Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 49, No. 1, March 2020
pages (34-48)

ISSN 1730-413X
eISSN 1897-3191

Dominant species drive seasonal dynamics of the fish community in the Min estuary, China

by

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DOI: **10.1515/ohs-2020-0004**
Category: **Original research paper**
Received: **May 5, 2019**
Accepted: **August 21, 2019**

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Abstract

Fishery resources are currently facing multiple stresses such as overfishing, pollution and climate change. Looking into processes and mechanisms of the dynamic fish community through detailed quantitative analyses contributes to effective conservation and management of fishery resources. The Min estuary plays an important role in maintaining fisheries in southeastern coastal China, therefore the fish community in the brackish area was investigated and analyzed in this study. A total of 127 species belonging to 91 genera, 49 families and 14 orders were sampled in 2015. Eight indices reflecting four aspects of fish communities were determined, i.e. species richness, species evenness, heterogeneity and taxonomy. Differences between the indices were nonsignificant, suggesting that the use of a single diversity descriptor could not provide a full explanation. Nine dominant species in the Min estuary showed seasonal turnover by rational use of resources and co-occurring species showed correspondingly adequate habitat preferences and feeding habits to avoid competition. The species *Harpadon nehereus* occurred as the dominant species in three seasons except spring. High values of niche overlap among common or rare species and lower values of niche overlap among all dominant species effectively brought the diversity of the fish community into a state of equilibrium.

Key words: composition, diversity, ecological niche, interspecific competition, migration

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Introduction

China has one of the longest coastlines in the world, stretching over 14 500 km from the border with North Korea in the north to Vietnam in the south (Liu 2013). Estuaries with mixed waters constitute a complex of different habitat types with sudden changes in temperature, salinity and depth, and are regarded as feeding grounds and nursery areas for both migrant and resident species (Blaber 1997; Elliott et al. 2007; Kerr et al. 2010; Potter et al. 2015), thus supporting high levels of fisheries (McLusky & Elliott 2007). Meanwhile, estuaries are also excellent sites for people to live and access to rivers and oceans helps to develop trade and communication. As anthropogenic impact continues to spread, it is crucial to improve the management of resources to protect and preserve habitats and maintain ecosystem functions (Banks-Leite et al. 2014; Lundquist et al. 2017).

In response to oceanographic dynamics and variation in solar irradiation, rainfall and wind conditions, estuaries show very strong environmental gradients, limiting some fish species to a particular section, which contributes to complex spatio-temporal patterns in fish communities (Nicolas et al. 2010; de Moura et al. 2012; Basset et al. 2013). Furthermore, the sequential immigration and emigration of fish species for spawning, nursing and wintering result in pronounced cyclical seasonal changes in the fish fauna composition (Hoeksema & Potter 2006; Eick & Thiel 2014). Such complexity makes it difficult to manage and control sustainable fisheries and it is therefore necessary to understand the processes and mechanisms of dynamic fisheries through detailed quantitative analysis of fish communities (Elliott & Hemingway 2002; Franco et al. 2008). Some measures, such as species composition, diversity, abundance and biomass provide information on the structure of fish assemblages and corresponding environmental conditions, thus offering complementary insights into fish assemblages for both theoretical and field studies (Magurran 2004; Eick & Thiel 2014). In addition to the classic index, i.e. species richness and, to a lesser extent, species evenness, which continue to play a dominant role as substitutes for diversity measures in many studies, the use of a multi-component diversity index should be encouraged to properly describe and monitor the main components of species diversity, e.g. Margalef's species richness, the Shannon–Wiener index, Pielou's index, Heip's evenness index, the Simpson concentration index, the taxonomic distinctness index, etc., in order to take full account of the ecosystem functions at different management scales (Gaertner et al. 2010; Loiseau et al. 2016).

Species of a given assemblage constituting the largest biomass in an ecosystem is considered a dominant species that can affect the distribution of other organisms and define that ecosystem and its characteristics. A dominant species may be more effective in obtaining resources, resisting disturbance or deterring competitors compared to other species (Miller et al. 2015). In addition, information on spatial niche overlap and segregation among species is essential for further understanding the population structure and dynamics (Cohen 1977; Navarro et al. 2013). Species with similar habitat preferences tend to engage in biological interactions and co-occur together (Mahon et al. 1998; Tews et al. 2003). Spatial patterns of fish movement can be determined by a number of factors, including the size of individuals and modes of reproduction (Dunlop et al. 2009; Enberg et al. 2010; Heino et al. 2015), interspecific and intraspecific competition for resources (Shulman 1985; Marshall & Elliott 1997; Svanbäck et al. 2008), habitat composition (Kamrani et al. 2016; Maree et al. 2016; Polansky et al. 2018), and abiotic factors (Bacheler et al, 2009; Payne et al. 2013; da Silva Jr et al. 2016). However, knowledge of niche partitioning among sympatric fish species in estuaries has remained scarce.

The Min estuary, located in the southeastern part of China, is a typical subtropical estuary. The complexity and variability of hydrodynamic characteristics of the Min estuary attract many types of fish and make the Min estuary an important fishery resource. The Min estuary is currently an important economic area with increasing industrialization, urbanization, population growth and rapidly developing agricultural practices (Yue et al. 2015; Gao et al. 2017), which pose a major challenge to the ecological health of the estuarine ecosystem. However, there is still a substantial lack of detailed information regarding the quantitative composition and seasonal variation of the fish fauna in the Min estuary, as well as the internal mechanism as to how the structure is maintained. The main objectives of the present work were: 1) to describe the composition and species diversity of the fish community; 2) to identify dominant species based on their abundance, biomass and seasonal turnover; 3) to explain the seasonal variation of the fish community through interspecific relationships and ecological niche overlap among dominant species.

Materials and methods

Study area

The study was carried out in the brackish area

(25°50′00″–26°20′00″N; 119°30′00″–120°00′00″E) of the Min estuary (Fig. 1). The climate of the area is characterized by a typical subtropical monsoon with seasonal variations. The mean annual temperature is 19.85°C with a range of 9.8–32.2°C (Hu et al. 2017). The mean annual discharge of the Min River is 1760 $m^3 s^{-1}$, with a seasonally uneven distribution as a maximum value occurs in April–July (average 3200 $m^3 s^{-1}$) and a minimum in October–March (average 620 $m^3 s^{-1}$; Yang et al. 2007; Hu et al. 2014). The mean depth of the river is 3 m upstream and the maximum depth is 30 m downstream (Zhang et al. 2015). The tide is irregular and semi-diurnal, and salinity significantly increases when the runoff drastically decreases (Fang et al. 2017).

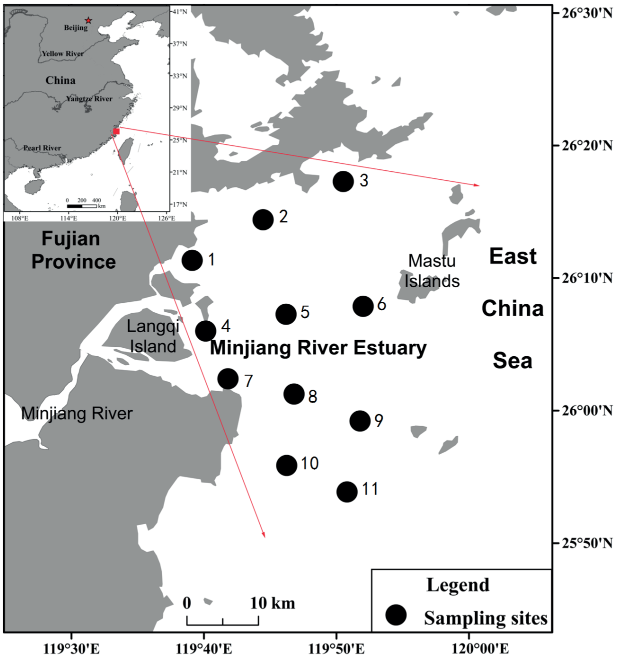

Figure 1

Sketch map of the study area (the Min estuary, southeastern China) with the sampling sites as solid circles

Sampling procedure

Fish surveys were performed seasonally (May in spring, August in summer, November in autumn and February in winter) at 11 sampling locations in 2015 (Table 1). Bottom trawling was used (horizontal aperture 7.5 m, vertical opening height 3 m, deploy distance 45 m, and mesh size 63 mm at the net opening and 25 mm at the cod end). The net was operated for half an hour at each sampling site at a towing speed of approximately 3.3–4.3 knots (corresponding to 6.02–7.85 km h^{-1}) to collect fish. Samples from each site were put into an ice container by site groupings for preservation and sent to the laboratory for further analysis. Species were taxonomically identified according to the monographs "Fishes of the Fujian Province" (Part I, II; Fishes of the Fujian Province Editorial Subcommittee, 1984; 1985), and scientific names were checked against www.fishbase.org. At each site, the number of individual species was counted to determine their abundance and each species was weighted to determine the biomass.

Data analysis

Non-metric multi-dimensional scaling (nMDS) was performed on species biomass across sampling locations in the Min estuary. The resulting ordinations were examined for seasonal groupings that indicate potential structuring within the fish community. The non-parametric analysis ANOSIM was used to test the statistically significant ($p < 0.05$) differences between the sampling seasons (Clarke & Gorley 2006).

To identify different aspects of the species diversity, the demersal fish community was analyzed

Table 1

Geological and environmental information on sampling locations in different seasons in the Min estuary

Location	Latitude	Longitude	Water temperature				Salinity				Water depth			
			Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
1	26.189	119.652	20.8	26.2	21.9	14.9	28.0	29.5	29.1	27.5	11.2	10.5	10.7	10.9
2	26.240	119.741	21.0	27.1	21.9	14.7	30.3	32.5	29.4	31.3	10.2	13.6	13.2	11.7
3	26.288	119.842	20.4	26.2	21.5	15.3	32.2	33.0	28.2	33.1	20.8	18.2	19.9	19.6
4	26.111	119.669	21.7	26.5	22.6	15.5	25.8	29.6	25.6	27.0	10.6	11.6	8.2	9.1
5	26.121	119.770	20.9	27.4	21.8	16.2	30.3	31.6	28.9	32.2	12.7	11.5	10.0	13.1
6	26.131	119.867	20.9	25.6	22.7	15.6	23.8	32.5	29.0	34.0	19.7	23.4	22.3	22.6
7	26.040	119.697	21.1	27.0	22.6	14.8	23.7	25.9	19.8	27.1	7.3	7.1	8.2	9.1
8	26.018	119.780	21.2	27.0	22.7	14.7	28.5	31.1	16.1	32.3	13.1	12.7	14.8	15.1
9	25.987	119.863	22.2	26.6	22.5	13.3	20.7	31.5	30.0	36.2	18.3	22.0	19.0	17.8
10	25.931	119.770	22.1	27.7	22.5	13.3	25.5	31.3	23.7	31.0	15.7	16.6	13.7	14.3
11	25.850	119.833	21.1	26.8	22.6	13.0	30.8	34.3	25.3	33.0	25.6	24.7	24.3	24.7

employing four types of indices representing the main components of the diversity (Table 2): 1) species richness, using two indices as the number of species *S* and Margalef's species richness index D (Margalef 1958); 2) species evenness, which refers to how close in numbers each species in a habitat is, e.g. Pielou's index *J'* (Pielou 1966), the most commonly used evenness index, despite significant controversy over its performance (Heip et al. 1998), and Heip's evenness index E_{Heip} (Heip 1974), mainly sensitive to the variation in rare species (Beisel et al. 2003). The less evenness in communities between the species, the higher *J'* value is. Unlike *J'*, E_{Heip} is less sensitive to variation in the number of species (Smith & Wilson 1996). 3) heterogeneity, described by the Shannon–Wiener index *H'* (Shannon & Weaver 1949) and the Simpson concentration index λ (Simpson 1949), which combine both the number of species and evenness components in a single value. The index *H'* is assumed to be sensitive to changes in the abundance of rare species, while λ is strongly weighted toward dominant species (Peet 1974). It is assumed that a high value of *H'* represents a high ecological quality status, while a high value of λ indicates a low ecological quality status. In our study, we chose an alternative one $1 - \lambda$ to maintain a similar trend of variation as *H'*; and 4) taxonomy, describing taxonomic and phylogenetic characters of the fish community and helping to improve knowledge for conservation purposes. The first three sets of indices were determined based on the abundance data. To avoid the bias of abundance and biomass, presence/absence data as well as the default value 1 for the branch length of each taxonomic category were used to determine the taxonomic indices, including: 1) average taxonomic distinctness Δ^{+}, an average distance tracing through the taxonomic tree between every pair of individuals in a sample; 2) variation in taxonomic distinctness $\wedge^{+}$, considering the evenness of taxa distribution across the hierarchical taxonomic tree (Warwick & Clarke 1995). Differences among all analyzed indices were examined using one-way ANOVA. Calculations of all indices and multivariate analysis were performed using the software PRIMER V6 (Clarke & Gorley 2006).

Index of relative importance

Dominant species were identified with the index of relative importance *IRI* (Pianka 1971) calculated as follows: $IRI = (N\% + W\%) \times F\%$, where *N*% and *W*% are the ratios of each fish species relative to the total species caught by number (*N*) and by weight (*W*) respectively, and *F* is the occurrence frequency of that fish species. In general, the criterion for defining dominant species varies. They were determined according to *IRI* values of the top species, e.g. in different areas; species with $IRI > 1000$ (Zhu et al. 1996), or $IRI > 500$ (Tan et al. 2012), or $IRI > 100$ (Wang et al. 2011) were used in a discriminatory way to identify dominant species. In this study, species with $IRI > 1000$ were grouped into dominant groups and species with values of 500–1000 into common groups.

Ecological niche

The ecological niche index, describing the n-dimensional space associated with survival and reproduction of living organisms, has been frequently

Table 2

Species diversity components and descriptors. x_i (i = 1, 2, ..., S) denotes the abundance of the *i*th species, N is the total number of individuals in the sample, P_i is the proportion of all individuals belonging to species *i*, ω_{ij} is the "distinctness weight" given to the path length linking species *i* to the first common node with species *j* in the hierarchical classification

Component	Descriptor name	Formula	Expected properties	Reference
Richness	Species density	S = number of species	Standardize species richness per unit area	
	Margelef	$D = \frac{S-1}{Ln(N)}$	Adjusted species richness by *N*	Margelef (1958)
Evenness	Pielou index	$J' = \frac{H'}{Log(S)}$	Evenness based on the Shannon-Wiener index *H'*	Pielou (1966)
	Heip	$E_{Heip} = \frac{exp(H') - 1}{S-1}$	Sensitive to rare species	Heip (1974)
Heterogeneity	Shannon-Wiener	$H' = -\sum_{i=1}^{S} P_i \ln P_i$	Sensitive to rare species	Shannon and Weaver (1949)
	Simpson diversity	$1 - \lambda = \sum_{i=1}^{S} P_i^2$	Sensitive to dominant species	Simpson (1949)
Taxonomy	Average taxonomic distinctness	$\Delta^{+} = 2\frac{\sum\sum_{i<j} \omega_{ij}}{S(S-1)}$	natural extensions of Simpson diversity including taxonomic relatedness	Clarke and Warwick (1998)
	Variation in taxonomic distinctness	$\wedge^{+} = 2\frac{\sum\sum_{i<j} (\omega_{ij} - \Delta^{+})}{S(S-1)}$	Evenness of the taxonomic level distribution in the taxonomic tree	Clarke and Warwick (1998)

used to analyze the shift of dominant species through interspecific relationship, and can be calculated as follows:

$$B_i = -\sum_{j=1}^{r} P_{ij} Ln P_{ij}$$

where B_i refers to the ecological niche breadth, P_{ij} is the ratio of species *i* at sampling site *j* relative to the total number of fish at sampling site *j*, and *r* is the total number of sampling sites (Levins 1968). To explain the competition between two species, the overlap of the niche breadth was calculated according to the formula:

$$O_{ik} = \sum_{p=1}^{n} \frac{(P_{ij} \times P_{kj})}{\sqrt{\sum_{j=1}^{n} P_{ij}^2 \sum_{j=1}^{n} P_{kj}^2}}$$

(Pianka 1973), where O_{ik} is the niche overlap between species *i* and *k*, with the value range of 0–100 expressed in percent; P_{ij} and P_{kj} are the ratios of the number of species *i* and *k* to the number of individuals at site *j*. Differences in ecological niches of the dominant species in different seasons were examined using one-way ANOVA.

Results

Taxonomic composition

Table 3 shows taxonomic characteristics of fish species, their abundance and biomass in different seasons. A total of 127 species belonging to 91 genera, 49 families and 14 orders were sampled. In total, 57 species were from Perciformes, accounting for about 45% of the total number of species, followed by about 10% from Clupeiformes and 9% from Pleuronectiformes. At the family level, both Sciaenidae and Gobiidae ranked first, each accounting for 8% of the total number of species, followed by Engraulidae (7%) and Tetraodontidae (7%). *Cynoglossus* and *Takifugu* were the dominant genera, each contributing 4% to the total number of species, followed by *Pampus*, *Thryssa* and *Dasyatis* with 3% respectively.

As far as the seasonal aspect is concerned, 64 species were sampled in spring and their number increased to 78 species in summer, then decreased to 49 species in autumn and 46 species in winter. In the non-metric multi-dimensional scaling analysis and the similarity test ANOSIM, the taxonomic composition of fish communities in different seasons could be effectively distinguished ($p < 0.01$), except between autumn and winter based on the abundance data, while considering the biomass data, fish assemblages in summer and winter showed significant differences compared to other seasons (Fig. 2).

Diversity

Table 4 shows eight diversity indices for different seasons. The two species-richness indices show a significant correlation at 0.823. They were not correlated with other indices, except for *D* and *H′* that showed correlation at 0.693. The evenness index E_{Heip} and *J′* showed significant relevance at 0.9249. Two heterogeneous indices *H′* and *J′* showed a high correlation at 0.9434, both of which were to some extent related to E_{Heip} and *J′*. Interestingly, *J′* showed higher relative values with *H′* and 1 – λ than E_{Heip}. The average taxonomic distinctness Δ^+ was negatively correlated with the variation in taxonomic distinctness Λ^+ with relevance –0.6708, and both were independent of other indices (Fig. 3).

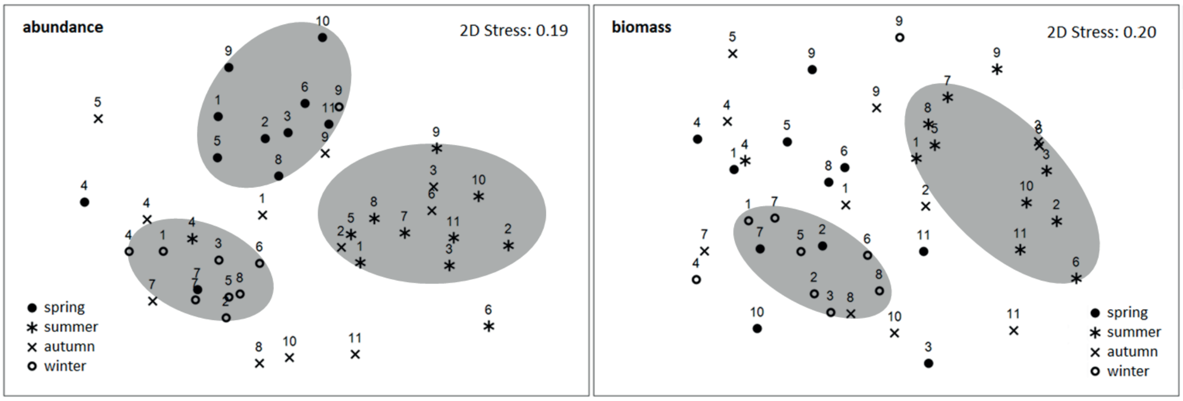

Figure 2

Non-metric multi-dimensional scaling ordination of the sampling locations in the Min estuary in 2015, ordered according to fish abundance (left) and biomass (right) recorded in each season

Table 3

List of fish with their taxonomic status, seasonal abundance and biomass in the Min estuary (-- denotes no samples)

Order	Family	Genus	Species	Spring		Summer		Autumn		Winter	
				abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)
Carcharhiniformes	Carcharhinidae	*Scoliodon*	*Scoliodon laticaudus*	--	--	7	409.6	--	--	--	--
Rajiformes	Rhinobatidae	*Rhinobatos*	*Rhinobatos hynnicephalus*	--	--	--	--	--	--	2	886.2
		Platyrhina	*Platyrhina tangi*	--	--	--	--	2	693.3	--	--
			Platyrhina sinensis	1	300.0	3	455.8	--	--	1	351.7
Myliobatiformes	Dasyatidae	*Dasyatis*	*Dasyatis akajei*	--	--	--	--	--	--	1	210.5
			Dasyatis laevigata	1	293.0	1	1468.0	--	--	--	--
			Dasyatis zugei	1	641.0	4	1478.5	7	1987.5	--	--
			Dasyatis navarrae	1	10018.0	--	--	2	4339.3	--	--
		Taeniura	*Taeniura meyeni*	1	299.9	--	--	--	--	--	--
Anguilliformes	Muraenesocidae	*Muraenesox*	*Muraenesox cinereus*	26	1120.4	52	2951.4	2	245.7	7	226.5
	Muraenidae	*Gymnothorax*	*Gymnothorax reticularis*	--	--	2	124.6	--	--	--	--
	Congridae	*Conger*	*Conger myriaster*	--	--	--	--	--	--	1	30.0
	Ophichthidae	*Pisodonophis*	*Pisodonophis cancrivorus*	9	211.8	4	151.2	11	214.3	--	--
			Pisodonophis boro	--	--	6	131.4	--	--	--	--
		Ophichthus	*Ophichthus apicalis*	--	--	31	707.5	--	--	--	--
		Neenchelys	*Neenchelys parvipectoralis*	--	--	2	61.0	--	--	--	--
Lophiiformes	Antennariidae	*Antennarius*	*Antennarius hispidus*	--	--	2	51.2	--	--	--	--
Gonorynchiformes	Gonorynchidae	*Gonorynchus*	*Gonorynchus abbreviatus*	--	--	5	140.5	--	--	--	--
Siluriformes	Bagridae	*Tachysurus*	*Tachysurus sinensis*	2	238.8	--	--	5	109.3	3	59.01
Clupeiformes	Clupeidae	*Konosirus*	*Konosirus punctatus*	49	1050.6	--	--	1	88.3	6	158.9
		Sardinella	*Sardinella zunasi*	20	312.8	1	4.5	--	--	--	--
	Pristigasteridae	*Ilisha*	*Ilisha elongata*	7	160.5	1	13.4	77	1913.2	4	150.7
	Engraulidae	*Setipinna*	*Setipinna taty*	110	1944.8	182	2829.6	90	866.2	1	3.3
		Coilia	*Coilia mystus*	211	2422.7	19	231.5	546	5261.7	1250	9977.8
		Thryssa	*Thryssa kammalensis*	330	1020.0	13	30.5	255	2002.1	20	44.3
			Thryssa vitrirostris	7	72.7	5	13.5	15	147.2	--	--
			Thryssa mystax	2	20.1	--	--	--	--	24	170.7
		Engraulis	*Engraulis japonicus*	--	--	--	--	3	22.2	--	--
		Stolephorus	*Stolephorus commersonnii*	99	102.4	8	21.1	8	7.3	--	--
			Stolephorus chinensis	30	52.2	--	--	--	--	--	--
Aulopiformes	Synodontidae	*Synodus*	*Synodus macrops*	1	3.9	--	--	--	--	--	--
			Synodus hoshinonis	--	--	5	6.5	--	--	--	--
		Harpadon	*Harpadon nehereus*	63	1505.8	1144	34623.2	2284	29280.9	279	9622.1
		Saurida	*Saurida undosquamis*	5	38.9	--	--	--	--	--	--
			Saurida elongata	4	258.2	56	2738.0	1	32.4	28	1612.3
Scorpaeniformes	Scorpaenidae	*Hoplosebastes*	*Hoplosebastes armatus*	--	--	1	1.7	--	--	--	--
		Scorpaena	*Scorpaena miostoma*	--	--	--	--	--	--	10	157.2
	Sebastidae	*Sebastiscus*	*Sebastiscus marmoratus*	2	1.8	4	30.2	2	152	--	--
	Synanceiidae	*Minous*	*Minous monodactylus*	--	--	--	--	1	1.0	--	--
	Platycephalidae	*Cociella*	*Cociella crocodilus*	--	--	7	61.4	--	--	--	--
		Grammoplites	*Grammoplites scaber*	5	208.4	2	108.2	4	42.8	1	13.1
		Platycephalus	*Platycephalus indicus*	2	169.9	4	52.1	1	85.2	--	--
	Triglidae	*Chelidonichthys*	*Chelidonichthys kumu*	328	2254.7	3	82.25	--	--	3	258.7
Mugiliformes	Mugilidae	*Moolgarda*	*Moolgarda cunnesius*	1	28.3	--	--	2	67.4	--	--
		Liza	*Liza carinata*	--	--	--	--	--	--	2	35.0
		Mugil	*Mugil cephalus*	1	26.9	3	80.1	--	--	--	--
Syngnathiformes	Syngnathidae	*Hippocampus*	*Hippocampus kelloggi*	--	--	1	0.9	--	--	--	--
	Fistulariidae	*Fistularia*	*Fistularia petimba*	--	--	5	13.5	--	--	--	--
Perciformes	Lateolabracidae	*Lateolabrax*	*Lateolabrax japonicus*	--	--	--	--	8	4273.0	5	1063.0
	Leiognathidae	*Leiognathus*	*Leiognathus brevirostris*	--	--	--	--	--	--	1	7.04
			Leiognathus berbis	--	--	3	1.3	--	--	--	--
		Equulites	*Equulites rivulatus*	--	--	--	--	1	9.9	--	--
		Nuchequula	*Nuchequula nuchalis*	6	79.37	--	--	--	--	3	22.15
		Secutor	*Secutor ruconius*	982	5120.7	1654	10399.9	299	1545.3	107	282.69
	Terapontidae	*Terapon*	*Terapon theraps*	--	--	1	11.1	2	30.4	--	--
	Siganidae	*Siganus*	*Siganus fuscescens*	--	--	4	35.35	--	--	--	--
			Siganus canaliculatus	--	--	168	1824.5	--	--	--	--
	Carangidae	*Alepes*	*Alepes djedaba*	--	--	10	340.8	--	--	--	--
		Decapterus	*Decapterus maruadsi*	--	--	141	2661.9	--	--	--	--
		Trachurus	*Trachurus japonicus*	2647	6918.6	--	--	--	--	--	--
	Sciaenidae	*Pennahia*	*Pennahia argentata*	1	32.1	6182	20174.7	52	1345.5	--	--
			Pennahia macrocephalus	--	--	--	--	--	--	7	31.34
		Nibea	*Nibea albiflora*	--	--	3	71.2	--	--	--	--

Table 3 (continuation)

Order	Family	Genus	Species	Spring		Summer		Autumn		Winter	
				abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)	abundance (ind.)	biomass (g)
		Chrysochir	*Chrysochir aureus*	6	465.3	--	--	21	643.9	5	405.2
		Larimichthys	*Larimichthys crocea*	17	1168.3	353	8112.0	3	250.8	--	--
			Larimichthys polyactis	1	100.7	--	--	--	--	--	--
		Johnius	*Johnius distinctus*	1	51.9	2	199.2	--	--	--	--
			Johnius belangerii	6	149.3	81	4839.3	54	1116.6	--	--
		Collichthys	*Collichthys lucidus*	130	3563.6	38	334.0	228	4161.3	544	12549.7
		Otolithes	*Otolithes ruber*	1	71.6	--	--	--	--	--	--
	Sparidae	*Pagrus*	*Pagrus major*	--	--	--	--	--	--	1	428.5
		Parargyrops	*Parargyrops edita*	357	1268.6	122	1601.0	--	--	--	--
		Acanthopagrus	*Acanthopagrus schlegelii*	1	218.9	--	--	--	--	--	--
		Rhabdosargus	*Rhabdosargus sarba*	--	--	6	401.8	--	--	--	--
	Priacanthidae	*Priacanthus*	*Priacanthus macracanthus*	--	--	156	2488.4	--	--	--	--
	Apogonidae	*Apogon*	*Apogon striatus*	--	--	--	--	4	7.3	--	--
			Apogon lineata	1	15.0	--	--	4	8.2	--	--
	Hapalogenyidae	*Hapalogenys*	*Hapalogenys analis*	--	--	1	3.8	--	--	--	--
			Hapalogenys nigripinnis	1	11.0	--	--	--	--	--	--
	Callionymidae	*Callionymus*	*Callionymus beniteguri*	--	--	17	148.0	--	--	--	--
			Callionymus curvicornis	--	--	3	21.5	--	--	--	--
	Uranoscopidae	*Ichthyscopus*	*Ichthyscopus lebeck*	--	--	3	105.5	--	--	--	--
		Uranoscopus	*Uranoscopus japonicus*	--	--	--	--	1	47.9	--	--
	Mullidae	*Upeneus*	*Upeneus japonicus*	--	--	1524	15023.7	--	--	1	17.3
	Sphyraenidae	*Sphyraena*	*Sphyraena pinguis*	--	--	6	203.4	--	--	--	--
	Sillaginidae	*Sillago*	*Sillago sihama*	2	116.1	31	175.7	4	149.2	26	854.8
	Stromateidae	*Pampus*	*Pampus cinereus*	--	--	4	190.0	--	--	--	--
			Pampus echinogaster	--	--	10	500.6	--	--	--	--
			Pampus argenteus	303	2227.8	24	2412.7	15	2391.2	3	45.5
			Pampus chinensis	--	--	25	1108.1	--	--	--	--
	Centrolophidae	*Psenopsis*	*Psenopsis anomala*	59	405.1	124	4162.3	--	--	--	--
	Trichiuridae	*Trichiurus*	*Trichiurus lepturus*	--	--	8	468.5	2	21.5	--	--
		Lepturacanthus	*Lepturacanthus savala*	1	31.6	151	7776.8	20	488.2	9	356.3
	Polynemidae	*Polydactylus*	*Polydactylus sextarius*	--	--	13485	30886.6	1929	13965.1	--	--
		Eleutheronema	*Eleutheronema tetradactylum*	--	--	--	--	3	234.5	--	--
	Scombridae	*Scomberomorus*	*Scomberomorus niphonius*	--	--	--	--	3	2056.1	6	3987.0
		Scomber	*Scomber japonicus*	16	106.3	--	--	--	--	--	--
	Gobiidae	*Acanthogobius*	*Acanthogobius hasta*	3	33.6	--	--	--	--	--	--
		Amblychaeturichthys	*Amblychaeturichthys hexanema*	448	2452.1	70	149.7	436	1899.4	160	1169.6
		Tridentiger	*Tridentiger barbatus*	2	25.8	--	--	--	--	2	29.7
		Trypauchen	*Trypauchen vagina*	9	108.4	60	593.9	8	80.2	81	840.3
		Odontamblyopus	*Odontamblyopus lacepedii*	67	1081.7	12	40.8	5	26.8	1	4.5
		Myersina	*Myersina filifer*	3	13.4	--	--	--	--	--	--
		Parachaeturichthys	*Parachaeturichthys polynema*	2	13.0	--	--	--	--	--	--
		Bathygobius	*Bathygobius cotticeps*	--	--	--	--	--	--	2	29.7
Pleuronectiformes	Paralichthyidae	*Pseudorhombus*	*Pseudorhombus arsius*	--	--	15	661.3	--	--	--	--
			Pseudorhombus oligodon	1	144.9	--	--	--	--	--	--
			Pseudorhombus quinquocellatus	1	15.7	--	--	--	--	--	--
	Pleuronectidae	*Pleuronichthys*	*Pleuronichthys cornutus*	1	4.2	--	--	--	--	--	--
	Cynoglossidae	*Cynoglossus*	*Cynoglossus puncticeps*	--	--	7	71.5	--	--	--	--
			Cynoglossus abbreviatus	233	8567.4	352	4290.4	145	2820.1	276	6396.6
			Cynoglossus roulei	--	--	--	--	--	--	1	23.3
			Cynoglossus joyneri	2	29.0	--	--	--	--	10	227.7
			Cynoglossus trigrammus	1	9.9	--	--	--	--	1	4.3
			Cynoglossus oligolepis	8	450.3	35	1899.2	6	500.5	9	631.03
	Soleidae	*Zebrias*	*Zebrias zebra*	--	--	19	191.1	--	--	--	--
	Monacanthidae	*Paramonacanthus*	*Paramonacanthus japonicus*	--	--	78.6	328.3	--	--	--	--
			Paramonacanthus sulcatus	--	--	5	33.5	--	--	--	--
	Tetraodontidae	*Takifugu*	*Takifugu poecilonotus*	4	118.6	4	23.9	--	--	5	132.6
			Takifugu vermicularis	--	--	--	--	2	38.7	--	--
			Takifugu oblongus	7	195.4	352	3805.1	65	2333.0	11	252.1
			Takifugu xanthopterus	--	--	--	--	--	--	2	280.7
			Takifugu alboplumbeus	--	--	1	9.9	--	--	--	--
			Takifugu bimaculatus	--	--	--	--	5	1296.0	--	--
		Lagocephalus	*Lagocephalus inermis*	--	--	12	397.5	--	--	--	--
			Lagocephalus wheeleri	--	--	--	--	--	--	3	430.79
			Lagocephalus spadiceus	--	--	616	13003.2	22	1714.7	--	--

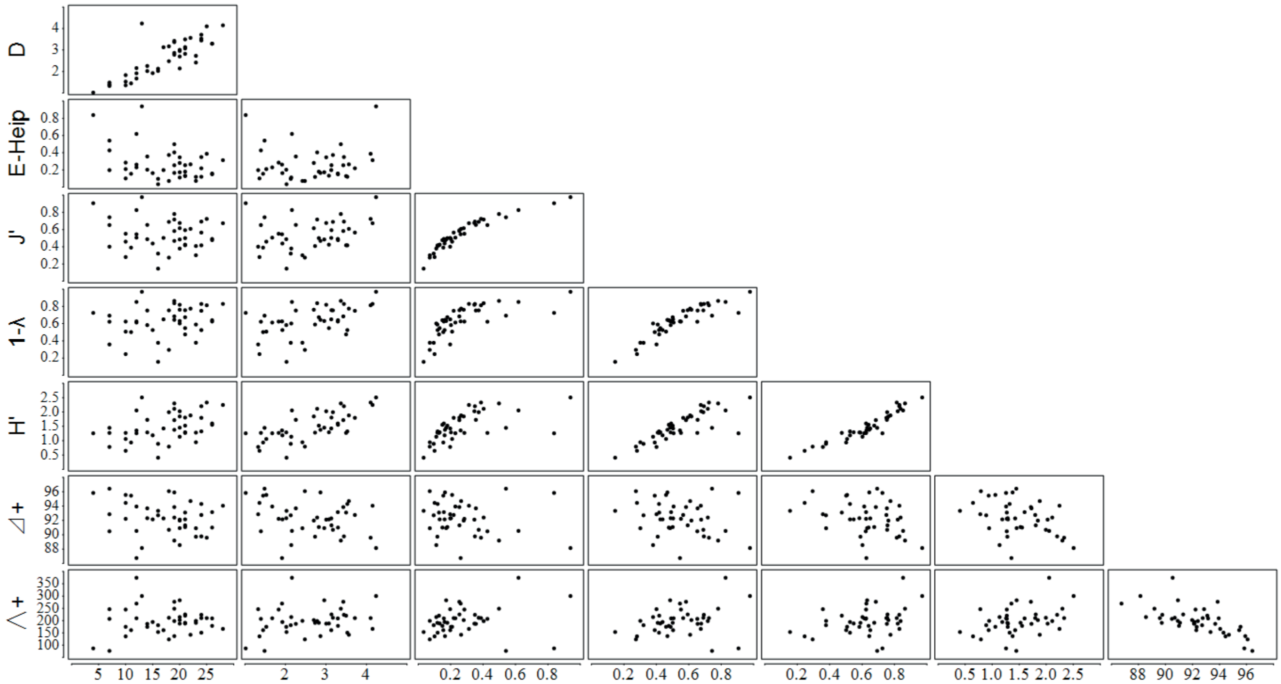

Figure 3

Plots of correlations of different diversity indices

Table 4

Seasonal variation in multi-component diversity indices of the fish community in the Min estuary

		Spring	Summer	Autumn	Winter
Species richness	*S*	64	78	49	46
	D	7.137	7.547	5.452	5.643
Evenness	*J'*	0.556	0.401	0.515	0.503
	E_{Heip}	0.144	0.061	0.134	0.123
Heterogeneity	*H'*	2.311	1.745	2.005	1.924
	$1 - \lambda$	0.811	0.688	0.782	0.757
Taxonomy	Δ^+	78.556	58.159	74.553	73.279
	Λ^+	96.900	84.564	95.342	96.832

Dominant species

The dominant species in the Min estuary showed seasonal variability. The species *Harpadon nehereus* occurred as the dominant species in three seasons, except for spring. Both *Cynoglossus abbreviatus* and *Polydactylus sextarius* occurred as dominant species alternatively in two seasons; the former in spring and winter and the latter in summer and autumn. In addition, *Trachurus japonicus* and *Secutor ruconius* were the dominant species in spring and replaced by *Pennahia argentata* and *Upeneus japonicus* in summer, followed by *Coilia mystus* and *Collichthys lucidus* in winter (Fig. 4).

Ecological niches among paired dominant species

Table 5 shows all Pianka values of niche overlap among the dominant species in each season. In spring, there were four pairs showing a high niche overlap, including *Harpadon nehereus* and *Pennahia argentata*, and three pairs among *Cynoglossus abbreviatus*, *Coilia mystus* and *Collichthys lucidus*. In summer, *Collichthys lucidus* and *Cynoglossus abbreviatus* showed the highest value of 94.70%; other relatively high values were 67.94% for *Harpadon nehereus* and *Pennahia argentata*, 54.28% for *Harpadon nehereus* and *Polydactylus sextarius*, and 51.16% for *Polydactylus sextarius* and *Pennahia argentata*. There were no significantly high values of niche overlap in autumn, while values between *Coilia mystus* and *Harpadon nehereus* – 59.23% and between *Coilia mystus* and *Cynoglossus abbreviatus* – 53.11% were considerably high. In winter, in addition to the overlap between *Collichthys lucidus* and *Cynoglossus abbreviatus* at 80.08%, the species pair of *Secutor ruconius* and *Upeneus japonicus* showed an almost complete overlap of the ecological niche at 99.99%.

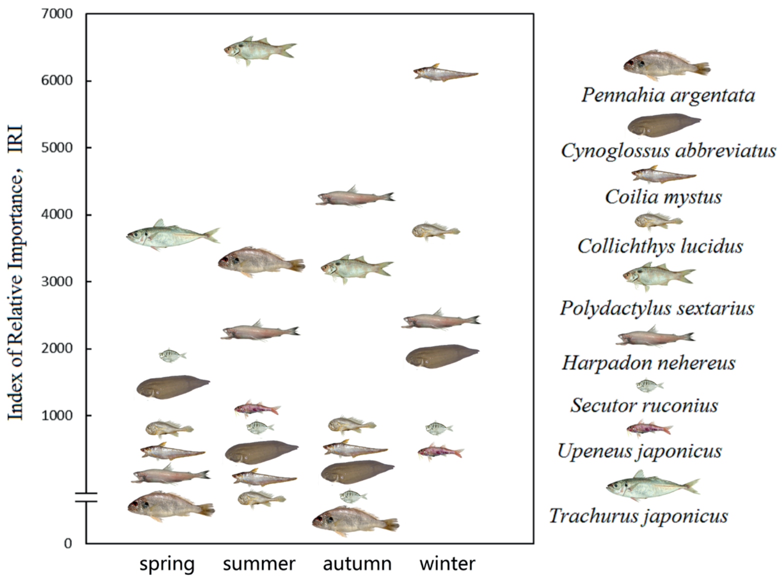

Figure 4

Seasonal variation of dominant species in the fish community in the Min estuary

Table 5

Pianka values (%) of the overlapping ecological niche of dominant species in different seasons

Species	Season	*C. abbreviatus*	*P. sextarius*	*C. mystus*	*C. lucidus*	*P. argentata*	*T. japonicus*	*S. ruconius*	*U. japonicus*
H. nehereus	spring	1.11		0.26	1.46	99.93	25.54	47.18	
	summer	33.63	54.28	61.96	21.79	67.94		13.75	20.40
	autumn	2.01	2.39	59.23	15.82	5.85		1.95	
	winter	33.46		34.99	21.90			24.35	23.56
C. abbreviatus	spring			87.28	90.83	0.73	12.24	19.59	
	summer		13.26	41.35	94.70	17.54		4.63	5.07
	autumn		8.39	53.11	19.31	19.24		23.54	
	winter			37.48	80.08			3.39	2.12
P. sextarius	summer			29.78	0.91	51.16		59.84	19.48
	autumn			0.47	3.06	37.21		37.00	
C. mystus	spring				93.40	0.00	2.65	14.49	
	summer				32.16	14.34		8.87	15.31
	autumn				11.99	0.00		1.20	
	winter				54.67			1.63	0.86
C. lucidus	spring					0.92	16.79	10.90	
	summer					14.95		0.27	0.12
	autumn					6.39		7.22	
	winter							0.88	0.00
P. argentata	spring						24.14	45.23	
	summer							19.86	0.12
	autumn							21.41	
T. japonicus	spring							28.13	
S. ruconius	summer								18.21
	winter								99.99

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Discussion

Fish community composition

The Min estuary is an important fishing area with a density of 997.36 kg km^{-2} of fish biomass, higher than that in coastal waters of the East China Sea (884.72 kg km^{-2}) and the Bohai Sea (275.30 kg km^{-2}), and lower than in the Yellow Sea (2323.57 kg km^{-2}; Huang et al. 2010). The Min estuary also borders on the famous eastern Mindong Fishing Ground and the southern Minnan-Taiwan Bank Fishing Ground with higher productivity in China, providing an important place for migratory fish species, e.g. *T. japonicus*, *H. nehereus* and *C. lucidus* etc., to spawn, nurse or winter. Knowledge of the taxonomic composition of fish assemblages, even on a seasonal basis, would be beneficial in terms of knowing how fish use this estuary for their development.

In 2015, a total of 127 fish species were sampled in the Min estuary, which is more than 77 species sampled in the Yellow River estuary in 1959–2011 (Shan et al. 2013) and 62 species sampled in the Yangtze estuary in 2010–2011 (Shi et al. 2014). Unlike the temperate character of the Yangtze and Yellow River estuaries, the Min estuary is subtropical with a higher water temperature, which supports higher species richness. In terms of taxonomic composition, Engraulidae were the common dominant family in fish catches in the Yellow River estuary during all years of sampling (Shan et al. 2013), similar to the Min estuary. Furthermore, Sciaenidae comprising more subtropical species also dominated in the fish community from the Min estuary, e.g. *Larimichthys crocea* and *Pennahia argentata* were abundant in summer, and *Collichthys lucidus* prospered in spring, autumn and winter. In addition to natural differences in fish assemblages between all these estuaries resulting from different environments, changes in fishing methods, tools and regulations could also affect the taxonomic composition of fish, e.g. harvest regulations significantly contributed to fish recruitment failure and catch-per-unit-effort decline of saltwater bass *Paralabrax* spp. (McClanahan & Mangi 2001). The exclusion of closed areas could potentially increase catch rates, while the exclusion of beach seines could lead to an increase in other types of fishing gear but a reduction in the total catch (Jarvis et al. 2014).

Biotic factors also play an important role in the estuarine fish community. Large seasonal environmental differences in a subtropical estuary lead to changes in seasonal composition. The content of nitrogen and phosphorus in the Min estuary was high, adjusted by diluted water of the Min River. As a phosphorus-limited eutrophicated estuary, phosphorus showed a relatively higher value in autumn and winter than spring and summer (Zheng 2010). Chlorophyll *a* is usually associated with the distribution of zooplankton, where its presence plays an important role in controlling the distribution of some dominant species (Marques et al. 2007; Ensign 2014). It showed significant seasonal variation, with productivity ranging from high to low in summer, autumn, spring and winter (Xiao 2014). Meanwhile, migratory species began to arrive at the Min estuary in spring, which led to an increase in species richness. In summer, with the arrival of an increasing number of species as well as an increase in primary production, fish species richness significantly increased compared to other seasons. Furthermore, a four-month (March–June) fishing ban in the Min estuary was in force (while scientific research was officially permitted). Sampling in the restricted season and just after the season could certainly lead to a better catch, with higher diversity and biomass. On the other hand, due to the aftereffects of compensatory fishing intensity after the fishing ban, the autumn fieldwork resulted in a poorer catch than expected from the theoretical natural composition. As a geologically southern estuary with warm water in winter, the estuary still maintains a number of fish species during this season.

Species diversity

Species diversity is a multi-component concept to expound thoroughly the biological and ecological characters of fish communities (Purvis & Hector 2000). Our results show not only that a single diversity descriptor cannot provide a complete description of species diversity, but also that in some cases it cannot even encapsulate a complete description of a specific diversity component. In addition, some of the descriptors considered complementary according to theoretical works proved to be redundant.

Estimates of the number of species (*S* and *D*) in the Min estuary were not correlated with other indices considered in our study, as was the case with the Gulf of Lions (Mérigot et al. 2007). Species richness remains the most comprehensive index for nature conservation purposes, despite such drawbacks as high sensitivity to difficulties in accurately estimating the actual number of species at different sample sizes (Gaston & Spicer 1998; Margules & Pressey 2000).

In the Min estuary, E_{Heip} and J' of the fish community showed the same pattern. Although these two indices were calculated based on H', E_{Heip} demonstrated greater reliability and could prove more efficient. The two most popular heterogeneous indices, H' and

1 – λ, were strongly related. The Simpson index is primarily a measure of dominance, especially of the first two or three species, whereas *H′* is more strongly affected by species in the middle of the species rank sequence (Whittaker 1972). Although *H′* and 1 – λ were significantly correlated with *D* and $E_{Heip,}$ with a correlation coefficient of 0.50–0.70, combining the number of species and evenness into a single diversity index does not facilitate the description of a fish community (Bell 2000) as the number of species and evenness are related to different aspects of diversity. In fact, the number of species and species evenness are related to different responses of species to environmental factors (Ma 2005; Nyitrai et al. 2012).

The taxonomic diversity is expected to allow for taxonomic relationships between individuals and thus to provide additional information to classical species diversity indices. The loss of taxonomic diversity of fish can lead to a loss of ecological responsiveness to environmental fluctuations and a loss of ecological functions providing goods and services to ecosystems (Miranda et al. 2005; Ramos-Miranda et al. 2005). To simply show the meaning of taxonomy and the evolution of fish in a sampling area, presence/absence data would be better to avoid any disturbance resulting from abundance and biomass. In our study, in addition to the negative correlation between the two taxonomic indices at –0.6708, they were independent of other indices and should be used in biodiversity conservation.

Seasonal turnover and ecological niche overlap of dominant species

The *IRI* index is a good indicator to describe fish communities by integrating abundance and biomass into a single index. In the Min estuary, the dominant species showed seasonal turnover by reasonable use of resources. In spring, *T. japonicus* was the most dominant species, with the IRI value twice as high as in the case of the subsequent dominant species, i.e. *C. abbreviatus* and *S. ruconius*. It is considered that geological features and oceanic dynamics of the Min estuary provide higher habitat diversity and thus can provide a wider range of potential microhabitats for fish to coexist (Shi et al. 2014). On the basis of ecological traits, it appears that these three species showed specific habitat preferences and feeding habits to avoid competition for food and space. For example, *T. japonicus* is a typical migratory species moving back and forth between different zones as well as between the lower and upper layers of the sea. It is highly predatory, feeding mostly on planktic crustaceans and small fish. In spring, it migrates to the estuary area for feeding and shows the highest feeding intensity in the whole year (Zhang et al. 2016; Yan et al. 2018). The species *C. abbreviatus* is a medium-sized fish that feeds on benthic invertebrates in the bottom sediments of the coastal area (Ni 2003; He et al. 2018). The species *S. ruconius*, which inhabits the lower water layer, lives in large groups mainly in coastal seabed sand and mud and feeds on small plankton. In spring, it arrives at the estuary for spawning in June–July (Du et al. 2010; He et al. 2018). In this season, higher niche values were determined for *C. abbreviatus*, *C. mystus* and *C. lucidus*, as well as for *H. nehereus* and *P. argentata*, where only *C. abbreviatus* was the dominant species at that time. High values of niche overlap among common or rare species and lower values of niche overlap among all dominant species, suggesting a difference in their feeding habits or habitat requirements, could effectively reduce the species competition to maintain the ecological balance. Although low overlapping cannot be expected to be an indication of strongly interspecific competition (Losos 1996), it may imply that these species can segregate spatially or overlap extensively, depending on the spatial distribution of their resources (Hofer et al. 2004).

In summer, after finishing their persistent migration, *T. japonicus* and *S. ruconius* abandoned the estuary, leaving a rich ecological space for new dominant species, including *P. sextarius*, *P. argentata*, *H. nehereus* and *U. japonicus*. Species *P. argentata*, *P. sextarius* and *U. japonicus* are also migratory and increasingly come to the Min estuary in May and June for spawning and then quickly dominate the area due to their varied feeding habit, e.g. *P. argentata* mostly feeds on nekton (especially fish and crustacean), *P. sextarius* feeds on shrimps and *U. japonicus* feeds on benthic invertebrates (especially macrura and mollusk). The species *H. nehereus* is a local resident in the middle-lower water layer and gradually increases its population. It is omnivorous, feeding mainly on zoobenthos. In this season, only pairs of *C. abbreviatus* (common species) and *C. lucidus* (rare species) showed a high niche overlap at 94.70. Interestingly, several dominant species, such as *H. nehereus*, *P. sextarius* and *P. argentata*, showed a significant overlap at 50–70, which could be explained by the highest productivity in summer to satisfy the resource demand of these species. Alternatively, the co-occurring pattern can be expressed by a complementary niche, e.g. a high overlap in one niche dimension (spatial dimension) compensated by a low overlap in at least one of the other dimensions (feeding or temporal gradient; Schoener 1974; Pusineri et al. 2008; Nagelkerke & Rossberg 2014).

In autumn, half of the *P. sextarius* population gradually abandoned the sampling area, but still kept the dominant position. Meanwhile, *H. nehereus* rapidly advanced to an absolutely dominant status. The *IRI* values of the two dominant species – *H. nehereus* and *P. sextarius* – were 4211 and 3209 respectively, about 5–8 times higher compared to other common species, and the two species showed no ecological niche conflicts.

In winter, *P. sextarius* continued to migrate from the sampling area and its ecological space was quickly occupied by *C. abbreviatus*. Two commercial species, *C. mystus* and *C. lucidus*, common species in other seasons, preponderantly dominated the assemblage. These two species always co-occurred together and showed similar feeding habits, preying mostly on zooplankton (e.g. copepods, Mysidacea). The species *Harpadon nehereus* preserved its status. The dominant species pair of *C. abbreviatus* and *C. lucidus* showed a high niche overlap at 80.08 and the pair of *C. mystus* and *C. lucidus* showed a considerable spatial niche overlap at 54.67. If resources for species are not in short supply, two organisms can share the resources without detriment to each other, even if they show relations in niche overlap and the competitive effect (Pianka 1974). The simultaneous occurrence of these dominant species indicated that there are enough food resources and habitat space in the Min estuary, which could be attributed to the absence of many migratory species and the decrease in feeding intensity in winter, despite decreasing temperature and primary production.

Acknowledgements

This study was funded by the National Natural Science Foundation of China (No. 41976091) and the National Program on Global Change and Air-Sea Interaction (GASI-02-PAC-YDaut). We express our sincere thanks to Chen Shen and Yan Shi for fieldwork.

Conflict of Interest: The authors declare no conflict of interest.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies: All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

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