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Investigating food web structure and system function of an artificial reef ecosystem based on carbon and nitrogen stable isotope analysis: implications for reef management

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Introduction: Food web is an important basis for identifying trophodynamic processes, and evaluating the structural and functional characteristics of ecosystems. The trophodynamics and system function of artificial reef (AR) ecosystems have rarely been examined.

Methods: Stable isotope analysis was used to investigate the food web structure and functions of an artificial reef (AR) ecosystem in this study.

Results and Discussion: The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of particulate organic matter (POM) in AR showed noticeable seasonal changes, and the $\delta^{13}\text{C}$ value of POM in autumn was significantly higher than that in other seasons ($p < 0.05$). There were no significant seasonal variations in the $\delta^{13}\text{C}$ values of solid organic matter (SOM), and no significant difference between SOM and POM was observed except in autumn. Moreover, macroalgae did not significantly affect the $\delta^{13}\text{C}$ values of SOM. Phytoplankton may be the primary nutrient source in the AR ecosystem. The $\delta^{13}\text{C}$ values of most crustaceans in the AR were approximately between $(-17.03 \pm 0.22) \text{‰}$ – $(-17.74 \pm 0.07) \text{‰}$, higher than those of most fish, indicating that they may have different basal nutrient sources. The trophic level (TL) of invertebrates was between 2.00 and 3.09, and that of fish was between 2.98 and 3.66. The distribution of $\delta^{13}\text{C}$ and TLs of crustaceans and fish showed that, except for crustaceans, bivalve shellfish and zooplankton might also be important food sources for fish in the AR ecosystem.

Conclusion: The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of most species in the AR showed good continuity, indicating that they may be mainly produced from the AR ecosystem. Migratory species such as *Lateolabrax japonicus* and *Sepiella maindroni* showed higher $\delta^{13}\text{C}$ values, indicating that they may have migrated from other sea areas. To maintain the stability of the ecosystem structure and function of the AR ecosystem, fishing activities should be carried out following the maximum sustainable yield theory. Future research needs to identify the nutritional relationship between AR and its adjacent sea areas, to depict the food web structure of the AR with higher accuracy.

KEYWORDS

artificial reef, food web, stable isotope, marine ranching, system function

1 Introduction

Inshore areas are well known for their rich biodiversity and high productivity, the major habitats and fishing grounds of many commercial species (Jin et al., 2015). Chinese inshore fisheries account for more than 90% of the total marine catches and are an essential source of high-quality proteins for Chinese people (Jin et al., 2015). However, due to overfishing and other excessive human activities (e.g., pollution, coastal construction), marine biodiversity and inshore fishery resources have markedly declined, and the coastal environment has seriously deteriorated (Liu, 2013; Jin et al., 2015). Therefore, the fishery production mode urgently needs transformation and upgrading in China's coastal areas, and the coastal environment requires protection expeditiously. As a new type of marine economy, marine ranching plays a vital role in enhancing fishery resources and restoring marine ecosystems, which is also of great importance for the sustainable development of marine fisheries in China (Yang et al., 2016).

Currently, the construction of marine ranching has developed rapidly in China owing to the strong social demand and government promotion (Yang et al., 2018). From 2015 to 2023, China has gradually established eight batches of 169 national marine ranching demonstration areas, and the total sea area for marine ranching has exceeded 850 km². Artificial reef (AR) construction is one of the most important ways to build marine ranching (Lin et al., 2020). By the end of 2018, ARs constructed in China's coastal waters reached 60.94 million cubic meters. AR influences the environment by changing the flow field, heterogeneity of spatial structure, and bottom sediment (Bohnsack et al., 1991; Harmelin and Bellan-Santini, 1997; Zalmon et al., 2014). The upwelling formed by the ARs brings nutrients from the deep seabed to the upper layers, providing nutrients for phytoplankton (Okano et al., 2011). In addition, the complex spatial structure of ARs provides shelter for low trophic-level organisms or species at a vulnerable life stage (Hixon and Beets, 1989; Charbonnel et al., 2002; Okumura et al., 2003; Ushiyama

et al., 2016). The deployment of artificial structures provides new hard substrata for marine fouling organisms to settle down, increasing food resources for other marine organisms (Boaventura et al., 2006; Walker et al., 2010). The environmental change caused by AR construction leads to a change in the biological environment, increasing the biomass of all the organisms in the reefs (Chen et al., 2002). Several studies have demonstrated that the increase in biological resources in AR ecosystems is due to increased biomass production (Polovina and Sakai, 1989; Bortone et al., 1994; Powers et al., 2003; Claisse et al., 2014; Cresson et al., 2014). However, protesters also insisted that the increased biomass is due to the attraction hypothesis, the ARs serve purely as an aggregation device without any increase in biomass production (Bohnsack et al., 1994; Grossman et al., 1997; Pitcher and Seaman, 2000).

Despite numerous studies of ARs, the attraction-production controversy persists as an unresolved research question (Smith et al., 2016). These two effects are closely associated with the fishery production of ARs (Bortone, 2008). The "attraction" effects made the ARs a more efficient fishing area by attracting fishery species with little or no production. Simultaneously, the "production" effects also gain a significant advantage of fishery production exports through the increased biomass production of fishery species in ARs. The settlement of this controversy will greatly help the scientific construction and management of ARs (Cresson et al., 2014).

Net production requires the availability of suitable food and recruitment of larvae (Bohnsack and Sutherland, 1985). The production of high trophic level (TL) species relies on food sources transferred from low TLs through food web structures (Tang, 1996), so the trophodynamics of ARs provide an essential solution to resolve the attraction-production controversy (Bohnsack and Sutherland, 1985). However, the trophodynamics of ARs have rarely been examined. In order to analyze the structure and function of the AR ecosystem, an investigation of AR's food web structure and trophodynamic processes are desperately needed (Lin et al., 2020).

Stable isotope analysis (SIA) is a powerful tool for identifying food sources (Phillips et al., 2014; Grey, 2016), calculating trophic position (Sahm et al., 2021; Stewart et al., 2021), and constructing food web structures (Mao et al., 2014; Gusha et al., 2021). Compared to the traditional stomach content analysis, which only represents food composition in a short period, the SIA provides data reflecting the long-term accumulation of food sources. It provides a more dependable approach for investigating marine food web ecology and increasing the credibility of the food web structure (Parnell et al., 2010; Feng et al., 2018).

Several studies have already used C and N stable isotope methods to study the structure of food webs in AR ecosystems. Meanwhile, Cresson et al. (Cresson et al., 2012; Cresson et al., 2014; Cresson et al., 2019) used C and N SIA to investigate the food web structure and assess the trophic function (production or attraction) of ARs. Zhang et al. (Zhang et al., 2020a; Zhang et al., 2020b) used SIA to investigate the food web structure prior to and following the construction of ARs. Wei et al. (2013), Xu et al. (2017), Xie et al. (2017), Lin et al. (2018) and Zhang et al. (2019) used stable isotope analyses to determine the basal food sources and TL of organisms in ARs. However, none of these studies explored the production or attraction functions of ARs in China.

The Fuhan AR ecosystem is located in the outer waters of Rushankou in the northern Yellow Sea. Until now, no research associated with food web structure and system function has been conducted for this AR ecosystem, and most of the construction and management activities associated with AR have been conducted based on empirical activities. This study used the Fuhan AR as the target to investigate the trophic structure and the AR ecosystem pathway, to depict a basic food web structure and explore the “attraction” and “production” functions of the AR ecosystem, thereby providing a scientific basis for AR construction and management.

2 Materials and methods

2.1 Study area

The Fuhan AR is located in the northern Yellow Sea, southeast of the Shandong Peninsula. The coordinates of the central point were 36° 42' 5.27" N, 121° 27' 31.16" E. The specific locations of the AR are shown in Figure 1. The Fuhan marine ranching was built by AR construction and stock enhancement to restore fishery resources and degraded habitats. Since 2013, 0.25 million cubic meters of ARs have been deployed in a 6.67 km² zone. The proliferation and release activities of sea cucumber *Stichopus japonicus* and Korean rockfish *Sebastes schlegelii* have also been conducted for several years. The average water depth of the Fuhan AR was approximately 12 m.

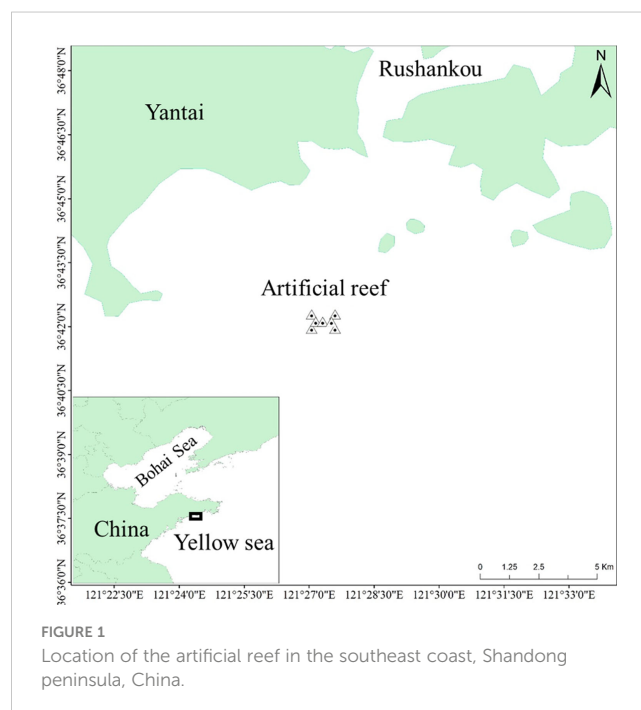
2.2 Sampling strategy

Samples of phytoplankton, zooplankton, particulate organic matter (POM), and solid organic matter (SOM) were collected in July, September, November 2017, and May 2018. Macroalgae were

collected in July 2017. Samples of swimming creatures and zoobenthos were collected in September 2017. POM was obtained by filtration, and approximately 1 L of seawater was filtered through a screen with a mesh size of 63 μm to remove large particles and zooplankton and then onto precombusted (450°C, 6 h) and preweighed Whatman GF/F glass fiber filters under vacuum suction of less than one-third atmospheric pressure. The residue on the filter papers was rinsed with distilled double deionized water to remove the salt adsorbed on the particle surface. Zooplankton samples were obtained by horizontal towing using a 63 μm plankton net, which was then held in filtered seawater overnight to allow the evacuation of gut contents. After that, zooplankton samples were dried at 60°C for 48 h and processed into a fine powder using a mortar and pestle. Macroalgae were hand-collected and rinsed with distilled water immediately after sampling. Sediments were collected using a sediment sampler, large benthic invertebrates of *Crassostrea gigas* and *A. japonicus* were collected by SCUBA diving, and *Perinereis aibuhitensis* were collected using a clam bucket dredger. All other benthic invertebrates and fish species were collected using cage nets and gillnets.

The white muscles of individual fish were removed from the dorsal part for SIA, the abdominal muscles of shrimp, the adductor muscles of shellfish, and the claw muscles of crabs were taken for SIA. Small invertebrates (e.g., *Caprella acanthogaster*) were prepared by pooling a suitable number (10–20 individuals) of whole specimens.

All samples were dried to a constant weight in an oven at 60°C. The dried tissue and sediments were pulverized into a fine powder using a mortar and pestle to ensure homogeneity. Samples for carbon SIA were acidized for 4 h with 1N HCl to remove carbonate and then dried at 60°C for 24 h. Samples for nitrogen stable isotope analysis were directly measured without the treatment of acidification (Cui et al., 2012). All samples were then stored at –20 °C prior to subsequent SIA.



2.3 Water quality determination

The water quality of marine ranching was measured in July, September, November 2017, and May 2018, respectively. The temperature, salinity, pH, and dissolved oxygen were measured by using a EXO2 multiparameter water quality detector (YSI co., USA). The mixed water samples (2 L) for determining inorganic nutrients (PO_4^{3-} , NH_4^+ , NO_3^- , NO_2^- , and SiO_3^{2-}) and Chlorophyll (Chl) a were taken from the surface, middle, and bottom layers of the marine ranching. The water samples for determining inorganic nutrients were first filtered through pre-combusted (450°C, 2 h) Whatman GF/F filters, and then measured according to the method of Lei (2006). The samples for determining Chl a were filtered through a 0.45 μm glass fiber filter, then the Chl a on the filter papers was extracted for 30 h with acetone (90%) under cold conditions (4 °C) and centrifuged. The absorbance values of the solutions were measured at 665 and 750 nm using a spectrophotometer. The concentration of Chl a was calculated following the method described by Lorenzen and Jeffrey (1980).

2.4 Measurement of stable isotope

The carbon and nitrogen isotope ratios of the prepared samples were measured using an elemental analyzer coupled with an isotope ratio mass spectrometer (EA-IRMS, Thermo Finnigan MAT Delta-plus) (Vander Zanden and Rasmussen, 2001). Stable isotope ratios are expressed in standard δ -unit notation, which is defined as follows:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \text{ ‰}$$

where X represents ^{13}C or ^{15}N , and R represents the $^{13}\text{C}:^{12}\text{C}$ ratio for carbon or the $^{15}\text{N}:^{14}\text{N}$ ratio for nitrogen. The results were reported relative to the Vienna Pee Dee Belemnite standard (PDB) for carbon and air N_2 for nitrogen. A laboratory working standard

(glycine) was run for every ten samples. The analytical precision for the carbon and nitrogen measurements was $\pm 0.01\text{‰}$.

2.5 Data analysis

Carbon and nitrogen stable isotopes are generally delivered along food chains with predictable stepwise enrichment between prey and consumers (Hobson and Welch, 1992). Therefore, TL was determined relative to the filter-feeding bivalves (*Crassostrea gigas*) as primary consumers, assumed to occupy the 2nd TL (Vander Zanden and Rasmussen, 2001). Using 3.4‰ enrichment of $\delta^{15}\text{N}$ per TL averaged over multiple TLs (Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002).

$$TL = 2 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{reference}}) / \delta^{15}\text{N}_{\text{TEF}}$$

where TL is the trophic level, $\delta^{15}\text{N}_{\text{consumer}}$ is the nitrogen isotopic ratio of consumers, $\delta^{15}\text{N}_{\text{reference}}$ is the nitrogen isotopic ratio of marine primary consumers (*Crassostrea gigas*), and $\delta^{15}\text{N}_{\text{TEF}}$ is the trophic enrichment factor. Because the primary consumers were at the bottom of the trophic ladder, they were assumed to occupy the 2nd TL in this study.

Data are presented as means and standard deviations (mean \pm SD). In addition, the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the measured samples were compared using one-way ANOVA followed by Duncan's multiple comparison test. The analyses were performed using SPSS software (version 17.0; SPSS Inc., Richmond, CA, USA), and values of $p < 0.05$ were considered significant.

3 Results

3.1 Water quality of the AR environment

The water quality data are listed in Tables 1, 2. During the sampling period, salinity varied between 30.29‰ and 32.54‰,

TABLE 1 Water quality of the marine ranching ecosystem1.

Sampling time	Temperature (°C)	Salinity (‰)	pH	dissolved oxygen (mg/L)
April	15.13 \pm 0.25	32.54 \pm 0.03	8.30 \pm 0.07	6.85 \pm 1.21
July	27.66 \pm 2.32	30.29 \pm 0.06	8.24 \pm 0.06	6.26 \pm 0.85
September	25.23 \pm 0.82	32.45 \pm 0.05	8.31 \pm 0.05	8.20 \pm 1.50
December	6.51 \pm 1.37	32.27 \pm 0.03	8.21 \pm 0.06	8.92 \pm 0.98

TABLE 2 Water quality of the marine ranching ecosystem2.

Sampling time	PO_4^{3-} (mg/L)	NH_4^+ (mg/L)	NO_3^- (mg/L)	NO_2^- (mg/L)	SiO_3^{2-} (mg/L)
July	0.03 \pm 0.02	0.08 \pm 0.07	0.08 \pm 0.07	0.004 \pm 0.003	0.04 \pm 0.03
September	0.01 \pm 0.01	0.08 \pm 0.08	0.14 \pm 0.13	0.008 \pm 0.007	0.06 \pm 0.04
December	0.02 \pm 0.016	0.03 \pm 0.01	0.18 \pm 0.062	0.013 \pm 0.008	0.17 \pm 0.14
April	0.03 \pm 0.028	0.04 \pm 0.04	0.18 \pm 0.135	0.021 \pm 0.011	0.11 \pm 0.04

temperature varied between 6.51–27.66 °C, pH varied between 8.21–8.31, and dissolved oxygen varied between 6.26–8.92 mg/L. The concentration of PO_4^{3-} varied between 0.01–0.03 mg/L, the concentration of NH_4^+ varied between 0.03–0.08 mg/L, the concentration of NO_3^- varied between 0.08–0.18 mg/L, the concentration of NO_2^- varied between 0.004–0.021 mg/L, and the concentration of SiO_3^{2-} varied between 0.04–0.17 mg/L. Seasonal fluctuations in Chl a concentration in the AR ecosystem were observed, as shown in Figure 2. The highest Chl a concentration was observed in autumn and lowest in winter.

3.2 Isotopic compositions of organic matters, and primary producers

The carbon and nitrogen stable isotope ratios of POM, SOM, and macroalgae are presented in Table 3 and Figure 3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of POM ranged from -21.40‰ – -18.20‰ and 7.19‰ – 8.68‰ during the four seasons, respectively. Significant differences among POM pools were observed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($p < 0.05$). The highest $\delta^{13}\text{C}$ value of POM was observed in autumn and lowest in winter. The highest $\delta^{15}\text{N}$ value of POM was observed in summer and lowest in autumn. No significant differences among the SOM pools were observed ($p < 0.05$). Among all the primary food sources, *Ulva pertusa* had the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. No significant differences were observed for the organic pools of POM and SOM, except for POM and SOM in autumn ($p < 0.05$), indicating transparent pelagic-benthic coupling processes.

3.3 Isotopic composition of consumers

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers in this AR ecosystem are presented in Table 4 and Figure 4. Comparison of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ revealed substantial isotopic differences ($p < 0.05$) among all invertebrate species, encompassing isotopic values of 5.09‰ for $\delta^{13}\text{C}$, and 3.70‰ for $\delta^{15}\text{N}$. The mean $\delta^{13}\text{C}$ values of the benthic invertebrates ranged from the most $\delta^{13}\text{C}$ depleted value of -20.43‰ for *C. gigas* bivalves, to the most enriched -15.34‰ for crab *Eucrate crenata*, with $\delta^{15}\text{N}$ values ranging from 7.97‰ for *C. gigas* to

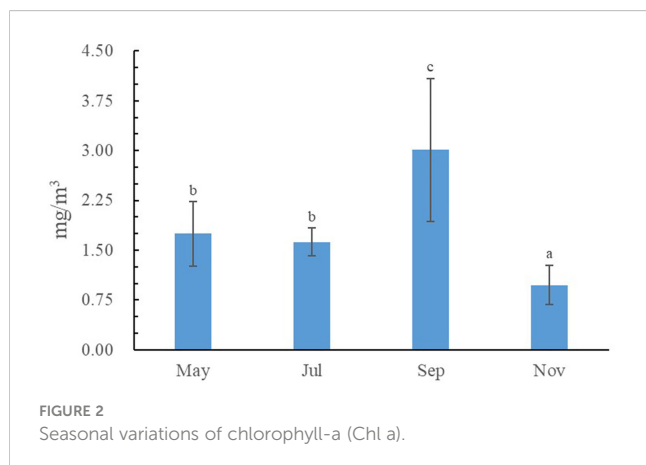


FIGURE 2
Seasonal variations of chlorophyll-a (Chl a).

TABLE 3 Carbon and nitrogen stable isotope ratios of food sources.

Food sources	n	$\delta^{13}\text{C}$ ‰	$\delta^{15}\text{N}$ ‰
POM-spring	6	-20.18 ± 1.05^{ab}	7.25 ± 0.75^{AB}
POM-summer	6	-20.66 ± 1.19^a	7.68 ± 1.15^A
POM-autumn	6	-18.20 ± 0.96^c	7.19 ± 0.63^A
POM-winter	6	-21.40 ± 0.77^a	8.41 ± 1.29^B
SOM-spring	3	-20.07 ± 0.37^{ab}	8.22 ± 0.16^{AB}
SOM-summer	3	-20.90 ± 0.29^a	8.08 ± 0.13^{AB}
SOM-autumn	3	-20.17 ± 0.36^{ab}	8.59 ± 0.14^B
SOM-winter	3	-21.11 ± 0.27^a	7.77 ± 0.19^{AB}
<i>Ulva pertusa</i>	3	-18.14 ± 0.16^c	9.94 ± 0.08^C
<i>Enteromorpha prolifera</i>	3	-19.05 ± 0.33^{bc}	8.75 ± 0.23^B
<i>Sargassum miyabei</i>	3	-18.42 ± 0.37^c	9.85 ± 0.12^c

The superscript letters within the same column indicate significant differences ($p < 0.05$).

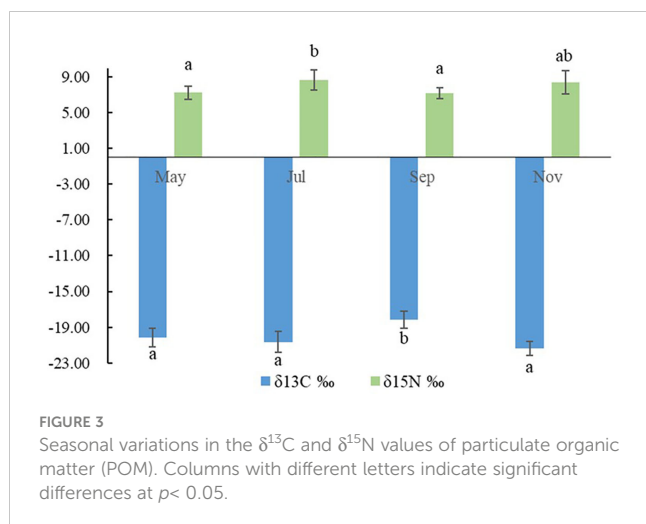
11.67‰ for shrimp *Oratosquilla oratoria*. Moreover, crabs of *Charybdis japonica* and cephalopoda *Octopus vulgaris* showed higher $\delta^{15}\text{N}$ values than the other invertebrates, with mean values of 11.50 . The TL of invertebrate species ranged from 2.0 – 3.09 , and *O. oratoria* displayed the highest TL (Figure 5).

A steady enrichment of $\delta^{13}\text{C}$ with an increasing trend from the filter feeders (bivalves) to deposit feeders of *P. aibuhitensis* and *A. japonicus*, then the omnivorous crustaceans and cephalopods. The crustaceans *C. japonica*, *Portunus trituberculatus*, *Crangon affinis*, *C. acanthogaster*, *Alpheus distinguendus*, and *O. oratoria*, were considered to have similar primary food sources, as most of them had similar $\delta^{13}\text{C}$ values.

The deposit-feeding species that graze organic content from the sediment on the seabed surface, including *P. aibuhitensis* and *A. japonicus*, showed higher $\delta^{15}\text{N}$ values relative to those of filter-feeding bivalves and zooplankton. In contrast to the stable nitrogen isotope, the zooplankton group showed higher $\delta^{13}\text{C}$ values than the main species of bivalves, annelids, and echinodermata. *Dorippe japonica* and *C. acanthogaster* have low $\delta^{15}\text{N}$ values among crustaceans and cephalopods, indicating lower TL among these species.

For fish species, the range of isotopic ratios measured in fishes was lower for $\delta^{13}\text{C}$ (2.54‰ only), but higher for $\delta^{15}\text{N}$ (5.19‰) than invertebrates. *Thryssa kammalensis* was the main pelagic fish in this ecosystem, which expressed the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among all the investigated fish, with mean values of -19.03‰ and 11.30‰ , respectively. The highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were observed for *Lateolabrax japonicus*, with mean values of -16.49‰ and 13.63‰ , respectively. *Oplegnathus fasciatus* and *Hexagrammos otakii* had the second-highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively. The TL of fish ranged from 2.98 – 3.66 , *T. kammalensis* displayed the lowest TL, and *L. japonicus* displayed the highest TL (Figure 5).

The position of fish groups on the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ biplot (Figure 4) indicated that all fish species fit well into the continuity of the position occupied by invertebrates in the trophic network of AR. This result was also consistent with the significant correlation observed between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of all consumers, invertebrates, and fish combined ($\delta^{15}\text{N} = 0.7952 \delta^{13}\text{C} + 24.539$; $R^2 = 0.3718$, $p <$



0.05), suggesting that most consumers belonged to a similar trophic pathway, with fish at its top.

4 Discussion

4.1 Basal nutrient sources of the AR ecosystem

POM (mainly composed of phytoplankton and other water detritus), SOM (mainly composed of microphytobenthos and organic detritus), macroalgae, and benthic microalgae are the primary food sources of AR ecosystems (Cresson et al., 2014; Xu et al., 2017; Zhang et al., 2021). The $\delta^{13}\text{C}$ of POM in this study ranged from $-21.40\text{‰} \pm 0.77\text{‰}$ – $-18.20\text{‰} \pm 0.96\text{‰}$, which was similar to the $\delta^{13}\text{C}$ value of POM usually ranged from -18‰ – -24‰ in temperate waters (Gearing et al., 1984; Fry and Wainright, 1991; Harmelin-Vivien et al., 2008). The $\delta^{13}\text{C}$ of POM in autumn was significantly higher than that in the other three seasons, which may be associated with a *Noctiluca scientillans* bloom outbreak in the AR in autumn. *N. scientillans* usually have a larger particle size than most other phytoplankton cells (Uhlig and Sahling, 1990; Sriwoon et al., 2010), its $\delta^{13}\text{C}$ value may also be higher, as phytoplankton with larger sizes were observed to have higher $\delta^{13}\text{C}$ values than smaller phytoplankton (Rau et al., 1990; Fry and Wainright, 1991; Grégori et al., 2001; Cresson et al., 2012).

Except in autumn, no significant differences were found between the $\delta^{13}\text{C}$ of SOM and POM in this AR ecosystem. These results differed from those of Cresson et al. (2012) and Xu et al. (2017), who found that the $\delta^{13}\text{C}$ value of SOM was significantly lower than that of POM in AR ecosystems. Microphytobenthos, POM, and macroalgae are considered the main contributors to SOM in neritic ecosystems (Cahoon, 1999; Letourneur et al., 2013; Briand et al., 2015; Zhang et al., 2021). Benthic microalgae are usually $\delta^{13}\text{C}$ enriched compared to planktonic microalgae because of differences in light temperature and photosynthesis mechanisms (Wiencke and Fisher, 1990; Fry and Wainright, 1991; France, 1995). In this study, the average Chl a of the benthic microalgae was only

3.5 mg C m^{-2} (unpublished data), which was very low compared to the other neritic ecosystems (Cahoon, 1999), indicating that benthic microalgae may not be an important energy source of SOM in this ecosystem. *U. pertusa* and *E. prolifera* were the main macroalgal species in the AR ecosystem, most imported from adjacent sea areas in summer. The outbreak of *E. prolifera* was considered a natural disaster in the Yellow sea (Chen et al., 2018; Xu, 2018), and a large part of *E. prolifera* was floated to Fuhun marine ranching in June and July (the covered area was approximately 20000 m^2). The significantly higher $\delta^{13}\text{C}$ value of the two macroalgal species than that of the SOM indicated that the macroalgae were also not a critical energy source for SOM. The similar $\delta^{13}\text{C}$ values of POM and SOM indicate that POM may be the main contributor of SOM, and strong coupling of benthic-pelagic mechanism existed in the AR ecosystem.

4.2 Food sources of consumers in the AR ecosystem

The sessile filter feeder, oyster *C. gigas*, is an ecosystem engineer that creates and maintains the oyster reef structure and provides resources for other organisms (Padilla, 2010), dominated in the fauna of this AR ecosystem, which showed a $\delta^{13}\text{C}$ value lower than that of the POM in autumn. This seems contradictory, as POM is usually considered the primary food source for oysters. The lower $\delta^{13}\text{C}$ value of oysters may be ascribed to its qualitative selection for microalgae, especially for diatoms (Riisgard and Larsen, 2000; Decottignies et al., 2007; Marin Leal et al., 2008; Kang et al., 2009), because most diatoms have a smaller particle size than *N. scientillans*, and the diatoms may have lower $\delta^{13}\text{C}$ values than that of the POM in this AR ecosystem (Sato et al., 2006; Sugie and Suzuki, 2015).

Snails of *Rapana venosa* are usually considered carnivorous predators, such as bivalves (Byon et al., 2015; Song et al., 2016). The oyster was inferred as its main food source in the artificial oyster reef (Xu, personal communication); however, the $\delta^{15}\text{N}$ value of *R. venosa* was only 1.66‰ higher than that of the oyster, and the TL of *R. venosa* was 2.55 in this study, indicating that almost half of its food originated from TL I. This seems contradictory to previous results: Qi (2017) discovered that adult *R. venosa* had a low amylase activity, which reflected that this species could only ingest a low level of plant food, and Yang et al. (2020) further discovered that *R. venosa* did not feed on phytoplankton based on fatty acid analysis. Moreover, it seems that only oyster production can support the high biomass of *R. venosa* in this AR (the biomass of *R. venosa* and oyster in this AR were approximately 270 g m^{-2} and 1500 g m^{-2} , respectively) (unpublished data). The relatively low $\delta^{15}\text{N}$ value of this species may be because *R. venosa* has a very low nitrogen fractionation. DeNiro and Epstein (1981) and Vanderklift and Ponsard (2003) demonstrated that the discrimination factor of $\delta^{15}\text{N}$ may vary among species. The $\delta^{15}\text{N}$ discrimination factors of *Assiminea japonica* and *Angustassiminea castanea* snails were lower than one (Kurata et al., 2001). The actual fractionation factor of this species needs to be estimated to provide a firm explanation for this phenomenon.

TABLE 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers in the artificial reef ecosystem.

Species	n	$\delta^{13}\text{C}$ ‰	$\delta^{15}\text{N}$ ‰
Zooplankton	3	-18.24 ± 0.26^{bc}	9.14 ± 0.39^B
Molluscs			
<i>Crassostrea gigas</i>	3	-20.43 ± 0.79^a	7.97 ± 0.18^A
<i>Rapana venosa</i>	3	-19.19 ± 0.72^b	9.63 ± 0.23^C
Polychaete			
<i>Perinereis aiubuhitensis</i>	3	-20.29 ± 0.72^{ab}	10.47 ± 0.08^D
Echinodermata			
<i>Apostichopus japonicus</i>	3	-19.43 ± 0.44^{ab}	9.26 ± 0.31^E
Crustacean			
<i>Dorippe japonica</i>	1	-18.87 ± 0.38^b	9.34 ± 0.14^{BC}
<i>Matuta planipes</i>	1	-15.88 ± 0.35^f	10.63 ± 0.23^D
<i>Eucrate crenata</i>	1	-15.34 ± 0.22^f	11.10 ± 0.26^E
<i>Crangon affinis</i>	3	-18.86 ± 0.30^b	11.30 ± 0.39^{EF}
<i>Charybdis japonica</i>	3	-17.03 ± 0.22^c	$11.50 \pm 0.12^{D^{FG}}$
<i>Caprella acanthogaster</i>	3	-17.28 ± 0.12^c	9.67 ± 0.19^C
<i>Portunus trituberculatus</i>	4	-17.18 ± 0.72^c	10.42 ± 0.08^D
Juvenile <i>Charybdis japonica</i>	3	-17.68 ± 0.14^{de}	10.62 ± 0.08^D
<i>Alpheus distinguendus</i>	3	-17.53 ± 0.15^{de}	11.45 ± 0.16^{FG}
<i>Oratosquilla oratoria</i>	3	-17.74 ± 0.07^{de}	11.67 ± 0.07^G
Cephalopoda			
<i>Octopus vulgaris</i>	3	-15.98 ± 0.38^f	11.29 ± 0.34^{EF}
<i>Sepiella maindroni</i>	3	-15.63 ± 0.13^f	11.50 ± 0.30^{FG}
Fish			
<i>Thryssa kammalensis</i>	3	-19.03 ± 0.49^a	11.30 ± 0.52^A
<i>Chaeturichthys stigmatias</i>	3	-18.10 ± 0.18^{bc}	12.33 ± 0.05^B
<i>Argyrosomus argentatus</i>	3	-18.28 ± 1.00^{bc}	12.38 ± 0.75^{BC}
<i>Sebastes schlegelii</i>	3	-18.29 ± 0.08^{bc}	13.05 ± 0.26^{BC}
<i>Cynoglossus joyneri</i>	3	-18.27 ± 0.65^{bc}	12.78 ± 0.17^{BCD}
<i>Sillago sihama</i>	3	-18.18 ± 0.22^{bc}	12.93 ± 0.13^{CDE}
<i>Lepidotrigla microptera</i>	1	-17.12 ± 0.07^d	12.43 ± 0.17^{BC}
<i>Odontamblyopus rubicundus</i>	3	-17.91 ± 0.67^c	12.56 ± 0.09^{BC}
<i>Platycephalus indicus</i>	3	-17.80 ± 0.18^c	13.13 ± 0.24^{DEF}
<i>Oplegnathus fasciatus</i>	3	-16.62 ± 0.14^d	13.14 ± 0.26^{DEF}
<i>Hexagrammos otakii</i>	3	-18.67 ± 0.29^{ab}	13.42 ± 0.17^{EF}
<i>Lateolabrax japonicus</i>	3	-16.49 ± 0.42^d	13.63 ± 0.13^F

The superscript letters within the same column indicate significant differences ($p < 0.05$).

The deposit feeder, *A. japonicus*, is an important economic species and has a high biomass in the AR ecosystem. It had a $\delta^{13}\text{C}$ value similar to that for SOM. Sun et al. (2012) discovered that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ discrimination factors of *A. japonicus* were 1.2‰

and 1.9‰, respectively. Based on these data, it can be speculated that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sea cucumbers were consistent with the POM. Therefore, POM may be the main food source for sea cucumbers in this AR. This result is similar to Yokoyama (2013),

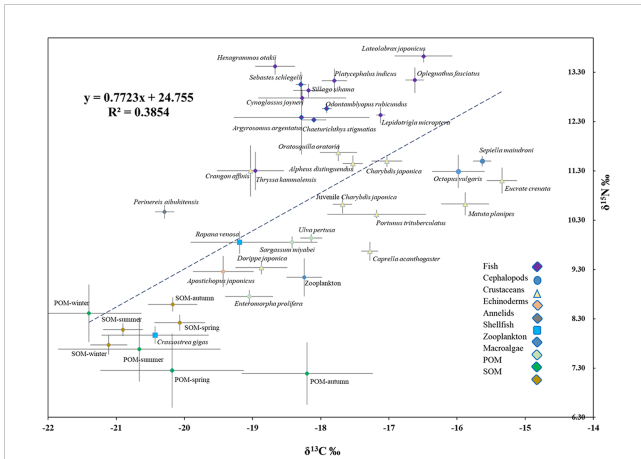


FIGURE 4 Bi-plots of $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ (mean \pm SD) of SOM, POM, zooplankton, and different species of fish, cephalopods, crustaceans, echinoderms, annelids, shellfish, and macroalgae in the artificial reef ecosystem.

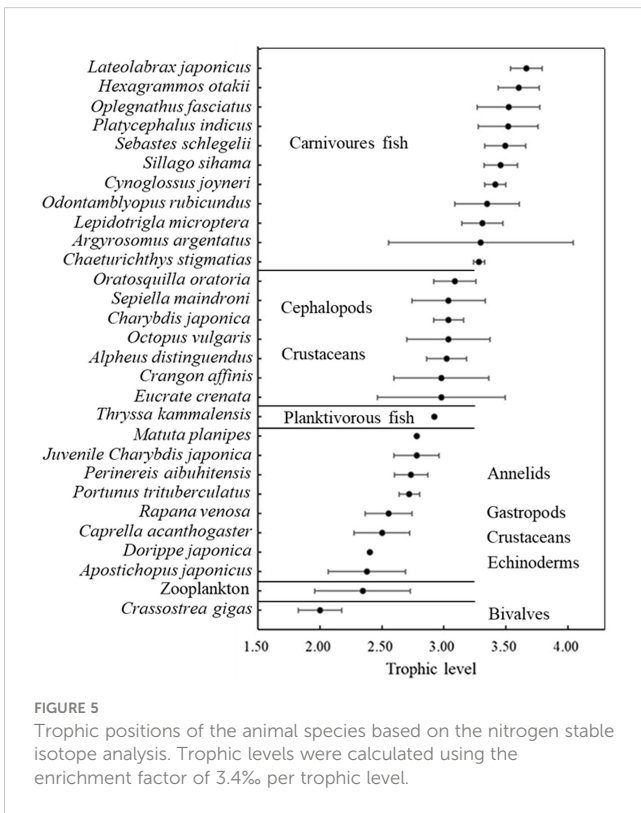


FIGURE 5 Trophic positions of the animal species based on the nitrogen stable isotope analysis. Trophic levels were calculated using the enrichment factor of 3.4‰ per trophic level.

who found that phytoplankton was the primary food source for *A. japonicus* in a sea cucumber-Pacific oyster integrated multi-trophic aquaculture ecosystem. Oysters may play an important role in supporting food sources for sea cucumbers. The filtering activity of oysters can transfer a large part of POM to the bottom of the AR (Cheung et al., 2010; Cresson et al., 2014), and the pseudofeces and feces from bivalves are an important food source for sea cucumbers (Yuan et al., 2008; Slater et al., 2009; Zamora et al., 2014).

Most crustaceans are omnivorous in marine ecosystems, usually positioned at intermediate levels, and play important roles in transferring energy from lower to higher TLs (Wilson et al., 2001). The crustaceans showed a narrow range of $\delta^{13}\text{C}$ values, except for *D. japonica* and *Matuta planipes*, indicating that most crustaceans may have similar primary food sources. The $\delta^{13}\text{C}$ of the crustaceans was close to that of POM in autumn, *U. pertusa*, and *S. muticum*. Considering the integration time of crustaceans (Fry and Arnold, 1982), $\delta^{13}\text{C}$ may reflect the diets of these crustacea–1–2 months ago, when a lot of macroalgae were floated into the AR. Therefore, the macroalgae *U. pertusa* and *S. muticum* were probably important food sources for these crustaceans. These results conformed to Feng et al. (2014), who found that macroalgae were an important contributor to the nutritional support of crustaceans.

Cephalopods *O. vulgaris* and *Sepiella maindroni* showed the lowest $\delta^{13}\text{C}$ values in the AR ecosystem, significantly lower than those of POM and macroalgae. The stable isotope signatures in animal tissues reflect the local food source where the animal resides (Peterson and Fry, 1987; Michener and Schell, 1994). The particularly low $\delta^{13}\text{C}$ values of these two species indicate that they may consume their food from entirely different surroundings. These results were consistent with our observation that these two species usually moved into the AR from other sea areas in autumn. Zhang et al. (1997) reported that *S. maindroni* usually stayed in coastal areas for spawning from May to November, suggesting that *S. maindroni* may have migrated into the AR ecosystem from another coastal sea area. Stomach content analysis indicated that *S. maindroni* and *O. vulgaris* mainly feed on fish and crustaceans (Yang, 2001; Yang et al., 2018), whose TLs were 4.2 and 4.5, respectively, in the Bohai Sea, which was significantly higher than those (3.04) in this study. However, the isotopic analysis conducted by Zhang et al. (2020) indicated that the TL of *O. variabilis* in AR was only 2.72. This may be ascribed to the differences between stomach content analysis and SIA, as the stomach content analysis only reflects the organism’s instantaneous food information, while the SIA provides integrated food information over a long period (Hobson and Welch, 1992; Qu et al., 2016).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish in this AR ecosystem ranged from -19.03‰ – -16.62‰ and 12.33‰ – 13.63‰ , respectively. The average $\delta^{13}\text{C}$ values of the fish species were quite similar, except for *O. fasciatus*, *L. japonicus*, and *T. kammalensis*. *T. kammalensis* is a pelagic predator that mainly feeds on plankton (Guo and Tang, 2000), so its $\delta^{13}\text{C}$ values were relatively lower and close to the phytoplankton. *L. japonicus* is a seasonal migratory predator whose food sources may come from a significantly larger area than the AR, thereby showing a different $\delta^{13}\text{C}$ value. *S. schlegelii* and *Hexagrammos otakii* are typical reef fishes that usually remain in the AR area (Zhang et al., 2015), which were discovered in the AR with high biomass (unpublished data). Similar $\delta^{13}\text{C}$ values of these fishes indicate that they may have similar primary food sources. Assuming a $\delta^{13}\text{C}$ discrimination factor of 0.75‰ or 1‰, phytoplankton should be their main primary food source. However, similar $\delta^{13}\text{C}$ values did not indicate similar food compositions. According to Zhang et al. (2018) and Zhang et al. (2021), no significant niche overlap was observed between *H. otakii*

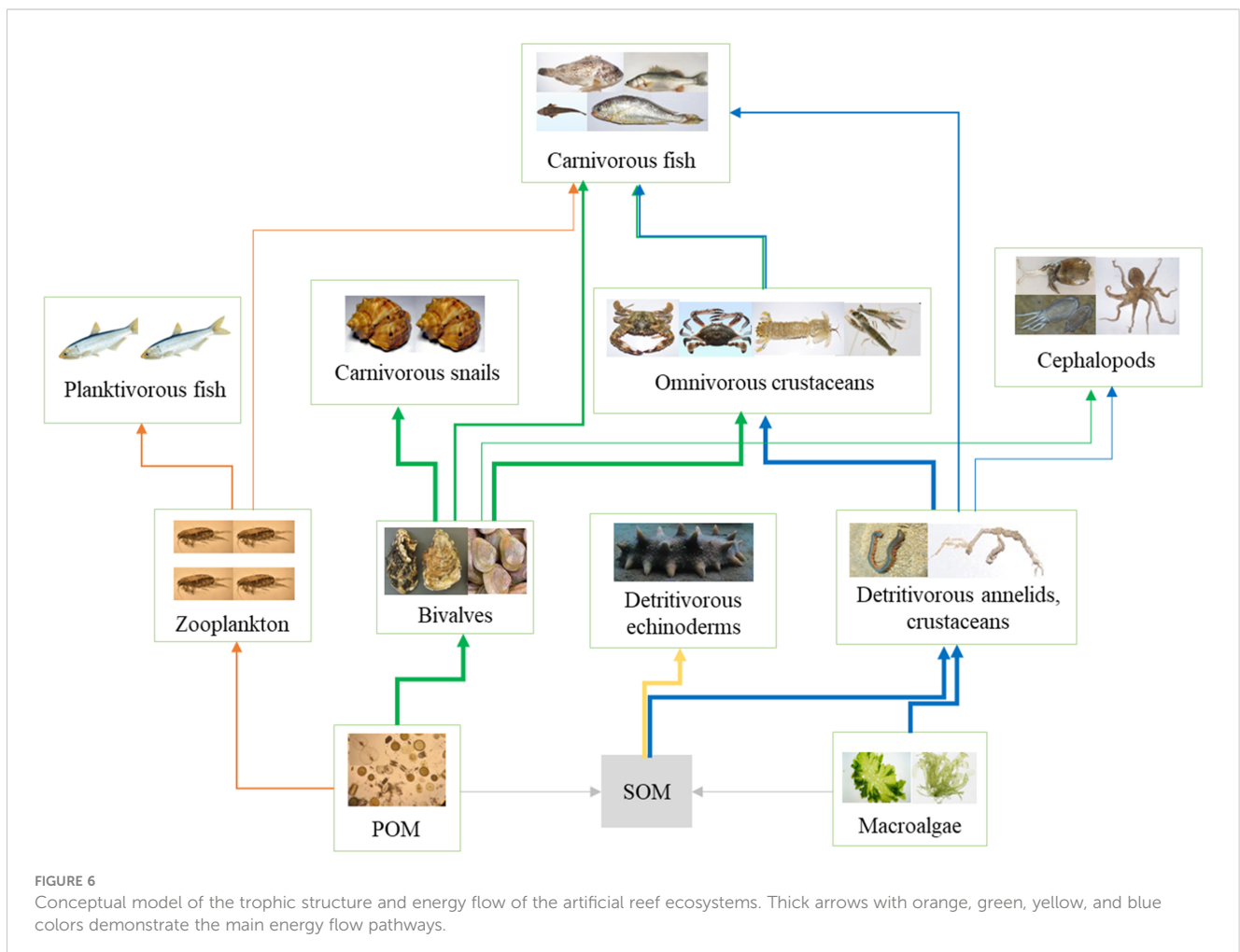
and *S. schlegelii* in ARs based on stomach content analysis and SIA. *H. otakii* tends to eat decapods and amphipods, whereas *S. schlegelii* tends to eat fish and shrimp (Wei and Jiang, 1992; Park et al., 2007; Ji, 2014; Zhang et al., 2014; Zhang et al., 2018; Zhang et al., 2021). The $\delta^{15}\text{N}$ values of these species also indicated that they had relatively different ecological niches. Cresson et al. (2014) highlighted that crustaceans are the most commonly ingested prey type in the AR ecosystem. However, most fishes in the Fuhan AR ecosystem showed lower $\delta^{13}\text{C}$ values than the crustaceans, and the TL of these fish mostly ranged from 3.00–3.66; the crustaceans mostly ranged from 2.40–3.04, these indicated that food sources such as zooplankton and bivalves with higher $\delta^{13}\text{C}$ values and lower TLs were also important food sources for fish. These results differed from Zhang et al. (2018) and Deng et al. (1997), who found that *S. schlegelii*, *P. argentata*, and *H. otakii* consumed very few bivalves, annelidas, and zooplankton as their food sources.

4.3 The TL and food web structure of the AR ecosystem

In this study, TLs of *C. gigas*, zooplankton, and *A. japonicus* were close to TL II. TLs of most crustaceans were close to but lower

than TL III, and TLs of most fish ranged from 3.28–3.66. Fish were the top predators of this ecosystem, however, even the fish with the highest TL did not reach four. The reason for the short food chain length of this ecosystem may be due to the fact that the most fish individuals are relatively small, even the largest fish sampled in the reef was not heavier than 500 g (unpublished data). These fishes were unable to consume large invertebrates or fish at high TL. The TL of *S. schlegelii*, *P. argentata*, and *H. otakii* was lower than that in the Bohai Sea, as reported by Yang (2001). These results were supported by Zhang et al. (2020), who found that TLs of fish in AR were lower than those in the natural ecosystem.

Based on the SIA, a simplified diagram of the food web in the AR ecosystem was obtained, as shown in Figure 6. Four energy flow pathways were observed in the simplified food web: (1) POM → zooplankton → planktivorous fish; (2) POM → bivalves → carnivorous snails/crustaceans → carnivorous fish; (3) SOM → detritivorous echinoderm; (4) SOM/macroalgae → detritivorous annelids and crustaceans → omnivorous crustaceans → carnivorous fish. As most species were benthic predators, the food web was mainly dominated by the benthic energy flow pathway in the AR. The bivalve *C. gigas* seemed to play a key role in the benthic food web structure, as *C. gigas* transported large amounts of phytoplankton to the bottom environment, which provided sufficient energy for benthic food webs.



4.4 The clues for “producer” or “attractor” of the AR

The AR ecosystem is the “producer” or “attractor” for swimming creatures is a controversial issue ((Bohnsack and Sutherland, 1985; Bortone 1998; Wilson et al., 2001; Cresson et al., 2014; Brickhill et al., 2015). In this study, most crustaceans showed similar $\delta^{13}\text{C}$ values, and were close to those of POM and macroalgae. The fish species showed similar $\delta^{13}\text{C}$ values, and their $\delta^{15}\text{N}$ values showed good continuity concerning crustaceans, indicating that the AR ecosystem may produce most crustaceans and fish species. However, it is worth noting that these native fish species tend to prey around ARs (Prince and Gotshall, 1976; Hueckel and Buckley, 1987), so the AR and its adjacent waters both play the role of producers. Species of *M. planipes*, *E. crenata*, *O. vulgaris*, *S. maindroni*, and *L. japonicus*, which are not typical species of the AR ecosystem, showed lower $\delta^{13}\text{C}$ values than other typical reef species, may only spend part of their lives in the AR. Another stable isotopic analysis research (unpublished data) revealed that the $\delta^{13}\text{C}$ of POM values from near shore in Rushankou were higher than those in the AR, and the $\delta^{13}\text{C}$ of POM values from the outer sea area were lower than those in the AR. It is quite probable that these species immigrated from the near-shore area.

4.5 Implications for AR management

Scientific management plays an important role in the sustainable development of AR ecosystems. Oyster *C. gigas* transferred a large part of POM to the bottom, which played a key role in coupling the pelagic-benthic environment and sustaining the benthic energy flow pathway. Therefore, it is necessary to protect it from excessive predation by predators, such as *R. venosa*. The fishing activities targeted for the migratory species (e.g., *O. vulgaris* and *L. japonicus*) should be conducted with sufficient caution, because excessive harvesting may make the AR a trap attracting these species, resulting in the decline of these resources in the surrounding waters. It is necessary to evaluate the carrying capacity and maximum sustainable yield of economic species in the AR, and the sustainable yields of the migratory species should be evaluated in an area larger than the AR. *S. maindroni* was once an important economic species on China’s coast, almost disappearing in China’s northern coast in the past 20 years due to habitat degradation and overfishing (Wu et al., 2010). It was discovered that this AR ecosystem was a spawning ground for this species (Zhang et al., 2020), indicating that the construction of ARs was beneficial for recovering the population of this species on the northern coast of China. Managers can specially design and introduce suitable spawning reefs to improve the resource restoration efficiency of this species.

4.6 Future prospects

This study shows that stable isotope technology is a useful way to investigate the food sources of organisms in AR. The investigated results can provide important clues for exploring the “production” or “attraction” issue of AR, and provide important data for constructing the energy flow model of the AR ecosystem. However, as the sampling area is limited in the marine ranching ecosystem, it is unable to clarify the possible impact of the adjacent sea area on the food web of the AR, which makes the research results have certain limitations. By measuring the distribution of stable isotopes of biotic and abiotic samples in the adjacent area of the marine ranching, we can further clarify the effects of nutrient inputs and biological migration on the food web structure of the AR. In addition, based on SIA, we can only roughly determine the possible food sources of consumers, but cannot determine the specific food composition. Combined with other methods, such as stomach content analysis and fatty acid analysis, we can further determine the food sources and composition of the consumers with higher accuracy to optimize the research results.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Ethics statement

The animal study was reviewed and approved by the Experimental Animal Ethics Committee of Institute of Oceanology, Chinese Academy of Sciences.

Author contributions

JF, XLZ, FB, WZ, and LZ: investigation, methodology, and writing - original draft; JLX and TZ: supervision, conceptualization, and writing- review and editing; HS, MJY, ZH, CZ, PS, PPH, and PZM: sample analysis; PFS and HJ: writing-reviewing. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

Author HJ was employed by the company Shandong Fuhan Marine Technology Co., Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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