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Research article

Taxonomic and functional diversities reveal different fish assemblage dynamics of stow net fishery in Haizhou Bay

Guangjie Fang[a,b,c,d], Yazhou Zhang[a,b,c,d], Haolin Yu[e], Chuanxi Chen[f], Jun Liang[a,b,c,d,*], Yanli Tang[g,**]

[a] Zhejiang Marine Fisheries Research Institute, Zhoushan, 316201, China
[b] Key Laboratory of Sustainable Utilization of Technology Research for Fishery Resources of Zhejiang Province, Zhoushan, 316021, China
[c] Scientific Observing and Experimental Station of Fishery Resources for Key Fishing Grounds, Ministry of Agriculture and Rural Affairs of the People's Republic of China, Zhoushan, 316021, China
[d] Marine and Fisheries Institute, Zhejiang Ocean University, Zhoushan, 316022, China
[e] Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China
[f] College of Ocean and Earth Sciences, Xiamen University, Xiamen, 361005, China
[g] Fisheries College, Ocean University of China, Qingdao, 266003, China

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ABSTRACT

Biodiversity is the cornerstone of marine fisheries. To ensure the prosperity of stow net fishery in Haizhou Bay, regular investigations of fishery resources are essential. However, most studies have primarily focused on taxonomic diversity while overlooking functional diversity. In this study, we examined both the taxonomic and functional diversity of fish assemblages based on abundance and functional traits from 2013 to 2018. Significant differences in taxonomic diversity were observed only between two seasons, whereas functional diversity showed significant differences across years, seasons and groups. Diversity indices exhibited negative linear relationships with catch per unit effort, except for functional evenness (*FEve*) and functional divergence. Twenty-seven out of 30 correlations between the two types of diversity indices were predominantly positive and synclastic, whether linear or nonlinear. Functional dispersion showed the most positive relationships with taxonomic diversities, while *FEve* exhibited gentle slopes. The functional redundancy curves indicated that the ecological stability and resilience of fish assemblages were vulnerable. The non-target fish group demonstrated a higher overlap in functions compared to the target fish group and the total fish group. In summary, the taxonomic and functional diversities revealed inconsistent statuses and trends of fish assemblages, with an evident decreasing trend in the non-target fish group requiring special attention. This study highlights that both taxonomic and functional diversity should be considered simultaneously in fish biodiversity investigations, which is crucial for establishing effective fish conservation systems.

1. Introduction

Biodiversity is essential for maintaining ecosystem functions, providing ecosystem services, ensuring biogeochemical cycles, and

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[*] Corresponding author. No. 28, Tiyu Road, Dinghai County, Zhoushan City, Zhejiang Province, China.
[**] Corresponding author.
E-mail addresses: jliang@zjou.edu.cn (J. Liang), tangyanli@ouc.edu.cn (Y. Tang).

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promoting human well-being and development [1,2]. However, global marine biodiversity has faced unprecedented challenges in recent decades, particularly in marine fisheries [3]. In 2020, China's marine fishing yield was 11.77 million tons, accounting for 14.9 % of the world's total production [4]. Fish constituted over 60 % of all catches. Faced with the immense demand for marine aquatic products, China's marine fisheries are under tremendous pressure of decline [5]. To address the challenges faced by the fisheries sector, the Chinese government has implemented multiple effective policies and regulations, such as summer fishing moratoriums and marine protected areas [6]. Accordingly, monitoring the dynamics of fish assemblages is crucial for the effective implementation of these policies.

Marine biodiversity is a prerequisite for the ocean's ability to provide abundant high-quality food for humanity [7]. In 2020, the global marine fish yield was 66,734 kilotons, representing approximately 84.7 % of the world's fisheries production [4]. Beyond their high catches, marine fish significantly impact ecosystem and biodiversity of the ecosystems [8]. Marine fish exhibit extremely high diversity in morphology, physiology, and behavior, influencing the entire aquatic ecosystem through nutrient cycling, predation, and interconnected effects within the food web, including on benthic organisms, plankton, and water quality [9]. Therefore, studying the biodiversity of marine fish assemblages is crucial for monitoring marine fisheries and providing policy optimization suggestions for fisheries management.

Currently, the loss of marine biodiversity in coastal areas is a pressing issue, especially concerning fish assemblages [2,10]. Marine fishing activities lead to the overexploitation of stocks, habitat degradation and the destruction of food webs, which have had and will continue to have significant impacts on biodiversity [6,11]. With the continuous increase in fishing pressure, both the size and economic value of target species are showing downward trends. Additionally, by-catch and abandoned, lost or otherwise discarded fishing gear (ALDFG) seriously threaten marine biodiversity, including fish, turtles and marine mammals [12–14]. Consequently, there are complex relationships between marine biodiversity and fishing, and balancing biodiversity protection with maintaining fishery yields is challenging.

Biodiversity generally encompasses three levels: taxonomic, functional, and phylogenetic diversity [15]. Ecologists historically focused on taxonomic diversity while often neglecting functional and phylogenetic diversity [7]. As a complement to taxonomic diversity, functional diversity has received increasing attention over the past decade. With the continuous deepening of research on functional diversity, its application has expanded to areas such as community aggregation mechanisms, biological strategies under environmental stress, interspecific competition, and biodiversity conservation [16]. Although significant progress has been made in understanding the functional diversity of fish assemblages, the internal responses of fish functional traits to fisheries are still unclear [17,18]. As more fish with varied functional traits are being targeted in global fisheries, the importance of functional diversity in marine biodiversity and ecosystem management under fishing pressure has become increasingly evident [19]. The relationships between fish functional diversity and marine fisheries sometimes have produced inconsistent and confusing results. Factors such as overfishing, climate change, marine areas, fish species, functional groups, and management policies can all influence outcomes [20–23]. Despite the lack of clear research conclusions and consensus, the compounded effects of fishing pressure on functional diversity are widely recognized. More systematic research is needed to evaluate marine fish functional diversities and its influencing factors across different temporal and spatial scales. Higher biodiversity in a community does not always equate to higher ecosystem stability [24,25]. In the face of environmental disturbances, communities with higher functional diversity are expected to have higher tolerance thresholds and greater resilience [26]. A regression curve of functional diversity and species richness, combined with a null model is applied to analyze whether there is functional redundancy in fish assemblages [27]. Three relationships between functional diversity and species richness are typically observed: saturating relationships, indicate functionally redundant communities; linear relationships, suggest equal contributions to functions by species; and other patterns, such as sigmoid curves [28]. For individual taxa, potential functional rarity is critical for maintaining ecosystem stability and ensuring ecosystem processes [29]. Functional rarity at the local scale is measured by functional distinctiveness and taxon scarcity [30]. The lower the distinctiveness and higher the scarcity of a species, the rarer it is in the community, and the greater its contribution to community functional redundancy [31].

Haizhou Bay is famous in China for its curved coastline and abundant fishing grounds. As one of China's eight major fishing grounds, it has long been renowned for its fishery resources, such as small yellow croaker (*Larimichthys polyactis*), large head hairtail (*Trichiurus lepturus*), swimming crab (*Portunus trituberculatus*), and Chinese shrimp (*Fenneropenaeus chinensis*) [32]. Participating in artisanal fisheries is an important source of income for coastal low-income residents. To date, stow net fisheries are the most representative operation method among local small-scale fisheries in Haizhou Bay, holding significant socio-economic importance. To promote the high-quality and sustainable development of fisheries in Haizhou Bay, China has adopted multiple management measures and monitoring methods, including summer fishing moratoriums, minimum mesh sizes, and artificial reefs [33]. In the present study, we estimated the dynamics of fish assemblages of stow net fishery of Haizhou Bay from 2013 to 2018. Our objectives were: (1) clarify the taxonomic and functional diversity of fish assemblages and their temporal trends; (2) reveal the potential relationships among taxonomic and functional diversity indices; and (3) assess the functional redundancy of fish assemblages and the contribution of individual species.

In summary, this study offers alternative viewpoints for analysing the conditions in the fish resources of stow net fishery of Haizhou Bay and helps to better understand the intrinsic mechanisms of changing fish assemblages, which are crucial for subsequent fishery management decisions. Given the rapidly changing and complex marine biodiversity conditions, regulatory measures must combine the species compositions with functional traits to achieve their goals successfully. Ideal implications for conservation and fishery resource management in China, based on the taxonomic and functional diversity, are promising.

2. Material and methods

2.1. Study area and data collection

Haizhou Bay is located in the southern Yellow Sea, China, with a total area of 7900 square nautical miles (Fig. 1). It is one of China's eight major fishing grounds and has long been renowned for high-value marine products. The temperature of the fishing ground is moderate, with an annual average surface water temperature of 14.4–15.7 °C. More than ten rivers flow into the sea along the coast, providing the bay with rich nutrients. Ideal natural conditions have nurtured abundant marine organisms, supporting the long-term development of small-scale fisheries, particularly the stow net fishery.

Stow net fishery is a typical artisanal fishery operated by several fishermen and is widely distributed along the coast of Haizhou Bay. The seabed of the fishing area is muddy, with of about 20 m. A small boat equipped with ten to twenty double-staked vertical bar stow nets is a typical production pattern in this fishery (Fig. 1). Stow nets are fixed on the seabed at all times and catch fish relying on currents. Fishermen go to the fishing areas daily to collect their catch from the cod-ends of stow nets. We conducted fishery surveys at three stations in the spring and autumn from 2013 to 2018. The three sampling stow net stations were deployed in the traditional fishing region with similar operating conditions, namely Daquangou (A), Lanshan (B), and Zhewang (C). The principal dimensions of the stow nets differed slightly between stations: the net mouth circumference and net length for stations A, B, and C were 46 m × 38 m, 47 m × 38 m, and 56 m × 39 m, respectively. Sampling surveys were conducted four times in the spring (March to April) and autumn (October to November), with each survey interval lasting about half a month. Ten kilograms of catches were randomly sampled at each station, and all samples preserved on ice, were taken to the laboratory. All fish individuals were sorted, identified, enumerated, and their biological characteristics (weight and total length), were measured to analyze the weight compositions of fish assemblages. Meanwhile, fishing logs were recorded by fishermen, including fishing dates, the number of nets, and daily catch weights. These two data sets were collected to compute catch per unit effort (CPUE).

2.2. Data analysis

2.2.1. Taxonomic diversity analysis

All fish were identified to the species level, and categorized into three groups: target fish group, non-target fish group, and total fish group. Target fish are defined as those with economic value collected by fishermen from their catches, and subsequently sold in the market. Non-target fish include all other fish. The daily catch of total fish was used to calculate the standardized catch per unit effort (CPUE), measured in kg/(net × day). The computational formula is as follows:

$$CPUE = \frac{W \times S}{n \times A} \tag{1}$$

In this formula, W is the daily catch weight (kg), S is the standard net mouth area (100 m^2), n is the daily number of stow nets, and A is the actual net mouth area (m^2).

Five taxonomic diversity indices (TD) were selected to analyze the inherent patterns of fish assemblages: fish number (N), Shannon-Weiner diversity (H'), Pielou's evenness (J'), Margalef diversity (D) and Simpson diversity (S). Shannon-Weiner diversity index (H') is the most widely used diversity index based on the number of fish and proportion of different species [34]. Pielou's evenness index (J') measures the degree of evenness in the distribution of individuals among species within a community [35]. Margelef diversity (D) emphasizes species richness [36]. The Simpson diversity index reflects the dominance of dominant species [37].

2.2.2. Functional traits

Functional traits of the fish were collected through literature reviews and professional databases (e.g., Fishbase). A total of 22 functional traits, classified into seven groups, were selected to characterize the roles of fish (Table S1). The seven functional trait

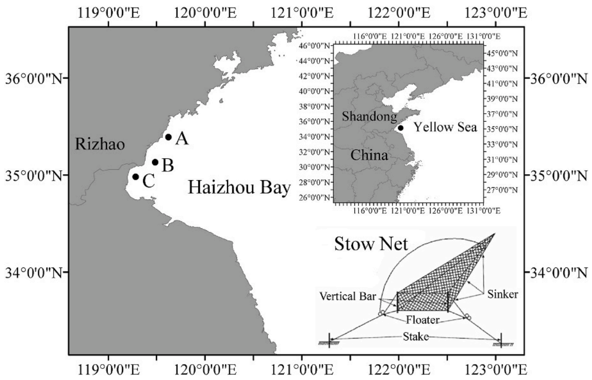

Fig. 1. Map of the study area with three stations and the sketch of the stow net. Three stations: A: Daquangou, B: Lanshan, C: Zhewang.

groups included food acquisition, locomotion, defense, ecological adaptation, reproduction, life history and population dynamics. The 22 traits comprised four numeric variables, five ordered variables and thirteen factors. According to the classification of functional traits, our study selected a combination of two response traits and sixteen effect traits, with four traits considered ambiguous [9,38,39]. These traits contain sufficient information to form a relatively comprehensive picture of functional diversity and are commonly adopted [40,41]. Additionally, one trait (maximum total length) was obtained by measuring fishery samples.

2.2.3. *Functional diversity analysis*

Six multidimensional functional diversity (FD) indices were quantified to analyze the functional characteristics of fish assemblages. To compute FD indices, the fish trait matrices were calculated using Gower dissimilarity. Principal coordinates analysis (PCoA) was then applied to obtain PCoA axes, which were used to study FD indices [42–45]. The functional richness index (*FRic*) measures the extent to which fish occupy ecological niche space within a community, without considering fish abundance [46,47]. The functional evenness index (*FEve*) measures the distribution pattern of fish traits in the trait space they occupy [47]. The functional divergence index (*FDiv*) represents the variability of trait values among fish [47]. The functional dispersion index (*FDis*) reveals the functional similarity among core fish [48]. Rao's quadratic entropy index (*RaoQ*) integrates information on both species richness and functional trait differences among species [49]. The functional redundancy index (*FRed*) indicates the abundance of fish with similar functional traits [50,51].

2.2.4. *Model and statistical analysis*

TD and FD indices were calculated using the "*vegan*" and "*FD*" packages in R 4.2.3 (www.r-project.org). Differences in TD and FD indices among years, seasons, and stations were tested using permutation-based analysis of variance (PERMANOVA) and multi-response permutation procedures (MRPP). To explore the relationships between TD and FD indices, we fitted curves using the generalized additive model. Pearson correlation analysis with multiple tests of "*fdr*" and heatmap were used to test the correlations among indices using the "*psych*" package. We also examined the relationships between TD, FD indices, and CPUE through ordinary least squares regression, to analyze the variations between biodiversity (TD and FD indices) and biomass (CPUE).

Second, we analyzed the functional redundancy of fish assemblages by computing functional redundancy index (*FRed*) and plotting functional redundancy curves [45]. The functional redundancy curve showed the relationships between *FDis* and species richness, revealing the real conditions of functional redundancy in fish assemblages. Assemblages above the curves were less redundant than

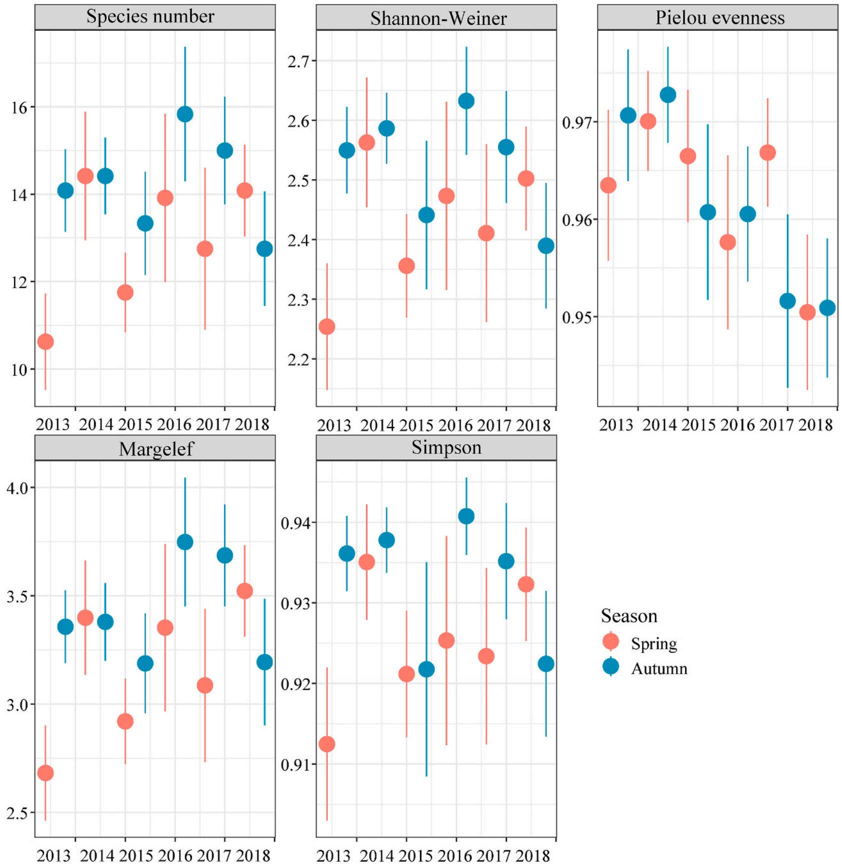

Fig. 2. Taxonomic diversity indices of fish of stow net fishery in Haizhou Bay from 2013 to 2018.

expected, while those below the curves were more redundant than expected. *FRed* revealed the number of species with the same functional traits in an assemblage, representing the degree of ecological niche overlap. Differences in *FRed* among fish groups, and stations were compared using the Wilcoxon rank sum test, Kruskal-Wallis rank sum test, and PERMANOVA.

Third, we calculated functional rarity using the "*funrar*" packages. The taxonomic and functional rarity of species were evaluated using taxon scarcity (*Scar*) and functional distinctiveness (*Dist*) to explain functional redundancy at the species level [30,31]. The higher the *Scar* value of a fish, the rarer the fish is. The lower the *Dist* value, the more it contributes to the functional redundancy of the community.

Finally, the Mann-Kendall trend test was applied to examine temporal trends in the TD and FD indices from 2013 to 2018 using the "*trend*" package. All analyses were performed in R. Figures were primarily created using the "*ggplot2*" package in R. The sampling map was produced using ArcGis 10.7 (www.arcgis.com).

3. Results

3.1. Taxonomic diversity of fish assemblages

A total of 70 fish species were collected, belonging to 12 orders, 36 families, and 55 genera (Table S2). Perciformes were the most abundant order, accounting for 48.6 % of all fish. The taxonomic diversity of fish assemblages showed significant temporal differences, but no spatial variation was observed among the three stations. Four taxonomic diversity indices in autumn were significantly higher than those in spring, except for J' (Fig. 2, Table 1). However, evident interannual changes were only detected in J'. For the target fish group and the non-target fish group, two diametrically opposite results were obtained. For the target fish group, four and two diversity indices showed interannual and seasonal differences, respectively; but for the non-target fish group, these differences were only observed in J'. For all five indices, no changes were observed among years or stations, just seasonal changes were found in the total fish group and the target fish group (Table 2). Temporal trends of TD indices for the three fish groups were consistent from 2013 to 2018, with significant decreasing trends observed for J' (Table 3).

3.2. Functional diversity of fish assemblages

Six functional diversity indices showed varied temporal and spatial changes, except for *FEve* (Fig. 3, Table 1). *RaoQ* and *FRed* had significant differences among years, seasons, and stations; *FDis* exhibited seasonal and station variations; *FRic* and *FDiv* only showed seasonal changes. For the target fish group, four functional diversity indices, including *FRic*, showed interannual differences; for the non-target fish group, five functional diversity indices showed significant interannual variability, and *FDiv* had seasonal variation. For all six indices, significant changes were observed among the six years, two seasons and three stations of the total fish group, while only seasonal and interannual differences were found for the target fish group and the non-target fish group, respectively (Table 2). No obvious temporal trends of functional diversity indices were detected for the total fish group and the target fish group; however, all

Table 1
Results of permutational multivariate analysis of variance (PERMANOVA) with three factors for taxonomic and functional diversity indices. *N*: fish number, H': Shannon-Weiner diversity, J': Pielou evenness, *D*: Margelef diversity, *S*: Simpson diversity. *FRic*: functional richness index, *FEve*: functional evenness index, *FDiv*: functional divergence index, *FDis*: functional dispersion index, *RaoQ*: Rao's quadratic entropy index, *FRed*: functional redundancy index.

Taxonomic diversity indices		*N*		H'		J'		*D*		*S*	
		F	P	F	P	F	P	F	P	F	P
Fish	Year	0.11	0.846	0.06	0.850	**13.51**	**0.001**	1.20	0.264	0.01	0.949
	Season	**12.76**	**0.002**	**10.57**	**0.002**	1.88	0.185	**12.80**	**0.001**	**8.52**	**0.002**
	Station	0.68	0.542	0.74	0.488	0.68	0.523	0.55	0.587	0.82	0.470
Target fish	Year	**4.12**	**0.037**	**5.30**	**0.027**	3.15	0.069	**3.79**	**0.032**	**4.92**	**0.001**
	Season	**8.06**	**0.003**	**8.66**	**0.007**	0.03	0.856	1.43	0.223	1.94	0.098
	Station	2.17	0.104	2.23	0.097	0.24	0.801	0.83	0.444	1.37	0.157
Non-target fish	Year	0.32	0.621	0.05	0.854	11.92	0.001	1.75	0.199	0.06	0.821
	Season	0.68	0.435	0.21	0.693	5.04	0.025	1.79	0.180	0.40	0.548
	Station	1.41	0.250	1.81	0.158	0.50	0.601	1.27	0.280	1.82	0.145

Functional diversity indices		*FRic*		*FEve*		*FDiv*		*FDis*		*RaoQ*		*FRed*	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	Year	2.58	0.068	0.88	0.399	0.11	0.787	2.72	0.060	**2.78**	**0.050**	**2.95**	**0.048**
	Season	**7.35**	**0.001**	0.25	0.661	**21.74**	**0.001**	**5.71**	**0.001**	**8.26**	**0.002**	**7.84**	**0.001**
	Station	1.40	0.224	1.58	0.193	1.09	0.331	**2.41**	**0.044**	**3.29**	**0.015**	**3.42**	**0.009**
Target fish	Year	**7.35**	**0.002**	1.66	0.182	–	–	**5.37**	**0.013**	**6.01**	**0.006**	**4.19**	**0.030**
	Season	1.07	0.328	1.22	0.285	–	–	0.20	0.790	1.84	0.187	1.17	0.266
	Station	1.19	0.306	0.36	0.798	–	–	2.61	0.070	2.01	0.112	1.77	0.140
Non-target fish	Year	1.36	0.231	**5.09**	**0.017**	**4.89**	**0.034**	**3.48**	**0.017**	**6.94**	**0.001**	**7.19**	**0.001**
	Season	0.33	0.740	0.27	0.660	**5.07**	**0.027**	1.31	0.214	1.07	0.339	1.10	0.287
	Station	0.74	0.566	0.38	0.690	1.35	0.249	0.48	0.940	0.42	0.961	0.49	0.898

Table 2

Results of multi-response permutation procedures (MRPP) with three factors for taxonomic and functional diversity indices.

		Taxonomic diversity indices			Functional diversity indices		
		Year	Season	Site	Year	Season	Site
Fish	observed delta	3.919	3.785	3.948	20.570	20.310	20.420
	expected delta	3.932	3.932	3.932	21.060	21.060	21.060
	A	0.003	0.037	−0.004	0.023	0.036	0.030
	P	0.352	**0.001**	0.650	**0.043**	**0.003**	**0.003**
Target fish	observed delta	2.013	1.738	2.018	10.530	9.303	10.410
	expected delta	2.042	2.042	2.042	10.580	10.580	10.580
	A	0.014	0.149	0.012	0.005	0.121	0.016
	P	0.137	**0.001**	0.110	0.310	**0.001**	0.055
Non-target fish	observed delta	3.178	3.186	3.187	11.770	12.820	12.930
	expected delta	3.179	3.179	3.179	12.820	12.820	12.820
	A	0.001	−0.002	−0.002	0.082	0.000	−0.008
	P	0.429	0.550	0.530	**0.001**	0.360	0.936

Table 3

Mann-Kendall trend test for taxonomic and functional diversity indices. *N*: fish number, *H*′: Shannon-Weiner diversity, *J*′: Pielou evenness, *D*: Margelef diversity, *S*: Simpson diversity. *FRic*: functional richness index, *FEve*: functional evenness index, *FDiv*: functional divergence index, *FDis*: functional dispersion index, *RaoQ*: Rao's quadratic entropy index, *FRed*: functional redundancy index.

Group	Factor	Taxonomic diversity indices					
		N	H′	J’	D	S	
Fish	***Z***	0.757	0.027	**−3.395**	1.218	0.000	
	P	0.449	0.979	**0.001**	0.223	1.000	
Target Fish	***Z***	0.757	0.027	**−3.395**	1.218	0.000	
	P	0.449	0.979	**0.001**	0.223	1.000	
Non-target Fish	***Z***	0.785	−0.053	**−3.191**	1.618	−0.284	
	P	0.433	0.958	**0.001**	0.106	0.776	
Group	Factor	Functional diversity indices					
		FRic	*FEve*	*FDiv*	*FDis*	*RaoQ*	*FRed*
Fish	***Z***	−0.880	−0.436	1.120	−0.578	−0.720	−0.702
	P	0.379	0.663	0.230	0.564	0.476	0.438
Target Fish	***Z***	−0.699	−0.314	-	0.027	−0.151	0.116
	P	0.484	0.756	-	0.979	0.88	0.908
Non-target Fish	***Z***	−0.151	**−2.249**	**−2.124**	**−2.178**	**−2.533**	**−2.711**
	P	0.880	**0.025**	**0.034**	**0.029**	**0.011**	**0.007**

indices except *FRic* for the non-target fish group showed significant decreasing trends (Table 3).

3.3. *The correlations between taxonomic diversity and functional diversity*

Decreasing directional shifts between diversity indices and CPUE were observed, including five taxonomic and four functional diversity indices (Fig. 4). *FEve* and *FDiv* had opposite correlations with CPUE, both showing increasing trends. The functional diversity and taxonomic diversity indices had significantly positive correlations (Fig. 5, Fig. S1). As for exceptions, only one significant positive correlation was found for *FEve*; and three correlations of all indices were negative, although not significant. For the target fish group, no significant relationship between the taxonomic diversity indices and functional diversity indices was found, and more proportional negative correlations occurred (Fig. S2). For the non-target fish group, the results were not consistent with those of the total fish group, more positive correlations were observed (Fig. S3).

3.4. *Functional redundancy and the contribution of species*

FRed among the three fish groups was significantly different, with the total fish group having the highest values, and the non-target fish group having the lowest (Fig. S4, Table S3). The relationship between *FDis* and species richness of the total fish group showed a general n trend of growth, while the curves of the target fish group and the non-target fish group were more saturated (Fig. 5, Fig. 6). To assess the contribution of fish to functional redundancy, we analyzed two species-level functional diversity indices (*Scar*, *Dist*). No correlation between two indices was observed ($r = 0.01$, $p = 0.91$). The Japanese seahorse (*Hippocampus mohnikei*) was the rarest species in the community, with a *Scar* value significantly higher than other species (Table S4). Two Sciaenidae species (*Collichthys niveatus*, *Collichthys lucidus*) and one anchovy (*Thrissa setirostris*) contributed the most to functional redundancy (Table S4).

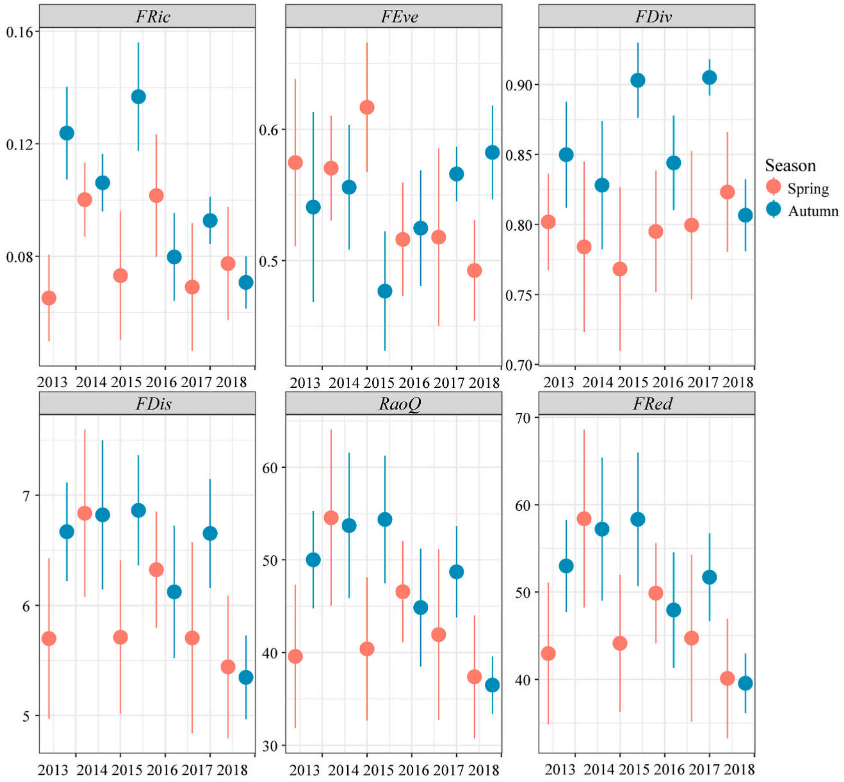

Fig. 3. Functional diversity indices of fish of stow net fishery in Haizhou Bay from 2013 to 2018. *FRic*: functional richness index, *FEve*: functional evenness index, *FDiv*: functional divergence index, *FDis*: functional dispersion index, *RaoQ*: Rao's quadratic entropy index, *FRed*: functional redundancy index.

4. Discussion

Our study depicted the fish assemblages of stow net fishery in Haizhou Bay from 2013 to 2018 based on taxonomic and functional diversity. TD indices showed significant temporal differences, but no significant spatial differences among the three stations. Pielou's evenness index (J') displayed significant interannual differences, but no seasonal differences, which was the opposite of the results seen with other TD indices (Table 1). J' measures the ratio of actual diversity to the theoretical maximum diversity. Our results revealed a decreasing trend over the study period, implying a decline in biodiversity to some extent. All three stations are all located in the traditional fishing area of the stow net fishery in Haizhou Bay, which covers a small spatial scale, resulting in similar TD indices of fish assemblages at three stations. Varied spatial scales could generate different results regarding the changing trends in biodiversity, and many initiatives have been proposed to form a scale-explicit framework to monitor and assess biodiversity [52,53]. Although the TD indices of fish assemblages at three stations were similar, we cannot assume that the three fish assemblages are highly consistent, so we need to explore the fish compositions, especially the dominant fish [54].

Six FD indices showed four types of disparate spatiotemporal differences (Table 1). These confusing results may stem from differences in the ecological implications of different indices. FD indices can effectively verify the mechanisms of biodiversity and ecosystem functions, but this requires linking functional diversity with ecosystem functions [55]. The three aspects of functional diversity (functional richness, functional evenness and functional divergence) can both indicate the characteristics of the same community and have unique ecological significance. *FRic* and *RaoQ* indicate the size of the functional space occupied by the species, *FEve* reflects the resource utilization efficiency by species, and *FDiv* and *FDis* reveal the degree of ecological niches complementarity among species. The multitude of indicators has brought dual impacts to the study of functional diversity [17]. On one hand, despite differences, various combinations of FD indices can more comprehensively demonstrate functional diversity. On the other hand, the presence of multiple FD indices can lead to inconsistent trends in functional diversity, making them challenging to explain. Thus, developing a conceptual framework to guide researchers in selecting appropriate indicators and quantities is essential for regulating functional diversity studies.

Nine taxonomic and functional diversity indices were higher in autumn than spring, while *FEve* and J' showed the opposite results (Fig. 2, Fig. 3). Ecological resources in spring were not fully utilized by fish, leaving extra niches available. In spring, fish in Haizhou Bay were mainly spawning fish (e.g., *L. polyactis*); however, some pelagic migratory fish (e.g., *Muraenesox cinereus*) migrated into the bay in autumn, which improved resource utilization and biodiversity [56]. The evenness indices (*FEve* and J') refer to the degree to which the characteristics of species within a community are evenly distributed in the ecological space [51]. The increase in the number

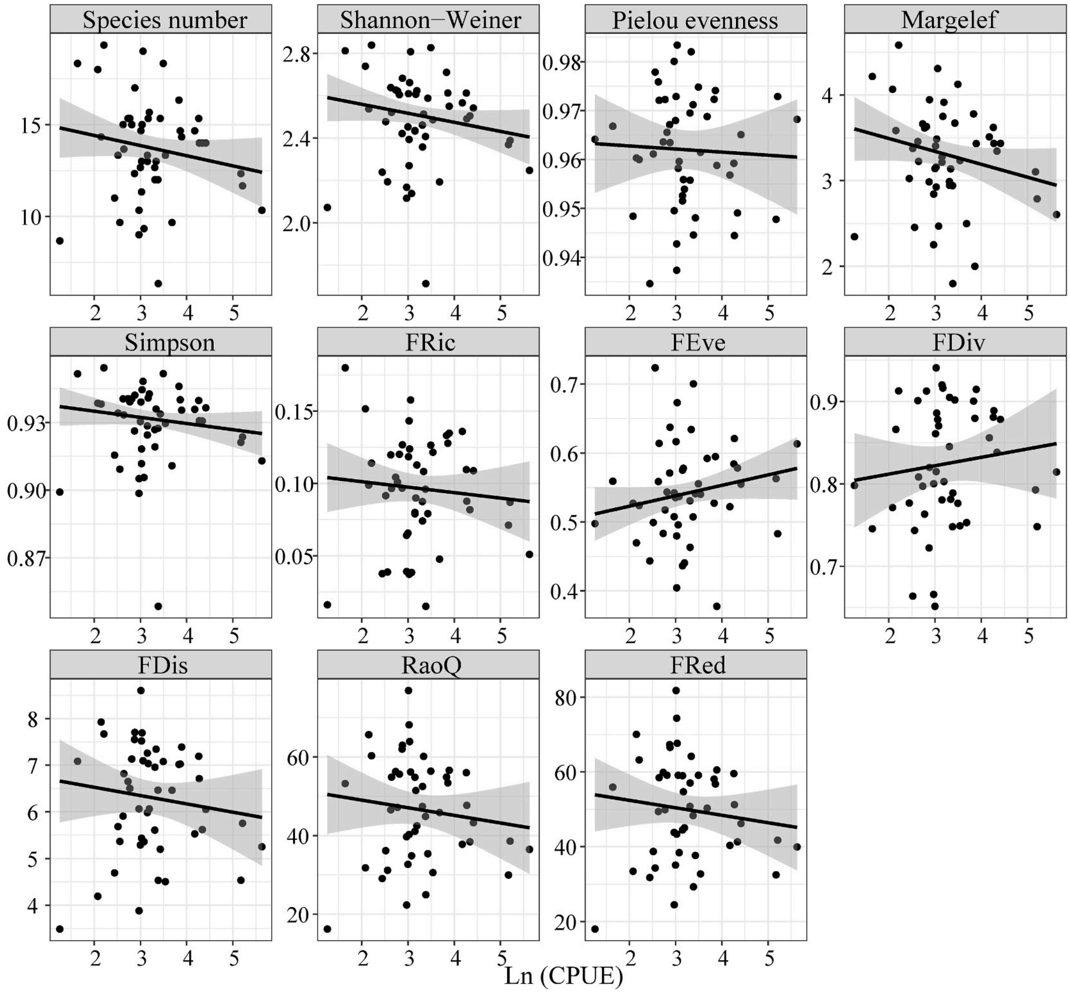

Fig. 4. Correlations between taxonomic and functional diversity indices and catch per unit effort (CPUE). The solid line was fitted through ordinary least squares regression. *FRic*: functional richness index, *FEve*: functional evenness index, *FDiv*: functional divergence index, *FDis*: functional dispersion index, *RaoQ*: Rao's quadratic entropy index, *FRed*: functional redundancy index.

of migratory fish in autumn reduced the evenness of fish assemblages, but contributed to the increased diversity. *FDiv* usually represents the degree of niche complementarity among species, higher values indicate weaker competition [57]. *FDiv* in autumn was significantly higher than in spring, showing that the degree of niche differentiation between species was relatively high. Spawning fish in spring were mostly demersal, while many migratory fish in autumn were pelagic [56]. These two types of fish utilize different ecological spaces, which not only improves space utilization efficiency and reduces interspecific competition, but also enhances biodiversity.

The three fish groups displayed different biodiversity dynamics (Tables 1–3). For instance, the TD indices of the target fish group showed significant interannual and seasonal differences, while those of the non-target fish group showed no difference. These results implied that the species and biomass of the target fish group have undergone drastic changes; conversely, the non-target fish group seemed stable (Table 1). The stow net fishery is a small-scale fishery, and fishery policies do not distinguish between target and non-target fish. Managers may strengthen their management strategy to target fish based on TD. However, the FD indices of both the target and non-target fish groups both fluctuated significantly from 2013 to 2018, which was inconsistent with TD (Table 1). Moreover, annual differences were only observed in two FD indices of the total fish group, while five FD indices showed seasonal differences. Seasonal variations in the target and non-target fish groups were not evident. Stow net fisheries are mixed fisheries with low selectivity, relying on currents to catch marine organisms. Due to varied distributions in the fishing grounds, species sizes, life histories, and exposure and sensitivity to fishing gear, causing variable fishing mortality and biological behavior of the target and non-target fish groups, resulted in differences in TD and FD indices [58,59]. Similar results were reported that the effects of marine protected areas were more beneficial to target fish, rather than non-target fish [60,61]. Bacheler and Smart [62] also pointed out that the abundance of non-target coral fish declined faster than target species over 25 years.

TD and FD indices showed disparate directional changing trends in the total fish group, target fish group and non-target fish group

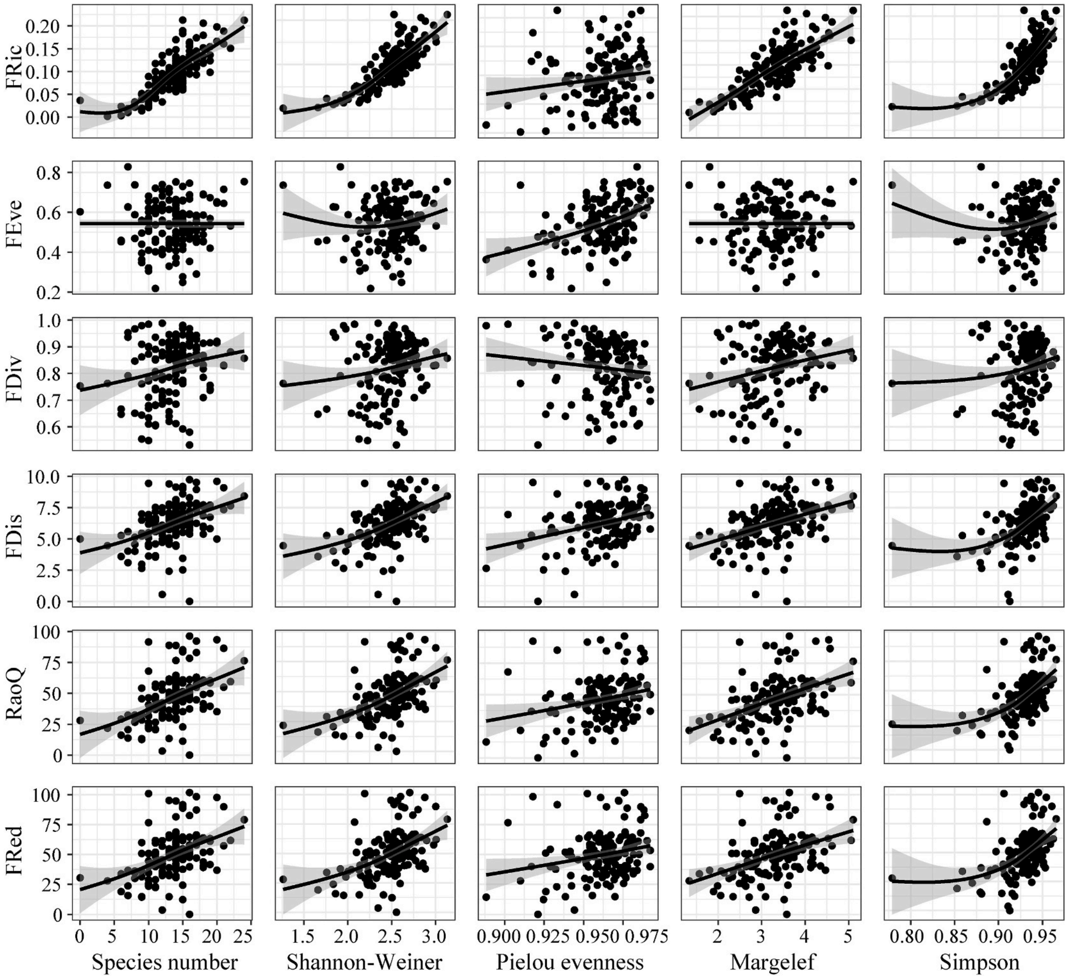

Fig. 5. Correlations between taxonomic diversity indices and functional diversity indices. The solid line was fitted through general additive model. *FRic*: functional richness index, *FEve*: functional evenness index, *FDiv*: functional divergence index, *FDis*: functional dispersion index, *RaoQ*: Rao's quadratic entropy index, *FRed*: functional redundancy index.

(Table 3). The overall J' of the three fish groups decreased significantly over six years, while other TD indices remained stable without obvious change. These results indicated that the community compositions changed to some extent during the study period. A possible reason is that continuous disturbances (e.g., overfishing, pollution) exist in the stow net fishery [63]. Fishermen in Haizhou Bay have been improving their fishing gear and changing their fishing targets to increase economic benefits [33]. Additionally, some sources of marine pollution, such as industrial sewage and aquaculture pollution could not be fully controlled. As for all six FD indices except *FRic*, we observed an incredible phenomenon: the non-target fish group, not the target fish group, showed a clear trend of decline. Some studies have also recognize the importance of this issue [64]. For example, a substantial and consistent decline of non-target demersal fish was detected along the coast of North Carolina and southeast Florida [62]. The vulnerability of target fish and non-target fish to fishing activities is not consistent [65]. The negative trends in the non-target fish group should be given attention by researchers and managers, as non-target fish are often small individuals that serve as important food sources for the target fish. To reduce the damage to non-target fish resources, changing fishing times and modifying fishing gear are recommended [66].

The higher the CPUE of fish assemblages, the lower the biodiversity (Fig. 4), which was consistent with Angulo-Valencia et al. [67]. A high abundance of dominant fish increased the yields of fishermen, and their dominance in communities suppressed other fish. Numerically dominant species had significant competitive advantages in a community, which could impede the colonization of other species [68]. Changing abundance is often the chief cause of the variation in biodiversity, and the complex interdependencies between biodiversity and abundance, evenness, and richness of communities deserve our increasing attention [69]. Higher TD indices generally heralded higher FD indices (Fig. 5), which supports the diversity-stability hypothesis [24]. Previous studies have also found that communities with abundant TD indices could have stronger resistance and maintain ecosystem stability when facing disturbances [70]. However, the target fish group and the non-target fish group exhibited completely different correlations between TD and FD indices (Fig. S2, Fig. S3). Lower correlations between FD indices of the target fish group were observed compared with the non-target fish group. Different FD indices have varied ecological implications and emphasis. We assumed that niche overlap among the target

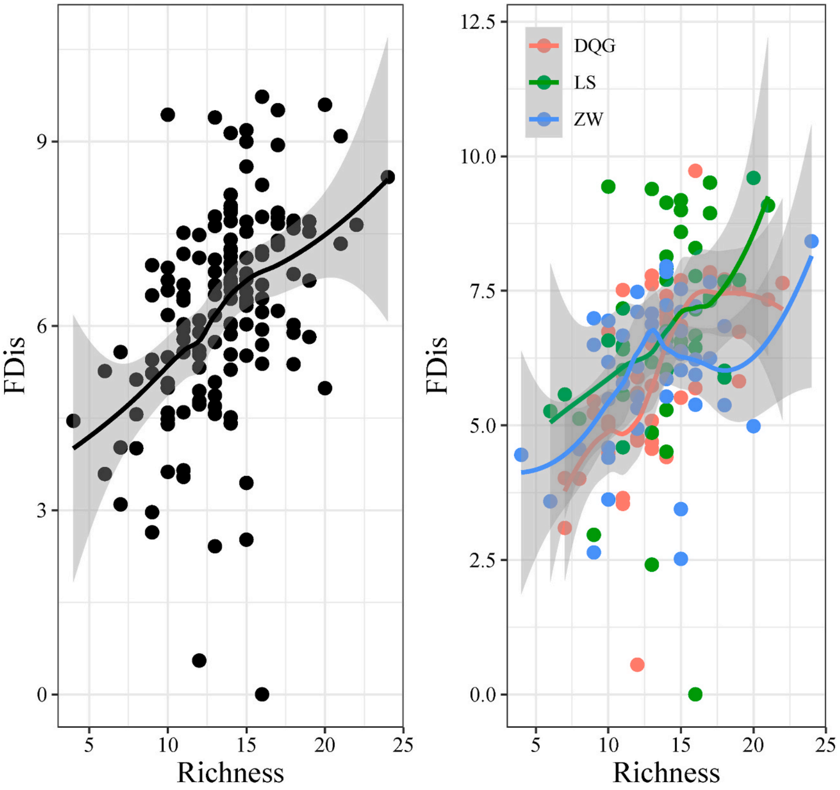

Fig. 6. The functional redundancy curve based on the functional dispersion index (*FDis*) and richness of the total fish group at three stations. Point means a fish assemblage. The solid line was fitted through method "loess". Three stations: DQG: Daquangou, LS: Lanshan, ZW: Zhewang.

fish was weaker. A total of 22 target fish belonging to eight orders were captured, and their characteristics compared with the non-target fish were larger bodies, lower abundance, and varied dietary habits. Differentiation in food habits and habitat space might reduce competition and strengthen the functional specialization of the target fish. For example, high-value fish such as *Pampus argenteus* mainly feed on jellyfish, benthic animals, polychaetes and diatoms; *Trichiurus lepturus* preys on fish and shrimps; and *Paralichthys olivaceus* prefers to feed on small demersal fish and cephalopods [71–73]. TD and FD are both important components of biodiversity. TD effectively reflects the richness and abundance of species in communities, while FD focuses on reflecting the differences in functional traits among species [40,74]. Although we often expect TD indices and FD indices to have consistent changing trends, incongruent cases often occur due to the heterogeneity of abiotic and biotic factors (e.g., water depth, temperature, migration) [75]. To minimize the limitations of these two diversity indices, many studies have integrated TD and FD to resolve ecological phenomena. For instance, different levels of biodiversity and vulnerability of fish assemblages were measured in the Min River, pointing out the hotspots based on the different facets of biodiversity and identifying vulnerable sites for conservation [40]. Fish assemblages facing invasion in Niagara Falls were depicted, and strategies for how combining TD and FD could reveal vital nuances of native fish assemblages were presented [76]. Meanwhile, the trade-offs among different levels of biodiversity are also a challenge. Comprehensive strategies integrated with ecological, environmental, social, and economic factors are encouraged when making conservation management decisions [77]. Additionally, some algorithms like *Marxan*, and *Zonation* are advanced tools that can help prioritize conservation actions [78].

In this study, we estimated the functional redundancy of fish assemblages by determining the relationships between the taxonomic richness and functional diversity [79]. This is of great significance for predicting the impacts of environmental disturbances and human activities on the ecosystem functions of fish assemblages. With the increase in fish species, the *FDiv* increased rapidly, with the gradient of the target fish group being higher than that of the non-target fish group (Fig. S5, Fig. S6). These results revealed that the target fish group had lower functional redundancy and poorer recovery ability after disturbances. In the face of tremendous and unforeseen disasters (e.g., overfishing, and extreme weather), the target fish may decline rapidly. Some factors, such as the choice of FD indices, the number of traits, and environmental gradients, all influence the relationship between functional diversity and richness [80,81]. Thus, applying multiple FD indices to fit two or more functional redundancy curves is recommended [28]. Functional redundancy originates from all fish, while the contributions of each fish vary (Table S4). Only one fish, *Hippocampus mohnikei*, could be considered unique in the stow net fishery based on the metric *Scar*. *H. mohnikei* swims slowly and inhabits the seaweed of shallow water, and is listed as vulnerable (VU) on the IUCN Red List of Threatened Species. Because of its special shape, nursery behaviors and predation, *H. mohnikei* is considered a special fish with a unique ecological niche [82]. *Collichthys niveatus* and *Collichthys lucidus* are high-value fish belonging to Epinephelinae, primarily inhabiting coastal waters like estuaries and bays. As one of the main fishing targets of the stow net and bottom trawl fishery, their fishing mortality rate is too high and overfishing has occurred [83]. Functional redundancy is the core component of functional insurance, so we should not only focus on the community level, but also on the species level [84]. When managers invest significant budgets and energy into high-value fish and rare fish, attention should also be paid to these important functionally rare fish. Only by understanding the contribution of each fish to the functional diversity can we accurately identify species at risk of functional extinction.

Non-target fish might face possible risks of resource decline (Table 3). Previous studies argued that the vulnerability of target and non-target fish to fishing activities is inconsistent [64,66]. Non-target fish are often abundant but have low economic value, which often leads to them being overlooked by researchers. However, non-target fish also play crucial roles in marine ecosystems (e.g., maintaining ecosystem stability and connecting the food web). We must directly address that the mismatch between protected fish and the fish that should be a concern in fisheries management. For example, some migratory fish with strong swimming capacity or high cryptic behaviour should be included in conservation lists, but this is difficult to implement in reality [85]. Special investigations targeting non-target fish are advocated by ecologists and policymakers. In the meantime, fish play an important role in aquatic ecosystems, and occupy different positions in the food web [86]. Therefore, it is important to consider not only competition among fish, but also the interactions and coexistence between fish and other organisms (e.g., crabs, and cuttlefish).

Biodiversity encompasses multiple facets, and biodiversity conservation must consider taxonomic diversity, functional diversity and phylogenetic diversity (PD) [87]. Taxonomic diversity effectively exhibits the number and relative abundance of species in communities, but struggles to convey relevant information about the ecological functions of species [40]. However, ecosystem functions are not only related to the number and abundance of species but also closely linked to the functional traits possessed by species. Functional diversity, as an important component of biodiversity, reflects the differences in functional traits among species and is used to analyze how organisms affect ecosystem functions and their response mechanisms to environmental changes [74]. Based on extensive research in the past, different diversity indices might produce contrasting changes and offer different management recommendations [88,89]. TD indices are the most widely accepted and applied indices, but they ignore the functional and evolutionary information of species. FD has seen significant advancements in recent decades, but, there is still controversy over the standardization of trait = selection and index calculation. PD is gradually being applied to species with different phylogenetic information in communities. As the advantages and disadvantages of different diversity indices vary, and the results differ, creating a comprehensive index that reflects the integral information of biodiversity is both crucial and challenging [40,90,91]. In addition to the biodiversity information of fish themselves, many other factors affect the biodiversity of communities. Geographical restrictedness, climate change and vulnerability to human activities are all shaping the biodiversity of the community in this area [92].

Stow net fisheries and biodiversity in Haizhou Bay are facing enormous pressure of decline. Marine protected areas (MPAs) is currently the one of most effective and important management measure for protecting marine biodiversity [61]. Despite achieving significant success and progress, many issues remain. First, the decisions on the locations and areas of MPAs were made based on TD, while FD and PD were ignored. Second, the significant importance of data deficient species to biodiversity and ecosystems has been overlooked. Lastly, the connectivity and policy consistency between MPAs are poor. As a developing country, the construction of MPAs in China is flourishing. Given international experience and current development situations, we propose four management suggestions. First, considering biodiversity at different facets simultaneously is crucial for accurately assessing biodiversity. Second, focusing on data deficient species by improving survey methods and establishing special investigations. Third, evaluating the integrity and connectivity of existing MPAs in China and exploring a comprehensive plan for the integration and consolidation of MPAs are imminent tasks [78]. Lastly, due to the numerous stakeholders involved in MPAs, especially the livelihood of artisanal fishermen, trade-offs between protection and fisheries need to be considered [60]. Overall, our study presents the taxonomic diversity and functional diversity of fish assemblages in the stow net fishery of Haizhou Bay, as well as their temporal trends. Of course, there are some limitations. The stow net is a passive fishing net with low fishing efficiency, making it difficult to capture large fish with strong swimming ability. We did not obtain environmental data that matched the biological data of fish, making it impossible to analyze the response mechanism of fish biodiversity to environmental factors. The functional traits we used were from the adult fish stage; however, these traits undergo significant changes from juvenile to adult stages. Despite some shortcomings, our findings have valuable implications. For one thing, the research area is located in an offshore bay with intensive human activities, making the driving mechanism of anthropogenic offshore engineering on fish aggregations an ideal topic. Additionally, forming a combined FD index is recommended to establish an integrative measure of functional diversity.

5. Conclusions

In summary, our study highlights the taxonomic and functional diversity status of fish assemblages in the stow net fishery of Haizhou Bay, revealing highly consistent correlations but inconsistent community characteristics and dynamics. Only one TD index (J') showed a declining trend in the three fish groups; however, five FD indices indicated that the non-target fish group faced the risk of resource decline. Moreover, the non-target fish group had higher functional redundancy compared to the target fish group, making an important contribution to the stability of fish assemblages. Given the inconsistency of FD indices, making management strategies based on the worst-case scenario may be effective, albeit conservative. Our results provide a new perspective for small-scale fisheries management, not only should we focus on fish with low abundance, but we should also consider their ecological functional traits. We especially recommend paying close attention to the non-target fish, including their behavioral habits, population dynamics and other relevant factors. Integrated and nuanced management strategies and research plans could be drafted based on these conclusions. Furthermore, to achieve higher validity and reliability in research, systematic studies involving environmental and anthropogenic factors are suggested.

CRediT authorship contribution statement

Guangjie Fang: Writing – original draft, Project administration, Funding acquisition, Conceptualization. **Yazhou Zhang:** Validation, Investigation. **Haolin Yu:** Software, Methodology. **Chuanxi Chen:** Formal analysis, Data curation. **Jun Liang:** Writing – review & editing, Funding acquisition. **Yanli Tang:** Writing – review & editing, Resources.

Data availability

The datasets generated and/or analyzed during the current study will be available from the corresponding author on reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e39428.

References

[1] A. Hussein, Links between biodiversity, ecosystems functions and services: systematic review, Int. J. Ecotoxicol. Ecobiol 6 (2021) 70–79, https://doi.org/10.11648/j.ijee.20210604.12.
[2] H.K. Lotze, Marine biodiversity conservation, Curr. Biol. 31 (19) (2021) R1190–R1195, https://doi.org/10.1016/j.cub.2021.06.084.
[3] E. Montes-Herrera, F. Muller-Karger, Global observational needs and resources for marine biodiversity, Front. Mar. Sci. 6 (2019) 367, https://doi.org/10.3389/fmars.2019.00367.
[4] FAO, The State of World Fisheries and Aquaculture 2022, Food and Agriculture Organization of the United Nations, Rome, 2022.
[5] L. Cao, Y. Chen, S. Dong, A. Hanson, B. Huang, D. Leadbitter, D.C. Little, E.K. Pikitch, Y. Qiu, Y. Sadovy de Mitcheson, U.R. Sumaila, M. Williams, G. Xue, Y. Ye, W. Zhang, Y. Zhou, P. Zhuang, R.L. Naylor, Opportunity for marine fisheries reform in China, Proc. Natl. Acad. Sci. USA 114 (3) (2017) 435–442, https://doi.org/10.1073/pnas.1616583114.
[6] G. Shen, M. Heino, An overview of marine fisheries management in China, Mar. Pol. 44 (2014) 265–272, https://doi.org/10.1016/j.marpol.2013.09.012.
[7] H. Hillebrand, B. Matthiessen, Biodiversity in a complex world: consolidation and progress in functional biodiversity research, Ecol. Lett. 12 (12) (2009) 1405–1419, https://doi.org/10.1111/j.1461-0248.2009.01388.x.
[8] J.Á. Payan-Alcacio, G.D.L. Cruz-Agüero, R. Moncayo-Estrada, Environmental drivers of fish community functional diversity in arid mangroves compared to a tropical estuary, Cienc. Mar. 46 (4) (2020) 193–210, https://doi.org/10.7773/cm.v46i4.3102.
[9] S. Villéger, S. Brosse, M. Mouchet, D. Mouillot, M.J. Vanni, Functional ecology of fish: current approaches and future challenges, Aquat. Sci. 79 (4) (2017) 783–801, https://doi.org/10.1007/s00027-017-0546-z.
[10] N.K. Dulvy, N. Pacoureau, C.L. Rigby, R.A. Pollom, R.W. Jabado, D.A. Ebert, B. Finucci, C.M. Pollock, J. Cheok, D.H. Derrick, Overfishing drives over one-third of all sharks and rays toward a global extinction crisis, Curr. Biol. 31 (21) (2021) 4773–4787. e8, https://doi.org/10.1016/j.cub.2021.08.062.
[11] J.A. Hutchings, I.M. Cote, J.J. Dodson, I.A. Fleming, S. Jennings, N.J. Mantua, R.M. Peterman, B.E. Riddell, A.J. Weaver, Climate change, fisheries, and aquaculture: trends and consequences for Canadian marine biodiversity, Environ. Rev. 20 (4) (2012) 220–311, https://doi.org/10.1139/a2012-011.
[12] H.L. Do, C.W. Armstrong, Ghost fishing gear and their effect on ecosystem services-Identification and knowledge gaps, Mar. Pol. 150 (2023) 105528, https://doi.org/10.1016/j.marpol.2023.105528.
[13] R. Law, M.J. Plank, Fishing for biodiversity by balanced harvesting, Fish Fish. 24 (1) (2023) 21–39, https://doi.org/10.1111/faf.12705.
[14] E. Gilman, M. Musyl, P. Suuronen, M. Chaloupka, S. Gorgin, J. Wilson, B. Kuczenski, Highest risk abandoned, lost and discarded fishing gear, Sci. Rep. 11 (1) (2021) 7195, https://doi.org/10.1038/s41598-021-86123-3.
[15] D. Tilman, Functional diversity, Encyclopedia of biodiversity 3 (1) (2001) 109–120, https://doi.org/10.1016/B978-0-12-384719-5.00061-7.
[16] L.M.O. Laureto, M.V. Cianciaruso, D.S.M. Samia, Functional diversity: an overview of its history and applicability, Natureza & Conservação 13 (2) (2015) 112–116, https://doi.org/10.1016/j.ncon.2015.11.001.
[17] S. Mammola, C.P. Carmona, T. Guillerme, P. Cardoso, Concepts and applications in functional diversity, Funct. Ecol. 35 (9) (2021) 1869–1885, https://doi.org/10.1111/1365-2435.13882.
[18] M. Emblemsvåg, L. Pecuchet, L.G. Velle, A. Nogueira, R. Primicerio, Recent warming causes functional borealization and diversity loss in deep fish communities east of Greenland, Divers. Distrib. 28 (10) (2022) 2071–2083, https://doi.org/10.1111/ddi.13604.
[19] I. Trindade-Santos, F. Moyes, A.E. Magurran, Global change in the functional diversity of marine fisheries exploitation over the past 65 years, Proceedings of the Royal Society B 287 (2020) 20200889, https://doi.org/10.1098/rspb.2020.0889, 1933).
[20] I. Cáceres, E.C. Ibarra-García, M. Ortiz, M. Ayón-Parente, F.A. Rodríguez-Zaragoza, Effect of fisheries and benthic habitat on the ecological and functional diversity of fish at the Cayos Cochinos coral reefs (Honduras), Mar. Biodivers. 50 (2020) 1–14, https://doi.org/10.1007/s12526-019-01024-z.
[21] M.P. Rincón-Díaz, N.D. Bovcon, P.D. Cochia, M.E. Góngora, D.E. Galván, Fish functional diversity as an indicator of resilience to industrial fishing in Patagonia Argentina, J. Fish. Biol. 99 (5) (2021) 1650–1667, https://doi.org/10.1111/jfb.14873.

[22] R. Frelat, A. Orio, M. Casini, A. Lehmann, B. Mérigot, S.A. Otto, C. Sguotti, C. Möllmann, A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea, ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 75 (7) (2018) 2463–2475, https://doi.org/10.1093/icesjms/fsy027.

[23] K. Zhao, Y. He, G. Su, C. Xu, X. Xu, M. Zhang, P. Zhang, Implications for functional diversity conservation of China's marine fisheries, Front. Mar. Sci. 9 (2022) 970218, https://doi.org/10.3389/fmars.2022.970218.

[24] M. Loreau, C. de Mazancourt, Biodiversity and ecosystem stability: a synthesis of underlying mechanisms, Ecol. Lett. 16 (s1) (2013) 106–115, https://doi.org/10.1111/ele.12073.

[25] B. Worm, E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, Impacts of biodiversity loss on ocean ecosystem services, science 314 (5800) (2006) 787–790, https://doi.org/10.1126/science.1132294.

[26] R.J. Standish, R.J. Hobbs, M.M. Mayfield, B.T. Bestelmeyer, K.N. Suding, L.L. Battaglia, V. Eviner, C.V. Hawkes, V.M. Temperton, V.A. Cramer, J.A. Harris, J. L. Funk, P.A. Thomas, Resilience in ecology: abstraction, distraction, or where the action is? Biol. Conserv. 177 (2014) 43–51, https://doi.org/10.1016/j.biocon.2014.06.008.

[27] M. Gerisch, Non-random patterns of functional redundancy revealed in ground beetle communities facing an extreme flood event, Funct. Ecol. 28 (6) (2014) 1504–1512, https://doi.org/10.1111/1365-2435.12272.

[28] K.A. Lamothe, K.M. Alofs, D.A. Jackson, K.M. Somers, Functional diversity and redundancy of freshwater fish communities across biogeographic and environmental gradients, Divers. Distrib. 24 (11) (2018) 1612–1626, https://doi.org/10.1111/ddi.12812.

[29] K.G. Lyons, C.A. Brigham, B.H. Traut, M.W. Schwartz, Rare species and ecosystem functioning, Conserv. Biol. 19 (4) (2005) 1019–1024, https://doi.org/10.1111/j.1523-1739.2005.00106.x.

[30] C. Violle, W. Thuiller, N. Mouquet, F. Munoz, N.J.B. Kraft, M.W. Cadotte, S.W. Livingstone, D. Mouillot, Functional rarity: the ecology of outliers, Trends Ecol. Evol. 32 (5) (2017) 356–367, https://doi.org/10.1016/j.tree.2017.02.002.

[31] M. Grenié, P. Denelle, C.M. Tucker, F. Munoz, C. Violle, funrar: an R package to characterize functional rarity, Divers. Distrib. 23 (12) (2017) 1365–1371, https://doi.org/10.1111/ddi.12629.

[32] Z.G. Li, Z.J. Ye, R. Wan, Spatial and seasonal patterns of ichthyoplankton assemblages in the Haizhou Bay and its adjacent waters of China, J. Ocean Univ. China 14 (6) (2015) 1041–1052, https://doi.org/10.1007/s11802-015-2603-3.

[33] G.J. Fang, H.L. Yu, X.M. Wang, H.X. Sheng, Y. Tang, C.D. Liu, C.X. Chen, Z.L. Liang, Y.L. Tang, Impact of summer moratorium on set-net fishery in Haizhou Bay, China, Journal of Oceanology and Limnology 40 (4) (2022) 1678–1691, https://doi.org/10.1007/s00343-021-0479-1.

[34] J.A. Ludwig, J.F. Reynolds, Statistical Ecology: a Primer in Methods and Computing, John Wiley & Sons, 1988.

[35] E.C. Pielou, Species-diversity and pattern-diversity in the study of ecological succession, J. Theor. Biol. 10 (2) (1966) 370–383, https://doi.org/10.1016/0022-5193(66)90133-0.

[36] R. Margalef, Dynamic aspects of diversity, J. Veg. Sci. 5 (4) (1994) 451–456, https://doi.org/10.2307/3235970.

[37] E.H. Simpson, Measurement of diversity, nature 163 (4148) (1949) 688, https://doi.org/10.1038/163688a0, 688.

[38] S.G. Bolam, K. Cooper, A.L. Downie, Mapping marine benthic biological traits to facilitate future sustainable development, Ecol. Appl. 33 (7) (2023) e2905, https://doi.org/10.1002/eap.2905.

[39] R.P. Streit, D.R. Bellwood, To harness traits for ecology, let's abandon 'functionality', Trends Ecol. Evol. 38 (5) (2023) 402–411, https://doi.org/10.1016/j.tree.2022.11.009.

[40] L. Lin, W. Deng, X. Huang, B. Kang, Fish taxonomic, functional, and phylogenetic diversity and their vulnerabilities in the largest river in southeastern China, Ecol. Evol. 11 (16) (2021) 11533–11548, https://doi.org/10.1002/ece3.7945.

[41] E.A. Frimpong, P.L. Angermeier, Trait-based Approaches in the Analysis of Stream Fish Communities, American Fisheries Society Symposium, Citeseer, 2010, p. 2010.

[42] S. Villéger, N.W.H. Mason, D. Mouillot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology, Ecology 89 (8) (2008) 2290–2301, https://doi.org/10.1890/07-1206.1.

[43] Z. Botta-Dukát, Rao's quadratic entropy as a measure of functional diversity based on multiple traits, J. Veg. Sci. 16 (5) (2005) 533–540, https://doi.org/10.1111/j.1654-1103.2005.tb02393.x.

[44] E. Laliberté, P. Legendre, A distance-based framework for measuring functional diversity from multiple traits, Ecology 91 (1) (2010) 299–305, https://doi.org/10.1890/08-2244.1.

[45] C. Ricotta, F. de Bello, M. Moretti, M. Caccianiga, B.E.L. Cerabolini, S. Pavoine, Measuring the functional redundancy of biological communities: a quantitative guide, Methods Ecol. Evol. 7 (11) (2016) 1386–1395, https://doi.org/10.1111/2041-210X.12604.

[46] W.K. Cornwell, D.W. Schwilk, D.D. Ackerly, A trait-based test for habitat filtering: convex hull volume, Ecology 87 (6) (2006) 1465–1471, 10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2.

[47] S. Villéger, N.W. Mason, D. Mouillot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology, Ecology 89 (8) (2008) 2290–2301, https://doi.org/10.1890/07-1206.1.

[48] E. Laliberté, P. Legendre, A distance-based framework for measuring functional diversity from multiple traits, Ecology 91 (1) (2010) 299–305, https://doi.org/10.1890/08-2244.1.

[49] Z. Botta-Dukát, Rao's quadratic entropy as a measure of functional diversity based on multiple traits, J. Veg. Sci. 16 (5) (2005) 533–540, https://doi.org/10.1111/j.1654-1103.2005.tb02393.x.

[50] D. Mouillot, S. Villéger, V. Parravicini, M. Kulbicki, J.E. Arias-González, M. Bender, P. Chabanet, S.R. Floeter, A. Friedlander, L. Vigliola, Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs, Proc. Natl. Acad. Sci. USA 111 (38) (2014) 13757–13762, https://doi.org/10.1073/pnas.1317625111.

[51] D. Schleuter, M. Daufresne, F. Massol, C. Argillier, A user's guide to functional diversity indices, Ecol. Monogr. 80 (3) (2010) 469–484, https://doi.org/10.1890/08-2225.1.

[52] P. Keil, J.C. Biesmeijer, A. Barendregt, M. Reemer, W.E. Kunin, Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae), Ecography 34 (3) (2011) 392–401, https://doi.org/10.1111/j.1600-0587.2010.06554.x.

[53] M.A. Jarzyna, W. Jetz, Taxonomic and functional diversity change is scale dependent, Nat. Commun. 9 (1) (2018) 2565, https://doi.org/10.1038/s41467-018-04889-z.

[54] O. Lepage, E.T. Larson, I. Mayer, S. Winberg, Serotonin, but not melatonin, plays a role in shaping dominant-subordinate relationships and aggression in rainbow trout, Horm. Behav. 48 (2) (2005) 233–242, https://doi.org/10.1016/j.yhbeh.2005.02.012.

[55] N.W. Mason, D. Mouillot, W.G. Lee, J.B. Wilson, Functional richness, functional evenness and functional divergence: the primary components of functional diversity, Oikos 111 (1) (2005) 112–118, https://doi.org/10.1111/j.0030-1299.2005.13886.x.

[56] W. Su, Y. Xue, C. Zhang, Y. Ren, Spatio-seasonal patterns of fish diversity, Haizhou Bay, China, Chin. J. Oceanol. Limnol. 33 (1) (2015) 121–134, https://doi.org/10.1007/s00343-015-3311-y.

[57] S.M. Scheiner, E. Kosman, S.J. Presley, M.R. Willig, Decomposing functional diversity, Methods Ecol. Evol. 8 (7) (2017) 809–820, https://doi.org/10.1111/2041-210X.12696.

[58] S.D. Foster, P.K. Dunstan, F. Althaus, A. Williams, The cumulative effect of trawl fishing on a multispecies fish assemblage in south-eastern Australia, J. Appl. Ecol. 52 (1) (2015) 129–139, https://doi.org/10.1111/1365-2664.12353.

[59] N.D. Walker, B. García-Carreras, W.J.F. Le Quesne, D.L. Maxwell, S. Jennings, A data-limited approach for estimating fishing mortality rates and exploitation status of diverse target and non-target fish species impacted by mixed multispecies fisheries, ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 76 (4) (2019) 824–836, https://doi.org/10.1093/icesjms/fsy205.

[60] D.L. Watson, M.J. Anderson, G.A. Kendrick, K. Nardi, E.S. Harvey, Effects of protection from fishing on the lengths of targeted and non-targeted fish species at the Houtman Abrolhos Islands, Western Australia, Mar. Ecol. Prog. Ser. 384 (2009) 241–249, https://doi.org/10.3354/meps08009.

[61] B.M. Fitzpatrick, E.S. Harvey, T.J. Langlois, R. Babcock, E. Twiggs, Effects of fishing on fish assemblages at the reefscape scale, Mar. Ecol. Prog. Ser. 524 (2015) 241–253, https://doi.org/10.3354/meps11077.

[62] N.M. Bacheler, T.I. Smart, Multi-decadal decline in reef fish abundance and species richness in the southeast USA assessed by standardized trap catches, Marine Biology 163 (2) (2016) 26, https://doi.org/10.1007/s00227-015-2774-x.

[63] S.L. Collins, F. Micheli, L. Hartt, A method to determine rates and patterns of variability in ecological communities, Oikos 91 (2) (2000) 285–293, https://doi.org/10.1034/j.1600-0706.2000.910209.x.

[64] T.R. McClanahan, Community biomass and life history benchmarks for coral reef fisheries, Fish Fish. 19 (3) (2018) 471–488, https://doi.org/10.1111/faf.12268.

[65] G. Moreno, L. Dagorn, G. Sancho, D. Itano, Fish behaviour from Fishers' knowledge: the case study of tropical tuna around drifting fish aggregating devices (DFADs), Can. J. Fish. Aquat. Sci. 64 (11) (2007) 1517–1528, https://doi.org/10.1139/f07-113.

[66] F.G. Forget, M. Capello, J.D. Filmalter, R. Govinden, M. Soria, P.D. Cowley, L. Dagorn, Behaviour and vulnerability of target and non-target species at drifting fish aggregating devices (FADs) in the tropical tuna purse seine fishery determined by acoustic telemetry, Can. J. Fish. Aquat. Sci. 72 (9) (2015) 1398–1405, https://doi.org/10.1139/cjfas-2014-0458.

[67] M.A. Angulo-Valencia, R.M. Dias, D.C. Alves, K.O. Winemiller, A.A. Agostinho, Patterns of functional diversity of native and non-native fish species in a neotropical floodplain, Freshw. Biol. 67 (8) (2022) 1301–1315, https://doi.org/10.1111/fwb.13918.

[68] B. Gilbert, R. Turkington, D.S. Srivastava, Dominant species and diversity: linking relative abundance to controls of species establishment, Am. Nat. 174 (6) (2009) 850–862, https://doi.org/10.1086/647903.

[69] S.A. Blowes, G.N. Daskalova, M. Dornelas, T. Engel, N.J. Gotelli, A.E. Magurran, I.S. Martins, B. McGill, D.J. McGlinn, A. Sagouis, Local biodiversity change reflects interactions among changing abundance, evenness, and richness, Ecology 103 (12) (2022) e3820, https://doi.org/10.1002/ecy.3820.

[70] D.G. Angeler, C.R. Allen, Quantifying resilience, J. Appl. Ecol. 53 (3) (2016) 617–624, https://doi.org/10.1111/1365-2664.12649.

[71] S. Dadzie, F. Abou-Seedo, T. Al-Shallal, Reproductive biology of the silver pomfret, *Pampus argenteus* (Euphrasen), in Kuwait waters, J. Appl. Ichthyol. 16 (6) (2000) 247–253, https://doi.org/10.1046/j.1439-0426.2000.00237.x.

[72] W.-D. Chiou, C.-Y. Chen, C.-M. Wang, C.-T. Chen, Food and feeding habits of ribbonfish Trichiurus lepturus in coastal waters of south-western Taiwan, Fisheries Science 72 (2006) 373–381, https://doi.org/10.1111/j.1444-2906.2006.01159.x.

[73] A. Hamidoghli, S. Won, S. Lee, S. Lee, N.W. Farris, S.C. Bai, Nutrition and feeding of olive flounder *Paralichthys olivaceus*: a Review, Reviews in Fisheries Science & Aquaculture 28 (3) (2020) 340–357, https://doi.org/10.1080/23308249.2020.1740166.

[74] M. Mouchet, F. Guilhaumon, S. Villéger, N.W.H. Mason, J.-A. Tomasini, D. Mouillot, Towards a consensus for calculating dendrogram-based functional diversity indices, Oikos 117 (5) (2008) 794–800, https://doi.org/10.1111/j.0030-1299.2008.16594.x.

[75] L. Kuczynski, J. Côte, A. Toussaint, S. Brosse, L. Buisson, G. Grenouillet, Spatial mismatch in morphological, ecological and phylogenetic diversity, in historical and contemporary European freshwater fish faunas, Ecography 41 (10) (2018) 1665–1674, https://doi.org/10.1111/ecog.03611.

[76] K.A. Lamothe, J.A.G. Hubbard, D.A.R. Drake, Freshwater fish functional and taxonomic diversity above and below Niagara Falls, Environ. Biol. Fish. 104 (6) (2021) 637–649, https://doi.org/10.1007/s10641-020-01044-w.

[77] W. Ma, W. Wang, C. Tang, G. Chen, M. Wang, Zonation of mangrove flora and fauna in a subtropical estuarine wetland based on surface elevation, Ecol. Evol. 10 (14) (2020) 7404–7418, https://doi.org/10.1002/ece3.6467.

[78] R.M. Daigle, A. Metaxas, A.C. Balbar, J. McGowan, E.A. Treml, C.D. Kuempel, H.P. Possingham, M. Beger, Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect, Methods Ecol. Evol. 11 (4) (2020) 570–579.

[79] G. da Silva Camilo, B. de Freitas Terra, F.G. Araújo, Using the relationship between taxonomic and functional diversity to assess functional redundancy in streams of an altered tropical watershed, Environ. Biol. Fish. 101 (2018) 1395–1405, https://doi.org/10.1007/s10641-018-0786-3.

[80] M.W. Cadotte, K. Carscadden, N. Mirotchnick, Beyond species: functional diversity and the maintenance of ecological processes and services, J. Appl. Ecol. 48 (5) (2011) 1079–1087, https://doi.org/10.1111/j.1365-2664.2011.02048.x.

[81] G. Legras, N. Loiseau, J.-C. Gaertner, J.-C. Poggiale, N. Gaertner-Mazouni, Assessing functional diversity: the influence of the number of the functional traits, Theor. Ecol. 13 (1) (2020) 117–126, https://doi.org/10.1007/s12080-019-00433-x.

[82] L. Aylesworth, J. Lawson, P. Laksanawimol, P. Ferber, T.L. Loh, New records of the Japanese seahorse *Hippocampus mohnikei* in Southeast Asia lead to updates in range, habitat and threats, J. Fish. Biol. 88 (4) (2016) 1620–1630, https://doi.org/10.1111/jfb.12908.

[83] S. Zhang, M. Li, J. Zhu, S. Xu, Z. Chen, An integrated approach to determine the stock structure of spinyhead croaker *Collichthys lucidus* (Sciaenidae) in Chinese coastal waters, Front. Mar. Sci. 8 (2021) 693954, https://doi.org/10.3389/fmars.2021.693954.

[84] C.R. Biggs, L.A. Yeager, D.G. Bolser, C. Bonsell, A.M. Dichiera, Z. Hou, S.R. Keyser, A.J. Khursigara, K. Lu, A.F. Muth, Does functional redundancy affect ecological stability and resilience? A review and meta-analysis, Ecosphere 11 (7) (2020) e03184, https://doi.org/10.1002/ecs2.3184.

[85] S. D`agata, D. Mouillot, L. Wantiez, A.M. Friedlander, M. Kulbicki, L. Vigliola, Marine reserves lag behind wilderness in the conservation of key functional roles, Nat. Commun. 7 (1) (2016) 12000, https://doi.org/10.1038/ncomms12000.

[86] C. Albouy, P. Archambault, W. Appeltans, M.B. Araújo, D. Beauchesne, K. Cazelles, A.R. Cirtwill, M.-J. Fortin, N. Galiana, S.J. Leroux, The marine fish food web is globally connected, Nature Ecology & Evolution 3 (8) (2019) 1153–1161, https://doi.org/10.1038/s41559-019-0950-y.

[87] M.A. Jarzyna, W. Jetz, Detecting the multiple facets of biodiversity, Trends Ecol. Evol. 31 (7) (2016) 527–538, https://doi.org/10.1016/j.tree.2016.04.002.

[88] A. Dubuc, J.P. Quimbayo, J.J. Alvarado, T. Araya-Arce, A. Arriaga, A. Ayala-Bocos, J. Julio Casas-Maldonado, L. Chasqui, J. Cortés, A. Cupul-Magaña, Patterns of reef fish taxonomic and functional diversity in the Eastern Tropical Pacific, Ecography (10) (2023) e06536, https://doi.org/10.1111/ecog.06536, 2023.

[89] B.L. Mindel, F.C. Neat, C.N. Trueman, T.J. Webb, J.L. Blanchard, Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea, PeerJ 4 (2016) e2387, https://doi.org/10.7717/peerj.2387.

[90] A.L. Strecker, J.D. Olden, J.B. Whittier, C.P. Paukert, Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity, Ecol. Appl. 21 (8) (2011) 3002–3013, https://doi.org/10.1890/11-0599.1.

[91] J.S.Y. Wong, Y.K.S. Chan, C.S.L. Ng, K.P.P. Tun, E.S. Darling, D. Huang, Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities, Coral Reefs 37 (2018) 737–750, https://doi.org/10.1007/s00338-018-1698-6.

[92] M. Grenié, D. Mouillot, S. Villéger, P. Denelle, C.M. Tucker, F. Munoz, C. Violle, Functional rarity of coral reef fishes at the global scale: hotspots and challenges for conservation, Biol. Conserv. 226 (2018) 288–299, https://doi.org/10.1016/j.biocon.2018.08.011.