Trophic structure and functional diversity reveal pelagic-benthic coupling dynamic in the coastal ecosystem of Daya Bay, China

Rui Ying[a], Yiting Cao[b], Fangmin Yin[a], Jianlin Guo[b], Jianrong Huang[a], Yingyong Wang[a,g], Lianming Zheng[c], Junxing Wang[d], Haoliang Liang[d], Zufu Li[a], Jianxiang Feng[e,f,*]

[a] Guangdong Province Key Laboratory for Improved Variety Reproduction of Aquatic Economic Animals, School of Life Sciences, Sun Yat-sen University, Guangzhou, Guangdong, China
[b] College of Biology and Food Engineering, Guangdong University of Education, Guangzhou, Guangdong, China
[c] College of Ocean and Earth Sciences, Xiamen University, Xiamen, Fujian, China
[d] Huizhou Marine Technology Center, Huizhou, Guangdong, China
[e] School of Marine Sciences, Sun Yat-sen University, Zhuhai, Guangdong, China
[f] Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Zhuhai, Guangdong, China
[g] The Museum of Biology, School of Life Sciences, Sun Yat-sen University, Guangzhou, Guangdong, China

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ABSTRACT

Offshore marine areas have diverse habitats and food sources which lead to dynamic exchanges of nutrients and energy between different water layers. Coupling of energy pathways is related to both physical (e.g., sedimentation) and biological (e.g., predation) processes. However, due to the biological processes affected by human influences, the variability and dynamics of this coupling are not well quantified. Daya Bay, a subtropical semi-closed gulf affected by human activities, was studied to assess dynamics of pelagic-benthic coupling affected by trophical interaction. Stable isotope analyses of three main functional groups (pelagic fish, demersal fish, and benthic crustaceans) were conducted to assess trophic interactions, and trait-based functional indices were calculated to reveal the changes of community structure. The environmental variations, including chlorophyll *a* concentration, phytoplankton, and zooplankton abundance were monitored to explain the potential causes. The results showed that pelagic-benthic coupling effects were strong and seasonally dynamic in Daya Bay. Most nekton organisms were largely (> 55%) fueled by pelagic production and exhibited high trophic overlap. In spring, when resources were limited, the proportion of the pelagic contribution to all the groups was highest, while greater trophic partitioning was observed. The trait-based functional diversity indices showed that the functional richness is extremely low in all seasons. However, the functional evenness and dispersion indices increased from winter to spring to summer. Our observation suggests that plankton abundance caused this seasonal pattern by controlling the strength of competitive interactions. Our study highlights the dynamic of pelagic-benthic coupling strength caused by trophic interaction across different environmental conditions of coastal ecosystems, this might provide important sighting on the coastal food web study and fishery management.

1. Introduction

Offshore ecosystem services are important for sustainable human development (Barbier, 2017). They provide a large amount of high-quality protein for humans through mariculture and fishery activities (He et al., 2014). These offshore ecosystems including mangroves, marshes, and coral reefs have high biodiversity and multiple basal energy sources which underlying the complex food webs (Barbier et al., 2011; Neres-Lima et al., 2016). These energy sources include many autotrophic basal sources, such as phytoplankton in the pelagic layer, microphytobenthos and seagrass in the benthic layer, and detritus suspending in the water body (Claudino et al., 2015). Additionally, allochthonous nutrients input, such as terrigenous sources and bird excrement, also increase the offshore ecosystem productivity (Careddu et al., 2015; Otero et al., 2018). The offshore ecosystems are typically of shallow depth and under intensive anthropogenic influences (e.g., fishing and input of extra organic matter). This leads to the complexity of the basic nutrient input and energy transfer of the food web and the

trend of coupling between various energy channels (Halpern et al., 2008; Rooney et al., 2006). In particular, the coupling between the two asymmetric energy pathways in the pelagic and benthic water layer (pelagic-benthic coupling hereafter) has been increasingly studied and appears to be beneficial for food web structure stability (Blanchard et al., 2010; Wolkovich et al., 2014).

The pelagic-benthic coupling process depends on both passive processes (e.g., sedimentation) and active processes (biological processes like predation). The deposition of pelagic-derived organic matter, such as fish fecal pellets, is an essential part of benthic secondary production (Morais and Bellwood, 2019; Saba and Steinberg, 2012), while the trophic interaction and energy exchange between pairwise species also exert important influence. For example, mobile invertebrates (e.g., mysids, squat lobsters) and suspension feeders (e.g., bivalves, scallops), feeding on plankton materials and caught by demersal predators, act to transfer energy from the pelagic to the benthic (Funes et al., 2018; Woodland and Secor, 2013; Zhou, 2006). Similarly, the oceanic diel vertical migration (DVM) community plays a significant role in the deep-sea carbon transport (Romero-Romero et al., 2019; Trueman et al., 2014). Previous studies have emphasized understanding of pelagic-benthic coupling, however, the coupling dynamics effects, particularly those caused by complex and dynamic biological processes (e.g., nutrient-cycling effects, ontogenetic shifts), remain poorly studied (Griffiths et al., 2017). General predators like demersal fish, which occupy a higher trophic level, have flexible feeding habitats and less prey size constraints. They are capable of feeding from different pathways and act as a coupler between these pathways (Vander Zanden and Vadeboncoeur, 2002; Woodland and Secor, 2013). The predation strength is also dynamic and regulated by body size (Woodland and Secor, 2013), population abundance (Bergström et al., 2015), and intraspecific competition (Svanbäck et al., 2011). Therefore, studies that include spatial and temporal variation are required to understand the linkage between energy flux and energy pathways coupling.

Stable isotopes (carbon: $\delta^{13}C$; nitrogen: $\delta^{15}N$; sulfur: $\delta^{34}S$) have been widely used for analyses of trophic interactions such as quantifying the contribution of different food sources to consumers (Duffill Telsnig et al., 2019; Giraldo et al., 2017; Morais and Bellwood, 2019). These isotopes have an important enrichment characteristic in the food web. For example, the nitrogen isotope ratio increases by about 3.4‰ for each trophic level, whereas the carbon isotope discrimination value is less than 1.5‰ (Post, 2002). Different basal food sources in an ecosystem often have different $\delta^{13}C$ values, species mainly feeding on pelagic prey tend to exhibit lower $\delta^{13}C$ values compared with benthic predators, so carbon stable isotope is often used to identify the diet sources of consumers (Kopp et al., 2015). The isotopic space has also been increasingly used as the proxy of ecological niche to study species coexistence mechanisms like the interaction between invasive and native species based on new methods, such as stable isotope Bayesian ellipses (Hayden et al., 2013; Hill et al., 2015; Jackson et al., 2011; Layman et al., 2007). However, in the real ecosphere with multi-dimensional ecological niches, it is species functional traits of different species (such as body size) that determine their competitive ability and trait-variations underlie species-interactions and community structure (McGill et al., 2006). For example, the abundant prey in the coastal ecosystem, herrings, can reverse its predator-prey relationship with cod by increasing its spawning stock biomass and inhibiting cod recruitment (Fauchald, 2010). On a community level, the functional diversity of food webs is also closely correlated with trophic niches. Isotopic niches increase with the functional richness of species in the food web (Dézerald et al., 2018), and trophic partitioning determines the functional redundancy of the native fish community (Comte et al., 2016). Overall, the combination of functional diversity and trophic niches helps explain the complicated trophic dynamics of ecosystems.

Although the trophic niche partitioning of separate pelagic and benthic populations or communities in coastal ecosystems have been well documented (Cabrol et al., 2019; Cherel et al., 2010; Choy et al., 2015; Divine et al., 2015; McTigue and Dunton, 2014), studies considering variation of functional structure as an indicator of ecosystem function are insufficient. The greatest biomass in coastal ecosystems is contributed by small forage fish, which have similar ecotypes and resource preferences (Ying et al., 2019). Therefore, the depletion of individual forage species will not necessarily result in widespread ecological effects. By contrast, such high functional redundancy can increase disturbance resistance of the ecosystem (Koehn et al., 2016; Raffaelli, 2006). Nevertheless, the relationship between trait similarity and trophic overlap is plastic. Similar species can have niche differentiation and this may depend on individual age and food availability (Cabrol et al., 2019; Zhao et al., 2014). Thus it is necessary to study the structure of food webs from complementary aspects (Gajdzik et al., 2018).

In this study, we used the nekton community of Daya Bay to study pelagic-benthic coupling effects in a coastal ecosystem. Daya Bay is a typical semi-closed offshore area that has been greatly affected by human activities (Wu and Wang, 2007). We studied the dynamics of trophic interactions between the three main functional groups: pelagic fish, demersal fish, and benthic crustaceans. We used isotopic trophic structure and analysis of various functional traits to study the dynamic relationship between pelagic-benthic coupling and nekton community structure (including the isotopic trophic structure and trait-based functional structure) within Daya Bay. We hypothesized that: (i) strong and dynamic pelagic-benthic coupling exists; (ii) such coupling is related to trophic interactions like competition; and (iii) seasonality is a major factor affecting the variability of trophic interactions. Based on functional diversity analysis results, we examined ecosystem functioning redundancy and the resilience of such gulfs under intensive exploitation. We also provide insights on effective practices for fishery management.

2. Materials and methods

2.1. Study site

Daya Bay is a subtropical semi-closed gulf located in the northern part of the South China Sea, between Shenzhen city and Huizhou city (22°30′–22°50′N, 114°30′–114°50′E). The bay covers about 600 km² area and has a shoreline of 92 km. The average water depth in Daya Bay is around 10 m and the annual average water temperature ranges from 15 °C to 32 °C. The bay has diverse habitats, including coral communities, mangroves, mudflats, rocky, and sandy shores. It is also a nursery, feeding, and breeding ground for more than 150 aquatic species (Wang et al., 2008). Daya Bay has been affected by intensive human activities, such as fishing, mariculture, and the construction of two nuclear power stations. Therefore, this area requires studies that will facilitate judicious future management and marine policies.

2.2. Sample collection and stable isotope analysis (SIA)

Fish and benthic invertebrate sampling were conducted through a seasonal survey in 2018 (January for winter, April for spring and July for summer) at Daya Bay. The nekton in epipelagic and bottom layer was sampled by pair trawl and bottom trawl respectively. A total of 16 sampling sites were deployed in the gulf and were divided into 4 sampling lines (i.e., East, West, Mouth, South of Daya Bay, Fig. S1). For pair trawl, all 16 sites were included, but only 8 sites (on the East and West side) were included in bottom trawl. Based on a previous study from Ying et al. (2019), the community structures in different stations were not significantly different and thus can be considered as replicates of the same population. Organisms in all the samples were identified to species level and the abundance, individual body mass, and length of each species were measured on site based on random sampling.

Chlorophyll *a* and plankton abundance were also sampled to test the importance of food availability. Surface seawater (0.5 m underwater,

200 mL) and bottom seawater (1 m above the seafloor, 200 mL) were sampled to measure chlorophyll content using plexiglass water sampler. The water sample was filtered through a 0.7 μm GF/F filter, frozen in liquid nitrogen and taken to the laboratory for extraction in 93% acetone for 20 h. The following extract was run on a Turner Design chlorophyll fluorescence instrument (non-acidification module, sigma chlorophyll standard, item number C6144 as standard correction). Phytoplankton samples were collected in 1000 mL of surface and bottom seawater using plexiglass water sampler. The water was filtered using a sieve (200 μm hole diameter), and then stored in white plastic bottles, fixed with Lugol's solution (1.5% of the sample volume), and stored in the dark. The fixed sample was taken to laboratory and stored for 24 h. After fully deposition, the supernatant was slowly aspirated by a siphon until 50 mL water sample containing the precipitate remained. The remaining 50 mL water sample was centrifuged and observed under a microscope. Zooplankton were horizontally collected using a plankton net (length: 145 cm, inner diameter: 50 cm, net mesh: 0.505 mm). The collected samples were placed in a 500 mL clear plastic jar and fixed with formalin, then were observed under a microscope. The identified zooplankton sample was sieved, filtered, and weighed using a balance accurate to 0.01 mg.

After sampling, 32 species, including 25 fish species and 7 crustaceans, were selected to conduct stable isotope analysis (SIA). These species represent the greatest percentage of biomass in Daya Bay (average 70.2% in pair trawl and 37.9% in bottom trawl) and are typical examples of the Daya Bay nekton community. These species were classified into 3 functional groups (pelagic fish FG1, demersal fish FG2, and benthic crustaceans FG3, respectively) according to their living layer, feeding habits, and taxonomic status (Table S2). Muscle samples were taken from the abdomen of shrimp, the chelipeds of crabs, and the dorsal of fish. At least 3 individuals were sampled for each species. Additionally, the foot-muscle of some bivalve species (Table S1) was sampled as an isotopic baseline. All of the muscle samples were dried in −55 °C for 48 h using a freeze dryer (Biocool, FD-1A-50), then ground to a powder and weighed in tin cups (about 200 μg in 4×6 mm tin cups). Carbon and nitrogen isotopes of these samples then were analyzed using an elemental analyzer (Flash EA 2000 HT, Thermo Fisher Scientific, Inc., USA) and an isotope ratio mass spectrometer (Finnigan Delta V Advantage, Thermo Fisher Scientific, Inc.) in Shenzhen Customs Food Inspection and Quarantine Technology Center. Laboratory standards (glycine and urea) were run every 12 samples to correct any instances of instrument drift. The analytical precision was ± 0.1‰ for δ^{13}C analysis and ± 0.2‰ for δ^{15}N analysis.

2.3. Seasonal variability of community abundance and biomass

A one-way ANOVA was used to determine the significance of seasonal effects on the abundance of chlorophyll *a*, phytoplankton, zooplankton, and biomass of pelagic and benthic community. Pairwise comparisons were made using Tukey's HSD post hoc test. Significant differences are indicated by different letters in Fig. 1. The significance level was $P < 0.05$.

2.4. Relative contribution of pelagic and benthic production to the nekton community

We calculated the relative contribution proportion of pelagic and benthic production using a two-source stable isotope mixing model (Duffill Telsnig et al., 2019; Giraldo et al., 2017; Kopp et al., 2015). A higher pelagic contribution proportion found in benthic communities (FG2 and FG3) could be a stronger coupling strength. The pelagic and benthic source isotope ratios data were from previous studies in Daya Bay (Arbi et al., 2018; Ke et al., 2019). The benthic detritivores (*Batillaria zonalis, Cerithidea cingulata, Petrolisthes miyakei, Paralacydonia paradoxa*) with similar δ^{13}C values to pelagic sources (particulate organic matter, about $-23‰ \sim -19‰$), and the grazers (*Clithon*

sowerbianus, Nerita undata, Monodonta neritoides, Planaxis sulcatus, Sesarma dehaani) with similar δ^{13}C values to benthic sources (microphytobenthos, about $-16‰ \sim -12‰$) were selected. These sources were taken as fixed. Fitting of the mixing model was performed using the R package "SIAR" (Parnell et al., 2010) and according to the guidelines in Phillips et al., (2014). The Markov Chain Monte Carlo (MCMC) sampling was run using function *siarmcmcdirichletv4* and following parameters: concdep = 0; chain length = 500,000; burn-in = 50,000; thin-by = 15. The model diagnostic test was conducted using function *siarhdrs* to test the convergence of mixing models. The mean proportional contributions are reported with 95% Bayesian Credible Intervals (95% BCI).

2.5. Ecological niche estimation of nekton community

Trophic structures were described by the ecological niche, which was composed of the isotopic niche and vertical space use. An iso-space plot (i.e., C-N biplot) was used to depict the feeding ecology. Isotopic niches were estimated using the standard ellipse area collected for small size (SEAc) in R package "SIBER" (Jackson et al., 2011). To visually show the habitat use on a vertical spatial scale, we plotted the relationship between relative habitat depth and δ^{13}C value. The relative occurrence depth (ROD) was simply proxied by occurrence frequency in two types of trawl methods (i.e., pair trawl and otter trawl); the calculation formula was $f_p - f_o$, where f_p is capture frequency in the pair trawl and f_o is capture frequency in the otter trawl. A higher ROD value of species means the tendency of occurring in the upper layer, while a lower value means occurring more frequently in the bottom layer. This simple method avoids determining feeding ecology only based on isotope ratio and helps provide the realized community resource use, including the vertical space of species and their seasonal dynamics.

Nitrogen isotope ratios (δ^{15}N) were transformed to trophic level (TL) data and sampled bivalves was used as baseline. Multiple species and repeats were set to reduce variation, but the seasonal variation wasn't considered here. Due to the narrowing trophic discrimination factor (Δ^{15}N) as the δ^{15}N value of prey increased, we adopted the scaled Δ^{15}N framework in Hussey et al. (2014) to achieve the precision of TL calculation. Based on the results, the trophic levels of 21 species appearing in all three seasons (common species hereafter, Table S1) were used to conduct one-way ANOVA to find the differences of trophic positions of species in different seasons.

### 2.6. Functional diversity of the nekton community

Both the isotopic functional diversity and trait-based functional diversity were estimated (Gajdzik et al., 2018). The three main modules (richness, evenness, and dispersion) were calculated. For the isotopic diversity indices, the IRich (isotopic richness) represents *iso*-space area occupied by all of the species as a convex hull area in (Layman et al., 2007); IEve (isotopic evenness) quantifies the regularity in the distribution of organism through the minimum spanning tree that links all of the points in isotopic space. The IDis (isotopic dispersion) represents distribution divergence in iso-space and it is the weighted-mean distance to the gravity center of all points. To calculate IEve, the first step was to determine the length of each branch linking a pair of points:

$$EW_l = \frac{dist(i, j)}{w_i + w_j}$$

where w_i and w_j mean relative abundances of i and j.

Then each EW_l was divided by the sum of EW to obtain the partially weighted evenness and it was compared to the perfect value $1/(N - 1)$, where N is species number. The specific equation is:

$$IEve = \sum_{l=1}^{N-1} \min\left(\frac{EW_l}{\sum_{l=1}^{S-1} EW_l}, \frac{1}{N - 1} \right) - \frac{1}{N - 1} \bigg/ 1 - \frac{1}{N - 1}$$
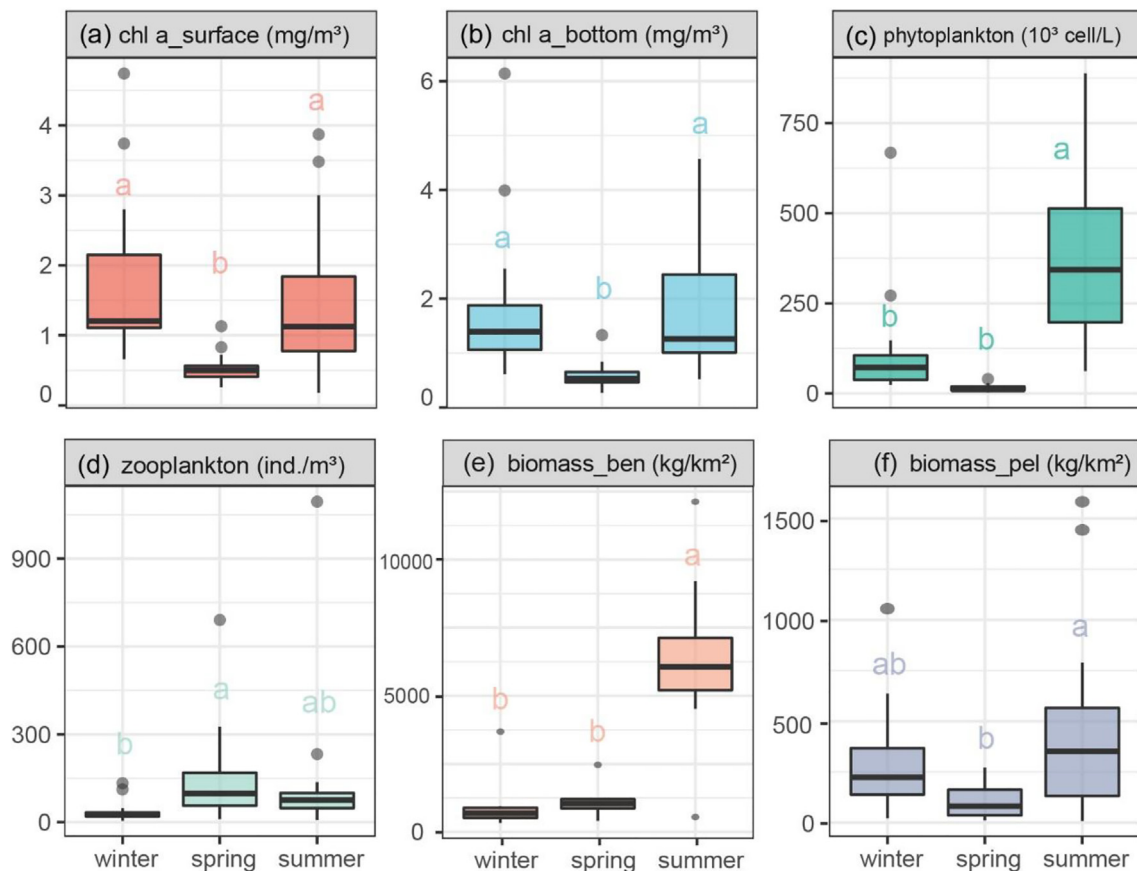
Fig. 1. Boxplot of seasonal variation of abundance/biomass of community in Daya Bay including (a) Chlorophyll *a* concentration in surface and (b) Chlorophyll *a* concentration in bottom layer, (c) Phytoplankton, (d) Zooplankton, (e) benthic fish and invertebrates and (f) pelagic fish community. Significant differences are indicated by letters, the significant level is 0.05.

For those communities having several dominant species, the gravity would be determined mainly by the dominant species.

$$IDis = \sum_{i=1}^{N} w_i \times dO_i / \max(dO_1, \cdots, dO_i, \cdots, dO_N)$$

where dO_i is the distance to the gravity of all points. The detailed definition, calculation, and functions of isotopic diversity are shown in Cucherousset & Villéger (2015). Finally, the overlap ratio of pair season (termed as nestedness), were calculated using the following equation:

$$INes = \frac{IRic(O_1 \cap O_2)}{\min(IRic(O_1), IRic(O_2))}$$

For the functional trait-based diversity calculation process, we followed Mouillot et al. (2013) and built a multidimensional functional space containing 11 biological traits. These traits included 7 category variables (taxonomic classification, feeding habits, grouping habit, movement ability, DVM habit, migration habit, and living layer) and 4 continuous variables (thermal preference, body length, body mass, and trophic level) (detailed information is shown in Table S1). The living habits (e.g., feeding habits and living environment) of species were obtained from FishBase (www.fishbase.com). Then a principal coordinate analysis (PCoA) was conducted on a Gower species distance matrix, which allows mixing both category and continuous variables while giving them equal weight (Mouillot et al., 2014). The first and second principal coordinate axes explained 32.1% and 18.0% of the variance, respectively. For a better explanation of PCoA axes, the correlation between functional traits and PCoA axes was tested and plotted. To visualize the trait-based dynamic, we plotted the abundance changes on two traits (body mass and thermal preference) as suggested

by (Mouillot et al., 2013). Two traits were selected because they are two of four continuous traits and reflect both the changes of individual size and adaption for environment. Trait-based functional diversity is also presented in the three indices. Similarly, the functional richness (FRi) represents the volume of multidimensional space occupied by all species. The functional evenness (FEve) represents the regularity of the distribution in functional space and the functional dispersion (FDis) quantifies the divergence of functional distribution.

We did not perform a null model approach randomly permuting species abundances and/or occurrences frequency as done in other studies (Comte et al., 2016; Fitzgerald et al., 2017; Mouillot et al., 2014). The present study focused on the overall change of communities rather than on the prediction variables that determine it. Because of this, we did not need to avoid effects caused by factors like species numbers. The functional diversity analyses were completed using R package "FD" (Laliberté and Legendre, 2010). The correlation between functional traits and the PCoA axis was tested using the *envfit* function in package "vegan" (Oksanen et al., 2007). All of these statistical analyses were performed in R version 3.6.0 (R Core Team, 2018).

3. Results

3.1. Abundance/biomass variance of the overall community

Abundance/biomass of the overall community varied seasonally (Fig. 1). The chlorophyll *a* concentration of surface and bottom showed similar values and patterns (Fig. 1a and b). In spring, chlorophyll *a* concentration was significantly lower than winter ($P < 0.001$) and summer ($P < 0.001$), which indicates the lowest productivity. Similarly, the abundance of phytoplankton in spring was lowest

$(13.8 \times 10^3 \text{ cell/L})$, but a phytoplankton bloom occurred in summer and caused significantly higher abundance than the other two seasons ($P < 0.001$, Fig. 1c). The zooplankton abundance of most sites was lower than 150 ind./m³ in all the seasons. Additionally, it showed an inverse seasonal dynamic with phytoplankton. Spring had the richest zooplankton population (121.5 ind./m³), followed by summer (69.5 ind./m³) and winter (25.4 ind./m³). The benthic nekton community exhibited the highest biomass in summer ($6.4 \times 10^3 \text{ kg/km}^2$), followed by spring ($1.1 \times 10^3 \text{ kg/km}^2$) and winter ($1.0 \times 10^3 \text{ kg/km}^2$). The pelagic nekton biomass was also highest in summer ($0.46 \times 10^3 \text{ kg/km}^2$), but winter ($0.29 \times 10^3 \text{ kg/km}^2$) had a higher biomass than spring ($0.10 \times 10^3 \text{ kg/km}^2$).

3.2. Relative proportion of pelagic contribution to the nekton

On the carbon isotope ratio (δ^{13}C) level, the entire community had a lower δ^{13}C mean value ($-17.3‰$ with 95% Bayesian Credible Interval, the same hereafter) in spring compared to winter and summer (both $-16.4‰$), and crustacean groups (FG3) showed a wider δ^{13}C ratio range ([$-18.8‰$, $-16.2‰$]) in spring. This indicates that the overall dietary preference was inclined to pelagic food sources in spring. Among the 3 functional groups, crustacean species always exhibited a higher δ^{13}C mean value than fish groups (average difference $+0.61‰$ in 3 seasons), while the two fish groups showed smaller difference (average 0.09‰ higher in FG2).

The stable isotope mixing model results show that the nekton community, including demersal fish and crustacea, was largely fueled by pelagic production (55%-82%, Fig. 2), indicating the strong pelagic-benthic coupling effects. Pelagic-derived food source fueled pelagic fish (mean 72.7%) are significantly higher than demersal fish (mean 67.0%) and crustaceans (mean 63.0%) ($P < 0.005$). For all the functional groups, the proportion of pelagic contribution in spring was significantly higher than in winter ($P < 0.001$) but is similar to summer ($P > 0.05$).

3.3. Ecological niches of functional groups in three seasons

The ROD results show that demersal fish assemblages have different vertical space use compared to pelagic fish (Fig. 3d-f). The pelagic fish typically live in the upper layer (ROD mean ± SE from winter to summer: 0.54 ± 0.40, 0.54 ± 0.35, 0.68 ± 0.26) and benthic

Fig. 2. Relative proportion of pelagic food contribution to different functional groups. Two-way ANOVA analysis shows that the pelagic contribution to the pelagic fish (FG1) is significantly higher than the other two groups ($P < 0.005$) and pelagic contribution in spring is significantly higher than winter ($P < 0.001$). The pelagic contribution in summer show no significant difference with winter and spring (both $P > 0.05$).

crustaceans basically live in the bottom layer (ROD mean ± SE from winter to summer: -0.60 ± 0.29; -0.78 ± 0.73; -0.78 ± 0.27). Demersal fish have various habitat use choices (ROD mean ± SE from winter to summer: -0.2 ± 0.48, 0.07 ± 0.71, -0.07 ± 0.45).

The trophic positions of nekton species in Daya Bay are mainly distributed at 2–4 TL. This indicates that they are basically secondary consumers. Mean scaled TL of all the species is lowest in winter (3.1) and higher in spring (3.5) and summer (3.7). For the 21 common species, winter showed a significantly lower TL than spring ($P < 0.05$) and summer ($P < 0.001$), while the difference among functional groups was not significant ($P > 0.05$).

Trophic niches of the 3 functional groups varied across seasons (Fig. 3). In winter, standard ellipse areas (SEAc) show that pelagic fish (FG1, 5.25) exhibit relatively wider isotopic niches than demersal fish (FG2, 4.12) and crustaceans (FG3, 2.78). However, in spring and summer, all the functional groups have similar isotopic niche breadth (FG1-FG3: 3.99, 4.67, 4.7 in spring, 3.25, 3.48, 3.35 in summer).

A high amount of overlap occurred between the isotopic niches of pelagic fish (FG1) and demersal fish (FG2) in winter and summer (isotopic nestedness ratio 72.1% and 80.8%). In spring, demersal fish showed a degree of isotopic niche partitioning with pelagic fish (nestedness ratio 49.1%). Nevertheless, the crustacean assemblage (FG3) showed relatively higher trophic partitioning with fish groups during all the seasons (nestedness ratio between FG1 and FG3: 54.3%, 10.8%, 21.4% from winter to summer).

3.4. Isotopic functional indices and trait-based functional structure of the nekton

All three isotopic functional indices increased with the season (Fig. 4a). The isotopic richness (0.64), evenness (0.44), and dispersion (0.50) in summer were the highest, followed by spring (IRic 0.63, IEve 0.33, IDis 0.42) and winter (IRic 0.39, IEve 0.08, IDis 0.16). The isotopic functional diversity in summer and spring were slightly different, and winter had the lowest isotopic diversity in all aspects. (Fig. 5).
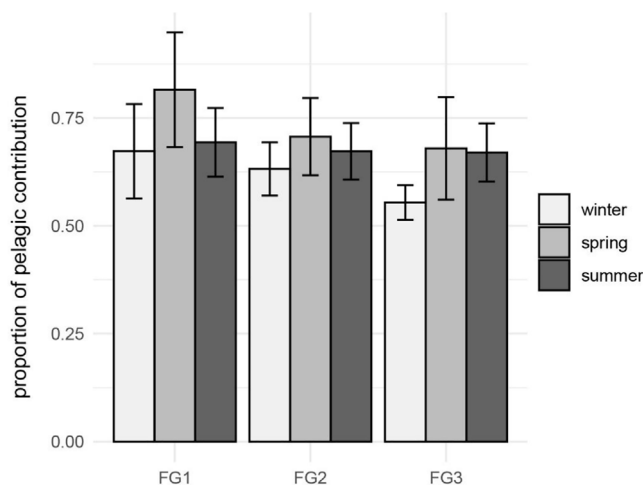
The PCoA result showed that the first and second principal coordinate axis accumulatively accounted for 50.1% of variance. The various functional traits are significantly correlated with PCoA axes ($P < 0.01$ for DVM and migration; $P < 0.001$ for the rest) and thus have some explanatory power (Fig. 6a). Trait-based functional indices showed that functional richness is extremely low all the time (near zero, but the value was set to 0.01 for visualization (Fig. 4b). This could be caused by the abundant, functionally homogeneous pelagic fish (Fig. 6b-c). The degree of functional dispersion in spring was the highest (0.284), followed by summer (0.246) and winter (0.031); functional evenness increased from winter to summer (0.163, 0.266, 0.428 respectively) (Fig. 4b).

The two-trait functional space shows that abundance change is the major factor causing functional diversity. From winter to spring, the entire Daya Bay community trended toward larger size and the fewer small fish resulted in a more even and dispersed functional structure (Fig. 6b). From spring to summer, the abundance of the entire community greatly increased except for the species preferring lower temperature (< 15 °C). However, the majority of changes still centered around the small fish (Fig. 6c).
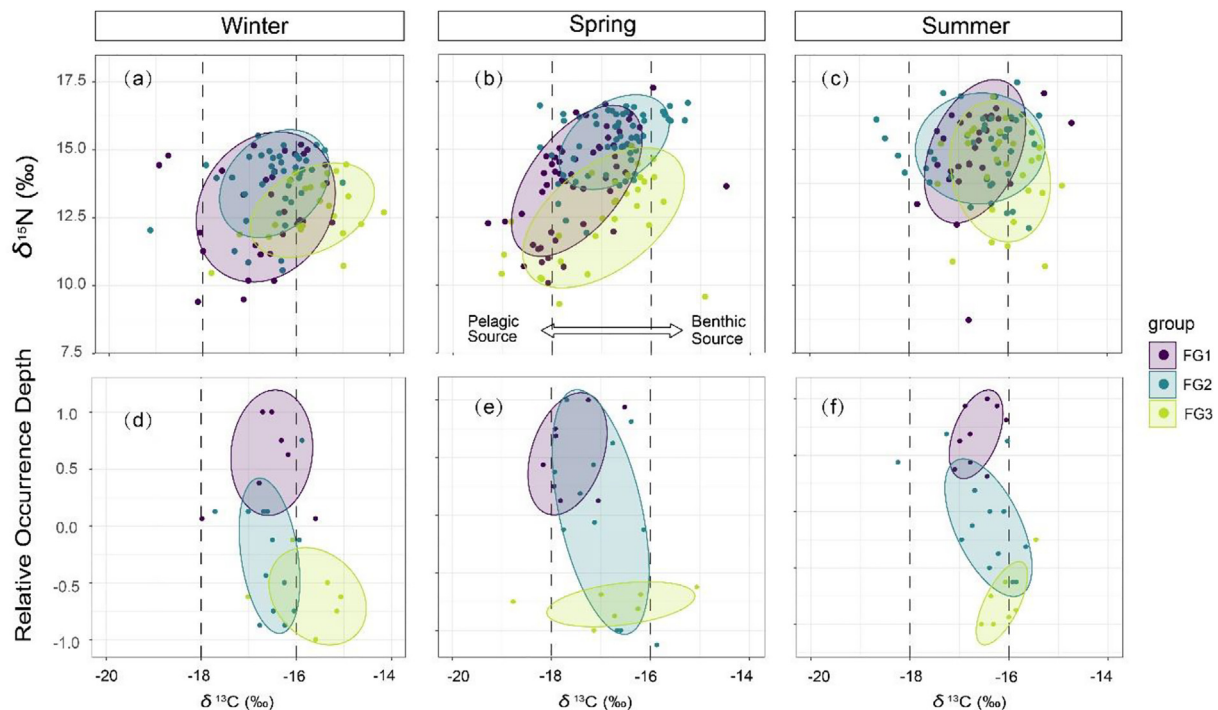
4. Discussion

4.1. The dynamic of pelagic-benthic coupling effects in Daya Bay

As our hypothesis, strong pelagic-benthic coupling effects exists in the Daya Bay. Both the pelagic and benthic community are largely fueled ($> 55\%$), directly or indirectly, by pelagic production. This is consistent with previous coastal studies that concluded strong pelagic-benthic coupling in shallow water (Giraldo et al., 2017; Kopp et al., 2015; McMeans et al., 2013). Shelf ecosystems are basically in the

Fig. 3. Trophic niche variation expressed by stable isotope biplot (a-c) and vertical habitat use (d-f) of pelagic fish (FG1), demersal fish (FG2), benthic crustacean (FG3). Points in (a-c) represent tested individuals, while points in (d-f) mean different species. The ellipses are colored by functional groups, overlapping between pairwise ellipses mean isotopic niche overlap. The confidence level of the ellipse is 70% to better visualize, while the confidence level of niche calculation is 95%. The lower carbon isotope ratio represents pelagic-derived food sources, while higher carbon isotope ratio represents benthic-derived sources. The black dashed lines are to facilitate the expression of $\delta^{13}C$ changes.

epipelagic layer where upper materials can rapidly reach the seabed, therefore the direct deposition of carbon can be significant. For example, Dunne et al. (2007) has estimated that 48% of the global flux of organic carbon reaching the seabed in shelf ecosystems. A recent study also show high productivity caused by pelagic subsidies in coral reef ecosystems (Morais and Bellwood, 2019). However, Griffiths et al. (2017) have pointed that the pelagic-benthic coupling effects caused by biological processes have been ignored. Our estimation of ecological niches (Fig. 3) confirms this: the carbon isotopes ratio of pelagic fish and demersal fish reveals highly overlapping of diet composition and direct competition, considering the high vertical mobility of demersal

fish and lower ability of pelagic fish, the energy coupling caused by direct predation of benthic fish should be significant. Our observation that more demersal fish occurred in upper layer in spring is the evidence (Fig. 3e), when the resources is limited (Fig. 1), the pelagic food demand of benthic community was significantly magnified.

Pelagic-benthic coupling caused by physical deposition is dependent on the physical condition of shelf ecosystem like depth and current speed (Giraldo et al., 2017; Jansen et al., 2018; Zhang et al., 2015). Nevertheless, in temporal scale, effects of depth within a certain coastal ecosystem are constant, and the current speed can be also slowed for the semi-closed gulfs (around 0.5 m/s in Daya Bay, unpublished data).
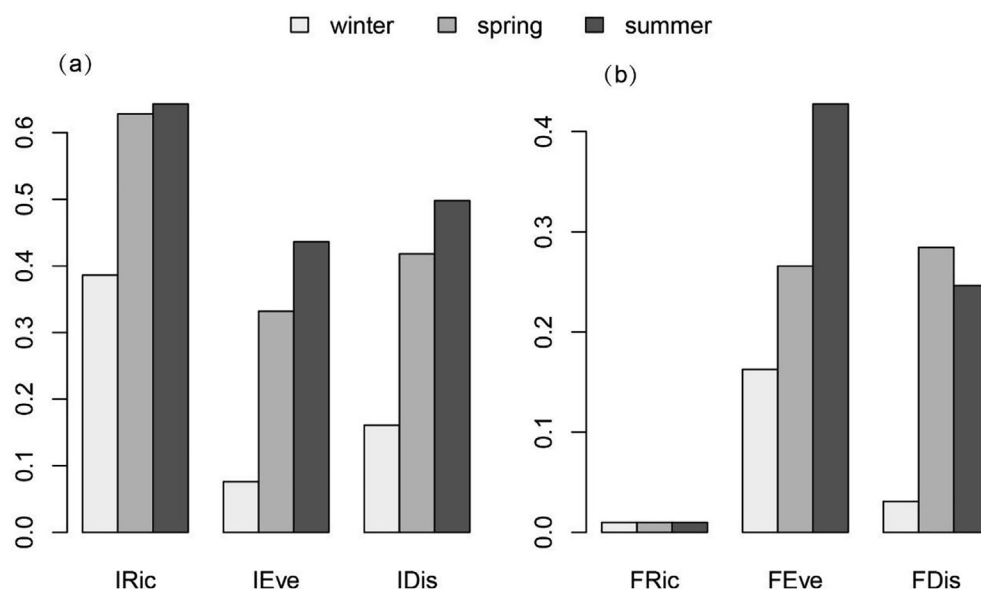
Fig. 4. Seasonal variation of (a) isotopic functional diversity and (b) trait-based functional diversity. The richness measures isotopic space use of community as convex hull area, the evenness measures the regularity of points distribution, the dispersion measures the weighted-mean distance to the center of gravity of all points in different season.
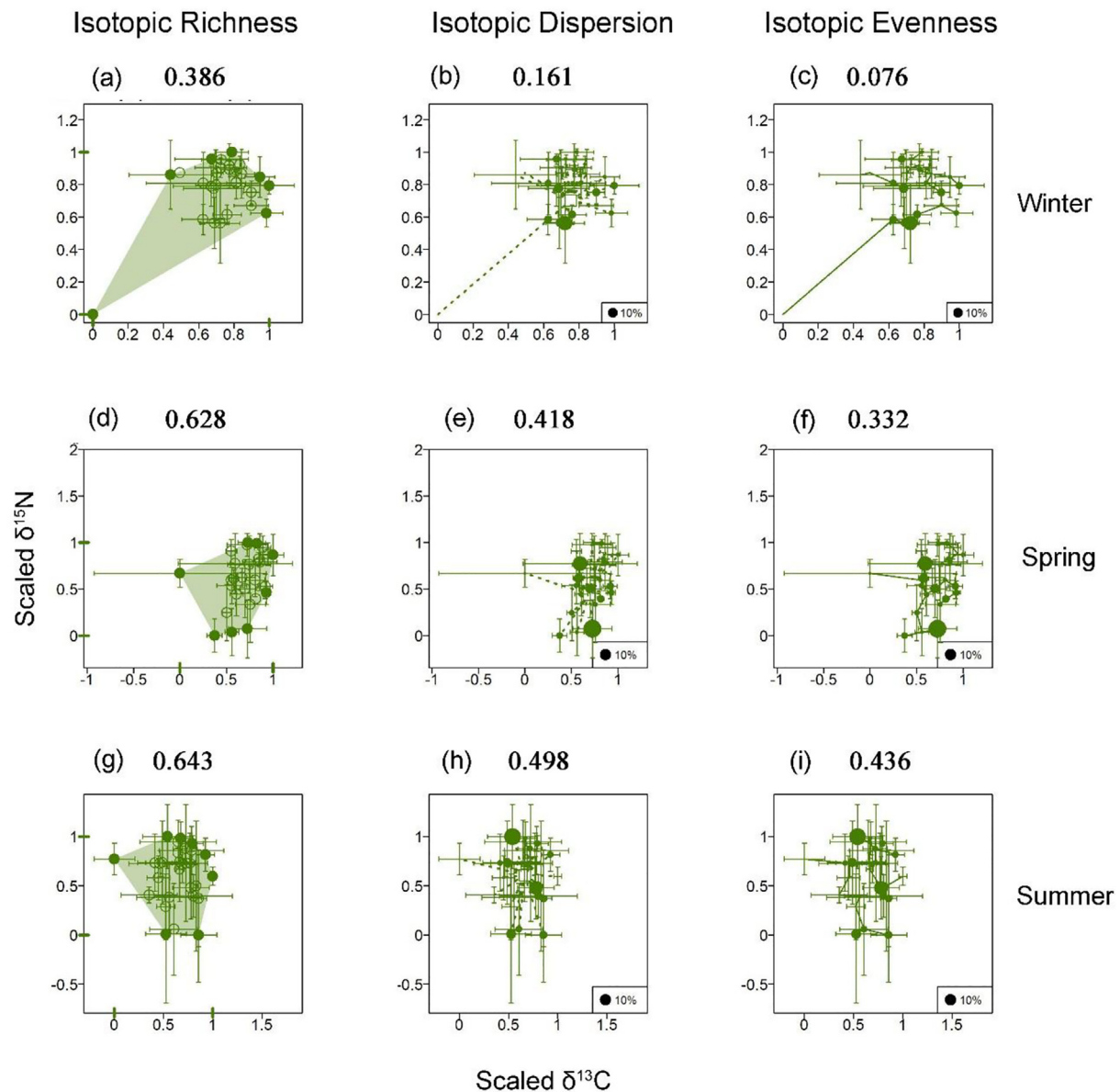
Fig. 5. The isotopic ratio distribution plot. The isotopic richness, isotopic dispersion, isotopic evenness from winter (a-c) to spring (d-f) and summer (g-i) were shown. The calculation is from Cucherousset and Villéger (2015).

Thus, we suggest that the seasonal variation of phytoplankton abundance is the dominant factor inducing the trophic cascade and pelagic-benthic coupling dynamic.

4.2. Effects of phytoplankton abundance on the pelagic and benthic energy pathways of Daya Bay

Seasonal variation of pelagic primary production can influence both pelagic and benthic communities, as shown in the previous finding in Zhang et al. (2015) that the phytoplankton bloom in spring will increase vertical carbon flux and cause rapid change of benthic community biomass. Similarly, the seasonal dynamic pattern of pelagic biomass is consistent with plankton abundance in Daya Bay. Many studies have suggested that phytoplankton is the main energy source supporting pelagic food webs through feeding zooplankton and transferring energy to higher trophic levels, such as marine mammals and sharks, despite of their diverse basal resources including microphytobenthos and corals (Søreide et al., 2006; Bird et al., 2018; McMeans et al., 2013). The pelagic energy pathway is highly active and

primary consumers of small size and short generation times greatly improve its turnover rate (Rooney et al., 2006). This may explain why it supports most of the large-size predators and why a higher fraction of pelagic fish are found in the tropics and subtropics (van Denderen et al., 2017).

The seasonal dynamic patterns of production (both surface and bottom) and benthic biomass are mismatched, but this can be another result of pelagic-benthic coupling. Shelf ecosystems are mostly photic zones, where the benthic macrophytes can receive sunlight and generate great primary productivity as pelagic phytoplankton (Fig. 1a and b). In addition to other energy sources from upper layer and slow energy turnover rate transferred to high-trophic-level predators through predation and assimilation, it is not surprising that benthic community biomass affected by various aspects other than from one single pathway. In long term, this also cause higher benthic biomass than pelagic biomass in Daya Bay (Fig. 1) and global coastal ecosystem (van Denderen et al., 2017).

Seasonal dynamic pattern of plankton and nekton community in Daya Bay show that the variability of pelagic-benthic coupling should
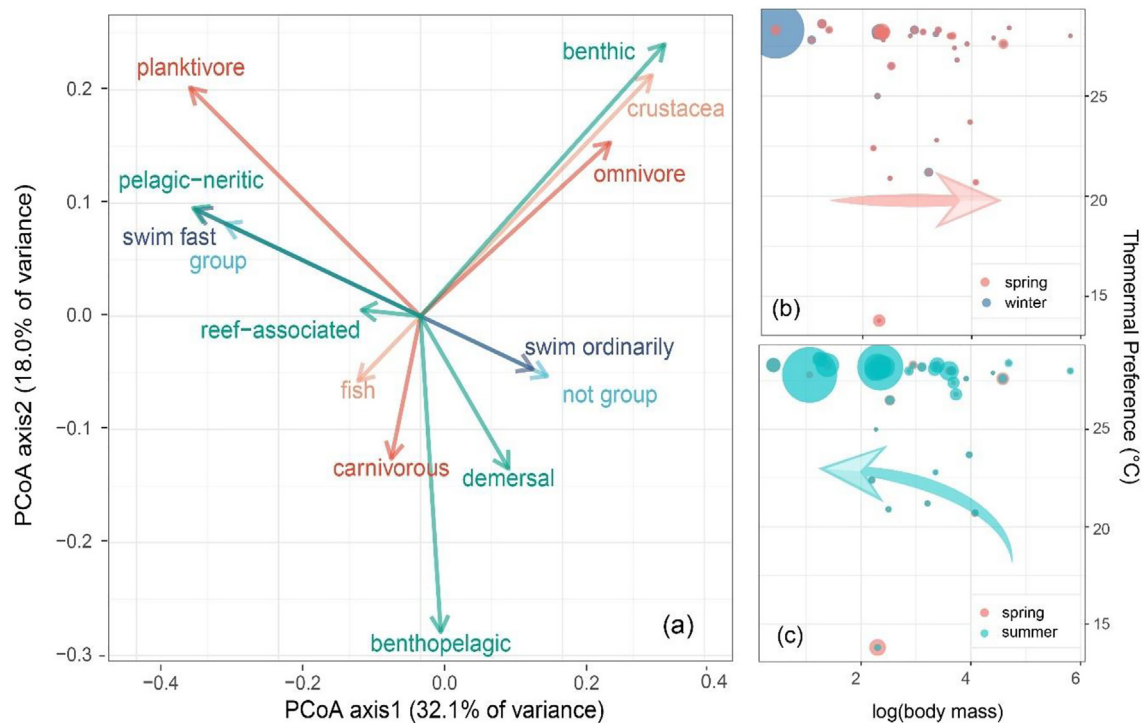
Fig. 6. Seasonal changes in the multidimensional functional structure described by 12 functional traits. (a) A principal coordinate analysis was conducted on a Gower distance matrix, the first and second principal coordinate axis explains 32.1% and 18.0% respectively. The functional traits owning high correlation ($r^2 > 0.4$, $P < 0.05$) are plotted, arrows with same color represent different levels of a trait. A more obvious and understandable two-traits (body mass and thermal preference) space was plotted (b) from winter to spring, and (c) from spring to summer. Point size represents relative abundance, and point color represent season. The arrow in (b) and (c) indicates the general trend of community towards larger size in spring, and smaller size, higher thermal preference in summer.

directly relate to the pelagic production. Future studies can focus on the detailed quantification of proportion of biological processes on pelagic-benthic coupling.

4.3. The effects of seasonal productivity dynamic on the trophic interaction and functional diversity

We determined the seasonal variation of the trophic structure of the fish and crustacean communities. The highly isotopic niche overlap of pelagic and demersal fish indicates their similar resource use, but when the resource is sufficient to support both communities (winter and summer), the niche segregation along other dimensions (vertical space here) might help to reduce the competition strength. Pelagic fish are adapted for fast movement (e.g., high gill surface area and streamlined body shape) and this improves their ability to use pelagic resources and avoid being captured (Killen et al., 2016). Demersal fish live at or near the bottom where human impacts are weak, and they often hunt for food at night. Such a pattern reflects a different adaptation strategy of the fish community and enhances their resilience to intensive fishing pressure.

However, when the entire community had the lowest primary production in the spring, we observed more demersal fish occurring in the upper layer (Fig. 3), while the proportion of pelagic production reach the highest (Fig. 2). Obvious trophic niche partitioning shows the competitive exclusion effect (i.e. only pelagic group can get more food), and confirm our argument that the pelagic group is more likely to capture pelagic prey. The strong competition and limited food availability also result in the low biomass yield of both pelagic and benthic community in spring. These phenomena indicate that greater resource opportunity can promote the coexistence of species with similar resource use and enhance the functional redundancy of the community (Figs. 5 and 6), while a relatively oligotrophic environment could intensify competition (Comte et al., 2016).

Trophic position variation of the fish functional groups also contributes to the niche shift. Previous observations of increasing biomass in the middle body size (4–64 g) and a sharp reduction of small size fish in spring indicates that the ontogenetic shift of the fish groups causes the $\delta^{15}N$ differentiation (Hammerschlag-Peyer et al., 2011; Ying et al., 2019). This facet of niche shift indicate the importance of body size and morphological characteristics in competition, which is consistent with the conclusions of Ríos et al. (2019).

We also found a seasonally variable relationship between productivity and functional diversity from winter (high productivity and overlap, low diversity) to spring (low productivity and overlap, high diversity) to summer (high productivity, high overlap and diversity). We suggest that competitive dominance along productivity gradients leads to such changes (Huss et al., 2012). High functional redundancy is caused by the abundant pelagic fish with similar functional traits (Fig. 6b and c). Thus, either the reduction of dominant species number (in spring) or the abundance of other species (in summer) might reduce their competitive dominance and narrow the gap of their resource use. This indicates the critical role of dominant species in the process of transforming productivity to total yield. Meanwhile, the relationship between functional diversity and trophic overlap also indicates that productivity can be critical when future studies consider if trophic partitioning result in higher functional diversity, because when productivity is high enough, the ecosystem is likely to support some trophically similar but functionally different populations (e.g., pelagic and benthic fish with similar food preference).

CRediT authorship contribution statement

Rui Ying: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing - original draft. **Yiting Cao:** Investigation. **Fangmin Yin:** Investigation. **Jianlin Guo:** Investigation. **Jianrong Huang:** Project administration, Supervision. **Yingyong Wang:** Project

administration, Supervision. **Lianming Zheng:** . **Junxing Wang:** Project administration. **Haoliang Liang:** . **Zufu Li:** Funding acquisition, Supervision. **Jianxiang Feng:** Writing - review & editing, Project administration, Supervision, Funding acquisition.

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.2020.106241.

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