the early stage of succession and found that the total biomass, coverage rate and bacterial counts of large attached organisms increased significantly over time. Bacterial communities underwent successional shifts in their structure, with Alphaproteobacteria and Flavobacteriia as pioneer primary colonizers and Actinobacteria and Planctomycetia as secondary colonizers. Fariñas-Franco and Roberts (2014) studied the attached community on artificial reefs (ARs) and found that the Shannon index, richness index and evenness index all increased with increasing time since construction. The limited ecological significance of the above indicators prevents full analysis of the ecological succession process. Existing studies focus only on the structure and composition of biological communities and ignore ecological functions, interspecific relationships, and stability in different successional stages.

ARs are artificial habitats that have been scientifically selected and placed on the seabed. They simulate rock or natural coral reefs by adding complex topography to flat and featureless ocean bottoms to optimize the ecological environment and protect and increase marine fishery resources. The attached community inhabiting the surface of ARs directly affects the ecological effect of the AR area (Zhou et al., 2010). In this study, we took ARs in Bailong Pearl Bay, Fangchenggang City, Guangxi Zhuang Autonomous Region, China, as an example. Based on traditional biological indicators, we applied the functional diversity index, niche overlap index, niche breadth index and biomarkers to analyse the change trends of richness, habitat resource supply, resource utilization degree and efficiency, and interspecific relationships during the succession process of the attached community to provide basic scientific data and a theoretical reference for research on the structure and function of artificial habitat ecosystems.

2 Materials and methods

2.1 Sampling and environmental measurements

Based on the lateral scan results of the reef space completed in November 2019 and December 2020, two investigation areas were set up in Bailong Pearl Bay, Fangchenggang City, Guangxi Zhuang Autonomous Region (O, constructed in 2016; N, constructed in 2020). Three sampling sites were randomly selected in each of the two investigation areas in March and April 2021. The locations of the sampling sites and the reef type (3.6 m×3.6 m×5.5 m) are shown in Figure 1 and Figure 2. Locally employed divers collected the attached organisms on the upper (0.5 m from the top of the ARs, O-ARU and N-ARU), middle (halfway point of the ARs, O-ARM and N-ARM) and lower (0.5 m from the bottom of the ARs, O-ARB and N-ARB) parts of

each reef. The sampling area of a single quadrat was 25 cm×25 cm. The obtained samples were kept in sealed bags and brought back to the laboratory on the same day for species identification, individual counting and weighing.

Water environmental data such as seawater temperature (T), salinity (Sal), pH and dissolved oxygen (DO) were measured on-site using a YSI water quality instrument (YSI, USA). For each AR, 1000 ml adjacent seawater was collected for measurement of water quality parameters, including active phosphate ($P - PO_4^{3-}$), nitrite ($N - NO_2^-$), nitrate ($N - NO_3^-$), ammonium ($N - NH_4^+$), total nitrogen (TN) and total phosphorus (TP).

2.2 Biological trait selection and assignment

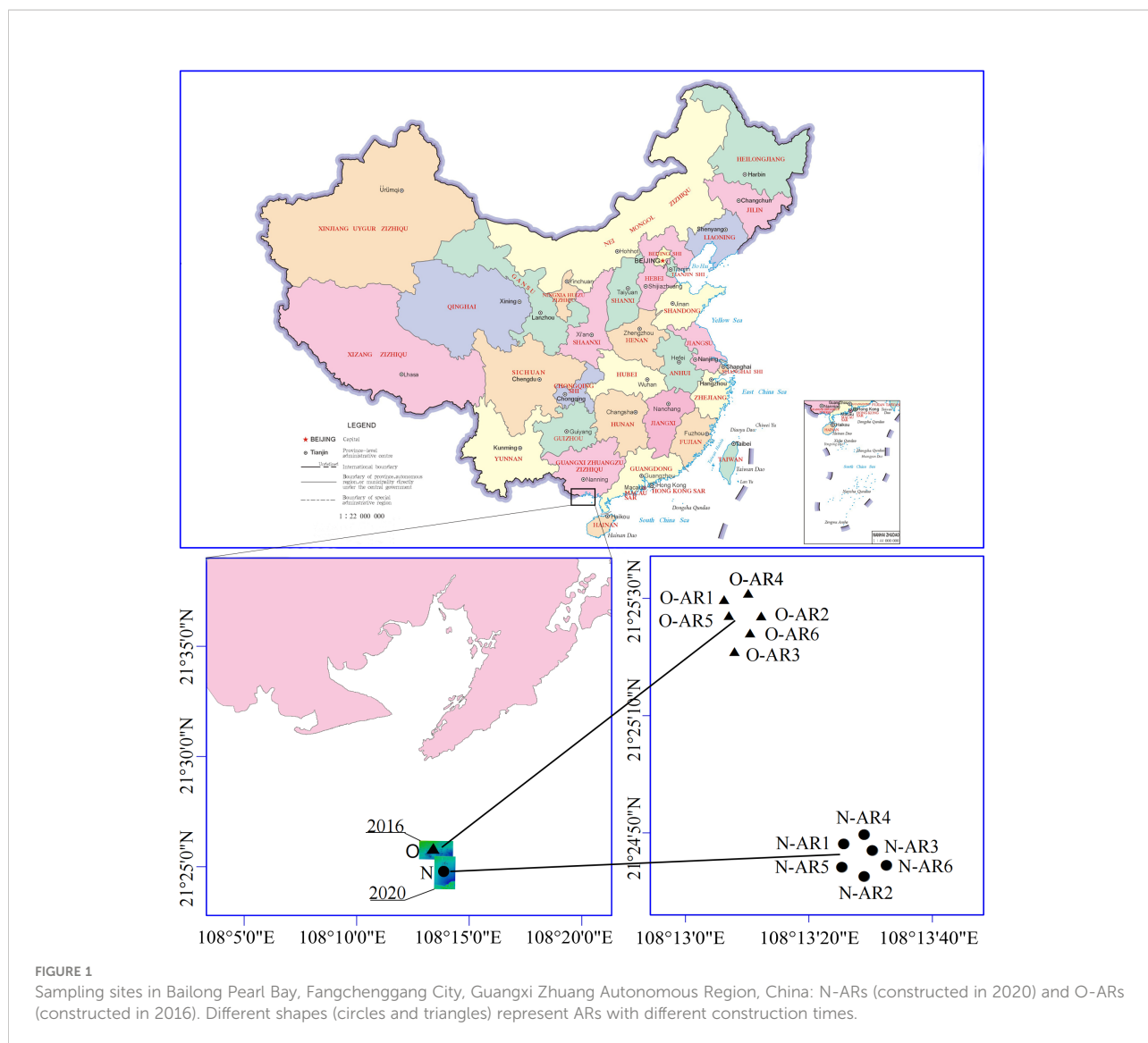
Five biological traits (divided into 18 types) were used to describe the functional properties of the attached community on the outer surface of ARs. The selected traits are known to influence ecosystem functioning, including morphology (physical flexibility), life history (life span), and behaviour (mobility, activity and feeding). The biological traits used in this study and their links to ecosystem function are listed in Table 1 (Li, 2019). Based on relevant books (Zhang and Qi, 1961; Xu et al., 2008), references (Li, 2019) and online database (WoRMS), the morphology of each species in the species × characteristic data matrix was assigned. When information on some functional characteristics of a species was lacking, a reference was made to the functional characteristic values at the genus or family level.

In this study, to avoid bias between different traits, the affinity score for each trait was normalized so that the sum equalled 1 (Linden et al., 2012). For a species with only one form of a biological characteristic, a value of 0 or 1 was assigned. For example, *Centroceras clavulatum* is a primary producer in terms of feeding habit, and it was assigned a value of 1 in the FH6 column, while the other columns were assigned a value of 0. For species with multiple morphologies for a biological trait, fuzzy coding was used to assign values (Chevenet et al., 1994). For example, *Portunus pubescens* is both a carnivore and a scavenger, so the values in the FH2 and FH4 columns were 0.5 and 0.5, respectively.

2.3 Indicator selection and statistical analysis

2.3.1 Community composition

In order to comprehensively reflect the differences in community composition between samples, we performed hierarchical clustering based on the Bray-Curtis dissimilarity to obtain a clustering tree of species composition, and then

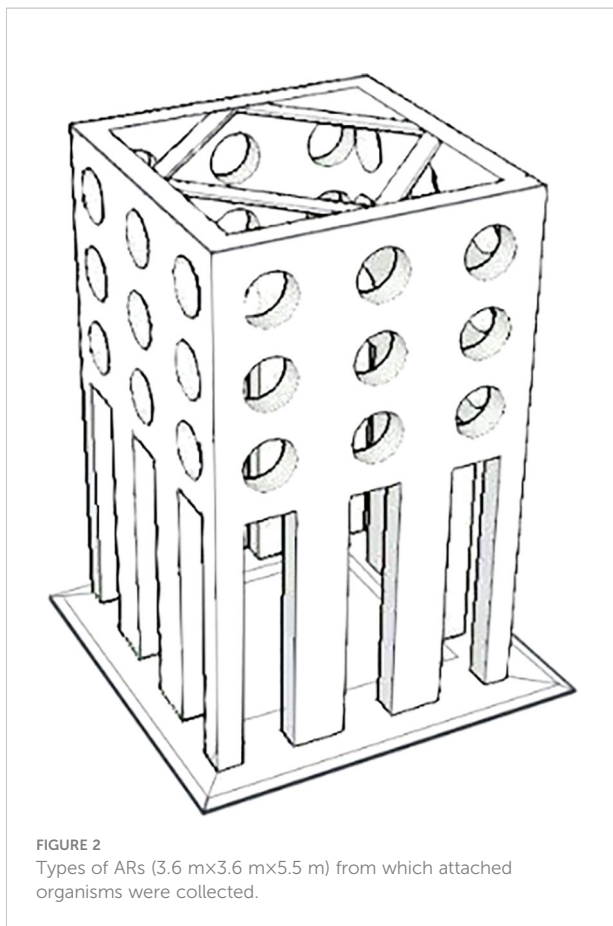


combined it with the relative abundance stacked column chart (at the phylum level). Two-way ANOVA was performed on the number of individuals of attached phyla at each sampling location on the ARs with different construction times. To explore the relationship between phylum abundance and multiple influencing factors (construction time, depth, T, Sal, DO, pH, NO_2^- , NO_3^- , NH_4^+ , PO_4^{3-} , TN and TP), we also performed redundancy analysis (RDA) based on Bray-Curtis dissimilarity. The *P*-values (Table S1) were obtained using the anova function of the vegan R package.

To assess possible differences among attached communities and test for significance, we ran the multivariate analysis of variance with 999 permutations (PERMANOVA) using the adonis function of the vegan R package based on Bray-Curtis dissimilarity.

2.3.2 α -Diversity

We used the α -diversity to analyse and compare the degree of species diversity within the attached communities. The α -diversity indexes of attached organisms on different parts of the ARs were calculated according to species abundance using the vegan R package, including the species richness index (*S*), Shannon index (*H'*), Simpson index (*D*), evenness index (*J*), Chao1 index and abundance-based coverage estimator (ACE). The calculation formula of each index is different, and it can provide different information, all of which have advantages. The species richness index is the sum of the number of species with abundance greater than 0 in the community. Shannon's index reflects the uncertainty of which species we can predict randomly selected individuals in the community. The Simpson index represents the probability that two randomly selected



individuals in a community belong to the same species. The Chao1 index is sensitive to rare species, and the ACE index can avoid low abundance species being ignored.

Boxplots of α -diversity indexes were drawn using the ggplot2 R package. The data in each group were tested for normality and homogeneity of variances, multiple comparisons (Tukey's honest significance difference (HSD) test) were performed, and the differences between groups were marked with different lowercase letters in the boxplot.

2.3.3 Functional diversity

Ecosystem function depends not only on the number of species but also on the functional characteristics that species possess (Diaz and Cabido, 2001; Coleman and Williams, 2002). Biodiversity depends on the difference in functional characteristics between species (characteristics closely related to ecosystem function) within the community; that is, functional diversity has a substantial impact on ecosystem function. Therefore, functional diversity is a key factor linking biodiversity and ecosystem functions, which can more clearly reflect the degree of resource complementarity among the species in a community (Jiang and Zhang, 2010). Similar to α -diversity, functional diversity is roughly divided into three categories: richness, evenness, and variation. These indexes not

only reflect different aspects of functions but also directly quantify functions. The functional richness index reflects the utilization degree of ecological space, and the functional evenness index is used to describe the utilization degree and efficiency of the effective resources of the community. The niche differentiation and resource competition degree of organisms in the community are characterized by the functional divergence index (Shuai et al., 2017), and the ecological significance of Rao's quadratic entropy index is between those of functional richness and the functional divergence index (Chen, 2017).

In order to deeply analyse the differences between the attached communities in terms of their ecological niche and resource utilization, we calculated various functional diversity indexes. Based on the assigned traits and species abundance, the FD R package was used to calculate the functional diversity of attached organisms on different parts of the ARs, including the number of single-function species (sing.sp), the functional richness index (*FRic*), the functional evenness index (*FEve*), the functional divergence index (*FDiv*), the functional dispersion index (*FDis*) and Rao's quadratic entropy index (*RaoQ*). The functional redundancy index was the ratio of *FDiv* to *H'* (*FD/H'*). Boxplots of functional diversity indexes were drawn using the ggplot2 R package. The data in each group were tested for normality and homogeneity of variances, multiple comparisons (Tukey's honestly significant difference (HSD) test) were performed, and the differences between groups were marked with different lowercase letters in the boxplot.

2.3.4 Niche characteristics and environmental factors

The ecological niche includes not only the physical space occupied by an organism but also its functional role in the community and its location along the environmental gradients of temperature, humidity, pH, soil and other living conditions. The most frequently quantified dimensions are niche breadth and niche overlap. Niche overlap occurs when two species (or other biological units) use the same resources or resemble each other in terms of other environmental factors (food, space, etc.). Niche breadth refers to the sum of the various resources utilized by a population (or other biological unit) in a community.

To further explain the differences in interspecific relationships between the attached communities of N-ARs and O-ARs, we calculated Levin's niche overlap index between pairs of species using the Spaa R package and visualized the relationships of species pairs using network graphs (only the relationship pairs with a niche overlap index greater than 0.5 are presented). Each serial number in network graphs represents a species (Table S2 and Table S3), and the type of line connecting the two serial numbers (reflected in the legend) represents the range of the niche overlap index. Levin's niche breadth index was also calculated with the permutation method of the EcoUtils R package for 1000 random rearrangements of the occurrence frequency of species, and the null distribution of the niche

TABLE 1 The biological characteristics and morphology of attached organisms.

Biological traits	Trait categories	Labels	Ecological function
Morphology			
Physical flexibility	High (>45)	FL1	This trait reflects the ability of organisms to respond to environmental changes.
	Low (10-45)	FL2	
	None (<10)	FL3	
Life history			
Life span	Short (≤ 2)	A1	This trait reveals the organism's ability to recover from disturbance.
	Medium (2-5)	A2	
	Long (>5)	A3	
Behaviour			
Mobility	Sessile	LS1	This trait can determine an organism's place in the community.
	Attached	LS2	
	Free	LS3	
Activity	None	MO1	This trait reflects the ability of organisms to seek advantages and avoid disadvantages in the environment.
	Semiactive	MO2	
	Active	MO3	
Feeding	Filter-feeder	FH1	This trait is a core factor affecting the community structure of attached organisms, and all feeding types contribute to production, nutrient support and nutrient cycling.
	Carnivore/omnivore	FH2	
	Herbivore	FH3	
	Scavenger	FH4	
	Deposit-feeder	FH5	
	Primary producer	FH6	

breadth index for these species was calculated. Generalist species have a broader fundamental niche than specialist species (Wilson and Hayek, 2015). Species whose actual niche breadth index exceeds the upper limit of the 95% confidence interval of the null distribution are defined as generalist species, those with an index below the lower limit of the 95% confidence interval are defined as specialist species, and those with an index falling within the 95% confidence interval are defined as neutral taxa (Wu et al., 2017).

To assess the potential impact of environmental factors on attached organisms, the psych, reshape2 and ggplot2 R packages were used to calculate the Spearman correlation coefficients for each environmental factor and the abundance of each species and to visualize the correlation coefficient matrix as a heatmap.

2.3.5 Biomarkers and dominant species

Linear discriminant analysis (LDA) effect size (LEfSe) (Segata et al., 2011) can identify biomarkers with significant differences between different groups. LEfSe emphasizes statistical significance, biological consistency, and effect relevance. It first robustly identifies taxa that are significantly different among groups. Then, it investigates biological consistency using a set of pairwise tests among subgroups. Finally, it uses LDA to estimate the effect size of each selected taxon. To explore possible differences between biomarkers on the ARs with different

construction times, we performed LEfSe analysis of attached organisms at each sampling location on the ARs using the online tool LEfSe (<https://www.bioincloud.tech>). The threshold of the *P*-value in the Kruskal-Wallis test among groups was 0.05. Only those taxa with a log LDA score >2 (more than four orders of magnitude) were considered in this study.

In order to compare the changes of dominant species in the attached communities on the ARs with different construction times, we used Excel 2016 to calculate the dominance (*Y*) of each species. It was stipulated that when $Y \geq 0.02$, the species is the dominant species.

2.3.6 Software and calculation formulas

Data analysis and graphical visualization, except for abundance, dominance and LEfSe, were performed in R software (v3.6.2). The Shannon index (*H'*) (Shannon, 1948), Simpson index (*D*) (Simpson, 1949), Chao1 index (Chao, 1984), richness index (*S*), evenness index (*J*) (Shannon, 1948), ACE (Chao and Yang, 1993), functional richness index (*FRic*) (Mason et al., 2005; Shuai et al., 2017), functional evenness index (*FEve*) (Mason et al., 2005), functional divergence index (*FDiv*) (Mason et al., 2005), Rao's quadratic entropy index (RaoQ) (Rao, 1982), niche breadth index (*B_i*) (Levins, 1968), niche overlap index (*O_{ik}*) (Levins, 1968) and dominance (*Y*) are calculated as follows:

$$H' = -\sum_{i=1}^S P_i \log_x P_i$$

$$D = 1 - \sum_{i=1}^S P_i^2$$

$$\text{Chao1} = S + \frac{F_1^2}{2F_2}$$

$$S = n$$

$$J = \frac{H'}{\log_2 S}$$

$$\text{ACE} = S_{abund} + \frac{S_{rare}}{C_{ace}} + \frac{F_1}{C_{ace}} \gamma_{ace}^2$$

$$\gamma_{ace}^2 = \max \left[\frac{S_{rare}}{C_{ace}} \frac{\sum_{i=1}^{10} i(i-1)F_i}{N_{rare}(N_{rare}-1)} - 1, 0 \right]$$

$$N_{rare} = \sum_{i=1}^{10} iF_i$$

$$C_{ace} = 1 - \frac{F_1}{N_{rare}}$$

In the above formulas, n is the total number of species with a number of individuals (abundance) greater than 0. Usually, $n = 10$ is used as the abundance threshold for distinguishing abundant and rare species. S_{abund} is the number of abundant species (abundance greater than 10). S_{rare} is the number of rare species (abundance less than or equal to 10). F_1 is the number of species represented by only 1 individual. γ_{ace}^2 is the estimated coefficient of variation of rare species. F_i is the number of species represented by i individuals.

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

$$FEve = \sum \min \left(P_i, \frac{1}{S} \right)$$

$$FDiv = \frac{2}{\pi \arctan \left[5 \times \sum_{i=1}^S \frac{1}{(ln C_i - ln x)^2 \times A_i} \right]}$$

$$\text{RaoQ} = \sum_{i=1}^{S-1} \sum_{j=(i-1)}^{S-1} d_{ij} p_i p_j$$

In the above formula, SF_{ic} refers to the niche occupied by species in the community; R_c is the absolute value of the characteristic; S is the number of species; P_i is the relative abundance of species i ; C_i is the value of the i -th functional characteristic; A_i is the abundance ratio of the i -th functional

feature; $\ln x$ is the natural logarithm of the species characteristic value; p_i and p_j are the relative abundances of species i and j , respectively; and d_{ij} is the dissimilarity of species i and j .

$$B_i = \frac{1}{\sum_{j=1}^r (P_{ij})^2}$$

$$O_{ik} = \frac{\sum_{j=1}^r (P_{ij} P_{kj})}{\sum_{j=1}^r (P_{ij})^2}$$

In the above formula, B_i is the niche breadth of species i ; P_{ij} is the proportion of species i at a given site j ; P_{kj} is the proportion of species k at a given site j ; r is the number of sites; and O_{ik} represents the overlap index between the resource utilization curve of species i and the resource utilization curve of species k .

$$Y = \frac{n_i}{N} \times f_i$$

In the formula, n_i is the number of individuals of the i -th species. N is the total number of individuals. f_i is the occurrence frequency of the i -th species.

3 Results

3.1 Community composition

In this study, 59 species of 8 phyla of attached organisms were identified, including Mollusca, Arthropoda, Echinodermata, Chordata, Cnidaria, Porifera, Bryozoa and Rhodophyta, among which Mollusca was represented by the most species (36), accounting for approximately 61.02% of the total species. The order of species numbers from high to low was Mollusca > Arthropoda > Echinoderm > Porifera = Chordata > Cnidaria = Bryozoa = Rhodophyta.

The composition of the attached community was significantly different between the N-ARs and O-ARs, and the numbers of phyla and species of attached organisms at each sampling location on the O-ARs were greater than those on the N-ARs. As shown in Figure 3, hierarchical clustering based on the Bray-Curtis dissimilarity divided the samples into two categories. The first category included O-ARU, O-ARM and N-ARB, and the second category included N-ARU, N-ARM and O-ARB. The phyla with the highest relative abundance differed between the two categories of samples. The dominant phylum of each sample in the first category was Arthropoda or Chordata, and the dominant phylum of each sample in the second category was Mollusca.

As shown in Table 2, it had a very significant impact on Mollusca ($P < 0.01$) and a significant effect on Arthropoda when the AR part was used as the source of variation ($P < 0.05$). When construction time was used as the source of variation, it had significant effects on Mollusca, Porifera, Bryozoa and

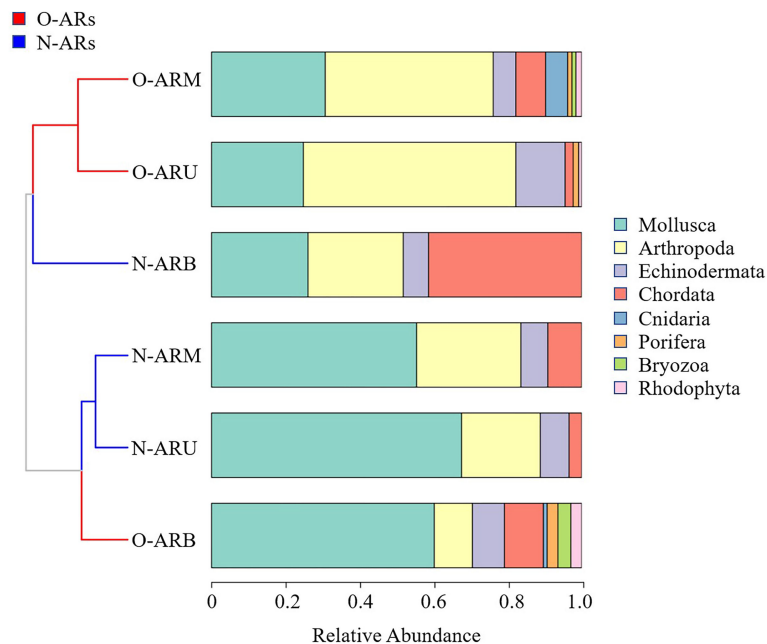


FIGURE 3

Analysis of the composition of attached organisms at each sampling location on the ARs with different construction times. The two colours of the cluster tree branches indicate that hierarchical clustering based on the Bray-Curtis dissimilarity divides the samples into two categories. Different colours in the histogram represent different phylum. The area size of the colour represents the relative abundance of its corresponding phylum.

Rhodophyta ($P < 0.05$) and a very significant effect on Arthropoda ($P < 0.01$). The interaction of the two sources of variation had a very significant effect on Mollusca ($P < 0.01$). The extremely significant correlation between construction time and depth and the difference in abundance of various phyla were also reflected in the redundancy analysis (Figure 4, $P = 0.0035$). In addition to the above two variables, the difference was also related to depth, NO_3^- and NH_4^+ ($P < 0.05$).

3.2 Community structure

The results in Table 3 revealed that different parts of the ARs with the same construction time showed significant differences in the attached communities structure between O-ARU and O-ARB and between N-ARU and N-ARB ($P < 0.05$). In the comparison of the same parts with different construction

times, the attached communities at the upper, middle and lower parts all changed due to construction time. There was an extremely significant difference between N-ARs and O-ARs in the upper and middle parts ($P < 0.01$) and a significant difference in the lower part ($P < 0.05$). In addition, a large difference was also revealed by the pairwise comparison of different parts of N-ARs and O-ARs. Except in the O-ARM and N-ARB comparison and O-ARU and N-ARB comparison, the pairs showed extremely significant differences ($P < 0.01$).

3.3 α -Diversity

The α -diversity of the attached communities showed significant differences among ARs with different construction times ($P < 0.05$), and the indexes of the O-ARs were generally larger than those of the N-ARs (Figure 5). When comparing the

TABLE 2 Two-way ANOVA for the number of individuals of attached phyla at each sampling location.

Source of variation	Mollusca	Arthropoda	Echinodermata	Chordata	Cnidaria	Porifera	Bryozoa	Rhodophyta
ARU-ARM-ARB	0.0021	0.0210	0.5312	0.1177	0.1512	0.8933	0.1453	0.7896
O-N	0.0143	0.0097	0.9062	0.1946	0.0846	0.0103	0.0110	0.0208
ARU-ARM-ARB and O-N	0.0045	0.0906	0.6981	0.3845	0.1512	0.8930	0.1453	0.7896

Bold P -values indicate significant effects ($P < 0.05$).

same parts, the richness, Shannon, Chao1 and ACE values of O-ARB were significantly higher than those of N-ARB ($P < 0.01$), and the Chao1 and ACE values of O-ARM were significantly higher than those of N-ARM ($P < 0.05$). There were no significant differences in the Simpson and Pielou indexes between N-ARs and O-ARs ($P > 0.05$). In addition, there were no significant differences in α -diversity between the upper, middle and lower parts of N-ARs and O-ARs in the comparison of different parts of the ARs with the same construction time ($P > 0.05$). From the upper to the lower part, the richness, Chao1 and ACE values first increased and then decreased on O-ARs but decreased on N-ARs. The Shannon, Simpson and Pielou indexes showed an increasing trend on O-ARs but first increased and then decreased on N-ARs.

3.4 Functional diversity

The functional diversity indexes of attached organisms showed significant differences between the middle and lower parts of the N-ARs and O-ARs (Figure 6, $P < 0.05$). The number of single-function species and functional evenness index of O-ARB were significantly higher than those of N-ARB ($P < 0.01$), and the functional richness, functional divergence and Rao's quadratic entropy index of O-ARB were significantly higher than those of N-ARB ($P < 0.05$). The functional richness index of O-ARM was significantly higher than that of N-ARM ($P < 0.05$). There were no significant differences in the functional dispersion

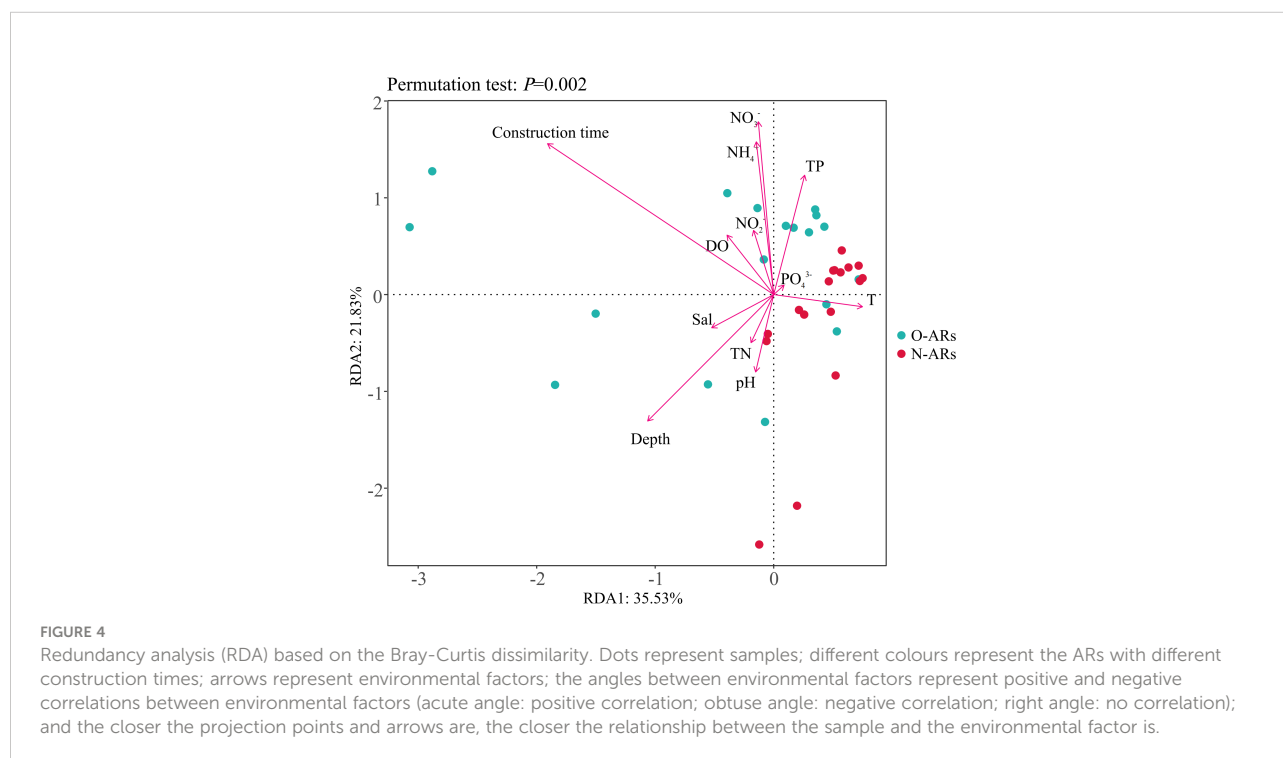
TABLE 3 PERMANOVA test for differences in sampling location and construction time.

Combination	R^2	P -value
O-ARU/O-ARM	0.0772	0.5754
O-ARM/O-ARB	0.1208	0.1968
O-ARU/O-ARB	0.2077	0.0260
N-ARU/N-ARM	0.1839	0.0679
N-ARM/N-ARB	0.1811	0.1409
N-ARU/N-ARB	0.3037	0.0320
O-ARU/N-ARU	0.3416	0.0070
O-ARM/N-ARM	0.2474	0.0050
O-ARB/N-ARB	0.2959	0.0140
O-ARU/N-ARM	0.3282	0.0060
O-ARU/N-ARB	0.2789	0.0270
O-ARM/N-ARU	0.2814	0.0090
O-ARM/N-ARB	0.1665	0.1109
O-ARB/N-ARU	0.4084	0.0020
O-ARB/N-ARM	0.3888	0.0030

Bold P -values indicate significant differences ($P < 0.05$).

index between the same sampling parts of the ARs with different construction times ($P > 0.05$). Except for the functional redundancy index, the functional diversity indexes of the attached community on the O-ARs were generally greater than those on the N-ARs.

In the comparison of different parts of the ARs, there were no significant differences in the functional diversity indexes



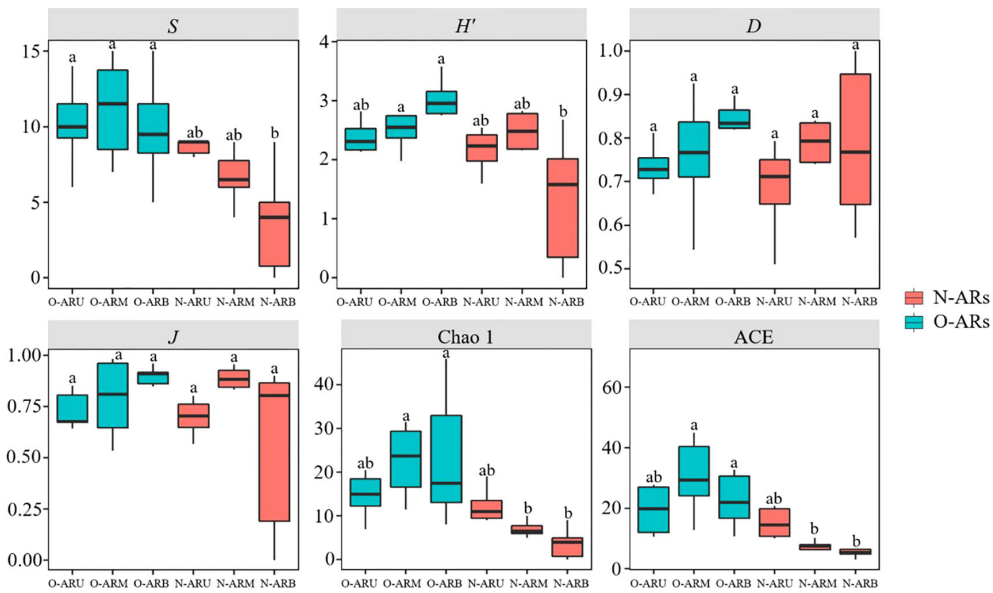


FIGURE 5
 α -Diversity analysis of attached communities at each sampling location on the ARs with different construction times: species richness index (*S*), Shannon index (*H'*), Simpson index (*D*), evenness index (*J*), Chao1 index and abundance-based coverage estimator (*ACE*). Different letters (a,b) above the bars indicate significant differences between sampling locations.

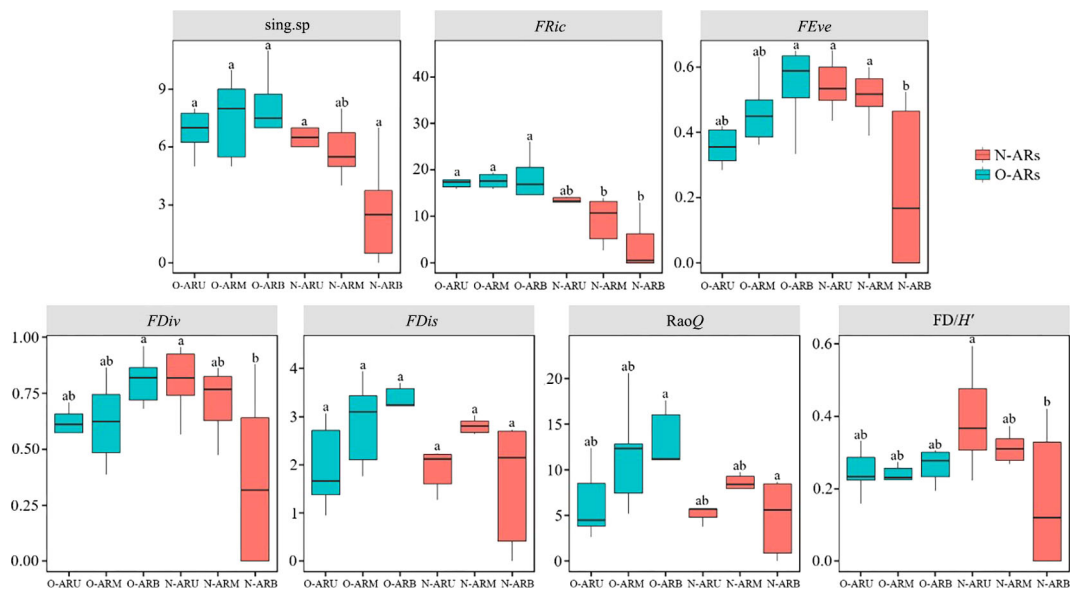


FIGURE 6
 Functional diversity analysis of attached communities at each sampling location on the ARs with different construction times: the number of single-function species (*sing.sp*), the functional richness index (*FRic*), the functional evenness index (*FEve*), the functional divergence index (*FDiv*), the functional dispersion index (*FDis*), Rao's quadratic entropy index (*RaoQ*) and the functional redundancy index (*FD/H'*). Different letters (a,b) above the bars indicate significant differences between sampling locations.

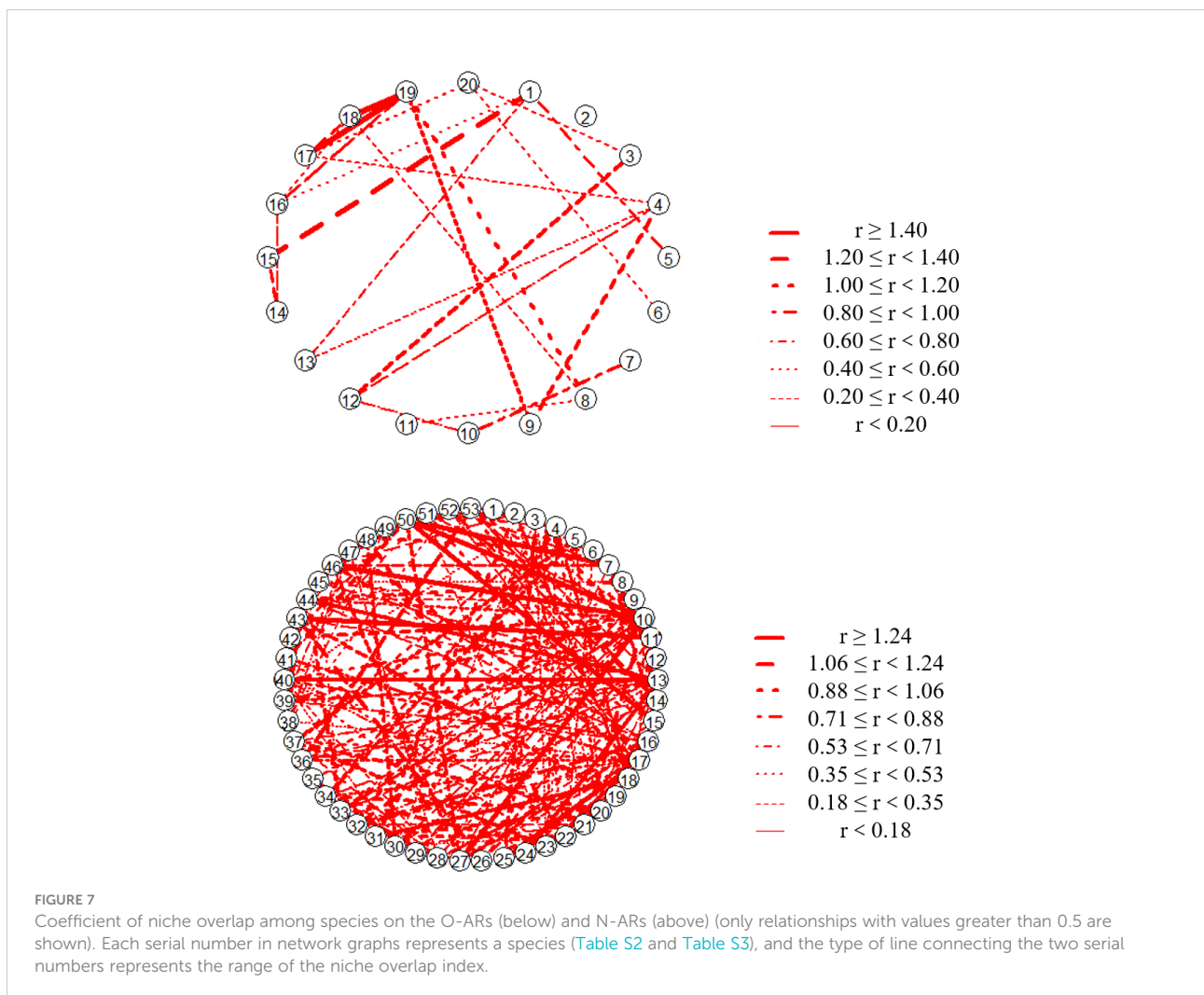
between the upper, middle and lower parts of the O-ARs ($P>0.05$), but there were differences among the parts of the N-ARs. The number of single-function species, functional divergence index and functional redundancy index of N-ARU were significantly greater than those of N-ARB ($P<0.05$), and the functional evenness index was extremely significantly greater than that of N-ARB ($P<0.01$). The functional evenness index of N-ARM was greater than that of N-ARB ($P<0.05$).

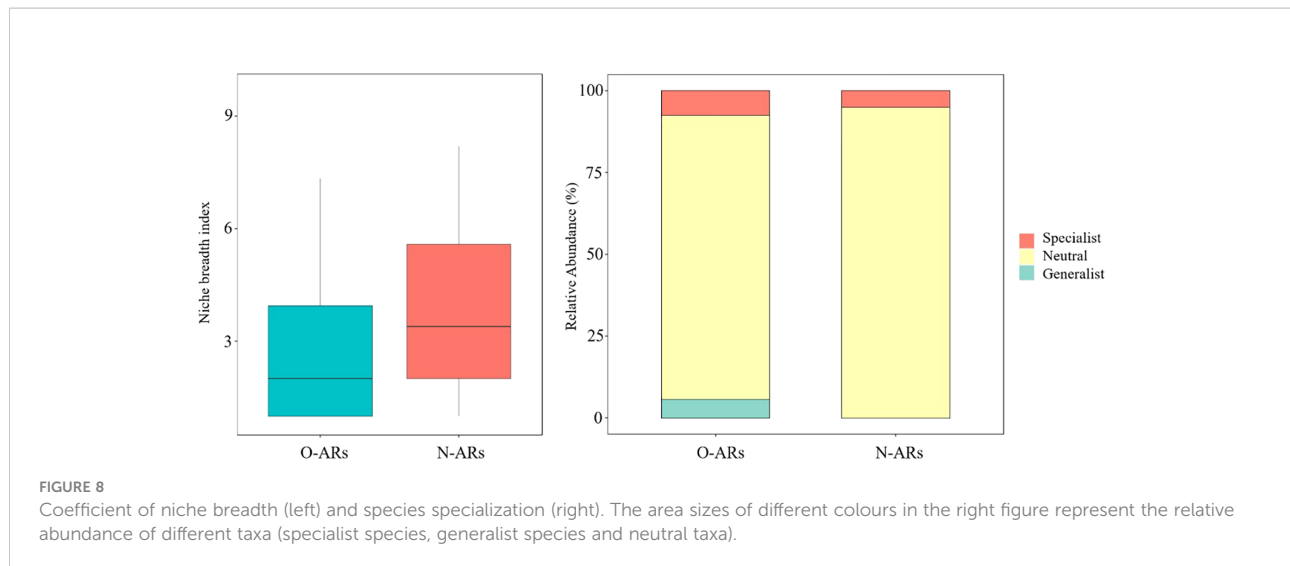
From the upper to lower parts, the functional diversity of N-ARs showed a decreasing trend, except for the functional dispersion index, which first increased and then decreased. Moreover, all the values were the smallest for N-ARB. The number of single-function species, functional evenness, functional divergence, functional dispersion and Rao's quadratic entropy of O-ARs all showed upwards trends. The functional redundancy index showed a trend of first decreasing and then increasing. All the values were the highest for O-ARB. The functional richness index showed a trend of increasing first

and then decreasing, with the weakest trend observed for O-ARB.

3.5 Niche overlap index and niche breadth

The results (Figure 7) indicated that the frequency of relationship pairs with a niche overlap coefficient of attached organisms greater than 0.5 on the O-ARs (11.39%) was greater than that on the N-ARs (11.05%). The overall niche breadth index of the O-ARs was smaller than that of the N-ARs (Figure 8). The average niche breadth of the community on the O-ARs was 2.92, compared to 4.10 on the N-ARs. Specialist species were found on the ARs with different construction times, and generalist species were also found on the O-ARs. On the O-ARs, the percentage of generalist species was 5.66%, the percentage of specialist species (7.55%) was slightly higher





than that on the N-ARs (5.00%), and the percentage of neutral taxa (86.79%) was lower than that on the N-ARs (95%).

3.6 Environmental drivers

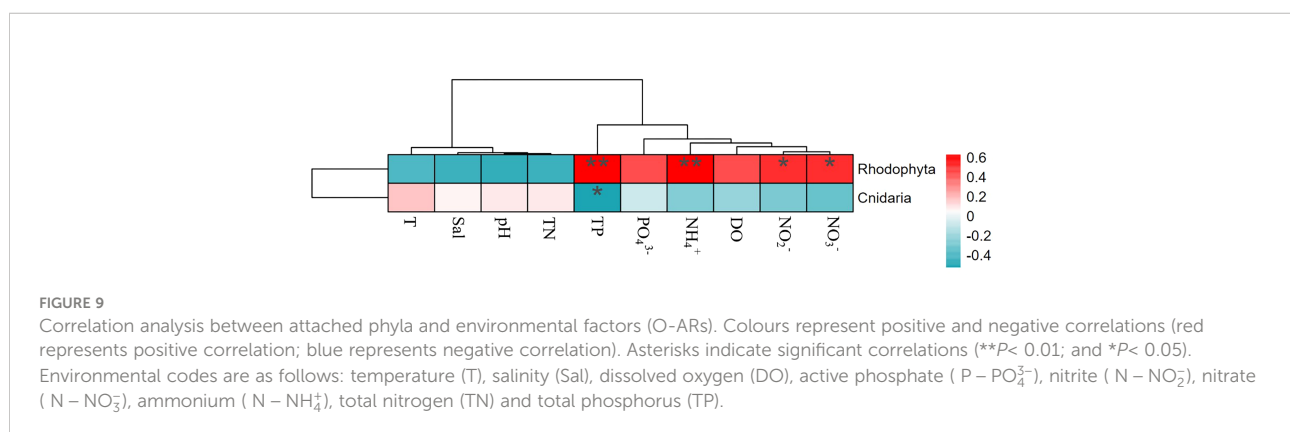
The heatmaps (Figure 9 and Figure 10) and *P*-values (Table S4 and Table S5) showing the correlations between environmental factors and phylum abundances indicated that the phyla affected by environmental factors were different between N-ARs and O-ARs. The environmental factors significantly correlated with phyla were different, and the degree of correlation varied widely. On the outer surface of O-ARs, TP had a very significant positive correlation with Rhodophyta ($P < 0.01$) and a significant negative correlation with Cnidaria ($P < 0.05$). NH_4^+ had a very significant positive correlation with Rhodophyta ($P < 0.01$), and NO_2^- and NO_3^- had a significant positive correlation with Rhodophyta ($P < 0.05$). On the outer surface of the N-ARs, all environmental factors except

DO were correlated with either Arthropoda or Chordata. Sal, pH, TN, NH_4^+ , PO_4^{3-} , T and NO_3^- were significantly correlated with Arthropoda and Chordata to varying degrees, and Chordata was also significantly negatively correlated with NO_2^- and TP ($P < 0.05$).

3.7 Biomarkers and dominant species

At the genus level, there was only one biomarker on the O-ARs (*Parahyotissa*), while there were five biomarkers on the N-ARs (*Scapharca*, *Saccostrea*, *Perna*, *Hyotissa* and *Lasaea*) (Figure 11). Thus, construction time plays an important role in the distribution pattern of attached organisms.

The dominant species of attached organisms on the N-ARs were *Balanus amphitrite*, *Anadara indica*, *Perna viridis*, *Saccostrea glomerata*, *Hyotissa hyotis*, *Herdmania momus*, *Styela plicata* and *Ophiactis savignyi*, which represent four phyla (Table 4). *Saccostrea glomerata* on the upper part of the



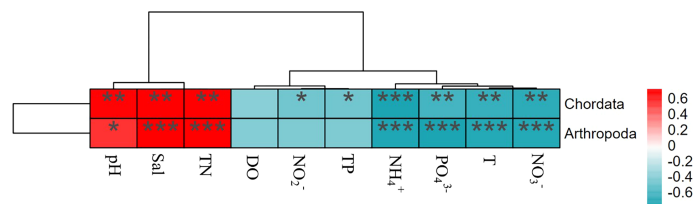


FIGURE 10

Correlation analysis between attached organisms and environmental factors (N-ARs). Colours represent positive and negative correlations (red represents positive correlation; blue represents negative correlation). Asterisks indicate significant correlations (*** $P < 0.001$; ** $P < 0.01$; and * $P < 0.05$). Environmental codes are as follows: temperature (T), salinity (Sal), dissolved oxygen (DO), active phosphate (P – PO_4^{3-}), nitrite (N – NO_2^-), nitrate (N – NO_3^-), ammonium (N – NH_4^+), total nitrogen (TN) and total phosphorus (TP).

N-ARs had the highest dominance among the dominant species. *Balanus amphitrite* in the middle of the N-ARs and *Herdmania momus* and *Balanus amphitrite* in the lower part of the N-ARs had higher dominance than other taxa. *Balanus amphitrite*, *Balanus amaryllis* and *Chama asperella* were dominant species on all parts of the surface of the O-ARs. The dominant species of organisms attached to the lower part of the O-ARs were relatively rich, including *Balanus amphitrite*, *Balanus amaryllis*, *Chama asperella*, *Scapharca kagoshimensis*, *Thais echinata*, *Herdmania momus*, *Styela plicata* and *Colochirus quadrangularis*. Compared with those on the lower part of the O-ARs, the dominant species on the upper and middle parts were more similar, including only species belonging to the *Balanus* and *Chama asperella*. The species belonging to the *Balanus* were absolutely dominant. Overall, the dominant species on the N-ARs were more abundant than those on the O-ARs. *Balanus amphitrite* was the dominant species at each sampling location.

4 Discussion

4.1 The close link between the α -diversity and functional diversity of attached organisms on ARs

Biodiversity is often used to evaluate the status and change trend of various communities in an ecosystem. However, species vary greatly in their physiological, ecological and morphological characteristics, and it is difficult for simple biodiversity indicators to truly reflect the important role of species characteristics in ecosystem processes. In a study of benthic invertebrates in the southern North Sea and the eastern English Channel, [Bremner et al. \(2003\)](#) compared the results of relative taxon composition analysis, trophic group analysis, and biological trait analysis. By comparing the amounts of variation explained by the axes in PCA, it was found that there may be trends in the ecological functions of the entire

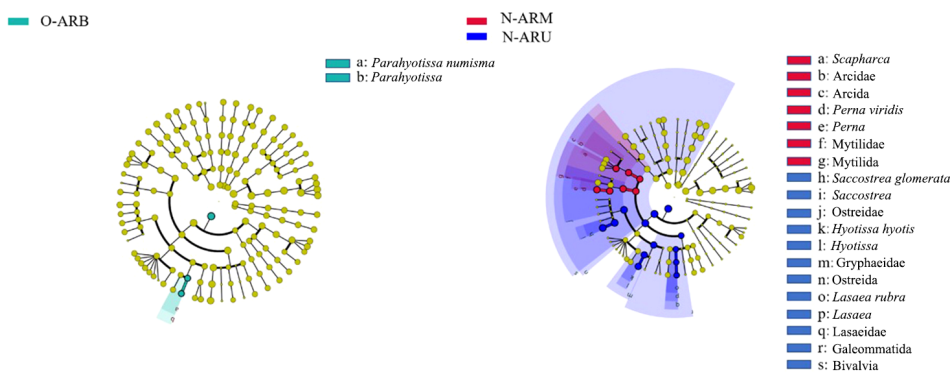


FIGURE 11

LEFSe results for the attached communities on the O-ARs and N-ARs. Nodes from inside to outside represent phylum, class, order, family, genus, and species. Biomarkers are represented by different colours, and yellow nodes represent taxa that do not play a significant role at each sampling location. The name of the taxa represented by the letters is shown in the legend on the right.

TABLE 4 Dominance of attached dominant species at each sampling location.

Dominant species	N-ARU	N-ARM	N-ARB	O-ARU	O-ARM	O-ARB
<i>Balanus amphitrite</i>	0.1994	0.2696	0.1324	0.2864	0.2007	0.0240
<i>Balanus amaryllis</i>	–	–	–	0.2068	0.1070	0.0267
<i>Balanus reticulatus</i>	–	–	–	0.0255	–	–
<i>Balanus trigonus</i>	–	–	–	–	0.0206	–
<i>Chama asperella</i>	–	–	–	0.0366	0.0557	0.2133
<i>Scapharca kagoshimensis</i>	–	–	–	–	–	0.0280
<i>Anadara indica</i>	–	0.0294	–	–	–	–
<i>Saccostrea glomerata</i>	0.4241	0.1797	0.0523	–	–	–
<i>Hyotissa hyotis</i>	0.1108	–	–	–	–	–
<i>Perna viridis</i>	–	0.1961	0.0261	–	–	–
<i>Thais echinata</i>	–	–	–	–	–	0.0360
<i>Herdmania momus</i>	–	–	0.1373	–	–	0.0373
<i>Styela plicata</i>	–	0.0425	0.0915	–	–	0.0280
<i>Ophiactis savignyi</i>	0.0475	–	0.0229	–	–	–
<i>Colochirus quadrangularis</i>	–	–	–	–	–	0.0200

benthic community that cannot be revealed by using only the relative taxon composition method. Analysis based on biological traits emphasizes small-scale heterogeneity, which can provide more ecological function information, reveal different relationships between combinations, and have the potential to describe the functional diversity of marine systems. In freshwater ecosystems, studies have also used functional characteristics to reflect the level of biome response to disturbance (Townsend and Hildrew, 1994; Charvet et al., 2000). Our study combined traditional α -diversity and functional diversity and found that the ecological implications of the two complemented each other when explaining the impact of construction time on the attached community.

α -Diversity showed significant differences between N-ARs and O-ARs ($P < 0.05$). The α -diversity indexes of attached organisms on the O-ARs were larger than those of attached organisms on the N-ARs, indicating that species richness (especially in the middle and lower parts) increased with increasing time since construction. The Shannon index and evenness index are two indicators used to characterize community stability. In general, the higher the Shannon index and evenness index of a community are, the more stable and mature the ecosystem to which the community belongs (Li et al., 2017). Although the above two indexes of the O-ARs were generally larger than those of the N-ARs, there was no significant difference between the same parts ($P > 0.05$). This showed that the stability and maturity of the two communities under different construction times differed only slightly. In this paper, functional diversity was used to deeply analyse the differences between the communities attached to N-ARs and O-ARs in terms of their ecological niche and resource utilization. The functional diversity showed significant differences between the middle and lower parts of the N-ARs and O-ARs ($P < 0.05$).

The parts with differences in each index were consistent with those identified using α -diversity and were most commonly the lower part. Except for the functional redundancy index, the functional diversity indexes of the attached community on the O-ARs were larger than those on the N-ARs. Based on the ecological significance of functional diversity, even though the stability and maturity were similar to those on the N-ARs, the communities attached to the O-ARs had a higher degree of utilization of ecological space, more comprehensive and efficient utilization of effective resources, a stronger degree of complementarity of organismal niches, and weaker interspecific competition. In addition, the ratio of functional diversity to the Shannon index was used as the functional redundancy index in this study. As the index decreases, the number of species exhibiting the same trait increases. The functional redundancy index of the attached community on the N-ARs was larger than that of the attached community on the O-ARs, indicating that species richness and functional diversity increased together with a gradual increase in the time since construction. While the number of species increased, those species exhibited different functional characteristics, and the number of species with identical traits decreased.

4.2 The supply of available resources is more abundant in the later successional stage of the attached community on ARs

Usually, the ecological niches of two species only partially overlap; that is, some resources are used jointly, while other parts are used independently. Although competition due to overlapping niches is often referred to as competition for resources, in reality, overlapping niches do not necessarily lead

to competition unless the supply of shared resources is insufficient. In this study, the species in the attached communities under different construction times were paired, and the niche overlap indexes of all pairs were calculated. The ratio of the number of pairs with a niche overlap index greater than 0.5 on the O-ARs was greater than that on the N-ARs. Combined with the conclusions represented by functional diversity, these findings suggested that ARs with longer times since construction had more available resources to support the survival and development of attached organisms, such that even though there was a high degree of niche overlap, interspecific competition was still weak. Li et al. (2013) pointed out that attached organisms can change the surface structure of the attachment base, increase the degree of spatial heterogeneity, and expand the surface area of the attachment base. Li et al. (1991) found that with increasing time since construction, multiple smaller individuals on the proliferation reefs often attached to larger oysters. This phenomenon reflected the species' full use of the expanded physical space.

In the case of fewer available resources, the niche breadth is generally increased to allow the population to obtain sufficient resources. In an environment with abundant available resources, selective utilization of resources and narrowing of the niche breadth occur. The average niche breadth index of the attached community on the O-ARs was smaller than that of the community on the N-ARs, indicating that the community selectively used the N-ARs in the face of a living environment with a sufficient supply of effective resources. There was a causal relationship between the niche overlap index and the conclusion inferred on the basis of the breadth index. Generalist species have a wide ecological niche and strong competitiveness. Specialist species have a narrow niche and are at a disadvantage in resource competition (Zhang, 2004). Specialist species were found on ARs with different construction times, and generalist species were also found on O-ARs. The proportion of specialist species on O-ARs was slightly higher than that on N-ARs. At the level of shared species, *Chama asperella* and *Herdmania momus* changed from neutral to generalist, and *Scapharca kagoshimensis* changed from specialist to neutral. The results showed that during ecological succession, some species tended to show strong competitiveness, and the ecological niches of these species were broadened without declines or replacement due to increasingly fierce competition for resources.

4.3 The community attached to ARs is more susceptible to external environmental factors in the early stage of succession

The structural composition of the marine attached community will be affected by factors such as temperature, pH, depth, salinity,

construction time, and attachment base materials (Huang et al., 2006; Nair, 2011; Li et al., 2017; Guo et al., 2020). In this study, the α -diversity indexes, the number of individuals and the number of phyla all increased with increasing construction time. This result was highly consistent with studies in other sea areas. For example, in a study of the sea area of Xuejia Island, Qingdao city, Shandong Province, it was found that with increasing time since construction, the average biomass and the number of species on ARs of five different cement types increased, and the dominant species also changed (Li et al., 2017). A survey by Dashentang in Tianjin showed that the impact of time series on the attached organisms of ARs was obvious in the early stage of construction. Although the impact was significantly weakened in the later stage, the biodiversity still gradually increased (Guo et al., 2020). In the early stage of the developmental process, the phyla affected by environmental factors accounted for a larger proportion of all phyla, were influenced by more environmental factors, and showed very significant correlations with those factors. This result indicated that ARs were more susceptible to external environmental factors during development and had a weaker ability to resist external disturbances and maintain their structures and functions.

4.4 The organisms attached to various parts of ARs tend to be similar

Depth is an important variable in determining patterns of marine community structure (Nair, 2011; Wu et al., 2017). We applied the LEfSe technique to compare and analyse different parts of ARs with different construction times and found that there were more biomarkers with significant differences in abundance between parts on N-ARs than on O-ARs. At the family level, O-ARs and N-ARs were consistent across Gryphaeidae. At the same time, there were similarities in the succession process of attached organisms on ARs. The dominant species on the upper and middle parts of the N-ARs were diverse. In the same parts of the O-ARs, only one species (*Chama asperella*) belonged to Mollusca, and the other four belonged to Balanidae (Arthropoda). The above results not only explained the fact that Arthropoda accounted for the largest proportion of the relative abundance of various phyla on O-ARs but also explained that during the long-term development of the system and the process of community succession, the species belonging to Balanidae were always members of the stable community on the ARs. Species belonging to Balanidae, often referred to as fouling organisms, are found in most disturbed waters, including Muara Port in Brunei, Songkhla Port in Thailand, and Balaclava Bay (Black Sea) (Shalaeva and Lisitskaya, 2004; Jolkifli and Wahab, 2018; Phuttapreecha et al., 2018). Barnacles are usually the predominant fouling group; they are small and settle in proportion to time (Su et al., 2008; Jolkifli and Wahab, 2018). In an investigation of Balaclava Bay, it was found that the relative abundance of *Balanus improvisus* was always high and that the species was mainly distributed on the artificial matrix in the innermost part of the bay (Shalaeva and Lisitskaya, 2004). The above

results are consistent with the change trend of barnacles in this study due to the time of construction. Studies on the impact of some fouling organisms on aquaculture species have shown that fouling organisms have little effect on the nutrient utilization of bivalves and can even cause an increase in some nutrients, thereby stimulating an increase in phytoplankton in the surrounding waters. Fouling organisms can provide a more abundant food source for bivalves that are also filter feeders (Leblanc et al., 2003). Based on this conclusion, it was likely that the positive effects of barnacles had created living conditions that can maintain the coexistence of various species, such that the number of attached organisms had not decreased due to competition for available space by barnacles.

5 Conclusions

Traditional taxonomic diversity was combined with functional diversity in this study, revealing that the species richness of the attached community increased along with functional diversity as the time since construction increased. While the number of species increased, the attached organisms showed different functional characteristics, and the number of species with identical traits decreased. The attached community in the later stage of development had a higher degree of utilization of ecological space, more comprehensive and efficient utilization of effective resources, a stronger degree of complementarity of organismal niches, and weaker interspecific competition. In the early stage of the developmental process, the attached community was affected by more environmental factors and very significantly correlated with them and had a weaker ability to resist external disturbances and maintain its structure and functions. The combination of the niche overlap index and the niche breadth index indicated that the resource supply supporting the survival and development of the attached organisms on the ARs with a long time since construction may be more abundant, and the organisms may selectively use it. The decrease in the number of biomarkers, the similarity of biomarkers belonging to the same family, and the similarity of dominance alternation all indicated that during the process of long-term development and community succession, the organisms attached to the various parts of ARs tended to become similar. The species belonging to Balanidae were always members of the stable community on the ARs. It was likely that the positive effects of barnacles had created living conditions that can maintain the coexistence of attached organisms.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

CQ conceived of the study and participated in its design. RL and YG drafted the manuscript and performed the field experiments. SZ provided scientific advice. HZ and AZ sorted the data. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.950151/full#supplementary-material>

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