



## Original Articles

# Spatial and temporal variabilities of coastal nekton community structure and phylogenetic diversity in Daya and Dapeng Bay, southern China

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## ABSTRACT

Coastal areas are important habitats for many species and strongly affected by anthropogenic activities. Management for sustainable coastal ecosystems benefits from a comprehensive assessment of species diversity. Here, we measured the spatio-temporal changes in community and phylogenetic structure of spring and autumn nektonic communities in Daya and Dapeng Bay among 12 sampling sites. We found that both the community structure and phylogenetic facets of nektonic communities in Daya and Dapeng Bay exhibited strong spatial and temporal patterns due to which we attribute to fishing intensity and mid-summer fishing moratorium. The relatively larger ratio of unexplained variation in the autumn community resulted from stochastic processes caused by the mid-summer fishing moratorium. Furthermore, the phylogenetic structure of the spring nektonic communities between Dapeng and Daya Bay were significantly different; obvious phylogenetic clustering was found in spring nektonic communities of Dapeng Bay. These results implied that we may consider the current fishing intensity as a strong stress for nektonic communities, which exceeds the effect of natural processes and environmental factors. We speculate that the immediate sweeping fishing efforts may rapidly deplete the recovered fish stocks in a short time as human activities exert great stress on the nektonic communities in the study area. To avoid permanent damage to the ecosystem and a loss of valuable marine resources, urgent attention is required for fishery management.

## 1. Introduction

Spatial and temporal variation in species composition is one of the most fundamental and conspicuous characteristics of biological communities (McKinney and Lockwood, 1999; Vandermeer et al., 2004; Vellend et al., 2007). Over the past 30 years, several hypotheses were proposed by ecologists to explain the maintenance mechanisms of species diversity (Palmer, 1994). However, despite there are many mechanisms that underpin the pattern of ecological communities, all of these mechanisms involve four kinds of processes: drift, speciation, dispersal and selection (Vellend and Agrawal, 2010). These four processes can be summarized into two theories which are mainly critical in determining a locality's biodiversity and species composition of community (Zillio and Condit, 2007). The first is the niche theory, which is essentially synonymous with selection. It emphasizes that environmental filtering is one of the main processes in structuring communities. Environmental

filtering includes organisms' responses to the abiotic environment and direct interactions between organisms (Chase and Leibold, 2003). The second is the neutral theory, which emphasizes the influence of stochastic processes shaping the composition of community (Hubbell, 2001). The core of the neutral theory is the concept of "ecological drift" (analogous to genetic drift in population genetics) leading to a balance between dispersal and assembly of ecological community (Bell, 2001).

Ecologists and evolutionary biologists agree that the interplay between ecological and evolutionary processes acts as a driver for community construction (Gerhold et al., 2018; Mouquet et al., 2012; Ricklefs, 1987; Weber et al., 2017). However, all above ideas of community ecology all focus on the number of species to explain the diversity pattern. The approach (base on species number) is not very accurate in predicting processes which involved in community assembly. For instance, despite two communities display a similar number of species, their evolutionary origins and processes might be quite

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different. For a long time, the studies for patterns in the species composition and dynamics of local communities have seldom employed information about the phylogenetic relatedness of interacting species within those communities (Brown, 1989; McGill et al., 2006; Paine, 1966). Since Webb (2000) first used phylogenetic relatedness to infer the common ecological preferences of Borneo rainforest trees, phylogenetic relatedness has been widely employed to investigate patterns in community structure (Mouquet et al., 2012). The idea hypothesized that the difference of community structures depends on both the ecological mechanisms (competitive exclusion and environmental filtering) and species status within the phylogeny (evolutionary history).

The interpretation of phylogenetic relatedness patterns mainly focused on environmental filtering and competitive exclusion, resulting in phylogenetic clustering and overdispersion. For example, if niche selection drives community assembly, environmental filtering tends to lead to a higher degree of co-occurrence of closely related species, hence a phylogenetic clustering pattern can be expected (Weiher and Keddy, 1999). Conversely, if competitive exclusion of species plays a driving role in community composition, then related species tend to compete more intensely for the same resource than distant species, leading to phylogenetic overdispersion (Cavender-Bares et al., 2009). Phylogenetic diversity (include phylogenetic alpha- and beta diversity) provides insights into how evolutionary history and ecological processes drive patterns of biodiversity. This is because phylogenetics may reflect a complex diversity of extrinsic (behavioral and environmental tolerance) and intrinsic (morphological and reproductive) traits (Graham and Fine, 2008). Phylogenetic alpha diversity measures the coexistence of phylogenetically distant or close species within a community, whereas phylogenetic beta diversity measures how phylogenetic relatedness changes among communities across space.

Recently, there are several examples from different ecosystems around the world to show the above phylogenetic approach have been expanded. For instance, Winter et al. (2009) revealed that floras of many European regions have partly lost and will continue to lose their phylogenetic distinctiveness. D'agata et al. (2014) reported that human activities have markedly reduced phylogenetic and functional diversity for a critically important fish family in the Pacific coral reef. Jiang et al. (2019) demonstrate that 50 years of anthropogenic disturbance was sufficient to obscure the phylogenetic features of evolutionary history of fish fauna from the Yun-Gui plateau in the last 5 million years. Massante and Gerhold (2020) found that the phylogenetic diversity of coastal vegetation in the Brazilian Atlantic forest increased with precipitation and latitude; the latter authors suggested the presence of ancient Gondwanan lineages colonizing from refugium at relative higher latitude. A rapid expansion of studies that apply phylogenies and methods to understand community ecology has been prompted by the increasing availability of phylogenetic information, computing power, and computational tools. The use of molecular phylogenetic data to investigate community assembly has gone "from an incidental application to a burgeoning subdiscipline" (Cavender-Bares et al., 2009; Mouquet et al., 2012; Pavoine et al., 2011; Vamosi et al., 2009).

Coastal ecosystems are the most productive and economically vital aquatic systems worldwide. In terms of fish, coastal ecosystems provide important habitats for foraging, spawn, nursery, and recruitment for most of species (Bergström et al., 2016; Eriksson et al., 2009; Myers et al., 2007). This contrasts with oceanic ecosystems which are mainly influenced by ocean exploitation and wide-range climate forcing; anthropogenic influences on coastal ecosystems are more extensive, such as overfishing, habitat degradation, eutrophication, invasive species, and pollution (Lotze et al., 2006; Pauly et al., 2002). Especially in the economically developed southern China coastal areas. In order to improve this situation, governments of many countries have implemented corresponding protection policy and management regulations. The annual fishing ban which has been in place by China's Ministry of Agriculture, lasts from May to August (since 1998), covering areas north of 12°N in the whole South China Sea. However, a number of species

that inhabit coastal areas may respond to environmental changes at different spatial and temporal scales, making it difficult to determine completely appropriate management actions (Guidetti et al., 2002; Snickars et al., 2015). Therefore, for policy development and efficient planning of these vital fishery resources, it is necessary to understand and evaluate the spatial and temporal variation of nekton community composition and diversity in coastal areas. Because southern China coastal areas is regarded as an important marine resource, support economic and social development.

Here, our purpose is to evaluate the contribution of local environmental factors on the variation of nektonic communities at spatial and temporal scales in two subtropical adjacent bays in South China, Daya Bay and Dapeng Bay. Due to natural conditions are quite similar in both bays, firstly, we tested the null hypotheses that there are no significant differences in the phylogenetic diversity of nektonic communities in these two adjacent bays. Secondly, we hypothesized that clearly seasonal variation of nektonic communities is expected in community composition and phylogenetic diversity in the two bays. To test our hypotheses, we sampled coastal nektonic communities, measured, and recorded environmental parameters in the two subtropical adjacent bays (i.e., Dapeng Bay and Daya Bay) in different seasons.

## 2. Material and methods

### 2.1. Study area

Daya Bay, located in the northern part of South China Sea, between Shenzhen city and Huizhou city, China. It is a subtropical semi-closed bay and covers about 600 km<sup>2</sup> area which has a shoreline of 92 km with water depth ranges from 6 to 16 m, and the water temperature between 15 °C and 32 °C (Wang et al., 2008). Dapeng Bay (i.e., Mirs Bay) is another natural semi-enclosed bay between Shenzhen city and Hong Kong city. Dapeng Bay covers about 390 km<sup>2</sup> area with water depth mostly less than 16 m, and the water temperature between 16.9 and 30.9 °C. Due to the presence of the mainland and the Hong Kong Islands as natural barriers, Dapeng Bay is less rough with a wave height of less than 0.7 m. The sea area has the largest container throughput of China's single port area - Yantian Port. Daya Bay and Dapeng Bay were separated by Dapeng Peninsula (Fig. 1). Daya Bay, Dapeng Bay and other series of large and important bays along the Pearl River mouth, are part of the Guangdong-Hong Kong-Macao Greater Bay Area. Hence, Daya Bay and Dapeng Bay are regarded as complex ecosystems strongly influenced by anthropogenic activities such as mariculture, petrochemical industries, overfishing, urban development and nuclear power stations (Wu et al., 2009).

### 2.2. Sampling and measurements

Nektonic communities were collected during the fisheries surveys conducted by the South China Sea Fisheries Research Institute on September 24th 2019 (autumn) and on April 4th 2020 (spring). The fishing activities were carried out by the commercial fishing vessel "Yueshanwei11092" using pair trawler nets and bottom trawler nets. A total of 12 sampling sites were deployed divided into two sectors, 6 sampling sites were laid out in each gulf (Fig. 1). The following data for each trawl were recorded: date, GPS position, duration time, depth, towing distance, and speed. Each trawl lasted 0.5 h. All the collected animals were counted, weighed, and identified to species using morphology. Water temperature (T), dissolved oxygen (DO), pH, and conductivity (Cond) were measured by a handheld multiparameter meter (YSI Pro Plus). For each site, 1500 mL water sample was collected from the bottom layer for measurements of phosphate, nitrite nitrogen, nitrate nitrogen, ammonia nitrogen, total nitrogen, chlorophyll *a*, and chemical oxygen demand. The collected water samples were stored in glass bottles and preserved at 4 °C until measurements were performed.

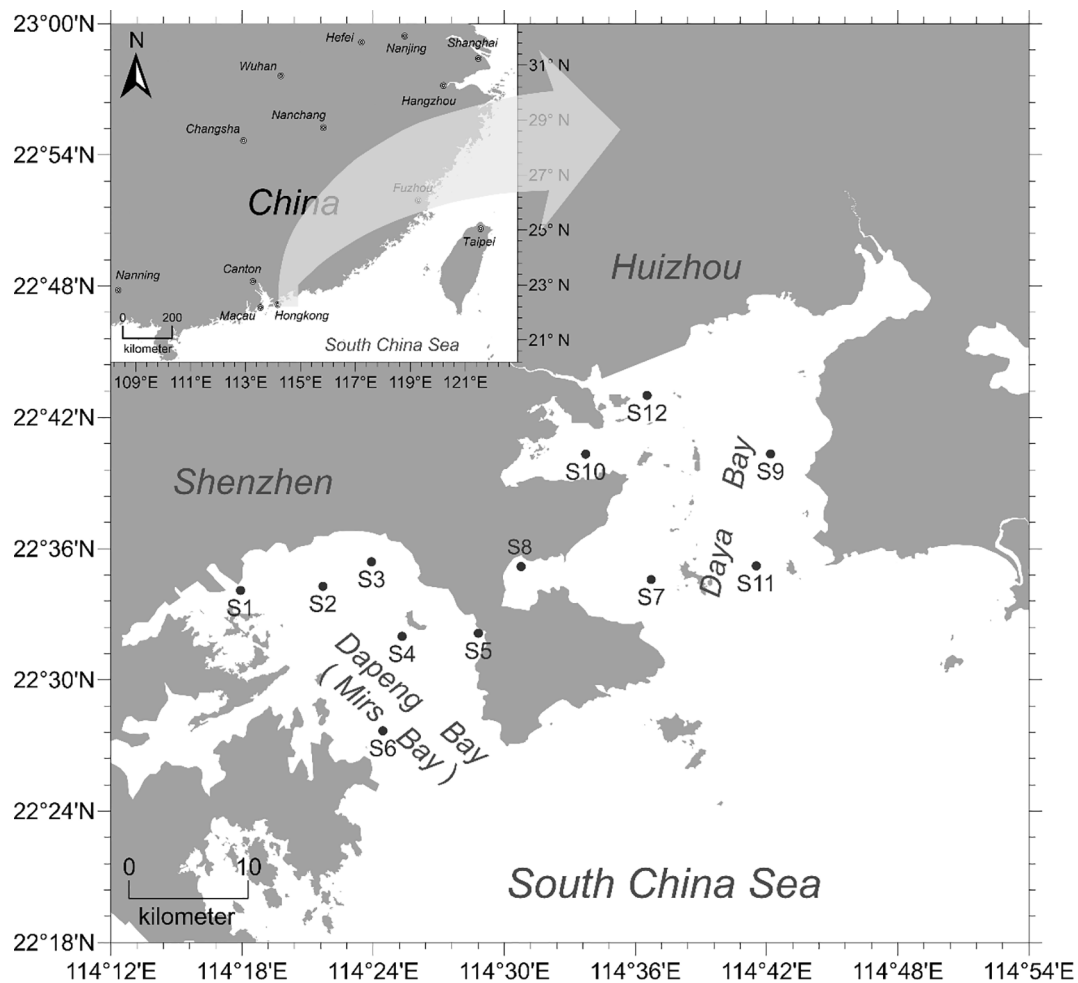


Fig. 1. Map showing study area and twelve sampling locations in Dapeng and Daya Bay.

### 2.3. Building the phylogenetic tree

We downloaded comparative sequences of the mitochondrial COI gene (cytochrome *c* oxidase subunit 1) from the public databases (GenBank or BOLD database) for each identified species (Table S1). All sequences (our collection and comparative sequences from databases) were collected and edited in BioEdit (Hall, 1999), and aligned using the CLUSTALW multiple algorithms. The phylogenetic tree was reconstructed on the COI dataset using Bayesian Inference (BI). For the Bayesian Inference tree, we used BEAST1.8.0 (Drummond et al., 2012). The parameters were set in BEAUti 1.8.0 assuming a coalescent model with constant population size, uncorrelated relaxed clock model, general time reversible (GTR) substitution model, and gamma shape site model with a chain length of 200,000,000 iterations for Markov chain Monte Carlo (MCMC). A maximum clade credibility consensus tree was obtained in TreeAnnotator v1.8.2, with the first 1,000,000 generations discarded as burn-in. The final consensus tree was displayed with Fig-Tree v 1.4.0.

### 2.4. Statistical analysis

The catch per unit area (CPUA  $\text{kg}\cdot\text{km}^{-2}$ ) was estimated based on Sparre and Venema (1998). Before multivariate statistical analyses, Hellinger transform was performed on abundance data to avoid subsequent analysis being dominated by only one or two abundant species/taxa. Environmental variables were checked for normality and homoscedasticity, then were standardized. To examine community patterns caused by spatial and environmental variables, we performed a

redundancy analysis (RDA) using spatial (distance-based Moran eigenvector maps, dbMEM) and environmental variables as independent variables (Borcard et al., 2004; Dray et al., 2006). The spatial variables (dbMEMs) were generated according to the longitude and latitude coordinates of sampling sites using principal coordinates of neighbor matrices analysis (Borcard and Legendre, 2002). We partitioned the community variation into pure spatial (S) and environmental (E) components, following the procedure in Peres-Neto and Legendre (2010). Before the RDA analysis, we first tested whether the overall model of spatial or environmental matrix was significant. If so, forward selection of variables was applied to produce a more parsimonious model. Only significant variables (*P* less than 0.05) were retained for subsequent variance partitioning. Variation partitioning was carried out to reveal the contribution of the significant spatial and environmental variables on community composition with adjusted  $R^2$  coefficient based on RDA (Peres-Neto et al., 2006). We estimated the proportions of spatial variables that determined community variation (S), environmental variables that determined community variation (E), joint effect (S + E), pure spatial variables (S|E), pure environmental variables (E|S) and their shared variance.

Phylogenetic structures of communities in the two gulfs were analyzed separately for spring and autumn data. We first calculated the phylogenetic diversity (PD) of nektonic communities to examine differences between Dapeng Bay and Daya Bay (Faith, 1992). The phylogenetic structure of nektonic communities was assessed by the net relatedness index (NRI), which is a standardized indicator to measure the mean pairwise phylogenetic distance of taxa in a sample, and quantifies the total clustering of taxa in a phylogenetic tree (Webb,

2000; Webb et al., 2002). Positive values of NRI indicate phylogenetic clustering of taxa, whereas values lower than zero indicate phylogenetic overdispersion.

For phylogenetic alpha diversity, we used two indices to evaluate the variation in phylogenetic diversity at different phylogenetic levels. Mean pairwise distance (MPD) calculates phylogenetic distances across the entire phylogenetic tree by averaging the pairwise distances of all species, while mean nearest taxon distance (MNTD) is the distance between the most closely related taxa, at shallower phylogenetic levels (at the tips of the phylogenetic tree) (Webb et al., 2002). For phylogenetic beta diversity, we used mean pairwise distance separating species in two sampling sites ( $D_{pw}$ ) and mean nearest taxon distance separating species in two sampling sites ( $D_{nn}$ ) (Swenson, 2011). We first applied Mantel tests with 999 randomizations to test the correlation of both spatial and environmental distances with phylogenetic beta diversity. Then we used multiple regression on distance matrices (MRM) (Lichstein, 2007) to reveal the effects of each environmental variable on both two phylogenetic beta indices ( $D_{pw}$  and  $D_{nn}$ ) of nektonic communities from the sampling survey in autumn 2019 and spring 2020. We also performed the nonmetric multidimensional scaling (nMDS) ordination to reveal differences in phylogenetic alpha diversity among the sampling sites. All analyses were carried out in R-3.5.3 with the packages *vegan*, *picante*, *splits*, *ape*, *packfor*, *ade4*, *PCNM*, *AEM*, *spacemakeR*, *spdep* and *ecodist* (Dray et al., 2006; Ezard et al., 2009; Goslee and Urban, 2007; Kembel et al., 2010; Oksanen et al., 2019; R Development Core Team, 2017).

### 3. Results

#### 3.1. Species composition and the catch per unit area

Totally, we identified 143 nektonic species from our samples in Dapeng and Daya Bay, including 92 species of fish, 40 species of crustaceans and 11 species of cephalopods. 63 species of fish, 40 species of crustaceans and 9 species of cephalopods were recorded during the sampling survey in autumn 2019, while 56 species of fish, 40 species of crustaceans and 8 species of cephalopods were identified from the sampling survey in spring 2020.

Mean CUPA of each sampling site for fish and invertebrates in Dapeng and Daya Bay are shown in Table S2. Both Dapeng and Daya Bay had higher total CUPA in the autumn survey than in the spring survey. Total CUPA in Dapeng Bay was higher in the autumn survey than that in Daya Bay, however it was the opposite in the spring survey (Fig. 2). Maximum CUPA of autumn survey was found in Daya Bay at S10 ( $2329.53 \text{ kg} \cdot \text{km}^{-2}$ ), while S6 in Dapeng bay ( $667.3 \text{ kg} \cdot \text{km}^{-2}$ ) represents the maximum CUPA of spring survey.

#### 3.2. Spatial and environmental factors associated with community composition

Our results revealed that the nektonic community composition of Dapeng and Daya Bay mainly related to spatial variables and a few environmental variables, both in the autumn and spring surveys. In the redundancy analyses of spring nektonic communities (Table 1), three spatial MEM variables (MEM1, MEM3 and MEM4) were selected in the spatial model (S) after forward selection. Small-scale (MEM4) and medium-scale (MEM3) spatial variation explained a smaller proportion of the community variation than large-scale spatial variation (MEM1) (Borcard et al., 2011). After considering covariation with environmental variables, pure spatial variation (S|E) still explained 38% of community variation. Only dissolved oxygen and temperature for environmental variables were retained after forward selection. When spatial variables were included as a covariable matrix, only 6.4% variation was explained as pure environmental variables (E|S). Combined spatial and environmental variables (S + E), all variables explained 60.1% of the variation in spring community. The spatially structured environmental variance amounted to 15.7%.

For autumn nektonic communities, two large-scale spatial variations (MEM1 and MEM2) and only one environmental variable (dissolved oxygen) were significantly related to the community variation. Purely spatial variation (S|E) explained 18%, while purely environmental variation (E|S) explained 3.9% of the autumn community variation. Both spatial and environmental variation (S + E) together explained 32% of the community variation. Shared environmental and spatial variables explained 9.4% of the variation in autumn community (Table 1).

#### 3.3. Phylogenetic diversity

The phylogenetic tree represented by sampled species is given in Fig. S1 and Fig. S2. There was no significant difference of phylogenetic biodiversity for autumn nektonic communities between Dapeng and Daya Bay ( $p = 0.219$ ) (Fig. 3a), while we noted a significant difference for spring nektonic communities ( $p$  less than 0.001) (Fig. 3b). NRI showed negative values for autumn nektonic communities both in Dapeng and Daya Bay which indicated phylogenetic overdispersion (Fig. 3c), whereas NRI showed positive values in spring nektonic communities of Dapeng Bay which indicated phylogenetic clustering (Fig. 3d).

For autumn nektonic communities,  $D_{pw}$  did not change with either spatial distance (Mantel  $r = 0.161$ ,  $p = 0.106$ ) or environmental distance between sampling sites (Mantel  $r = 0.022$ ,  $p = 0.429$ , Fig. 4 a, b).  $D_{nn}$  also did not change with spatial distance (Mantel  $r = 0.18$ ,  $p = 0.063$ ),

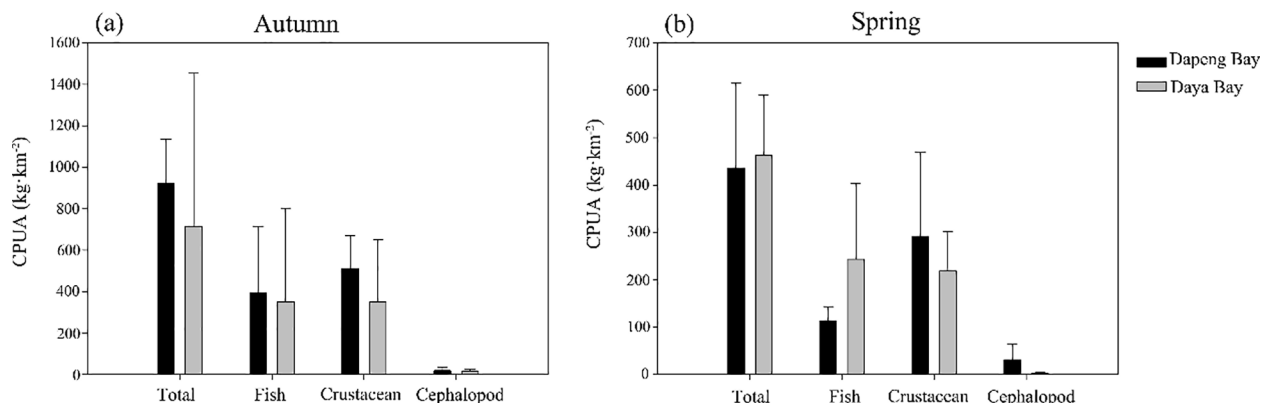
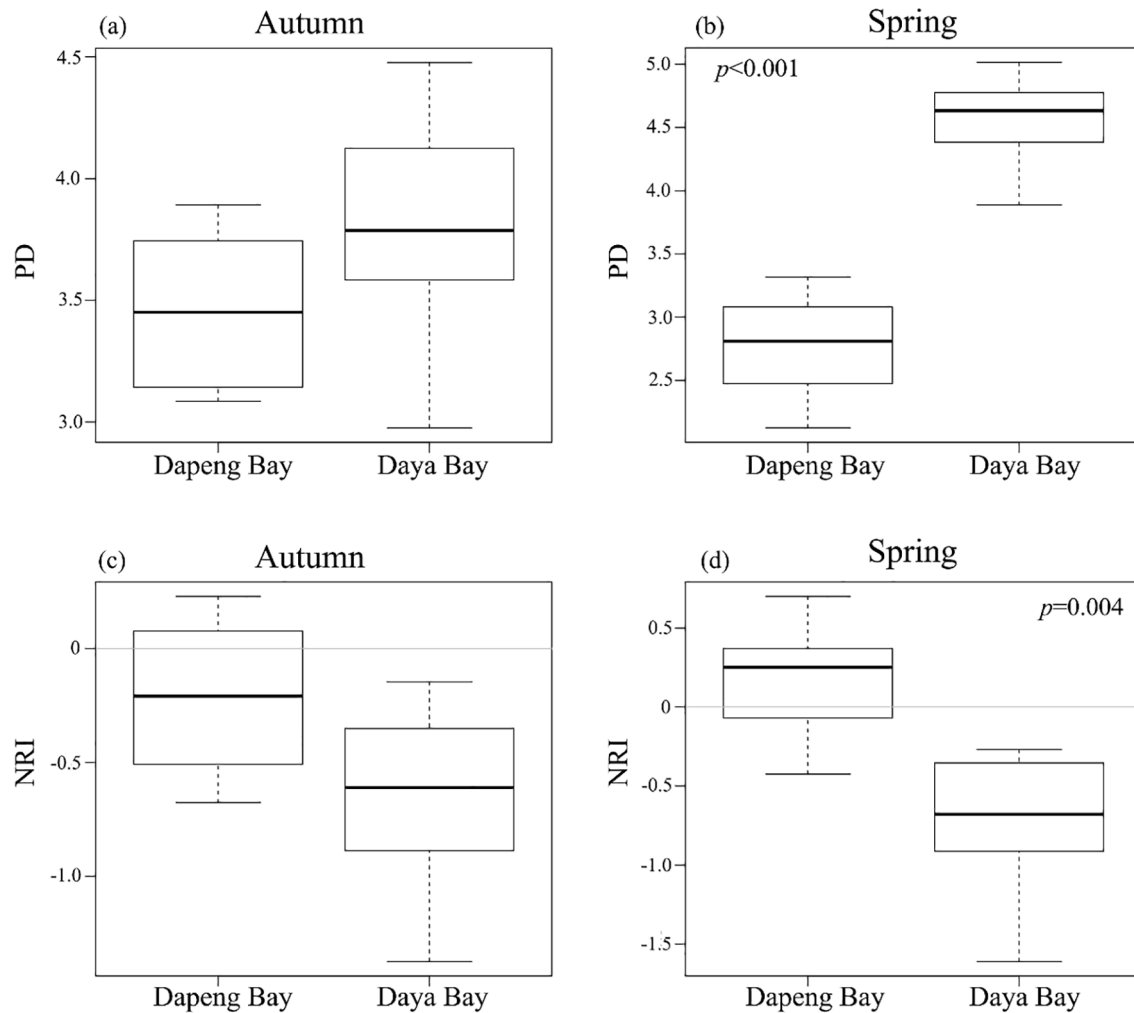


Fig. 2. Catch per unit area estimates for fish and benthic invertebrate in Dapeng and Daya Bay in autumn 2019 (a) and spring 2020 (b).

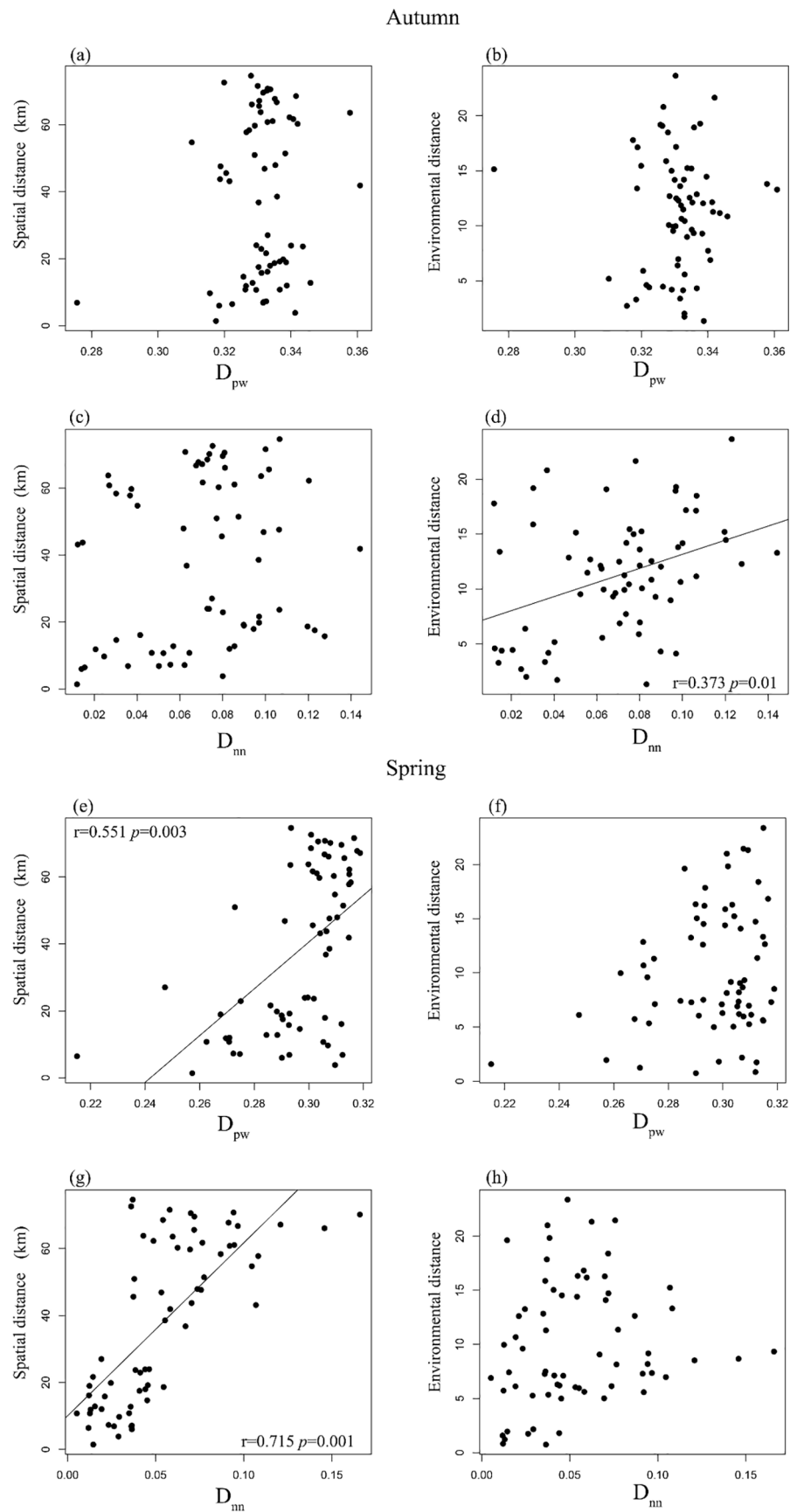
**Table 1**

Results of the redundancy analysis to test for the contributions of space and environment to community patterns in Dapeng and Daya Bay in autumn 2019 and spring 2020. Global model, overall model performance; FS, forward selection performance; E, environmental variables; S, spatial variables; S + E, all variables; E|S, the pure contribution of environmental variables; S|E, the pure contribution of space; Shared, explained variance that cannot be attributed uniquely to spatial or environmental variables; Unexplained, the variance not explained by variables included in the model.

Spring				Autumn			
RDA model	R <sup>2</sup>	R <sup>2</sup> <sub>adj.</sub>	p	RDA model	R <sup>2</sup>	R <sup>2</sup> <sub>adj.</sub>	p
<b>S</b>				<b>S</b>			
Global model	0.747	0.546	0.009	Global model	0.733	0.511	0.001
FS	0.664	0.533	0.002	FS	0.412	0.281	0.001
dbMEM1	0.559		0.001	dbMEM1	0.215		0.022
dbMEM3	0.053		0.008	dbMEM2	0.197		0.006
dbMEM4	0.051		0.002				
<b>E</b>				<b>E</b>			
Global model	0.875	0.543	0.041	Global model	0.592	0.252	0.033
FS	0.606	0.519	0.002	FS	0.177	0.095	0.043
Dissolved oxygen	0.435		0.005	Dissolved oxygen	0.177		0.042
Temperature	0.171		0.013				
S + E	0.782	0.601	0.001	S + E	0.567	0.32	0.008
S E	0.42	0.38	0.001	S E	0.277	0.188	0.009
E S	0.119	0.064	0.036	E S	0.155	0.039	0.04
S ∩ E		0.157	/	S ∩ E		0.094	/
Unexplained		0.399	/	Unexplained		0.68	/



**Fig. 3.** Variance analysis with permutation tests for values of phylogenetic diversity (a, b) and net relatedness index (c, d) in nektonic communities of Dapeng and Daya Bay in autumn 2019 and spring 2020.



**Fig. 4.** The relationship between phylogenetic beta diversity and (deep phylogenetic levels, D<sub>pw</sub>; shallow phylogenetic levels, D<sub>nn</sub>) spatial or environmental distance between sampling sites in Dapeng and Daya Bay in autumn 2019 (a-d) and spring 2020 (e-h).



but increased with environmental distance between sampling sites (Mantel  $r = 0.373$ ,  $p = 0.01$ , Fig. 4 c, d). For spring nektonic communities, both  $D_{pw}$  and  $D_{nn}$  increased with spatial distance (Mantel  $r = 0.551$ ,  $p = 0.003$ ; Mantel  $r = 0.715$ ,  $p = 0.001$ , Fig. 4 e, g), but did not change with environmental distance between sampling sites (Mantel  $r = 0.241$ ,  $p = 0.059$ ; Mantel  $r = 0.154$ ,  $p = 0.148$ , Fig. 4 f, h).

NMDS analysis did not detect clear ordination differentiations of phylogenetic alpha diversity both at deep and shallow phylogenetic levels in the autumn nektonic communities (Fig. 5 a, b). However, obvious ordination differentiations of phylogenetic alpha diversity were observed both at deep and shallow phylogenetic levels in the spring nektonic communities, following a clear trend for separation of Dapeng and Daya Bay (Fig. 5 c, d).

The MRM models significantly predicted the effect of environmental variables in phylogenetic beta diversity both at shallow and deep phylogenetic levels for spring nektonic communities. The MRM models explained 34.4% of environmental variance in phylogenetic beta diversity at deep phylogenetic levels ( $D_{pw}$ ) and 42.1% at shallow phylogenetic levels ( $D_{nn}$ ). Dissolved oxygen ( $p = 0.043$ ) and pH ( $p = 0.001$ ) significantly explained the variation in phylogenetic beta diversity at deep phylogenetic levels for spring nektonic communities, while Salinity ( $p = 0.02$ ), pH ( $p = 0.003$ ) and water temperature ( $p = 0.021$ ) were significantly related to the variation in phylogenetic beta diversity at shallow phylogenetic levels. For autumn nektonic communities, however, the effect of environmental variables in phylogenetic beta diversity were not significantly predicted by MRM models both at deep and shallow phylogenetic levels (Table 2).

#### 4. Discussion

Several studies have revealed the importance of considering both spatial and temporal variations to explain nektonic communities' structure and distribution (Eby and Crowder, 2004; Ramos-Miranda et al., 2008; Raposa et al., 2003). Our results further support this view that both spatial and temporal variabilities contribute to explaining the heterogeneous patterns of community structure and phylogenetic diversity of coastal nekton in Daya and Dapeng Bay in South China Sea.

A large part of overall variance in autumn nektonic communities was explained by spatial variables included in the analyses (18.8%), whereas this part increased to 38% in spring nektonic communities. The total unexplained variation went down from 68% to 39.9%. These percentages indicated that the nektonic communities in the two subtropical adjacent bays have clear spatial and seasonal patterns. One of the main factors responsible for the difference of spatial component that explained variation between autumn and spring was the difference of degree of stochastic processes (ecological drift). In addition, the large unexplained variability in autumn also implied a strong effect of stochastic processes in structuring communities of the two adjacent bays. The larval dispersal and settlement in the open-sea systems supports the existence of strong stochastic forces in the assembly of many nektonic communities (Ford and Roberts, 2018; Waltho and Kolasa, 1996). It has been shown that the stochastic forces caused by climate variations influence rates of fecundity and recruitment by altering water temperature, the availability of spawning grounds, or coastal circulation patterns (Hilborn et al., 2003). Many fish and invertebrates in coastal ecosystems have a life cycle that includes pelagic larval stage and benthic adult stages. These relatively sedentary adult stages release

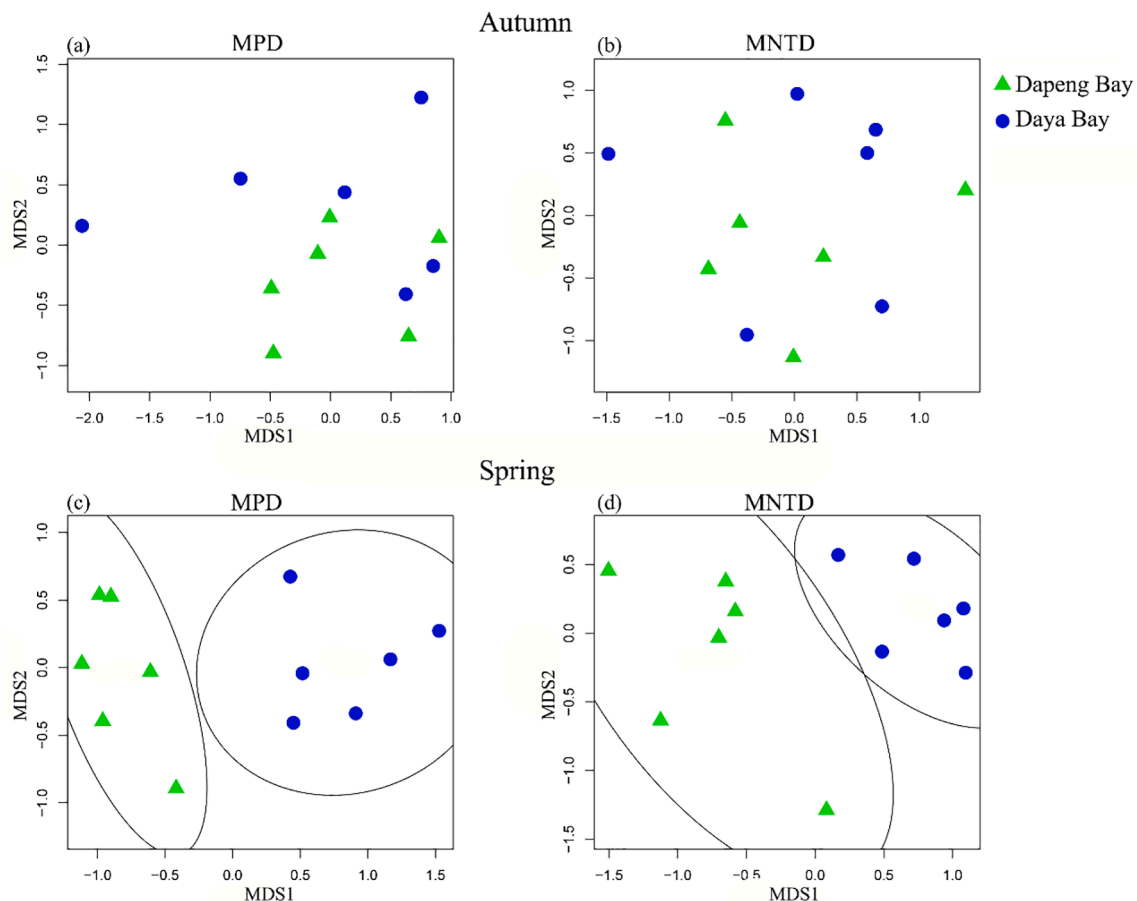


Fig. 5. nMDS ordination plots of nektonic communities occurring in Dapeng and Daya Bay in autumn 2019 (a, b) and spring 2020 (c, d) based on mean pairwise distance and mean nearest taxon distance.

**Table 2**

Results of multiple regression on distance matrices (MRM) analyses for the effect of environmental variables in phylogenetic beta diversity both at shallow and deep phylogenetic levels from autumn and spring nekton communities in Dapeng and Daya Bay. Significant variables are in bold.

predictor	autumn				spring			
	D <sub>pw</sub>		D <sub>nn</sub>		D <sub>pw</sub>		D <sub>nn</sub>	
	coefficient	p	coefficient		coefficient	p	coefficient	p
Intercept	0.324	0.214	0.033	0.999	0.277	0.057	0.027	0.963
Chl-a	−0.005	0.329	0.014	0.315	0.004	0.627	−0.017	0.128
pH	0.066	0.505	0.225	0.469	<b>0.451</b>	<b>0.001</b>	<b>0.605</b>	<b>0.003</b>
Salinity	0.003	0.765	0.002	0.965	0.018	0.207	<b>0.053</b>	<b>0.02</b>
Dissolved oxygen	−0.001	0.99	0.008	0.581	<b>−0.014</b>	<b>0.043</b>	−0.016	0.476
Temperature	0.015	0.022	0.028	0.186	0.008	0.328	<b>0.038</b>	<b>0.021</b>
Transparency	0.001	0.737	0.008	0.41	0.027	0.169	−0.012	0.25
Depth	−0.001	0.312	−0.001	0.685	−0.001	0.364	−0.003	0.068
Nutrients	0.001	0.31	−0.001	0.968	0.001	0.578	0.001	0.722
R <sup>2</sup>	0.207	0.109	0.266	0.144	<b>0.344</b>	<b>0.023</b>	<b>0.421</b>	<b>0.01</b>

millions of larvae that passively are widely dispersed by ocean currents (Jackson and Strathmann, 1981; James et al., 2002).

The results suggest that the recruitment of marine organisms affected by chaotic coastal circulations might increase the stochasticity in structuring communities of the Daya Bay and Dapeng Bay, particularly in autumn. Mid-summer fishing moratorium may be one of the main reasonable explanations of the increased stochasticity in structuring nektonic communities. In recent decades, many productive coastal fishing grounds have disappeared or moved away from the shoreline due to the overexploitation of fisheries resources and other anthropogenic impacts (Zhong and Power, 1997). Since the 1980 s, the Chinese government has launched a series of actions to protect conventional species such as fishing bans during the reproductive seasons. The annual fishing ban covered the spawning seasons of most nektonic species, mostly from May to August in summer, hence named “mid-summer fishing moratorium”. It was reported as being successful in recovering fish stocks (Yu and Yu, 2008). Even Bryde’s whale has recently been found swimming and preying in Dapeng Bay. According to the previous studies, the summer fishing moratorium in the East China Sea has the effect of increasing fishery resources, and fishes contribute the most to the increase of resource output. However, the current fishing moratorium only serves as a short-term temporary conservation, and the effect of the increasing fishery production during the fishing moratorium is limited to the current year (Yan et al., 2019). Zhang et al. (2020) reported the current fish biomass in autumn is higher than that in spring in Dapeng Bay due to fishing moratorium, and the community structure is affected by an external disturbance in spring and stable in autumn. In our case, without fishing pressure, fish stocks and diversity had been effectively recovered and recruited in Daya Bay and Dapeng Bay, through the random nature of vacant habitat becoming available and successful settlement from the larval pool.

In general, the broad scale distribution pattern of nekton could be primarily affected by oceanographic factors, such as circulation and water currents, which can greatly impact larval dispersal distance. Nevertheless, at small spatial scales, such as coastal ecosystems, or estuarine ecosystems, the composition and distribution of nektonic communities are also related to heterogeneity in the habitat types or environment (La Mesa et al., 2011; Letourneur et al., 2003; McClanahan and Arthur, 2001). Only a small part of the overall variance in nektonic communities was explained by environmental variables in our study (3.9%–6.4%). MRM also showed that changes at deep and shallow phylogenetic dissimilarities for spring nektonic communities were weakly related to a few environmental variables (e.g. pH, salinity, dissolved oxygen and temperature). These low percentages and weak relationship indicated the lack of certain environmental variables able to add explanatory capability to the analyses, or these environmental variables are bad predictors for seasonal change of species composition and community structure of nekton in these two bays. Indeed, the way of each species perceives and responds to the environmental variability

may be quite different and be influenced by their ability to move and position in coastal ecosystems. In addition, in coastal areas, physical conditions can change very quickly and variables such as wind speed, atmospheric pressure or currents also could contribute explain part of the variation in nekton community structure. Implement long-term environmental monitoring would be able to effectively assess true environmental factors structuring nektonic communities in these coastal areas.

Studying phylogenetic structural patterns of communities can reveal the potential mechanisms that drive community composition (Cavender-Bares et al., 2009). Here, we found strongly spatial and temporal pattern of phylogenetic structure in nektonic communities between Daya and Dapeng Bay. In the autumn dataset, there were no differences of phylogenetic biodiversity for nektonic communities between Dapeng and Daya Bay. These results supported our previous discussions on the effect of stochastic processes on community structure, as nektonic communities both in Dapeng and Daya Bay showed higher negative values of NRI and indicated phylogenetic overdispersion. The autumn community dataset was collected only one week after the mid-summer fishing moratorium. That is, nektonic communities in both bays became progressively more evenness due to the lack of strong selection pressure (fishing) lasting more than three months.

However, both phylogenetic biodiversity and NRI showed heterogeneous patterns (see below) between Dapeng Bay and Daya Bay in spring nektonic communities. Phylogenetic biodiversity significantly decreases while NRI changed from negative to positive in Dapeng Bay throughout the winter. Strong phylogenetic clustering was found in spring nektonic communities of Dapeng Bay. After the mid-summer moratorium, fishing becomes more intense as fishermen try to catch as much fish as possible in the shortened period by using more efficient gear and methods (high number of artisanal shrimp trawlers, see below), especially for some commercial species. These results implied that we could consider the fishing intensity as a strong stress for nektonic communities, which even exceeds the effect of environmental forces. The phylogenetic structure of the spring nektonic communities between Dapeng Bay and Daya Bay were significantly different, associated with their distinct fishing intensity. Both total and fish CPUE in Dapeng Bay were higher in the autumn survey than that in Daya Bay, whereas it was the opposite in the spring survey. There was an increased fishing intensity that occurred in Dapeng Bay rather than Daya Bay after mid-summer fishing moratorium. According to the statistical data on agriculture, the marine fishing production in Shenzhen city (Dapeng Bay) was much higher than that in Huizhou city (Daya Bay). The total marine fishing production was 91,776 tonnes and crustaceans fishing production was 8,102 tonnes in Shenzhen city, while that 20,134 tonnes and 2,875 tonnes in Huizhou city, despite Dapeng Bay only covers about 390 km<sup>2</sup> area by comparison with Daya Bay which covers about 600 km<sup>2</sup> of area (Editorial Committee of Guangdong Statistical Yearbook on Agriculture, 2019).



Moreover, different taxa do not have the same sensitivity to fishing equipment and fishing method. According the data from Guangdong Statistical Yearbook on Agriculture (2019), the number of commercial trawlers in Shenzhen city are nearly twice of Huizhou city, most of are artisanal shrimp trawlers. The gross tonnage of commercial trawler in Shenzhen city reached to 5,505 tonnes, while 826 tonnes in Huizhou city. The crustaceans in Dapeng Bay are under even higher fishing pressure. The nektonic community in Dapeng Bay present strong phylogenetic clustering in spring. Therefore, we suggested the differentiation in nekton species diversity and composition in the two bays was also associated with an increased fishing activity as well as differences in fishing equipment (Zhang et al., 2020).

## 5. Conclusion

The nektonic communities in Daya and Dapeng Bay showed strong spatial and temporal patterns in both community structure and phylogenetic facets because of the change of fishing intensity and mid-summer fishing moratorium. The differentiation of spatial components explained the variation in the two bays between autumn and spring, which are related to the stochastic processes. However, the low percentages explained by environmental variables indicated the lack of certain environmental variables able to add explanatory capability to the analyses. The differentiation of temporal pattern in both community and phylogenetic structure mainly related to increasing stochasticity in structuring nektonic communities caused by mid-summer fishing moratorium, and different fishing intensity in the two bays. Therefore, fishing intensity is a strong stress for nektonic communities that even exceeds the effect of environmental forces. In our view, the immediate and sweeping fishing efforts may rapidly deplete the recovered fish stocks in a short time and exert enormous pressure on resources. Our study also provided insights into effective practices for fishery management for the future.

## CRediT authorship contribution statement

**Lei Xu:** Conceptualization, Data curation, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Lianggen Wang:** Formal analysis, Methodology. **Xuehui Wang:** Formal analysis, Methodology. **Kay Van Damme:** Writing - original draft. **Jiajia Ning:** Formal analysis, Methodology. **Yafang Li:** Formal analysis, Methodology. **Delian Huang:** Formal analysis, Methodology. **Shuangshuang Liu:** Formal analysis, Methodology. **Hong Li:** Formal analysis, Methodology. **Feiyan Du:** Funding acquisition, Project administration, Resources.

## 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.ecolind.2021.108226>.

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