




# Drivers of temporal variations in fish assemblages from mangrove creeks in Beihai, southern China

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Received: 17 May 2021 / Accepted: 30 January 2022 / Published online: 17 February 2022  
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## Abstract

Mangroves are regarded as important settlement grounds and nurseries for fishes due to the sheltered nature of these ecosystems. To identify the drivers of temporal variations in fish assemblages, seasonal variations of fish assemblages and environmental variables were investigated in Nanliu River Estuary, China, from July 2019 to May 2020. In total, 17,680 individuals weighing 24,724.73 g belonging to 23 families and 45 species were collected. The dominant species were *Ambassis urotaenia*, *Mugil cephalus*, *Coptodon zillii*, *Gambusia affinis*, and *Bostrychus sinensis*. Fish assemblages were significantly different in seasonal periodicity according to the results of nonmetric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA). Kruskal–Wallis test results revealed that species richness, fish abundance, and biomass were significantly different, seasonally. The highest number of fish specimens captured was recorded in winter and summer, while the highest biomass was observed in autumn. Different ecological types of fish utilized mangroves in different ways. Hence, the findings in this study are instrumental in understanding and the conservation of mangroves even coastal wetland and fish resources in the process of mangrove restorations.

**Keywords** Environmental factors · Fish assemblages · Mangrove creeks · Nanliu River Estuary · Temporal variations

## Introduction

Located between the land and the sea on tropical and subtropical coastlines, mangroves are essential habitats for a variety of fish, which support and enhance fishery resources and species diversity (Nagelkerken et al. 2008; Igulu et al. 2013). Mangrove ecosystems contain complex creek systems which expand the scope of mangrove areas and promote the

migration of fish within the shallow coastal zone (Mwandya et al. 2010). Fish resident species and transient species enter mangroves through tidal creeks for foraging, refuge, and rearing (Rehage and Loftus 2007; Vaslet et al. 2012).

Numerous studies have been carried out about seasonal differences of fish assemblages in estuarine mangroves (Ikejima et al. 2003; Wainaina et al. 2013; Huang et al. 2016). Seasonal variations of freshwater discharge and tidal changes throughout a year may cause huge fluctuations in salinity and other physicochemical conditions so that seasonal changes in the immigration and emigration of freshwater and marine species in estuarine mangroves affected fish assemblage structures (Barletta et al. 2008; Mandal et al. 2013; Shahraki et al. 2016). In the mangrove creeks of Qeshm Island, higher numbers of resident species existed during the wet season when the salinity was very low, and fish abundance and biomass were the highest in winter due to the migration of dominant marine transient species at high salinity (Shahraki et al. 2016). It is also found that the seasonal pattern of the fish assemblages was caused by the reproductive characteristics of dominant species (Tsai et al. 2015). Ikejima et al. (2003) showed that fish abundance and species richness in the rainy season was significantly higher

Responsible Editor: V.V.S.S. Sarma

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than that in the dry season, and this change may be caused by the breeding patterns of fishes and seasonal changes in food availability. In addition, Barletta's view was that seasonal changes of fish assemblages may be determined by a combination of temporal fluctuations in the fish assemblages induced by rainfall, reproduction, recruitment of resident estuarine species, and recruitment of marine or freshwater species in tidal mangrove creeks of the lower Caeté Estuary (Barletta et al. 2003). Therefore, it is very important to explore the temporal variation characteristics and causes of the fish assemblages in estuarine mangroves for the protection and utilization of fish resources (Desmond et al. 2002; de Azevedo et al. 2016).

Nanliu River is the largest independent river flowing into the sea in Guangxi province, and its estuary is a complex subtropical estuary ecosystem that integrates freshwater ecosystems, seawater ecosystems, brackish water-freshwater mixed ecosystems, tidal flat wetland ecosystems, estuary islands, and sandbar wetland ecosystems. Many scholars have conducted extensive studies on the fish community in mangrove forests listed as nature reserves (Wang et al. 2009; Wu et al. 2018; Zhang et al. 2019). Fish data from mangroves in Nanliu River Estuary (NRE), as a nonnatural reserve, were rarely reported. Therefore, based on the investigation of fish assemblage structures in mangrove creeks on different seasons, we analyzed the differences of fish utilization patterns in mangroves and the relationship between fish assemblages and environmental factors. These will clarify the temporal variation characteristics and main driving factors of the fish assemblages in estuarine mangroves and provide the basis for the protection and utilization of fish resources.

## Materials and methods

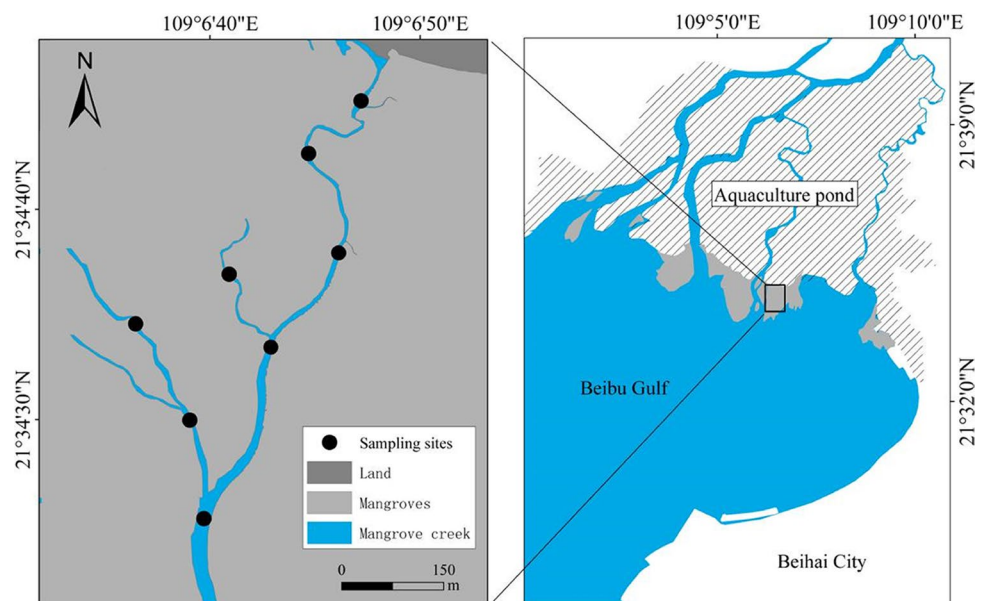
### Study area

This study was carried out in the NRE, which was divided into four main branches and debouched into Beibu Gulf, the northwestern part of the South China Sea (Fig. 1). The NRE is influenced by irregular diurnal tide, ranging in height from  $-2.15$  during neap tide to  $3.37$  m during spring tide. Mangroves are distributed within the estuary and fringe the river banks up to  $7$  km upstream. These forests are dominated by dwarf *Aegiceras corniculatum* intermixed with patches of *Kandelia candel*, and the total mangrove area increased significantly in recent decades (Liu et al. 2017, 2020). NRE belongs to a subtropical monsoon climate with a dry season in winter-spring and a wet season in summer-autumn (Wu et al. 2008). Human activities in the estuary are mainly aquaculture ponds. Ponds on both sides of the estuary area cover more than  $6500$  ha, and pond water emissions are restricted during the two short harvesting periods in summer and autumn (Kaiser et al. 2013). The land-based pollutants carried by rivers and the discharge of aquaculture water lead to serious eutrophication in the estuary (Yang et al. 2015).

### Sampling methods

Sampling sites were set up according to the length of each creek, that is, more sampling sites were set up in the longer creek, and fewer sites were arranged in the shorter creek. A total of eight sites were set up in three creeks, five were in the longest creek into which the shrimp pond water was

**Fig. 1** Study area and sampling sites of fish assemblages and environmental variables in Nanliu River Estuary (NRE) (land use in shaded area on the right: aquaculture pond)



directly discharged, and three were in two shorter creeks (Fig. 1). The width of the longest creek varies from about 3.8 upstream to about 20.7 m downstream. The width of the shorter creeks varies from 2.5 to 9.3 m.

Fishes were collected from July 2019 (summer), October 2019 (autumn), January 2020 (winter), and May 2020 (spring) using a fyke net (mesh 5 mm; high 1 m; length about 5–20 m) and one trap (mesh 8.5 mm;  $35\text{ cm}^2 \times 10\text{ m}$  for 1 unit). For every season, samples were taken at day tides and night tides. For everyday tides and night tides, samplings lasted for three consecutive tidal cycles. Day and night tides were defined as those in which the flood occurred primarily during day or night, respectively. For each tidal cycle, we set the nets before flowing tide, and fish samples were then collected after ebbing tide at all sites. Therefore, a total of 192 fish samplings were conducted during the study. All fish were removed from the net, stored in 10% formalin solution, and taken back to the laboratory for identifying, weighing, counting, and then were subsequently stored in 5% formalin solution.

Environmental parameters were measured at each site during sampling. Water temperature (WT), pH, dissolved oxygen (DO), and salinity were measured using a handheld multiparameter meter provides (YSI Professional Plus). The measurement of turbidity was applying a portable turbidimeter (HACH 2100Q). Chlorophyll-a (Chl-a) was measured using a portable algal detector (ALGAE-Wader). At the same time, surface water samples (0.5 m) were collected and brought back to the laboratory to measure chemical indices including chemical oxygen demand (COD), total nitrogen (TN), total organic carbon (TOC), and total phosphorus (TP) (General Administration of Quality Supervision and Administration 2007). Besides, tidal ranges were the difference between the maximum and minimum tide levels of the day, and tidal level data was obtained from the State Oceanic Administration People's Republic of China (<http://ocean.cnss.com.cn/>).

## Species classification

The identification and biological characteristics of fishes were determined according to reference books (Lai and He 2016; Liu et al. 2017) and Fishbase ([www.fishbase.org](http://www.fishbase.org)) (Froese and Pauly 2020). Fish species were categorized into bioecological groupings depending on their utilization of mangroves/estuary following Wainaina (Wainaina et al. 2013) and Potter (Potter et al. 2015). The functional three groups were as follows:

**Mangrove/estuary-transient species (MT):** those fish species that may use the estuary as transit routes between the marine and freshwater environments.

**Mangrove/estuary-resident species (MR):** those fish species that may use the estuary as foraging habitats, and their life history are associated with the estuary.

**Mangrove/estuary-occasional species (MO):** Those fish species that inhabit freshwater and marine and their life history are not related to the estuary.

## Data analyses

All the fish captured on the day tides or night tides at each site for each season were collected as the catch per unit effort (Jin et al. 2007). Therefore, a total of 64 samplings participated in the analysis. Index of relative importance (IRI) was used to determine the dominant species in this region (Pinkas et al. 1971). IRI was calculated based on abundance, biomass, and frequency of occurrence as follows:  $IRI = (N\% + W\%) \times F\%$ , where  $N\%$ ,  $W\%$ ,  $F\%$  are percentage contribution of abundance, the contribution of biomass, and frequency of occurrence. When the IRI value of a species was greater than 1000, it is recognized as the dominant species. Kruskal–Wallis test was carried out for fish abundance, species richness, biomass, as well as the environmental variables with the R package agricolae due to these parameters running counter to assumptions of ANOVA, even after the log transformation of data.

PERMANOVA was performed by the adonis function in R package vegan to test the difference of fish assemblages among seasons based on log-transformed fish abundance data (Anderson 2001; Ruppert et al. 2018). NMDS was used to visualize temporal patterns revealed by PERMANOVA. Then, similarity percentages (SIMPER) analysis was used by PAST3.0 to analyze the dissimilarity of fish assemblages and identify those fish species that contributed most to the average dissimilarity of the seasonal period determined the percentage contribution of each fish species to the overall dissimilarity (Clarke 1993; Kindong et al. 2020).

Redundancy analysis (RDA) was used to investigate the associations between fish species' abundance and environmental variables (Ruppert et al. 2018; Huang et al. 2019). Firstly, rare species were removed with an occurrence frequency lower than 10%. Then, detrended correspondence analysis (DCA) on the log-transformed species abundance was carried out, and the longest gradient length of 2.38 along the first axis was obtained, which suggested that RDA was effective (Šmilauer and Lepš 2014). The significance of fish abundance and environmental variables was tested by using the Monte Carlo permutation test (permutations = 999). Only if it was significant, a forward stepwise selection procedure of environmental variables

**Table 1** List of species captured from the mangrove creek in the NRE, showing ecological guild (EG), total number of individuals (*N*), total biomass (*W*), frequency of occurrence (*F*%), and index of relative importance (IRI) (The fish species with IRI > 1000 were indicated in bold)

Family	Species	EG	<i>N</i>	<i>W</i> (g)	<i>F</i> %	IRI
Elopidae	<i>Elops machnata</i>	MR	1	0.91	1.56	0.01
Ophichthyidae	<i>Pisodonophis boro</i>	MR	35	2836.41	34.38	401.15
Engraulidae	<i>Thryssa vitrirostris</i>	MR	77	215.37	17.19	22.46
	<i>Encrasicholina heteroloba</i>	MR	1	1.09	1.56	0.02
CluPidae	<i>Sardinella aurita</i>	MO	10	7.38	9.38	0.81
	<i>Sardinella gibbosa</i>	MO	80	35.38	17.19	10.24
Salangidae	<i>Salanx ariakensis</i>	MT	1	3.19	1.56	0.03
Mugilidae	<b><i>Mugil cephalus</i></b>	MT	<b>2712</b>	<b>3976.01</b>	<b>98.44</b>	<b>3092.95</b>
Atherinidae	<i>Hypoatherina tsurugae</i>	MO	7	1.67	6.25	0.29
Scorpaenidae	<i>Scorpaenopsis gibbosa</i>	MO	11	8.5	9.38	0.91
Poeciliidae	<b><i>Gambusia affinis</i></b>	MO	<b>2548</b>	<b>473.98</b>	<b>76.56</b>	<b>1250.17</b>
	<i>Poecilia latipinna</i>	MO	1	2.69	1.56	0.03
Cyprinidae	<i>Hypophthalmichthys nobilis</i>	MO	1	8.57	1.56	0.06
Ambassidae	<i>Ambassis interrupta</i>	MR	71	96.15	20.31	16.05
	<b><i>Ambassis urotaenia</i></b>	MR	<b>7048</b>	<b>1810.34</b>	<b>68.75</b>	<b>3324.05</b>
Serranidae	<i>Epinephelus fuscoguttatus</i>	MO	2	3.35	1.56	0.04
Sillaginidae	<i>Sillago sihama</i>	MR	9	45.64	10.94	2.57
Malacanthidae	<i>Branchiostegus argentatus</i>	MO	1	0.35	1.56	0.01
Sparidae	<i>Acanthopagrus latus</i>	MR	102	37.38	30.06	28.44
Teraponidae	<i>Terapon jarbua</i>	MT	871	671.32	29.68	226.86
Cichlidae	<b><i>Coptodon zillii</i></b>	MO	<b>725</b>	<b>5059.22</b>	<b>75</b>	<b>1842.21</b>
	<i>Oreochromis niloticus</i>	MO	15	794.68	18.75	61.86
Scatophagidae	<i>Selenotoca multifasciata</i>	MR	12	9.4	12.5	1.32
Eleotridae	<b><i>Bostrychus sinensis</i></b>	MR	<b>198</b>	<b>3451.44</b>	<b>78.13</b>	<b>1178.07</b>
	<i>Butis butis</i>	MR	347	815.45	76.56	402.79
	<i>Butis koilomatodon</i>	MR	2	3.98	3.13	0.09
Gobiidae	<i>Synechogobius ommaturus</i>	MR	299	2374.77	81.25	917.80
	<i>Acentrogobius viridipunctatus</i>	MR	93	540.63	67.19	182.25
	<i>Acentrogobius chlorostigmatoides</i>	MR	50	92.57	18.75	12.32
	<i>Acentrogobius brevirostris</i>	MR	25	50.9	28.13	9.77
	<i>Acentrogobius caninus</i>	MR	8	44.41	7.81	1.76
	<i>Glossogobius olivaceus</i>	MR	69	274.34	31.25	46.87
	<i>Glossogobius giuris</i>	MR	1	15.63	1.56	0.01
	<i>Mugilogobius abei</i>	MR	13	8.6	9.38	1.02
	<i>Mugilogobius chulae</i>	MR	1	0.4	1.56	0.01
	<i>Pseudogobius javanicus</i>	MR	2034	307.75	60.94	776.91
	<i>Mahidolia mystacina</i>	MR	3	2.42	4.68	0.13
	<i>Oligolepis acutipennis</i>	MR	1	0.26	1.56	0.01
	<i>Periophthalmus modestus</i>	MR	89	265.23	54.69	86.19
	<i>Boleophthalmus pectinirostris</i>	MR	40	150.5	34.38	28.70
	<i>Taenioides cirratus</i>	MR	4	41.27	4.69	0.89
	<i>Trypauchen vagina</i>	MR	32	169.94	21.88	19.00
Osphronemidae	<i>Macropodus opercularis</i>	MO	1	1.12	1.56	0.02
Tetraodontidae	<i>Lagocephalus spadiceus</i>	MO	16	2.56	14.06	1.42
Soleidae	<i>Solea ovata</i>	MO	13	11.58	10.94	1.32

with a permutation test (999 permutations) was used to obtain the reduced environmental variables (Huang et al.

2019). The DCA and the RDA analysis were performed in the Canoco 5.

## Results

### Fish assemblage composition

A total of 45 species (17,680 individuals weighing 24,724.73 g) belonging to 23 families were caught in the NRE (Table 1). *Ambassis urotaenia*, *Mugil cephalus*, *Coptodon zillii*, *Gambusia affinis*, and *Bostrychus sinensis* were dominant species throughout the year ( $IRI > 1000$ ). The most numerically abundant species were *A. urotaenia* (39.86%), *M. cephalus* (15.34%), *G. affinis* (14.41%), and *Pseudogobius javanicus* (11.50%), while the most fish species in biomass were *C. zillii* (20.46%), *M. cephalus* (16.08%), *B. sinensis* (13.96%), and *Pisodonophis boro* (11.47%).

The majority of fish surveyed were mangrove/estuary-associated species (28 species) and mangrove/estuary-occasional species (14 species) (Table 1). The remaining species were mangrove/estuary-transient species (3 species). Throughout the year, we found a seasonal variation in the abundance and relative abundance of mangrove/estuary-associated species, which were more abundant in autumn and winter (Fig. 2). The maximum abundance and relative abundance of mangrove/estuary-occasional species were observed in summer (Fig. 2). The peak abundance of mangrove/estuary-transient species appeared in summer and winter (Fig. 2). Maximum relative abundance occurred in summer, and the increasing trend of relative abundance from autumn to spring of the second year existed on these guilds (Fig. 2).

### Seasonal variation of fish assemblages

Kruskal–Wallis test results showed that species richness, fish abundance, and biomass were significantly different seasonally (Fig. 3). There were significant differences in

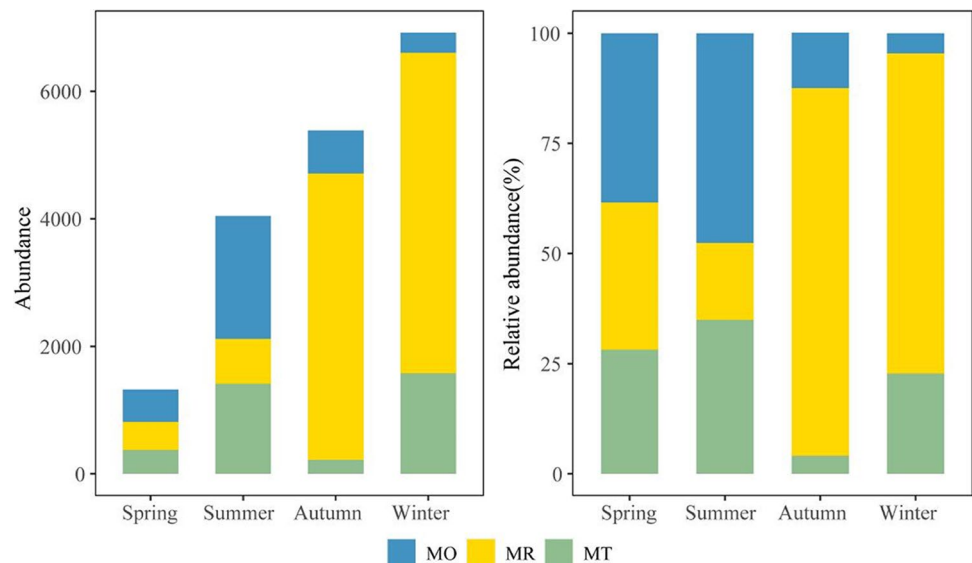
fish abundance among the three seasons (spring, autumn, and winter) ( $p < 0.05$ ) (Fig. 3), and the higher fish abundance captured was recorded in winter, followed by autumn and the lowest in spring. The fish abundance in summer was significantly higher than that in spring, but there was no significant difference with that in autumn and winter. The seasonal significant difference of species richness only existed between summer and autumn, and the higher species richness captured was recorded in summer than that in winter (Fig. 3). The seasonal significant difference of fish biomass only existed between autumn and other seasons, and the fish biomass in autumn was the highest (Fig. 3).

A clear separation of fish samples with a clockwise direction was found for different seasons (Fig. 4), which indicated a gradual change in fish assemblages over the seasons. PERMANOVA analysis further revealed a highly significant effect of the time of seasons ( $R^2 = 0.4512$ ,  $p = 0.001$ ) on fish assemblages. A 79.61% average dissimilarity was found among seasons based on SIMPER analysis, and *A. urotaenia*, *M. cephalus*, *G. affinis*, *T. jarbua*, and *C. zillii* were the major fish species that contributed to seasonal dissimilarity, those which contributed 27.96%, 17.68%, 14.20%, 8.992%, and 7.380% of the difference, respectively (Table 2).

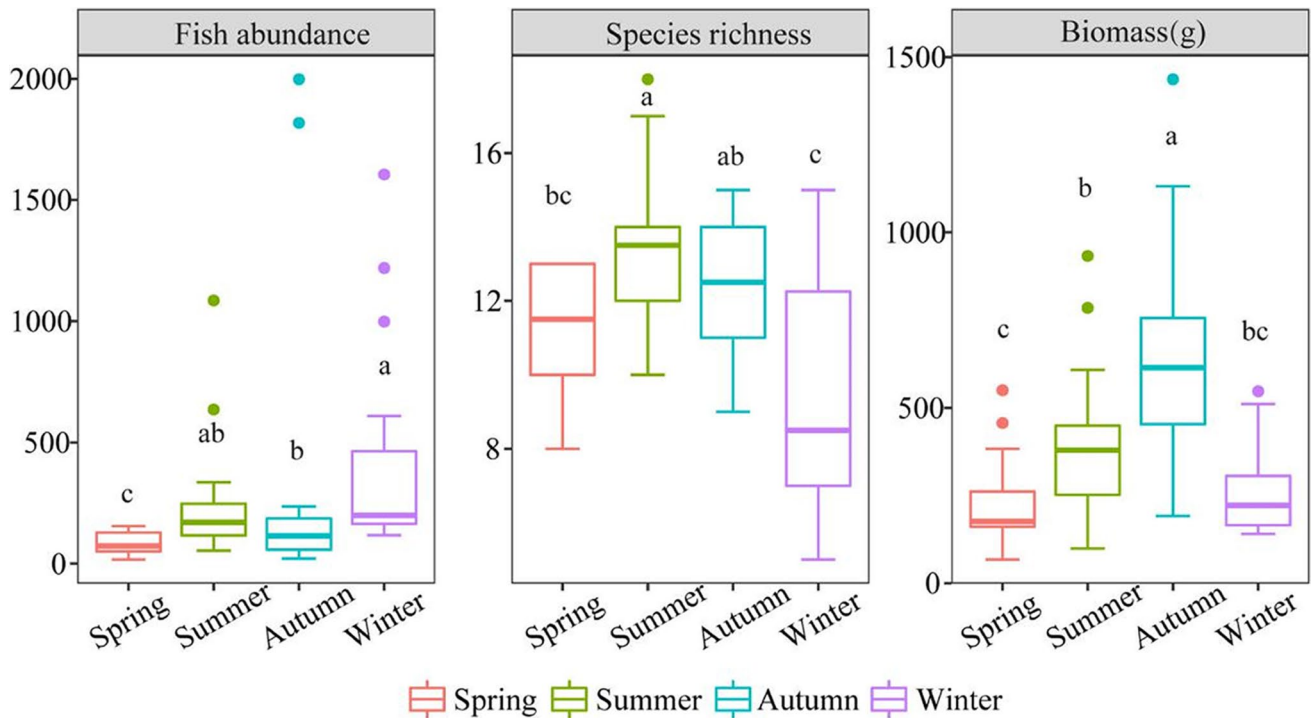
### Relationship between fish assemblages and environmental variables

All the environmental variables were significantly different between seasons (Fig. 5). For water temperature, significantly higher values were observed in summer compared with other seasons, whereas significantly lower values were found in winter ( $p < 0.05$ ); conversely, salinity in

**Fig. 2** The abundance and relative abundance of ecological guilds of fish among seasons (MO, mangrove/estuary-occasional species; MR, mangrove/estuary-resident species; MT, mangrove/estuary-transient species)





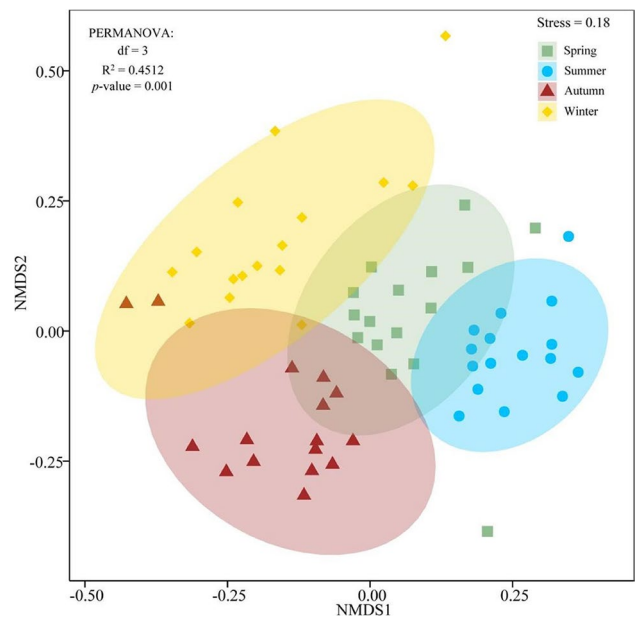


**Fig. 3** Seasonal changes for fish abundance, species richness, and biomass from mangrove creek in the NRE. Different letters (a, b, c, d) indicate significant differences (Kruskal–Wallis test,  $p$ -values < 0.05)

winter was the highest, and that in summer was the lowest ( $p < 0.05$ ). TOC, COD, and turbidity in summer and autumn were greater than that in spring and winter ( $p < 0.05$ ). The peak concentrations for TN recorded in autumn were significantly higher than those in other seasons ( $p < 0.05$ ). Tidal ranges in spring were significantly higher than those in other seasons ( $p < 0.05$ ).

A total of 26 fish species were selected for analysis with occurrence frequency higher than 10% (Table 1), and 6 environmental variables were selected after a forward stepwise selection including salinity, TN, COD, water temperature, TOC, and tidal ranges (Table 3). In the RDA ordination biplot, two axes totally explain 42.0% of species–environment variations. Among the axes, the first axis explains 20.11% and the second axis 8.44% of species–environment variations. *T. jarbua*, *Butis butis*, *Ambassis interrupta*, *Scorpaenopsis gibbosa*, and *Selenotoca multifasciata* were positively related to water temperature but negatively related to high salinity (Fig. 6). While *A. urotaenia*, *Acanthopagrus latus*, *Lagocephalus spadicus*, *Trypauchen vagina*, and *M. cephalus* were positively associated with salinity. In addition, *Trypauchen vagina*, *Acentrogobius viridipunctatus*, *Oreochromis niloticus*, and *Glossogobius olivaceus* were positively associated with TN. Moreover, *C. zillii*, *Synechogobius ommaturus*, *Sillago sihama*, and *P. boro* were positively associated with

COD and TOC. *Solea ovata* and *P. javanicus* were positively associated with tidal ranges.



**Fig. 4** NMDS ordination of and PERMANOVA test of fish assemblages among seasons based on Bray–Curtis similarity

**Table 2** Results of the SIMPER analysis, showing average dissimilarity of most representative species (%), contributory species, as well as their cumulative contribution (%) and their sum of fish abundance for seasons

SIMPER analysis				Fish abundance			
Seasons (average dissimilarity: 79.61%)				Seasons			
Species	Av. diss (%)	Contrib (%)	Cumulative (%)	Spring	Summer	Autumn	Winter
<i>Ambassis urotaenia</i>	22.26	27.96	27.96	93	3	3974	2978
<i>Mugil cephalus</i>	14.07	17.68	45.64	373	548	215	1576
<i>Gambusia affinis</i>	11.30	14.20	59.84	455	1716	111	266
<i>Terapon jarbua</i>	7.159	8.992	68.83	0	867	4	0
<i>Coptodon zillii</i>	5.875	7.380	76.21	35	127	548	15
<i>Pseudogobius javanicus</i>	5.165	6.488	82.70	53	133	3	1845
<i>Selenotoca multifasciata</i>	2.273	2.856	85.56	0	12	0	0
<i>Synechogobius ommaturus</i>	2.030	2.55	88.11	23	77	176	23
<i>Bostrychus sinensis</i>	1.305	1.639	89.74	80	60	34	24
<i>Trypauchen vagina</i>	0.9403	1.181	90.93	0	0	77	0
<i>Ambassis interrupta</i>	0.7799	0.9796	91.91	0	71	0	0
<i>Acanthopagrus latus</i>	0.7420	0.932	92.84	9	9	0	84
<i>Sardinella gibbosa</i>	0.6990	0.878	93.72	0	80	0	0
<i>Periophthalmus modestus</i>	0.6300	0.7914	94.51	32	46	5	6
<i>Glossogobius olivaceus</i>	0.6252	0.7853	95.29	4	21	30	14

## Discussion

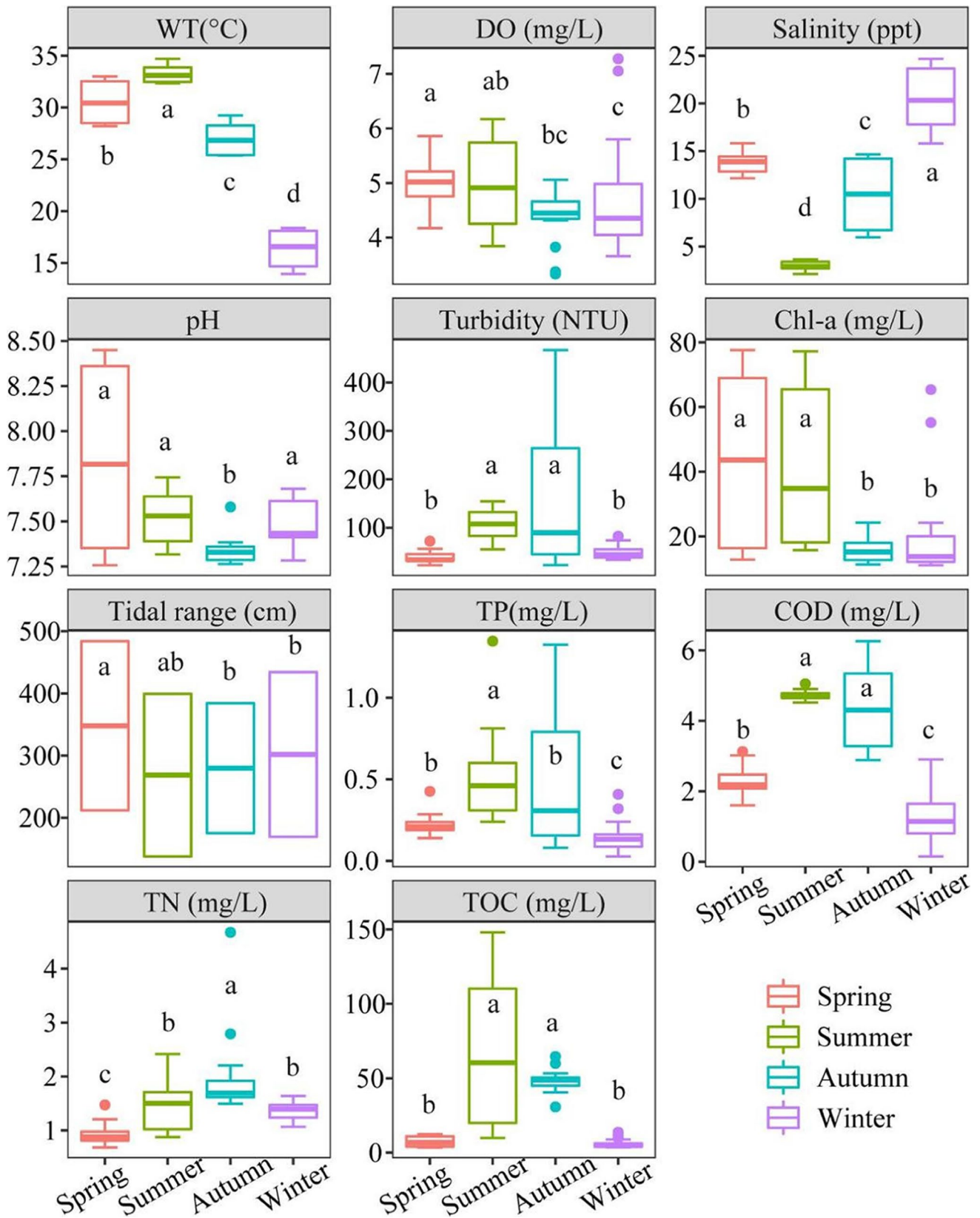
### Seasonal variations on fish assemblages

Fish assemblage structures in mangrove creeks in this study were seasonally different, and this temporal distribution pattern, generally, occurs in mangroves in other regions all over the world (Wainaina et al. 2013; Castellanos-Galindo and Krumme 2015; Mahesh and Saravanakumar 2015). The seasonal variation of the contributing species abundance was the reason for the seasonal difference of fish assemblages (Table 2), which may be related to the breeding dates of some species (*M. cephalus*, *G. affinis*, and *T. jarbua*) as found in estuary mangroves in Taiwan (Tsai et al. 2015). Firstly, this difference was reflected in the reproductive cycles to anadromous species (*M. cephalus*) and catadromous species (*T. jarbua*). The spawning period of the *M. cephalus* occurred from November to February, reaching the highest intensity in January (Ibáñez Aguirre and Gallardo-Cabello 2004); other studies have also found that *M. cephalus* reproduced from December to January in China and India (Hsu et al. 2007; Rekha et al. 2021). The breeding season of *T. jarbua* is from April to October every year (Miu et al. 1990). In their own breeding season, the individuals of these fish were higher than that in other seasons (Table 2), which supported our guess that the seasonal difference was reflected in the reproductive cycles of contributing species. The annual reproductive cycles with a distinct breeding season for *G. affinis* extends from about mid-spring until mid-autumn with a peak in summer, meanwhile, its foraging time

also varied seasonally, with a peak in summer and a trough in winter (Pyke 2005). Overall, it may explain the high abundance of *G. affinis* in summer (Table 2).

### Influence of environmental variables in fish assemblages

The seasonal pattern of fish assemblages was also related to the change of environment and fish-specific tolerance (Rousseau et al. 2018). The most influential environmental variables were salinity, water temperature, and COD (Fig. 6). Higher species richness captured were recorded in summer than that in winter in this study (Fig. 3) and might be explained by the comprehensive effects of seasonal variation in salinity and water temperature (Fig. 3). As a response to high salinity, low species richness has been recognized in tropical estuaries (Sloterdijk et al. 2017). With the increase of salinity in autumn and winter, only marine species (*A. latus*, *L. spadiceus*) with high salinity preference and some resident species (*A. urotaenia*, *T. vagina*) were suitable for the environmental characteristics of mangroves (Fig. 6), resulting in the absolute predominance of a few species of fish and lower species richness (Fig. 3). Meanwhile, the increase of primary and secondary productivity from freshwater inflows and supplementing this productivity in the case of warmer water temperatures in the wet season facilitated faster juvenile fish growth (Pichler et al. 2015). *T. jarbua* and *G. affinis* preferred high temperature and low salinity environments (Fig. 6). So, these species, together with the resident species, entered with every flood tide to



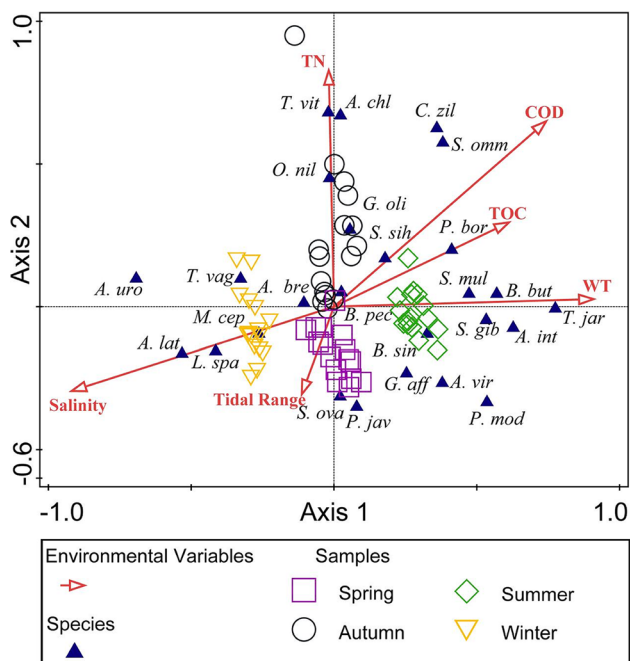
**Fig. 5** Seasonal comparisons for environmental variables from the mangrove creek in the NRE. Different letters (a, b, c, d) indicate significant differences (Kruskal–Wallis test,  $p$ -values < 0.05). (WT,

water temperature; Chl-a, chlorophyll-a; COD, chemical oxygen demand; TN, total nitrogen; TOC, total organic carbon)



**Table 3** Results of forward stepwise selection of environment variables

Environmental variables	Contribution %	Pseudo-F	p-value
Salinity	41.2	17	0.002
TN	15.2	6.8	0.002
Water temperature	8.4	4.0	0.002
Tidal range	7.6	3.7	0.002
COD	7.0	3.6	0.004
TOC	5.6	3.0	0.006
TP	3.3	1.8	0.090
pH	3.1	1.7	0.100
Chlorophyll-a	2.6	1.4	0.170
Turbidity	2.5	1.3	0.188
DO	2.4	1.3	0.238

**Fig. 6** RDA ordination of fish assemblages and environmental variables from the mangrove creek in the NRE. (Notes: species names were used by generic acronym and the first three letters of the species name in Table 1. WT, water temperature; COD, chemical oxygen demand; TN: total nitrogen; TOC, total organic carbon)

exploit mangroves, resulting in higher species richness in summer (Fig. 3). *C. zillii* had a positive correlation with TOC and COD (Fig. 6). The sources of TOC and COD in mangroves were the combination of degradation and release of mangrove litter, benthic microalgae, and plant detritus imported with tides, which provided ample food for *C. zillii* (Tsutsumi et al. 2006; Kristensen et al. 2008). It was worth noting that the input of emissions from shrimp ponds in summer and autumn increased organic nutrition for *C. zillii*,

which was consistent with the higher TOC and COD in summer and autumn (Fig. 5). Nevertheless, *C. zillii* abundance peaked in the autumn rather than in the breeding peak season (summer) (Table 2) (El-Sayed, H.K.A.; Moharram 2007), which was caused by the maximum values of feeding activity that was during autumn before overwintering (Shehata et al. 2017; Gu et al. 2018). The most fish species in biomass were *C. zillii* (20.46%), and this was the reason that fish biomass in autumn was the highest (Fig. 3).

### Mangrove utilization of different ecological guild

Mangrove/estuary-resident species are composed of 28 species, mainly Gobiidae (16 species), Leotridae (3 species), Ambassidae (2 species), *Pisodonophis boro*, *Thryssa vitrirostris*, *Encrasicholina heteroloba*, *Sillago sihama*, *Acanthopagrus latus*, *Elops machnata*, and *Selenotoca multifasciata*. This group was considered euryhaline due to their adaptability to variable salinities and also since most species appeared in all four seasons, indicating that mangrove ecosystems provide habitats and/or food sources for these species (Krumme et al. 2015; Wu et al. 2018). Estuarine resident species had higher relative abundances in winter at a small estuary of the Portuguese coast and was more abundant during the wet season in Indian estuaries (Cardoso et al. 2011; GB et al. 2020), which indicated seasonal variations were found in the abundances of estuarine-resident species. In our study, the abundance of mangrove-resident species in autumn and winter was higher than that in spring and summer, which was the result of a large number of *A. urotaenia* and *P. javanicus* moving into mangroves (Fig. 2; Table 2). The reasons for the remarkably larger-sized individuals of *A. urotaenia* and *P. javanicus* in the mangrove creeks in autumn and winter are unclear and deserve further study. Functions such as feeding, rearing, or predator avoidance may have been involved.

Mangrove/estuary-transient species were formed by diadromous species (those that migrate between freshwater and marine habitats), including *M. cephalus*, *T. jarbua*, and *Salanx ariakensis*. From last winter to the next summer, this group occupied a certain proportion in mangrove creeks, and the number of individuals was the most in summer and winter (Fig. 2). During their own spawning migration season, the abundance of *M. cephalus* and *T. jarbua* was higher than that in the other three seasons (Table 2) (Miu et al. 1990; Ibanez et al. 2012). These species stayed in mangroves and regulated osmotic pressure to adapt to salinity changes after moving into seawater/freshwater (Kültz 2015). Thus, the mangrove creeks were used as a breeding migration transit area for these two species.

The mangrove/estuary-occasional species consists of 14 species, including 6 freshwater species (*G. affinis*, *Poecilia latipinna*, *Hypophthalmichthys nobilis*, *C. zillii*,

*Oreochromis niloticus*, and *Macropodus opercularis*) and 8 marine species (*Sardinella aurita*, *Sardinella gibbose*, *Hypoatherina tsurugae*, *Scorpaenopsis gibbose*, *Epinephelus fuscoguttatus*, *Branchiostegus argentatus*, *Lagocephalus spadiceus*, and *Solea ovata*). Except for *G. affinis* and *C. zillii*, the frequency and the abundance of these species were low in this category (Table 1), which was washing into mangroves by tides or freshwater runoff accidentally. Besides, *G. affinis* moved into mangroves for foraging and avoiding the pressure of high temperature in the shade of mangrove creeks (Hendy et al. 2020). *C. zillii* took mangrove creeks as a temporary transit place for overwintering. Hence, the mangrove creeks were used as a refuge for these two species.

## Conclusion

This study was conducted in an estuarine mangrove of an unnatural reserve. Our findings emphasized that fish assemblages had seasonal variations in the mangrove creeks system in NRE. Mangrove creeks provided habitats for mangrove/estuary-resident species. It also was a breeding migration transit area for mangrove/estuary-transient species and provided refuges for mangrove/estuary-occasional species that migrated to mangroves intentionally. Mangrove restoration has been currently carried out in China, and the mixed forests to increase habitat complexity of the mangrove should be taken into account in the restoration process to ensure good connectivity between mangroves and other types of habitats.

**Acknowledgements** We gratefully acknowledge the support of Guangxi Key Laboratory of Environmental Pollution Control Theory and Technology for Science and Education Combined with Science and Technology Innovation Base for their vital help during samplings. Thanks to Dr. Liu Qi for improving this manuscript and thanks to Saeed Rad for helping to polish this manuscript.

**Author contribution** L.L. Huang and X. Huang developed the basic idea and designed the investigation. X. Huang, L.L. Huang, H. Liu, J.L. Chen, and L.Y. Gui performed the sampling collection and processing. X. Huang and H. Liu performed the data analyses. X. Huang led the original writing. L.L. Huang reviewed and made corrections to improve the paper. All authors read the full paper and agreed to its publication.

**Funding** This research was supported by the National Natural Science Foundation of China (Grant Number: U20A2087), Natural Science Foundation of Guangxi Province (2018GXNSFAA281022), the Guangxi “Bagui Scholar” Construction Project (2016A10), and “Chunhui Planning” Project from the Ministry of Education, China.

**Data availability** All data generated or analyzed during this study are included in this published article.

## Declarations

**Ethics approval and consent to participate** The experimental protocol was established, according to the ethical guidelines of the Council for Laboratory Animal Science of the Guilin University of Technology. Written informed consent was obtained from individual or guardian participants.

**Consent for publication** Not applicable.

**Competing interests** The authors declare no competing interests.

## References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46. <https://doi.org/10.1046/j.1442-9993.2001.01070.x>
- Barletta M, Amaral CS, Correa MFM et al (2008) Factors affecting seasonal variations in demersal fish assemblages at an ecocline in a tropical-subtropical estuary. *J Fish Biol* 73:1314–1336. <https://doi.org/10.1111/j.1095-8649.2008.02005.x>
- Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G (2003) Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar Ecol Prog Ser* 256:217–228. <https://doi.org/10.3354/meps256217>
- Cardoso I, França S, Pais MP et al (2011) Fish assemblages of small estuaries of the Portuguese coast: a functional approach. *Estuar Coast Shelf Sci* 93:40–46. <https://doi.org/10.1016/j.ecss.2011.03.016>
- Castellanos-Galindo GA, Krumme U (2015) Tides, salinity, and biogeography affect fish assemblage structure and function in macrotidal mangroves of the neotropics. *Ecosystems* 18:1165–1178. <https://doi.org/10.1007/s10021-015-9887-4>
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- de Azevedo MCC, da Cruz AG, Araujo FG (2016) Mangrove habitat use by fishes in Southeastern Brazil: are there temporal changes in the structure of the community? *Mar Ecol Evol Perspect* 37:1223–1238. <https://doi.org/10.1111/maec.12302>
- Desmond JS, Deutschman DH, Zedler JB (2002) Spatial and temporal variation in estuarine fish and invertebrate assemblages: analysis of an 11-year data set. *ESTUARIES* 25:552–569. <https://doi.org/10.1007/BF02804890>
- El-Sayed HKA, Moharram SG (2007) Reproductive biology of *Tilapia zillii* (Gerv, 1848) from Abu Qir Bay, Egypt. *Egypt J Aquat Res* 33:379–393
- Froese R, Pauly D (2020) FishBase. World Wide Web electronic publication
- GB S, AK J, HB S et al (2020) Fish composition and assemblage structure in tropical monsoonal estuaries: estuarine use and feeding guild approach. *Estuar Coast Shelf Sci* 244:106911. <https://doi.org/10.1016/j.ecss.2020.106911>
- Gu DE, Yu FD, Xu M et al (2018) Temperature effects on the distribution of two invasive tilapia species (*Tilapia zillii* and *Oreochromis niloticus*) in the rivers of South China. *J Freshw Ecol* 33:511–524. <https://doi.org/10.1080/02705060.2018.1517698>
- Hendy IW, Burt O, Clough S et al (2020) Mosquitofish avoid thermal stress by moving from open water to the shade of the mangrove *Rhizophora mangle*. *Mar Ecol Prog Ser* 637:103–116. <https://doi.org/10.3354/meps13253>

- Hsu C, Han Y, Tzeng W (2007) Evidence of flathead mullet *Mugil cephalus* L. spawning in waters northeast of Taiwan. *Zool Stud* 46:717–725
- Huang J, Huang L, Wu Z et al (2019) Correlation of fish assemblages with habitat and environmental variables in a headwater stream section of Lijiang River, China. *Sustain* 11:1–14. <https://doi.org/10.3390/su11041135>
- Huang LL, Huang DL, Wu ZQ et al (2016) Temporal variation of fish diversity and assemblages and their associations to environmental variables in the mangrove of Qinzhou Harbor, Guangxi Province, China. *Turkish J Fish Aquat Sci* 16:297–310. [https://doi.org/10.4194/1303-2712-v16\\_2\\_10](https://doi.org/10.4194/1303-2712-v16_2_10)
- Ibáñez Aguirre AL, Gallardo-Cabello M (2004) Reproduction of *Mugil cephalus* and *M. curema* (Pisces: Mugilidae) from a coastal lagoon in the Gulf of Mexico. *Bull Mar Sci* 75:37–49
- Ibanez AL, Chang CW, Hsu CC et al (2012) Diversity of migratory environmental history of the mullets *Mugil cephalus* and *M. curema* in Mexican coastal waters as indicated by otolith Sr:Ca ratios. *CIENCIAS Mar* 38:73–87. <https://doi.org/10.7773/cm.v38i1A.1905>
- Igulu MM, Nagelkerken I, van der Velde G, Mgya YD (2013) Mangrove fish production is largely fuelled by external food sources: a stable isotope analysis of fishes at the individual, species, and community levels from across the globe. *Ecosystems* 16:1336–1352. <https://doi.org/10.1007/s10021-013-9687-7>
- Ikejima K, Tongnunui P, Medej T, Taniuchi T (2003) Juvenile and small fishes in a mangrove estuary in Trang province, Thailand: seasonal and habitat differences. *Estuar Coast SHELF Sci* 56:447–457. [https://doi.org/10.1016/S0272-7714\(02\)00194-4](https://doi.org/10.1016/S0272-7714(02)00194-4)
- Jin B, Fu C, Zhong J et al (2007) Fish utilization of a salt marsh intertidal creek in the Yangtze River Estuary, China. *Estuar Coast Shelf Sci* 73:844–852. <https://doi.org/10.1016/j.ecss.2007.03.025>
- Kaiser D, Unger D, Qiu G et al (2013) Natural and human influences on nutrient transport through a small subtropical Chinese estuary. *Sci Total Environ* 450:92–107. <https://doi.org/10.1016/j.scitotenv.2013.01.096>
- Kindong R, Wu J, Gao C et al (2020) Seasonal changes in fish diversity, density, biomass, and assemblage alongside environmental variables in the Yangtze River Estuary. *Environ Sci Pollut Res* 27:25461–25474. <https://doi.org/10.1007/s11356-020-08674-8>
- Kristensen E, Bouillon S, Dittmar T, Marchand C (2008) Organic carbon dynamics in mangrove ecosystems: a review. *Aquat Bot* 89:201–219. <https://doi.org/10.1016/j.aquabot.2007.12.005>
- Krumme U, Grinvalds K, Zagars M et al (2015) Tidal, diel and lunar patterns in intertidal and subtidal mangrove creek fish assemblages from southwest Thailand. *Environ Biol Fishes* 85:208–216. <https://doi.org/10.1007/s10641-015-0393-5>
- Kültz D (2015) Physiological mechanisms used by fish to cope with salinity stress. *J Exp Biol* 218:1907–1914. <https://doi.org/10.1242/jeb.118695>
- Lai T, He B (2016) Marine osteichthyes fishes in Guangxi Beibu Gulf of China. Science Press, Beijing
- Jing L, Wu R, Kang B, Ma L (2016) Fishes of Beibu Gulf. Science Press, Beijing
- Liu T, Liu SF, Wu B et al (2020) Increase of organic carbon burial response to mangrove expansion in the Nanliu River estuary, South China Sea. *Prog EARTH Planet Sci* 7. <https://doi.org/10.1186/s40645-020-00387-3>
- Liu T, Tao Y, Liu Y (2017) Mangrove swamp expansion controlled by climate since 1988: a case study in the Nanliu River Estuary, Guangxi, Southwest China. *Acta Oceanol Sin* 36:11–17. <https://doi.org/10.1007/s13131-017-1097-9>
- Mahesh R, Saravanakumar A (2015) Temporal and spatial variability of fin fish assemblage structure in relation to their environmental parameters in Pichavaram mangrove ecosystem, India. *Indian J Geo-Marine Sci* 44:910–923
- Mandal B, Mukherjee A, Banerjee S (2013) A review on the ichthyofaunal diversity in mangrove based estuary of Sundarbans. *Rev Fish Biol Fish* 23:365–374. <https://doi.org/10.1007/s11160-012-9300-8>
- Miu T-C, Lee S-C, Tzeng W-N (1990) Reproductive biology of *Tetraodon lineatus* from the estuary of Tamshui River. *J Fish Soc Taiwan* 17:9–20. 10.29822/JFST.199003.0002
- Mwanda AW, Gullstrom M, Andersson MH et al (2010) Spatial and seasonal variations of fish assemblages in mangrove creek systems in Zanzibar (Tanzania). *Estuar Coast Shelf Sci* 89:277–286. <https://doi.org/10.1016/j.ecss.2010.08.002>
- Nagelkerken I, Blaber SJM, Bouillon S et al (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat Bot* 89:155–185. <https://doi.org/10.1016/j.aquabot.2007.12.007>
- Pichler HA, Spach HL, Gray CA et al (2015) Environmental influences on resident and transient fishes across shallow estuarine beaches and tidal flats in a Brazilian World Heritage area. *Estuar Coast Shelf Sci* 164:482–492. <https://doi.org/10.1016/j.ecss.2015.07.041>
- Pinkas L, Oliphant SM, Iverson L.K.I (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. State of California, Dept. of Fish and Game, State of California
- Potter IC, Tweedley JR, Elliott M, Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish Fish* 16:230–239. <https://doi.org/10.1111/faf.12050>
- Pyke GH (2005) A review of the biology of *Gambusia affinis* and *G. holbrooki*. *Rev Fish Biol Fish* 15:339–365. <https://doi.org/10.1007/s11160-006-6394-x>
- Rehage JS, Loftus WF (2007) Seasonal fish community variation in headwater mangrove creeks in the southwestern everglades: an examination of their role as dry-down refuges. *Bull Mar Sci* 80:625–645
- Rekha MU, Tomy S, Sukumaran K et al (2021) Comparison of the reproductive biology of two stocks of Indian subcontinental *Mugil cephalus* (Linnaeus, 1758) with special reference to reproductive isolation and philopatry. *Indian J Geo-Marine Sci* 50:130–140
- Rousseau Y, Blanchard F, Gardel A (2018) Spatiotemporal dynamics of larval fish in a tropical estuarine mangrove: example of the Mahury River Estuary (French Guiana). *Can J Fish Aquat Sci* 75:235–246. <https://doi.org/10.1139/cjfas-2016-0267>
- Ruppert JLW, Vigliola L, Kulbicki M et al (2018) Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs. *Glob Chang Biol* 24:E67–E79. <https://doi.org/10.1111/gcb.13882>
- Shahraki M, Saint-Paul U, Krumme U, Fry B (2016) Fish use of intertidal mangrove creeks at Qeshm Island. *Iran. Mar Ecol Prog Ser* 542:153–166. <https://doi.org/10.3354/meps11546>
- Shehata S, Ghanem M, Ragab A (2017) Effect of some environmental factors on the food and feeding habits of the cichlid fish, *Tilapia zillii*, inhabiting Lake Qarun, Egypt. *Egypt Acad J Biol Sci B Zool* 9:55–70. 10.21608/eajbsz.2017.13457
- Sloterdijk H, Brehmer P, Sadio O et al (2017) Composition and structure of the larval fish community related to environmental parameters in a tropical estuary impacted by climate change. *Estuar Coast Shelf Sci* 197:10–26. <https://doi.org/10.1016/j.ecss.2017.08.003>
- Šmilauer P, Lepš J (2014) Multivariate analysis of ecological data using CANOCO 5, 2nd edn. Cambridge University Press, Cambridge, UK
- Tsai CH, Wang YK, Te TS, Wu SH (2015) Seasonal and diel changes of the fish assemblage employing the fyke nets in a subtropical mangrove estuary of Puzih River, Taiwan. *J Mar Sci Technol* 23:109–116. <https://doi.org/10.6119/JMST-014-0110-3>
- Tsutsumi H, Srithongouthai S, Inoue A et al (2006) Seasonal fluctuations in the flux of particulate organic matter discharged from net pens for fish farming. *Fish Sci* 72:119–127. <https://doi.org/10.1111/j.1444-2906.2006.01125.x>

- Vaslet A, Phillips DL, France C et al (2012) The relative importance of mangroves and seagrass beds as feeding areas for resident and transient fishes among different mangrove habitats in Florida and Belize: evidence from dietary and stable-isotope analyses. *J Exp Mar Bio Ecol* 434:81–93. <https://doi.org/10.1016/j.jembe.2012.07.024>
- Wainaina MW, Kaunda-Arara B, Njiru JM (2013) Seasonality in fish assemblage structure in an East African mangrove creek. *African J Mar Sci* 35:163–173. <https://doi.org/10.2989/1814232x.2013.769904>
- Wang M, Huang Z, Shi F, Wang W (2009) Are vegetated areas of mangroves attractive to juvenile and small fish? The case of Dongzhaigang Bay, Hainan Island, China. *Estuar Coast Shelf Sci* 85:208–216. <https://doi.org/10.1016/j.ecss.2009.08.022>
- Wu DX, Wang Y, Lin XP, Yang JY (2008) On the mechanism of the cyclonic circulation in the Gulf of Tonkin in the summer. *J Geophys Res* 113:10. <https://doi.org/10.1029/2007jc004208>
- Wu Z-Q, Zou Q, Chang T et al (2018) Seasonal dynamics of the juvenile fish community structure in the Maowei Sea mangroves. *PLoS One* 13. <https://doi.org/10.1371/journal.pone.0192426>
- Yang J, Zhang R, Zhao Z, et al (2015) Temporal and spatial distribution characteristics of nutrients in the coastal seawater of Guangxi Beibu Gulf during the past 25 years. *Ecol Environ Sci* 24:1493–1498. 10.16258/j.cnki.1674-5906.2015.09.011
- Zhang Y, Ding Y, Wang W et al (2019) Distribution of fish among *Avicennia* and *Sonneratia* microhabitats in a tropical mangrove ecosystem in South China. *Ecosphere* 10. <https://doi.org/10.1002/ecs2.2759>

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