



# Trophic interactions of reef-associated predatory fishes (*Hexagrammos otakii* and *Sebastes schlegelii*) in natural and artificial reefs along the coast of North Yellow Sea, China

Rongliang Zhang<sup>a,b,d</sup>, Hui Liu<sup>a,c</sup>, Qianqian Zhang<sup>a,c</sup>, Hua Zhang<sup>b</sup>, Jianmin Zhao<sup>a,c,\*</sup>

<sup>a</sup> Research and Development Center for Efficient Utilization of Coastal Bioresources, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, People's Republic of China

<sup>b</sup> Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, People's Republic of China

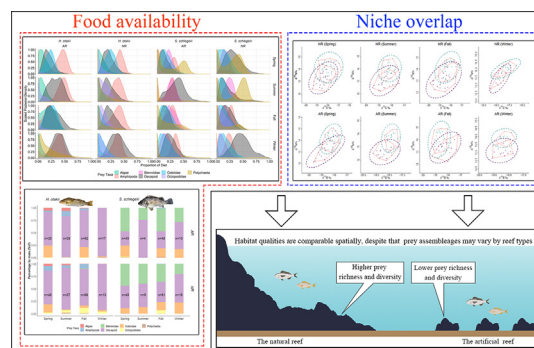
<sup>c</sup> Muping Coastal Environment Research Station, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, People's Republic of China

<sup>d</sup> University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

## HIGHLIGHTS

- Biomass of *H. otakii* and *S. schlegelii* were comparable or higher at artificial reefs.
- Prey assemblages perhaps varied between the artificial reef and the natural reef.
- Both niche width and niche overlap were smaller at artificial reefs.
- Artificial reefs could supply reef predatory fish with high habitat quality.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Large reef-associated predatory fishes play important roles in aquatic ecosystem along coast because of their ecological functions and economic values to recreational and commercial fisheries. This study was carried out to assess the function of artificial reefs as alternative habitats for two common reef-associated predatory fishes in the north of Yellow Sea, China, Fat Greenling *Hexagrammos otakii* and Korean rockfish *Sebastes schlegelii*. According to the catch per unit effort (CPUE), the biomass of predatory fishes at the artificial reef was comparable (*H. otakii*) to or higher (*S. schlegelii*) than the natural reef, highlighting the environmental fitness of the artificial reef. Gut content analysis (GCA) showed that *H. otakii* preyed primarily on Decapod and Amphipoda, while *S. schlegelii* exhibited higher dependence on fish (Blenniidae and Gobiidae) and Decapod. Collectively, prey richness and diversity were greater at the natural reef relative to the artificial reef, and prey availability may be different between the two reef types. Stable isotopic analysis (SIA) in conjunction with the Bayesian mixing model (MixSIAR) revealed spatial and interspecific difference on the diet composition of *H. otakii* and *S. schlegelii* as well. Based on GCA and MixSIAR result, the habitat-specific effect on the prey availability was confirmed. Additionally, comparisons on trophic niche breadth and niche overlap indicated higher trophic diversity but relatively lower food resources partitioning degree for both species at the natural reef than at the artificial reef. Our results suggest that artificial reefs may harbor a different prey assemblage comparing to natural reef but can support large populations of predatory reef-associated fishes and accommodate their coexistence.

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\* Corresponding author at: Research and Development Center for Efficient Utilization of Coastal Bioresources, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, People's Republic of China.

E-mail address: [jmzhao@yic.ac.cn](mailto:jmzhao@yic.ac.cn) (J. Zhao).

## 1. Introduction

As an important element in the restoration of the degraded coastal marine habitats, artificial reefs have been established globally to mimic the ecological functions of natural reefs (Baine, 2001; Carr and Hixon, 1997; Layman and Allgeier, 2020). It was reported that artificial reefs had a great effect on the diet of reef-associated fish species, especially on the upper trophic level species with great commercial and ecological values (Cresson et al., 2019; Lowry et al., 2014). Usually, large predatory fishes can exert top-down effects in regulating population with lower trophic levels and structuring local community by consumption directly or being a predator risk indirectly, and their feeding strategies will influence on the distribution of resource and transmission of energy through the ecosystems resources and transmission of energy through the ecosystems (Heithaus et al., 2013; Terborgh and Estes, 2010; Williams et al., 2004). Thus knowledge of the trophic ecology of these reef-associated predators is important in understanding and evaluating the function of artificial reefs in the maintenance of fish populations.

Over the past decades, many studies have been conducted on the trophic ecology of reef habitat-specific fishes in artificial reefs, with most have carried in Gulf of Mexico (Brewton et al., 2020; Schwartzkopf et al., 2017; Simonsen et al., 2015; Tarnecki and Patterson, 2015; Wells et al., 2008). Relevant studies performed rigorous comparison on the feeding ecology of reef-associated fishes (e.g. red snapper *Lutjanus campechanus*) and highlighted the effect of the habitat structures, seasons and ontogeny on the feeding strategies. However, most of these studies have been conducted at reefs formed by oil platforms, while very few have concerned the reefs designed for fishery enhancement or habitat restoration. Moreover, the previous studies mainly focused on the diet variation of one single fish species, which overlooked the trophic interactions among species with similar trophic levels. The potential trophic overlap or divergence among upper trophic level fishes commonly determines the degree of trophic redundancy or complementary, which are important for the community stability (Bascompte et al., 2005; Heithaus et al., 2013; Kondoh, 2008). At present, there is a lack of studies regarding to the trophic interactions among the reef dwelling predatory fishes living in artificial reefs, including the direct (e.g., predator-prey) and indirect (e.g., competition for a shared resource) interactions.

The Fat Greenling *Hexagrammos otakii* and Korean rockfish *Sebastes schlegelii* are two common upper level predatory fish species in Yellow Sea of China, both usually spend the major life history amid reef-associated water (Kwak et al., 2005; Kang and Shin, 2006; Zhang et al., 2015). They used to serve a prominent role in supporting local near-shore fishery in terms of their abundance and commercial values. In past decades, loss and degradation of the original coastal environments have threatened the populations of these two species, as a result of a variety of human activities (e.g. coastal development, overfishing and pollution). Development of artificial reefs has been increasingly carried out in the Yellow Sea coast as one of the major restoration approaches to support the fish living. Although the feeding ecology of both *H. otakii* and *S. schlegelii* in artificial reefs in Yellow sea, China have been reported in a few previous researches (Wu et al., 2018; Zhang et al., 2018). Trophic interaction between the two species with similar trophic level has yet been addressed. Moreover, how the feeding strategy and trophic interaction of/between these two predatory fishes vary from artificial to natural reefs have not explored. As artificial reefs are always constructed to supplement or enhance natural rocky areas, a comparative study between artificial reefs and relatively undisturbed natural reefs are not doubt imperative and necessary, to provide more robust and informative evidence for the function of artificial reefs in supporting predatory fishes living and accommodating their coexistence.

In this study, we studied the trophic ecology of *S. schlegelii* and *H. otakii* and their potential niche partitioning at both the artificial reef and natural reefs of Yellow Sea coast, based on Gut content analysis

(GCA) and stable isotopic analysis (SIA). We present two questions: 1) Are the feeding strategy of both two species different between the artificial reef and the natural reef? 2) Are the trophic overlap between *S. schlegelii* and *H. otakii* at the artificial reef comparable to those at the natural reef. Via the two questions, we sought to compare the habitat quality of the artificial reefs relative to their natural counterparts in supporting these two reef-associated predators, and give an interpretation to their coexistence in reef habitat. This information is expected to provide insights into the ecological role of artificial reefs and guide the optimization of their deployment and management in the future.

## 2. Material and methods

### 2.1. Study area and sampling collection

This study was conducted in south coast of Northern Yellow Sea, China, with approximately 18 km distance between the natural reef and the artificial reef (Fig. 1). The artificial reef has been established over seven years (started from 2009 to 2013), with material mainly composed of quarry rocks and concrete cubes 3m × 3m × 3m. The depth at both artificial reef and natural reef ranges from 10 to 20 m. At each site, six sampling stations were evenly installed. At each station, 10 fishing traps connected with each other (defined as one gear unit) were used to collect predatory fish samples. Our sampling was carried out in May 2018, August 2018, November 2018, and February 2019, representing spring, summer, fall, and winter seasons, respectively. Benthic fish and macro-invertebrates were collected using fishing traps placed at sea bottom for 48 h, and small benthos were sampled from oyster bags placed a few days in advance. Once brought on boat, all biota samples were stored in the refrigerator until they were transported to the laboratory. Then all samples were identified to species level for fish and at least genus level for macrobenthos. Fish were measured standard length (SL) in mm and weighted (wet weighted in g) prior to being labeled for subsequent GCA and stable isotopes determination. For fish, dorsal white muscle and gut were dissected, and the latter was preserved with 70% ethanol for subsequent analysis. For benthos, only abdomen muscle if possible or the whole body was used for stable isotopic analysis.

### 2.2. Community structure analysis

To estimate the relative biomass of each species, fishery yields at each station was calculated as Catch-per-unit-effort (CPUE) (Calkins, 1961), which is defined as:

$$CPUE = \frac{\sum C_i}{\sum f_i} \quad (1)$$

where  $C_i$  is the catch (expressed in wet weight) of species  $i$ ,  $f_i$  is its fishing efforts, and  $i$  represents *H. otakii* or *S. schlegelii* here. In the current study, one unit of effort was defined as one gear unit in one day and night, and CPUE was denoted by  $g \cdot unit^{-1} \cdot d^{-1}$ .

### 2.3. Gut content analysis (GCA)

Following the fixation, prey items in gut contents were identified to the lowest possible taxon by using a stereoscopic microscope, and their wet weight was measured up to 0.01 g. Otoliths, large pincers, and other hard structures were considered when present to help identify heavily degraded prey items. A vacuity coefficient (%VC) was calculated as the percentage of stomach with preys account for total stomachs. To examine the relative importance of different prey taxa, frequency of occurrence (%FO), percentage by number (%N), percent weight (%W) were calculated, then index of relative importance (IRI) and corresponding %IRI was calculated.

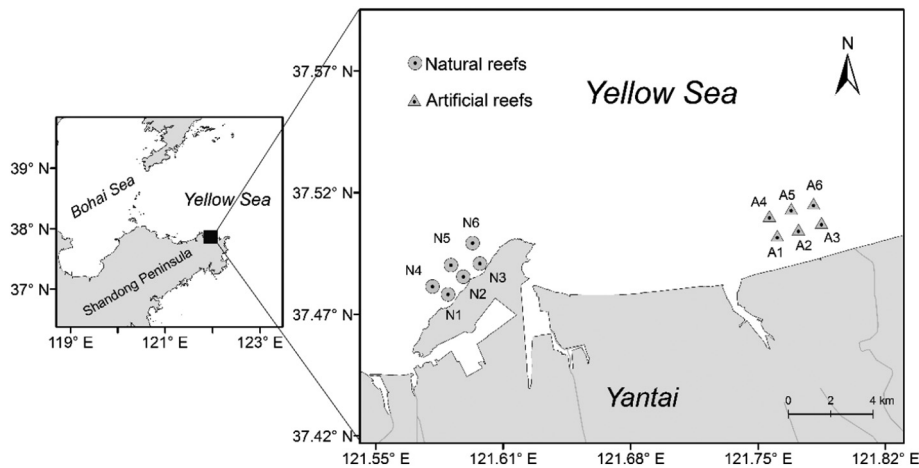


Fig. 1. Location of study sites in the south coast of North Yellow Sea, China, showing two habitat types including natural reefs (N1 to N6) and artificial reefs (A1 to A6).

To minimize the influence of dominate food items, the %W data of all identifiable preys was square root transformed to build a Bray-Curtis resemblance matrix, Shannon-Wiener Diversity Index ( $H'$ ) based on scaled prey %W was used to reflect the forging diversity of each species. Moreover, permutation multivariate analysis of variance (PERMANOVA) using 99,999 permutations and subsequent pairwise comparisons were then employed to examine whether season, species, season  $\times$  species interaction would impact on the stomach contents (measured by %W). Subsequently, similarity percentages (SIMPER) tests were undertaken to further explore prey items most accounting for driving any dissimilarities observed as a function of species and seasons. All statistical analysis of GCA was finished in R using “vegan” packages (Oksanen et al., 2020).

#### 2.4. Stable isotopes analysis (SIA)

Prior to stable isotopes determination, all muscle samples were freeze-dried for at least 48 h and ground to a fine and homogeneous powder using a mortar and pestle, then both 1 M HCl and 2:1 mixture of chloroform and methanol were used to minimize the difference of  $\delta^{13}\text{C}$  values caused by inorganic carbonates and lipid content. No such treatment was necessary in  $\delta^{15}\text{N}$  measurement. SIA was carried out using a mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, US) connected to an elementary analyzer (Flash EA 1112, Thermo Fisher Scientific, US) via an interface (ConFlo III, Thermo Fisher Scientific, US). The stable isotopic ratios were denoted as  $\delta$  notation, as the following equation:

$$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 10^3 \quad (2)$$

where X means  $^{13}\text{C}$  or  $^{15}\text{N}$  and R represents  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ .  $R_{\text{sample}}$  was measured for biota samples and  $R_{\text{standard}}$  is an international standard (Vienna Pee Dee belemnite limestone carbonate for carbon and atmospheric air for nitrogen). For both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , measurement precision was within 0.2‰. Additionally, to examine whether ontogenetic shift had impact on forging habit, simple linear regressions were conducted to determine the relationship between SL and each of carbon and nitrogen stable isotope value, respectively.

Apart from *S. schlegelii* and *H. otakii*, SIA was limited to include species taxonomically similar to prey items presented in gut samples, to make the assessment of food contribution more reliable. Food items which were not captured from traps and oyster bags were collected from the guts of each species of scorpionfish. Multiple analysis of variance (MANOVA) based on stable isotopes signatures was executed to access the variation of dependent variables ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) within

factors (species and seasons). Significant dependent variables identified from MANOVA were followed with univariate analysis of variance (ANOVA) or Kruskal-Wallis tests, depending on whether the requirements of variance homogeneity coupled with normality were fulfilled, on a given factor to examine which level leads to the difference. Afterwards, the pairwise test was applied to distinguish the source of significance within significant factors. The ANOVA or Kruskal-Wallis test, in combination with post hoc tests, were also applied to investigate the interspecific or spatial difference of CPUE, prey diversity ( $H'$ ) and other parameters present in this study. Statistical analyses were performed in R using the “multcomp” and “pgirmess” package (Hothorn et al., 2008).

#### 2.5. Bayesian mixing models

Bayesian mixing models were adopted to estimate the contribution of a potential prey resource to the diet of each species using Bayesian Mixing Models in R (MixSIAR) (Stock and Semmens, 2016). The MixSIAR model allows for uncertainties associated with isotopic signatures and diet-to-tissue discrimination factors (Parnell et al., 2010; Parnell et al., 2013; Phillips et al., 2014), which were set  $1 \pm 0.1\%$  and  $3.4 \pm 0.11\%$  for  $^{13}\text{C}$  and  $^{15}\text{N}$  respectively as recommended in Post (2002). Food items used in the model was derived from GCA, as well as a prior knowledge about their feeding preferences (Kwak et al., 2005; Zhang et al., 2014, 2018; Wu et al., 2018).

In order to obtain more constrained and logically interpretable results, prey items with similar taxonomic status were grouped as a potential source, and mean  $\pm$  SD of their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values was calculated. Final groups of sources used as input for the mixing models were seven categories in total, namely algae, Decapod, Gobiidae, Blenniidae, Amphipoda, polychaetes, and Octopodidae. Since no significant spatial difference on stable isotope values of specific sources was detected, sources from the natural reef and the artificial reef were treat as common ones. It's important to note that some prey species were not identified based on GCA, hence all suspect preys collected from external environment and with similar morphological characteristics were treated as members within a specific group. For instance, assume a prey item in gut content was identified as a member of Gobiidae but unrecognized to species level, taxonomically similar individuals (e.g., *Chaeturichthys stigmatias* or *Tridentiger trigonocephalus*) sampled by fishing gears would be included in the Gobiidae group.

Mixing models were performed with 300,000 iterations (200,000 burns-in), with informative priors from %W of each source group based on the GCA were specified. To examine whether the model run correctly, Gelman-Rubin, Heidelberger-Welch and Geweke tests were used in examining the convergence in the model (Stock and Semmens, 2016).

The trophic niche breadth was measured by corrected Standard Ellipse Area (SEAc), which was estimated as a quantification of the isotopic  $\delta$ -space, to avoid bias owing to small sample sizes (Jackson et al., 2011). Potential isotopic niche overlap between species was also quantified as a percentage of shared SEAc (niche overlap ratio, %OA). It was considered significant when %OA greater or equal to 0.6, representing a heavy diet overlap between two specific populations (Dance et al., 2018; Guzzo et al., 2013; Schoener, 1968). All calculations of trophic niche metrics were completed using the Stable Isotope Analysis in R with "SIAR" package (Parnell and Jackson, 2013) and Stable Isotope Bayesian Ellipses in R with "SIBER" package (Jackson et al., 2011). All statistical analyses significant at  $\alpha = 0.05$  were further tested with appropriate post hoc tests.

### 3. Results

#### 3.1. Fishery yields

Seasonal fluctuation of CPUE for both species at two habitat types was exhibited in Table 1. Overall, *S. schlegelii* has higher CPUE than *H. otakii* in both natural reef ( $231.4 \pm 153.7$  vs.  $205.9 \pm 135.9$  g·unit<sup>-1</sup>·d<sup>-1</sup>) and artificial reef ( $367.4 \pm 281.7$  vs.  $166 \pm 186.5$  g·unit<sup>-1</sup>·d<sup>-1</sup>) (Kruskal-Wallis test,  $p < 0.05$ ). The CPUE estimate of *S. schlegelii* was higher at the artificial reef than at the natural reef, whereas there is no significant difference for *H. otakii* between the two reef habitats.

#### 3.2. GCA results

During all sampling periods, a total of 410 *H. otakii* (184 and 226 for the artificial and natural reefs) and 430 *S. schlegelii* (200 and 230 for the artificial and natural reefs) were collected. The standard length (SL) of *H. otakii* ranged from 8.6–20.0 cm at the artificial reef and 8.2–26.4 cm at the natural reef, respectively; SL of *S. schlegelii* ranged from 7.3–30 at the artificial reef and 9.6–35.3 cm at the natural reef, respectively. Information of stomach number with identifiable prey items and %VC for both *H. otakii* and *S. schlegelii* is displayed in Table 1. Overall, *S. schlegelii* displayed higher %VC than *H. otakii*, as well as higher vacuity values obtained at the artificial reef for both species.

The summaries consist of %W and %IRI of each prey items in gut content were depicted in Table S1 and %W of each prey categories in Fig. 2. Of totally 309 *H. otakii* informative stomachs, at least 28 prey species (22 and 26 for the artificial and natural reefs, with 20 in common) were discerned, which were categorized into seven taxonomic groups: Decapod, Amphipoda, Polychaeta, Octopodidae, algae, Gobiidae, Blenniidae. Of the 239 *S. schlegelii* informative stomachs, at least 21 species (16 and 20 for the artificial and natural reefs, with 15 in common) were detected, with similar taxonomic composition (except algae) as *H. otakii*. Generally, Amphipoda and Decapod were two predominate prey categories for *H. otakii* at both sites. Compared to those living at natural reefs, *H. otakii* at the natural reef consumed more Amphipoda (%W: 7.79% vs. 3.18%, %IRI: 63.38% vs. 40.75%) and less Decapod (%W: 80.53% vs. 74.37% and %IRI: 51.96% vs. 29.06%). In contrast, *S. schlegelii*

fed primarily on Decapod at both the artificial and the natural reef (%W: 46.84% vs. 46.25%, IRI: 42.25% vs. 44.3%) and fish, which is constituted of Blenniidae (%W: 35.73% vs. 33.95%, IRI: 35.59% vs. 34.84%) and Gobiidae (%W: 16.32% vs. 16.52%, IRI: 15.93% vs. 17.71%). According to the Shannon-Wiener Diversity Index ( $H'$ ) calculations result (Table 1), higher diversity of prey compositions was found in specimens dwelling at the natural reef than those at the artificial reef for both species (seasonal averaging  $H'$ : 2.07 vs. 1.85 for *H. otakii*, 1.91 vs. 1.76 for *S. schlegelii*).

Based on the PERMANOVA ( $p < 0.05$ ), spatial differences of the *H. otakii* stomach compositions were detected in all seasons except winter, though magnitudes of the difference were relatively low in all cases ( $R < 0.1$ ). Specifically, the prey *Palaemon ortmanni* in spring (SIMPER, % dissimilarity contribution, hereafter as dif con = 17.8%), *Alpheus distinguendus* in summer (dif con = 20.07%), *P. ortmanni* (dif con = 16.50%) and *Caprellidae sp.* (dif con = 14.89%) in fall were the typifying species driving the regional differences. In contrast, spatial difference of the *S. schlegelii* gut content were not observed in any season, where Gobiidae and *Enedrias fangi* made up similar proportion of the prey composition all year round at both reef types.

Significant interspecific differences of the gut content were observed in fish organisms living at both reef in all seasons except fall (PERMANOVA,  $p < 0.05$  for all cases), albeit with magnitudes at a relatively low level ( $R < 0.2$  for all cases). Based on the subsequent SIMPER, the disparities at the natural reef were mainly as a result of that Decapod (mean dif con = 23.17%) played a principal role in the diet of *H. otakii*, while Blenniidae (mean dif con = 11.17%) and Gobiidae (mean dif con = 10.83%) contributions were greater to *S. schlegelii* than to *H. otakii*. The pattern of interspecific difference at the artificial reef was consistent with that at the natural reef except in fall, with same divergent categories as well, and the mean dif cons were 19.45% for Decapod, 9.82% for Gobiidae and 11.72% for Blenniidae, respectively.

#### 3.3. Isotopic signatures

Totally 184 *H. otakii* (85 and 99 for the artificial and natural reefs, respectively) and 200 *S. schlegelii* (94 and 106 for the artificial and natural reefs, respectively) individuals were used for carbon and nitrogen isotopic analysis. Result of the MANOVA test showed notable discrepancies on both isotopic signatures between species and habitat types ( $p < 0.05$  for all cases), both of which also had strong interactions with seasons ( $p < 0.05$  for both cases). Unexpected, relationships between SL and either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  were not significant for both species at each habitat type ( $p > 0.05$  for all cases).

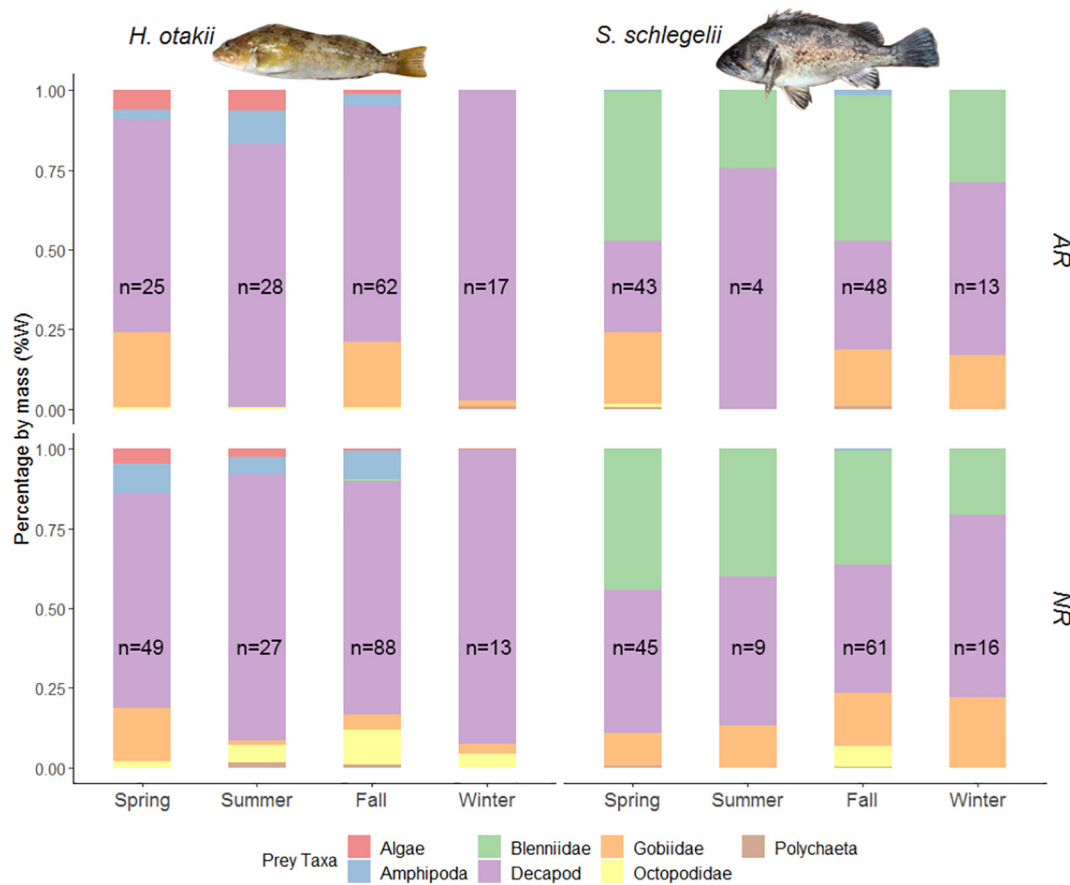
The isotopic characteristics of each species across seasons were displayed in Table 2. Generally, *S. schlegelii* exhibited more enriched isotopic signatures than *H. otakii* (ANOVA,  $p < 0.05$ ) at both reef sites, with one exception that no significant difference was detected for  $\delta^{13}\text{C}$  at the artificial reef. For *S. schlegelii*, both the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were significantly lower at the artificial reef ( $-18.42 \pm 0.38\text{‰}$  and  $13.97 \pm 0.53\text{‰}$ ) than at the natural reef ( $-18.04 \pm 0.5\text{‰}$  and  $14.11 \pm 0.48\text{‰}$ ) (ANOVA,  $p < 0.05$  for both cases). In contrary, no significant spatial differences were observed for *H. otakii* on either the  $\delta^{13}\text{C}$  ( $-18.55 \pm 0.57\text{‰}$  and

**Table 1**

Seasonal variation of CPUE, %VC, prey species number (PSN), and Shannon-Wiener Diversity Index of preys in stomachs ( $H'$ ) of *H. otakii* and *S. schlegelii* at the artificial reef (AR) and the natural reef (NR) in Yellow Sea, China (2017–2018), where \* represents significant difference within two reef types.

Season	<i>H. otakii</i>								<i>S. schlegelii</i>							
	AR				NR				AR				NR			
	CPUE	%VC	PSN	$H'$	CPUE	%VC	PSN	$H'$	CPUE	%VC	PSN	$H'$	CPUE	%VC	PSN	$H'$
Spring	95.7* $\pm$ 45.2	39.02%	14	1.9	211 $\pm$ 154.2	35.53%	13	2.11	347.5 $\pm$ 179.7	35.82%	13	2.21	221.2 $\pm$ 127.1	51.09%	13	2.13
Summer	92.1 $\pm$ 77.4	47.17%	11	1.78	132.9 $\pm$ 72.5	30.77%	13	1.88	147.7 $\pm$ 131.7	92.59%	4	1.19	253.6 $\pm$ 79.7	75%	7	1.48
Fall	442.4 $\pm$ 216.3	15.07%	15	2.05	394.4 $\pm$ 145.5	10.20%	21	2.44	770.7* $\pm$ 358.7	26.15%	13	2.08	412.8 $\pm$ 93.8	29.07%	17	2.33
Winter	33.6 $\pm$ 33.3	0	10	1.67	85.4 $\pm$ 83.3	0	12	1.85	203.6* $\pm$ 139.5	7.14%	6	1.55	37.9 $\pm$ 28.3	0	9	1.68
Mean	165.9 $\pm$ 186.5	25.23%	12.5	1.85	205.9 $\pm$ 135.9	19.13%	16	2.07	367.4* $\pm$ 281.7	40.43%	9	1.76	231.4 $\pm$ 153.8	38.79%	11.5	1.91





**Fig. 2.** Percent by mass (%W) of prey categories consumed by *H. otakii* and *S. schlegelii* based on gut content analysis at the natural reef (NR) and the artificial reef (AR) and across seasons, where "n" represents numbers of informative stomachs.

−18.46 ± 0.55‰ for the artificial and natural reefs, respectively) or the  $\delta^{15}\text{N}$  (13.03 ± 0.54‰ and 13.19 ± 0.55‰ for the artificial and natural reefs, respectively).

The isotopic values of potential prey groups (e.g., algae, Decapod, Gobiidae, and Amphipods) displayed seasonal variations, though species composition of each group might vary by seasons (Table S2). The isospace plot of both *H. otakii* and *S. schlegelii* together with their potential food resources was exhibited in Fig. 3, where the mixture data were inside of the source polygon made of each prey taxa, supporting that our MixSIAR estimation on diet proportions make sense.

Our MixSIAR results (as exhibited in Fig. 4) revealed Decapod and Amphipoda were two typical prey taxa for *H. otakii*, with Gobiidae and algae acting as supplement food. Differently, Blenniidae and Gobiidae were principal prey of *S. schlegelii*, which also showed different degree of dependence on Decapod and Amphipoda. In terms of the prey taxa contribution to *H. otakii* at different reef types, prey taxa were more diverse at the natural reef than the artificial reef, especially in summer and

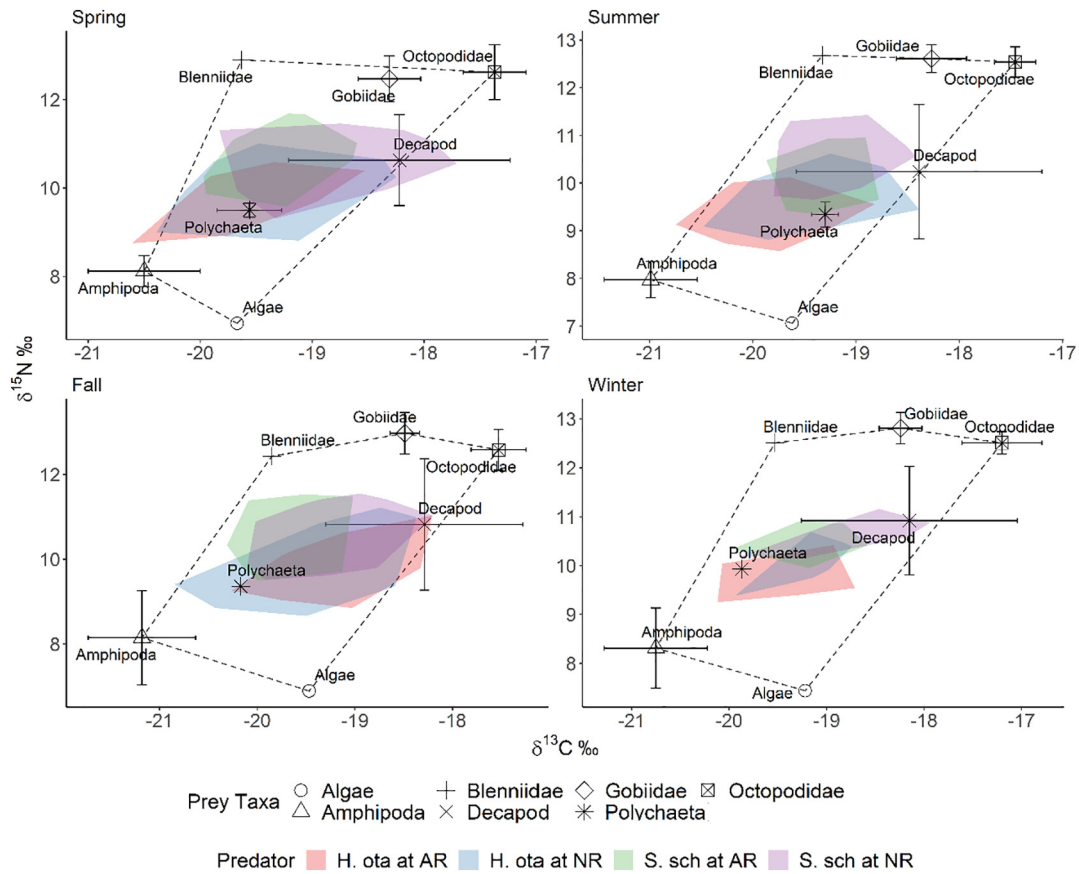
fall. There were more prey taxa with estimated contributions of median over 3% at natural reefs (6 vs. 4 in summer; 5 vs. 4 in fall; Fig. 4). Overall, the prey taxa contributions were more evenly for *H. otakii* at the artificial reef.

Contribution pattern of prey to *S. schlegelii* varied by habitat types and across seasons. For instance, Amphipoda's contribution to the *S. schlegelii* was higher at the artificial reef in spring and summer, with contribution of median 0.201 and 0.254, together with 25%–75% Bayesian credible interval [CI] 0.015–0.303 and 0.152–0.307, respectively, whereas the depletion of Polychaete was greater at the artificial reef, with 0.297, 0.054–0.417 [CI] and 0.43, 0.002–0.522 [CI] in spring and summer, respectively. Moreover, *S. schlegelii* displayed reliance on Octopodidae to some extent (0.105, 0.044–0.184 [CI]) at the natural reef in fall and preyed more on Decapod at the natural reef (0.455, 0.348–0.566 [CI]) relative to their artificial counterpart (0.237, 0.168–0.319 [CI]) in winter. The summary statistics of MixSIAR models on both species across seasons were exhibited in Table S3.

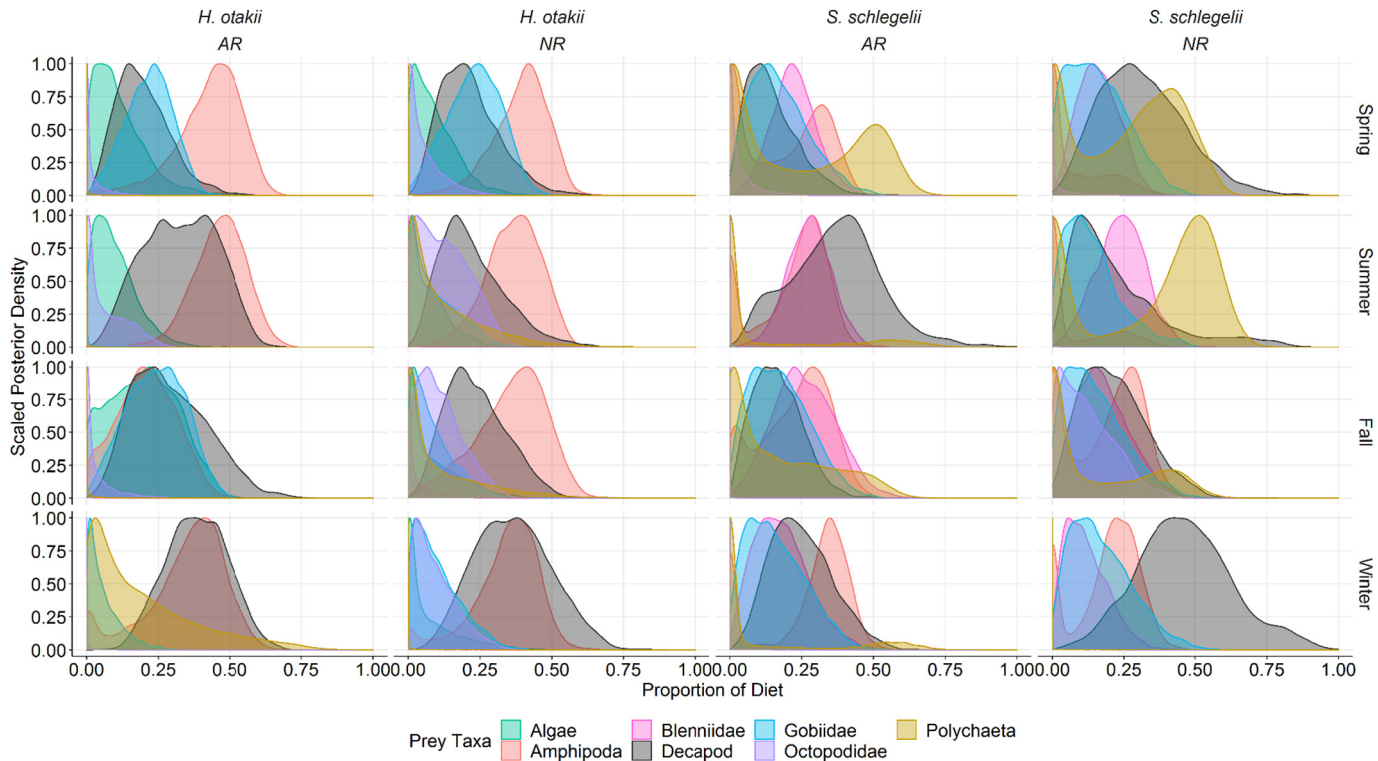
**Table 2**

Standard length (SL) and Stable isotopic characteristics of *H. otakii* and *S. schlegelii* at the artificial reef (AR) and the natural reef (NR) in different seasons.

Date	Species	AR				NR			
		n	SL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	SL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Spring	<i>H. otakii</i>	20	14.66 ± 2.8	−18.69 ± 0.6	13.06 ± 0.6	34	15.32 ± 3.4	−18.38 ± 0.6	13.3 ± 0.5
	<i>S. schlegelii</i>	33	14.69 ± 4.5	−18.28 ± 0.4	14.15 ± 0.5	32	15.59 ± 2.9	−17.89 ± 0.5	14.14 ± 0.5
Summer	<i>H. otakii</i>	24	12.44 ± 2.4	−18.84 ± 0.5	12.61 ± 0.4	26	15.96 ± 4.7	−18.53 ± 0.5	13.06 ± 0.5
	<i>S. schlegelii</i>	21	15.09 ± 4.5	−18.38 ± 0.3	13.66 ± 0.5	26	16.31 ± 3.7	−18.13 ± 0.4	14.03 ± 0.4
Fall	<i>H. otakii</i>	24	14.59 ± 3.2	−18.21 ± 0.5	13.37 ± 0.5	27	14.67 ± 3.0	−18.61 ± 0.7	13.09 ± 0.6
	<i>S. schlegelii</i>	26	17.27 ± 6.7	−18.69 ± 0.4	14.03 ± 0.6	32	19.51 ± 6.9	−18.26 ± 0.5	14.17 ± 0.6
Winter	<i>H. otakii</i>	17	14.02 ± 2.5	−18.47 ± 0.4	13.12 ± 0.3	12	16.33 ± 3.3	−18.2 ± 0.3	13.44 ± 0.4
	<i>S. schlegelii</i>	14	22.3 ± 4.6	−18.32 ± 0.4	13.9 ± 0.2	16	19.54 ± 5.5	−17.77 ± 0.5	14.07 ± 0.3



**Fig. 3.** Isospace plot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values at the natural reef (NR) and the artificial reef (AR) across different seasons, where dashed polygon corrected by prey categories can wrap colored polygon made up of TDF corrected data of both *S. schlegelii* (*S. sch*) and *H. otakii* (*H. ota*).



**Fig. 4.** MixSIAR revealed posterior distributions of feasible contribution of each prey group (Algae, Blenniidae, Gobiidae, Amphipoda, Decapod, and Octopodidae) to the *H. otakii* and *S. schlegelii* at the natural reef and the artificial reef across different seasons.

**Table 3**

Seasonal variations of SEAc values and %OA values of/between *S. schlegelii* and *H. otakii* at the natural reef (NR) and the artificial reef (AR).

Date	NR			AR		
	<i>H. otakii</i>	<i>S. schlegelii</i>	%OA	<i>H. otakii</i>	<i>S. schlegelii</i>	%OA
Spring	0.87	0.89	37.2%	0.80	0.58	23.0%
Summer	0.73	0.54	28.3%	0.61	0.44	25.2%
Fall	1.21	0.82	38.8%	0.77	0.72	33.0%
Winter	0.32	0.31	27.5%	0.45	0.28	13.5%

### 3.4. Niche width and niche overlap

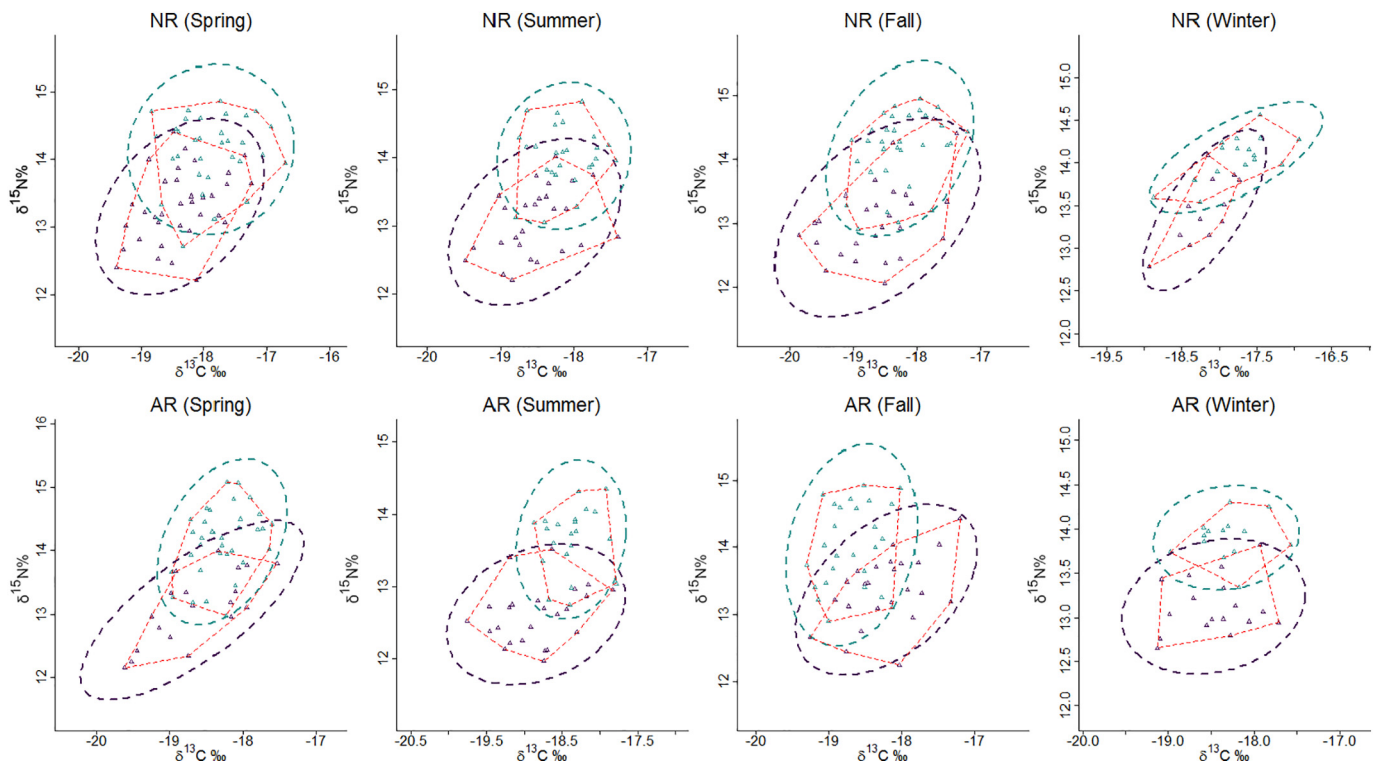
Both *S. schlegelii* and *H. otakii* generally displayed higher niche width at the natural reef (SEAc:  $0.64 \pm 0.27$  vs.  $0.78 \pm 0.37$ , on seasonal average) compared the artificial reef (SEAc:  $0.51 \pm 0.19$  vs.  $0.66 \pm 0.16$ , on seasonal average) (ANOVA,  $p < 0.05$  for both cases). Furthermore, *H. otakii* generally displayed higher SEAc value than *S. schlegelii* at the artificial reef (ANOVA,  $p < 0.05$ ), whereas marked interspecific difference of SEAc value was absent at the natural reef (ANOVA,  $p > 0.05$ ). No significant niche overlap was observed between *H. otakii* and *S. schlegelii* across all seasons at both reef types (%OA < 60%), but %OA were lower at the artificial reef (seasonal average %OA =  $23.7 \pm 8.06\%$ ) than at the natural reef (seasonal average %OA =  $33.0 \pm 5.89\%$ ). The maximum niche overlap was present in spring (%OA = 33.0% and 38.8% for the artificial and natural reefs, respectively), while the minimum was present in winter (%OA = 13.5% and 27.5% for the artificial and natural reefs, respectively) at both sites. The seasonal variation of SEAc and %OA for both species at the natural reef and the artificial reef are displayed in Table 3 and Fig. 5.

## 4. Discussion

Based on GCA and SIA adopted on *H. otakii* and *S. schlegelii* in four seasons, differences on trophic ecology within two species and between the natural reef and the artificial reef were examined, reflecting that the habitat-specific effects on the trophic ecology of both reef species. Information of the trophic ecology of two reef-associated fishes provided in our study can not only give insights to the habitat quality of the artificial reefs in supporting biological and ecological needs of large reef predators, but also allow for a deeper understanding of the trophic diversity and the stability of community structures.

### 4.1. Fish biomass comparisons between habitats types

Comparable or even higher biomass at the artificial reef were observed for *H. otakii* and *S. schlegelii* relative to those at the natural reef, supporting the verified conclusion that the artificial reef can be an efficient tool in enhancing reef fish biomass (Bohnsack et al., 1994; Lima et al., 2019; Lowry et al., 2014). This result provides direct evidences that artificial reefs are suitable habitats for both reef-associated species in the coast of Yellow Sea, China. Many previous studies have demonstrated habitat complexity generally is positively associated with the abundance, biomass and richness of reef-associated fish assemblage (Hackradt et al., 2011; Komyakova et al., 2013; Lowry et al., 2014). The introduced hard substrate improved the complexity of habitat structure, such as general complexity, vertical relief and presence of small holes or crevices, which reef fishes and their benthic prey can be used as shelters (Bohnsack, 1989; Komyakova and Swearer, 2019; Leitao et al., 2007; Scarcella et al., 2011). Moreover, the rough rock surface can also be colonized by algae and sessile filter feeders, which promote the pelagic organic matter flux towards benthic community because of their strong filtration ability (Cresson et al., 2014). Hence,



**Fig. 5.** The corrected standard ellipse area (SEAc) and niche overlap of/between *H. otakii* (cyan points) and *S. schlegelii* (purple points) at the natural reef (NR) and the artificial reef (AR) across four seasons, where the red dashed polygon showed the realized isotopic niche of each species with empirical data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the increased primary or secondary production would transfer along the trophic network, which would facilitate the upper level predatory fish in the end.

#### 4.2. Interspecific and spatial differences on diet composition

Based on GCA, both species displayed diverse feeding choices, with at least 28 prey items identified in *H. otakii* and 21 in *S. schlegelii*, supporting the conclusion that they are opportunistic carnivorous predators (Wu et al., 2018; Zhang et al., 2018). Decapods were observed to be most selected for by *H. otakii* at both sites, even though proportion of the diet represented by prey items within this category varied by habitat types, while *S. schlegelii* displayed a largely dependence of Gobiidae and Blenniidae irrelevant to habitat types. Our result is consistent with previous studies on trophic ecology of *H. otakii* and *S. schlegelii*, reporting that these two species were both shrimp and fish feeders, where *H. otakii* preyed more on Decapod while *S. schlegelii* relied more on teleosts (Kwak et al., 2005; Wu et al., 2018; Zhang et al., 2018).

Notable spatial disparities were detected on %VC values, prey diversity, and gut content compositions for both species, reflecting to some extent the environmental condition and prey availability varied between the artificial and natural habitats. The occurrence of vacant stomachs is likely associated to either the shortage of available food supply or ceasing foraging because of the unfavorable external conditions. In both *H. otakii* and *S. schlegelii*, high %VC was observed in spring and summer, while lower values were detected after summer. This can be explained by that *S. schlegelii* and *H. otakii* are temperate fishes which may reduce foraging frequency when facing dissatisfactory environmental conditions. The extreme high %VC values (up to 80% and 90% at the natural reef and the artificial reef, respectively) of *S. schlegelii* were identified in summer. The high vacuity was less possibly caused by the food scarcity considering that the bloom of macroalgae and phytoplankton in spring and summer can supply substantial organic matters to secondary consumers. Therefore, the high %VC values in summer might be explained mainly by high temperature and low dissolved oxygen at bottom water layer, which drastically inhibited the feeding behavior of *S. schlegelii*. On another hand, the natural reef displayed a lower %VC than the artificial reef, suggesting that the natural reef provided more flexible conditions (e.g. more micro-habitats or food source) for predatory fishes to cope with poor conditions.

Diets of both species were more diverse at the natural reef than the artificial reef. On one hand, this may suggest natural reefs may support a broader feeding choice than artificial habitats do. On the other hand, a diverse diet of predators represents not only an omnivore or an opportunism feeding strategy but also a lower supplement of preferred prey items (Svanback and Bolnick, 2007). A predatory with preferential prey taxa may have to expand their feeding range to fulfill their food requirements. James et al. (2020) has reported more diverse food resources were exploited at the restored oyster reef than their natural counterparts, implying that resources use variability was caused by the lower productivity at the restored habitats. However, cases may be different and not consistent in this study, due to the high vacuity for each species in particular seasons. For instance, if the food supply is not sufficient for *H. otakii* in spring and summer, which assumes to be the main explanation of the vacant stomachs at both sites, the higher prey diversity at the natural reef would suggest more varied feeding choice than that at the artificial reef. Instead, lower vacuity for each species can be indicative of a relatively adequate supply of food for them, and the lower prey diversity in fall and winter at the artificial reef probably reflects *H. otakii* can derive enough energy from particular prey items, without necessary to seek for other food resources.

Habitat differences in stomach contents were observed in *H. otakii* across all seasons except winter, while absent for *S. schlegelii*, which relied mainly on Gobiidae and Blenniidae and partly on Decapod independent of habitat types. The principal differences for *H. otakii* were mainly contributed by proportion variation of fish and Decapod, implying

distinct prey (fish and Decapod) availability associated with the habitats. Previous studies have reported that artificial reefs may support distinct community structure compared to natural reefs, taking account of impacting factors such as habitats complexity (Connell, 1998; Mills et al., 2017), reef ages (Perkol-Finkel and Benayahu, 2004, 2007), hydrologic condition (Feyrer et al., 2011; Fowler and Booth, 2012) and the distance between the artificial and natural reefs (Sanabria-Fernandez et al., 2018; Strelcheck et al., 2005). In this study, higher-relief characteristics, much bigger reef area, and more densely coverage of macro algae (especially in summer) were observed by the diving observation at the natural reef relative to the artificial reef (data not shown), which may also be limited in relatively flat layout and short deployed duration. Result of this work was consistent with the work by Carvalho et al. (2013), which suggested that epibenthic assemblages differed between artificial reefs deployed more than 16 year and natural reefs in terms of composition, structure and trophic function. Similarly, Page et al. (2007) also observed a different amphipod assemblage in the diet of a resident reef fish (*Oxylebius pictus*) at the artificial reef and the natural reef based on the GCA. Schwartzkopf et al. (2017) and Brewton et al. (2020) reported higher diversity of prey items in the natural reef and little overlap in prey species consumption between the natural and artificial reefs in Red Snapper (*L. campechanus*). As preys can affect the quality and quantity of food available to the consumer (also called “bottom-up” process), habitat related variability in prey resources would probably lead to the specific habitat related consumers assemblages. Nowadays, researches on community structure at the artificial reef have paid more attention to the high mobility or relative larger species, overlooking those less conspicuous species which are common but hard to catch or quantify with standing techniques, especially in water with low transparency (Sanabria-Fernandez et al., 2018). This work highlights the appropriateness of GCA method in comparing the role of artificial reefs on prey assemblages to their natural counterparts, albeit with many disadvantages. More techniques therefore are still awaited in future studies to accurately describe the assemblages of prey.

Despite allowing for the identification of what a targeted fish actually consumed recently, the GCA could not reveal dietary information in long terms (Ahlbeck et al., 2012; Hyslop, 1980; Layman et al., 2012; Peterson and Fry, 1987; Phillips and Eldridge, 2006; Votier et al., 2003). Hence, in order to incorporate the uncertainties related to multiple sources and obtain more robust results on feeding ecology of both species, SIA coupled with Bayesian mixing models was introduced to complement the GCA (Parnell et al., 2010; Phillips, 2012).

Source contribution estimates are important for understanding trophic pathways, as well as identifying essential food resources to consumers. Based on the MixSIAR model, spatial and interspecific differences on stable isotopic values were disclosed, revealing that Decapod and Amphipoda were major contributors of *H. otakii* diet, while *S. schlegelii* mainly depend on fish, Decapod and Amphipoda. This result is generally consistent with GCA results, such as the overall contribution of each prey taxa. Nevertheless, disparities also occurred within the two methods. For example, algae accounted for a certain degree of proportion to the *H. otakii* diet based on MixSIAR, while GCA result only claimed a negligible role of algae; MixSIAR revealed potential contributions of Amphipoda prey to the diets of *S. schlegelii*, where the importance of this prey category was not mirrored by GCA. Moreover, habitat-specific effects on sources contributions to *S. schlegelii* were revealed by the MixSIAR, reflecting the reliance of Blenniidae, Gobiidae, and Amphipoda varied by habitat types. It appears likely that the GCA may have inflated the importance of some prey items, which are easier to identify due to persistent hard structures, such as crabs and shrimps. Additionally, the digestion ability may be varied among species, which would also bias the actual diet difference within species. And the loss of unknown preys caused by stomach eversion during collection can also obscure the GCA results. Hence, the quantification for contribution estimate of each source derived from MixSIAR might be more representative in reflecting the potential prey availability difference between the natural and artificial reefs.



### 4.3. Trophic niche width and niche overlap comparison

Niche theory is one of the commonly used theories to explain the mechanism of coexistence and competition between species, in which niche width and niche overlap are important for understanding the status, role and inter-specific relationships of species in the community (Alley, 1982; Pocheville, 2015). In current study, isotopic niches represented by the SEAc indicated trophic diversity was higher at the natural reef than at the artificial reef for either of species, which is similar to the findings reported for red snapper (*L. campechanus*) at the Gulf of Mexico (Schwartzkopf et al., 2017). These findings might on another aspect reflect that natural reefs play better roles in supporting the predators by exploiting higher diverse array of prey taxa. Furthermore, although low niche overlap values (%OA < 0.6) were detected between two species at both reef sites, our results still showed higher values at the natural than artificial reef, indicating larger overlap of the food resources. The larger niche overlap at the natural reef might be due to that both species have to increase their dietary diversity in response to low prey availability and relatively stronger mutual exploitation on similar food resources (Batzner and Boix, 2016; Schindler et al., 1997; Svanback and Bolnick, 2007; Vander Zanden et al., 2000). It seems likely the case at the artificial reef is that either *H. otakii* or *S. schlegelii* can catch sufficient prey items with preference, it may be un-imperative for them to seek for higher diet diversification. As the comparable biomass of both species (even higher for *S. schlegelii*) at the artificial reef, a conclusion can thus be drawn that the quality of habitat at the artificial reef may be comparable or even better in supporting these two species livelihood, for the environmental fitness, sufficient food and to less extent interspecific food overlap.

In ecology, the competitive exclusion principle states that two species competing for same resources can only coexist when there is niche differentiation (Hardin, 1960; Pocheville, 2015), which generally include partitioning of food and space (Michael et al., 2005). Our result revealed no significant niche overlap between the two upper level reef-associated fishes, which may give insights into the mechanism of their coexistence in artificial reefs. Similar findings have also been reported by Dance et al. (2018), which revealed Gray triggerfish (*Balistes capricus*) had larger SEAc, with no significant overlap across all size classes relative to red snapper (*L. campechanus*) at the artificial reef in the northwest Gulf of Mexico, which probably be due to the different feeding strategies. Mablouke et al. (2013) also observed significant niche overlap among three commercial fish species at artificial reefs in south-western Indian Ocean caused by resource partitioning. Nevertheless, we should also be aware that, as the ecological niche occupied by one species also depend on other ecological factors such as population size, climate factors, landscape characteristics, disease (Pocheville, 2015; Svanback and Bolnick, 2007), which means the trophic interaction would be changed once the species' niche modified. Therefore, to uncover the effect of artificial reefs on the trophic interaction of reef-associated predators in long terms, persisting surveillance and corresponding follow-up studies are warranted.

## 5. Conclusion

Our field investigation in the nearshore reef habitat of Yellow Sea, China showed the biomass of predatory fishes at the artificial reef was comparable (*H. otakii*) to or higher (*S. schlegelii*) than those at the natural reef, implying environment fitness of the artificial reef *in situ*. Besides, the different prey availability between two reef habitats was revealed based on GCA and SIA analysis, and we detected more diverse trophic niches but relative lower food resource partitioning degree at the natural reef. Overall, our results implied that artificial reefs can be an alternative management practice in providing high quality habitat for predatory reef-associated fishes and accommodate their coexistence.

## CRediT authorship contribution statement

**Rongliang Zhang:** Formal analysis, original draft writing-; **Qianqian Zhang:** Writing - review & editing, **Hui Liu:** Data curation, Validation; **Jianmin Zhao:** Supervision, Funding acquisition, Writing - review & editing; **Hua Zhang:** Supervision, Writing - review & editing;

## 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.scitotenv.2021.148250>.

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