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Research Paper

Stable isotopic niche analysis of the food web in the typical coral reefs of the South China Sea*

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Abstract The South China Sea (SCS), due to its unique geographical location and marine environment, harbors a diverse and representative coral reef ecosystem. This study examines the trophic structure of major marine organisms within the coral reef ecosystem of the southern SCS through stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$). The analysis is based on field samples collected during the spring of 2023 and 2024. The $\delta^{13}C$ values of consumers spanned from -21.72‰ to -3.26‰, and the $\delta^{15}N$ values ranged from 2.42‰ to 10.97‰, which indicates a well-defined and continuous trophic spectrum. The trophic levels (TLs) of fish varied from 1.80 to 3.35, whereas those of invertebrates ranged from 1.08 to 2.76, suggesting a structured ecosystem in the study area. MixSIAR modeling revealed that macroalgae, plankton, and organic matter on coral surfaces (OMCs) were the predominant basal food sources, supporting five major trophic groups: carnivores, corallivores, planktivores, macroalgae-consuming herbivores and omnivores. Notably, several species that traditionally feed on coral, such as *Chaetodon ornatissimus* and *Heniochus chrysostomus*, demonstrated an increased reliance on algal resources, implying a possible change in feeding strategy. Additionally, the diet preference of *Acanthaster planci* showed a strong reliance on crustose coralline algae (CCA), with juveniles experiencing growth stagnation or adults suffering from long-term starvation being the predominant individuals. This highlights the importance of food-source monitoring for understanding the population dynamics of *A. planci*. This study provides basic data and novel perspectives for coral reef conservation and sustainable management in the coral reef ecosystems of the western Pacific Ocean.

Keyword: coral reef; stable isotope; food source; trophic level (TL)

1 INTRODUCTION

Coral reefs, predominantly found in tropical oceans, are primarily composed of calcareous skeletons produced by reef-building corals and are often associated with other calcareous organisms such as corallina algae, mollusc shells, and foraminifera (Liu et al., 2022). Recognized as the most biodiverse marine ecosystems, coral reefs support a vast array of species that form intricate interaction networks. These ecological relationships play a critical role in shaping the structure, function, and resilience of coral reef ecosystem (Fey et al., 2021). The ecological and economic significance of coral reefs is evident in their contributions to coastal protection, fisheries support, tourism promotion, and biodiversity maintenance. Moreover, coral reefs contain valuable natural resources, including potential oil and gas reserves, while their sedimentary layers may give rise to various metal deposits (Hannington

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et al., 2017). However, climate change and recurrent outbreaks of *Acanthaster planci* have led to an increase in coral bleaching events in recent years. Therefore, it is essential to intensify research efforts and implement stronger conservation strategies (Yu et al., 2024).

The biodiversity of coral reefs plays a crucial role in shaping the complexity of the cross-food chains and the formation of food webs. Food webs are defined as networks of organisms within an ecosystem that are interconnected through intricate trophic relationships, representing both material cycles and energy flow (Link, 2002). Therefore, identifying the primary pathways of energy transfer between organisms and abiotic factors in coral reef ecosystem is essential. This not only aids in evaluating the complex trophic interactions and resilience of coral reef food webs (McLeod et al., 2019), but also facilitates predictions regarding the impacts of global climate change (Hughes et al., 2020).

The diverse organisms and habitats of coral reefs in the western Pacific Ocean constitute ecosystems characterized by complex food webs. These ecosystems exhibit efficient nutrient transfer and energy circulation pathways, playing a crucial role in biogeochemical cycles (Brandl et al., 2019; Zhao et al., 2022). Nearly all islands and reefs in the western Pacific Ocean are composed of coral reefs, which represent the most important landforms in this region (Xu et al., 2022). However, contemporary coral reef ecosystem is experiencing significant decline due to increasing environmental pressures at both global and local scales, including sea-level rise, elevated sea surface temperature, and outbreaks of *A. planci* (Bellwood et al., 2004; Carpenter et al., 2008; Li et al., 2019). These changes not only threaten the biodiversity of coral reef ecosystem in the western Pacific Ocean but also disrupt food web structure and trophic relationships within marine ecosystems, thereby compromising their overall health (Rassweiler et al., 2020). The degradation of coral reef ecosystem can lead to shifts in consumer feeding strategies, potentially resulting in alterations or even collapse of the coral reef food web. Such disruptions further impede energy transfer across trophic levels (TLs). Therefore, there is an urgent need for effective management and restoration strategies for coral reef ecosystem. Investigating the trophic structure of degraded coral reef ecosystem and identifying the underlying drivers of these ecological transformations can facilitate such efforts.

Currently, domestic and foreign studies on coral reef fishes in the western Pacific Ocean primarily focus on community structure (Dai et al., 2022), the feeding ecology of certain fish species (Ke et al., 2022), and changes in coral reef resources (Xu et al., 2021). However, due to the inherent complexity of coral reef ecosystem and the limitations of current sampling methodologies, there remains a lack of comprehensive research examining coral reef food webs from primary producers to the higher TLs of fish. This knowledge gap significantly hinders our understanding of coral reef ecosystem dynamics. To achieve a more thorough and systematic understanding of energy flow and material cycling within coral reef ecosystem, as well as to enhance efforts in restoration and reconstruction, it is essential to conduct in-depth investigations into the trophic structure of coral reef ecosystem.

Stable isotope analysis (SIA) has emerged as a powerful tool for elucidating trophic structures and TLs in food webs based on $\delta^{15}N$ values, as well as for identifying food sources and their contributions to aquatic organisms through $\delta^{13}C$ analysis (Davenport and Bax, 2002). The $\delta^{13}C$ value remains relatively stable across the TLs, making it an effective tracer for distinguishing food sources when studying the trophic characteristics of coral reef communities (Christianen et al., 2017). During the metabolic process in animals, $\delta^{15}N$ is enriched as lighter isotopes are excreted, resulting in progressively higher $\delta^{15}N$ values at higher TLs. Therefore, $\delta^{15}N$ serves as a reliable indicator for determining the TLs of organisms within coral reef ecosystem. SIA not only reveals the long-term food sources sustaining organismal life activities, but also clarifies trophic linkages and energy flows within food webs (Cárcamo, 2015), thus becoming one of the most effective approaches for describing food web structure and dynamics (Layman et al., 2012).

In this study, we quantified the contributions of primary food sources to coral reef organisms in southern South China Sea (SCS), a marginal sea of the western Pacific Ocean, and evaluated the current trophic structure of the coral reef community. Additionally, we analyzed trophic relationships among primary producers, primary consumers, and higher TL consumers using $\delta^{13}C$ and $\delta^{15}N$ analysis, aiming to provide fundamental data and scientific insights for the conversation and sustainable management of coral reef living resources in the western Pacific Ocean.

2 MATERIAL AND METHOD

2.1 Sample collection and treatment

Samples for SIA were collected in May 2023 and May 2024 from several coral reef areas, including those near the Meiji Islands, located in the southern SCS (Fig.1). The samples included primary producers such as macroalgae as well as consumers comprising plankton, macrobenthos and fish. Moreover, organic matter adhering to the surface of 39 coral species (OMCs) was also collected using a dental scaler. Fish were collected using a trawl winch, while invertebrate samples were obtained through diving expeditions. This study focuses on the trophic structure within the coral reefs in the study sea area in the spring. The sampling conducted during these two periods was complementary (May 2023 and May 2024), ensuring comprehensive coverage of dominant species and maintaining the integrity of the ecosystem's trophic structure. Throughout the sampling period, the environmental factors of the adjacent sea areas exhibit similarities, having a relatively minor influence on the isotopic patterns. All samples were identified, processed, and prepared for analysis according to established protocols (Fang and Lv, 2019; Ryanskiy, 2019; Huang et al., 2020). Taxonomic details are provided in Supplementary Tables S1–S4.

We used sterilized tweezers and scissors to carefully remove the skin and bones of the fish, collecting only the back muscle below the dorsal fin for subsequent analysis. For invertebrate cephalopods such as squid, tentacle muscles were collected; for shellfish, adductor muscles were sampled; for shrimp, abdominal muscles were extracted after shell removal; and for crab, muscle tissues from the cephalothorax were obtained following carapace removal. The collected tissues were then cut into small pieces, dried at 60 ℃ in an oven until reaching a constant weight, ground into fine powder, and transferred into sample tubes for further analysis. The macroalgae were thoroughly rinsed with deionized water to remove surface salts and debris, dried at 60 °C for 48 h, and ground into a fine powder. The OMCs were freeze-dried at -60 ℃ for 72 h until achieving a constant weight, finely ground, and stored in centrifugal tubes for subsequent analysis. Among these samples, crustose coralline algae (CCA) and invertebrate specimens selected for $\delta^{13}C/^{12}C$ analysis underwent acid fumigation for 5 h to eliminate the influence of inorganic carbonates prior to isotopic analysis. In contrast, non-CCA macroalgae were not subjected to acid-treated and were directly analyzed for both $\delta^{13}C$ and $\delta^{15}N$.

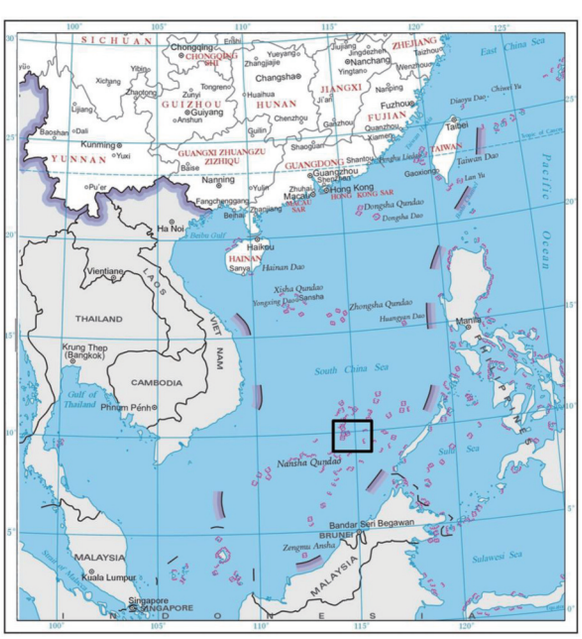

Fig.1 Study area (black rectangle), coral reefs in the Nansha Islands, South China Sea (SCS), China
Map review No. GS(2019)1708.

2.2 Analysis of carbon and nitrogen stable isotopes

The carbon and nitrogen stable isotope signatures of these samples were analyzed using an isotope ratio mass spectrometer (IRMS) coupled with an elemental analyzer (Flash EA 1112 HT-Delta V Advantage). Isotopic ratios were expressed in δ notation as the deviation in parts per thousand (‰) from a standard reference material:

$$\delta R = \left[\left(X_{\text{sample}} / X_{\text{standard}}\right) - 1\right] \times 1000‰, \quad (2.2.1)$$

where R represents either ^{13}C or ^{15}N; X refers to the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standards for $\delta^{13}C$ and $\delta^{15}N$ were VPDB (Vienna Peedee Dee Belemnite) and atmospheric N_2, respectively.

2.3 Data processing and analysis

The $\delta^{15}N$ value of consumers within the coral reef ecosystem of southern SCS was used to estimate the TL of these organisms. The formula for calculating the TL is as follows:

$$\text{TL} = \left(\frac{\delta^{15}\text{N}_{\text{sample}} - \delta^{15}\text{N}_{\text{baseline}}}{\text{TEF}}\right) + \lambda, \quad (2.3.1)$$

where $\delta^{15}N_{sample}$ represents the stable nitrogen isotope ratio in consumers; $\delta^{15}N_{baseline}$ denotes the average stable nitrogen isotope ratio in reference organism; λ indicates the TL of the reference organism, TEF refers to the trophic enrichment factor, which quantifies the degree of isotopic enrichment per TL. In this study, trophic positions were estimated using $\delta^{15}N$ values with a TEF of 3.4‰. This TEF value represents the average per-TL enrichment that is widely adopted in marine food-web studies (Post, 2002; Fey et al., 2021; Yin et al., 2023). It provides a standardized basis for TL estimation in diverse marine ecosystems, and its use enhances comparability with existing studies.

In numerous marine food-web studies, primary consumers like bivalves are commonly used as baseline organisms and assigned a TL value of 2, which reflects their herbivorous or suspension-feeding behaviors (Yin et al., 2023). Nevertheless, coral reefs represent a critical element of the ecological structure in the southern SCS and form the basis of the coral reef food web (Liu et al., 2022; Xu et al., 2022). Thus, within coral reef ecosystems, utilizing OMCs as baseline organisms can more precisely mirror the food-web structure of coral reef ecosystems compared to using bivalves. Based on this, OMCs were chosen as the λ baseline for TL calculations in this study. Significantly, OMCs not only trap exogenous organic matter but also establish a symbiotic relationship with algae, thereby supplying essential nutrients. As a result, OMCs occupy an intermediate trophic position between primary producers (TL=1) and classical primary consumers (TL=2) because of their dual nutritional functions. Subsequently, we further refined the TL of OMCs by referring primary producers.

As marine primary producers, macroalgae have a clearly defined TL of 1. Hence, in this study, the collected macroalgae could be used to calibrate the TL values of OMCs using the following formula:

$$TL_{OMCs} = \left(\frac{\delta^{15}N_{OMCs} - \delta^{15}N_{macroalgae}}{TEF} \right) + \lambda_{macroalgae}, \quad (2.3.2)$$

where $\delta^{15}N_{OMCs}$ and $\delta^{15}N_{macroalgae}$ represent the mean nitrogen isotopic values of OMCs and macroalgae, respectively, TEF denotes the trophic enrichment factor (3.4‰), and $\lambda_{macroalgae}$ is the TL of macroalgae, which is assigned a value of 1 as primary producers.

Based on the results obtained through the approach described above, the mean TL of OMCs was estimated to be approximately 1.75. Therefore, in subsequent TL calculations, OMCs were assigned a TL of 1.75 and used as the λ baseline for estimating the trophic positions of consumers (λ_{OMCs}=1.75).

The TLs of all consumers were then calculated using the equation:

$$TL_{consumer} = \left(\frac{\delta^{15}N_{consumer} - \delta^{15}N_{OMCs}}{TEF} \right) + \lambda_{OMCs}, \quad (2.3.3)$$

where $\delta^{15}N_{consumer}$ represents the nitrogen isotopic values of consumers.

To determine the dietary composition of marine fauna within the coral reefs of study area, the mean proportional contribution of potential food sources to high-TL consumers, along with their associate 95% creditable intervals, were estimated using the software MixSIAR (stable isotope analysis in R) (Stock et al., 2018). This analysis was based on the average $\delta^{13}C$ values of organisms in the coral reef ecosystem. The primary potential food sources were macroalgae, OMCs, and plankton.

Based on the calculations of food source contributions and TLs, organisms in the study area were categorized into five trophic groups. Organisms with TLs greater than 3 were classified as pure carnivores; organisms receiving more than 40% of their dietary carbon from OMCs were categorized as corallivores, suggesting a strong preference for OMCs over plankton or macroalgae; organisms with contributions exceeding 40% from plankton or macroalgae were identified as planktivores or macroalgae-consuming herbivores, respectively, reflecting their dominant reliance on those specific food sources. Specifically, a subset of organisms exhibited either mixed diets where more than two food sources each contributed over 40%, or balanced diets where no single food source contributed more than 40%. These species were classified as omnivores due to their relatively even consumption across all three basal resources. Thus, in this study, omnivores are defined as individuals utilizing multiple or mixed food source without a dominant preference. Additionally, the identification of organisms with different feeding strategies in this study was further verified and supplemented based on the book "*Ecological Atlas of Coral Reef Fish in Nansha Islands*" (Liu et al., 2021).

3 RESULT

3.1 Species composition of marine organisms in the coral reefs of the southern SCS

A total of 132 species of organism samples were collected in the coral reef ecosystem of the southern SCS, including 27 species of invertebrate, 58 species of fish. To construct the trophic structure of the food web in spring in this particular area of the southern SCS, the primary food source, including 7 species of macroalgae, OMCs from 39 species of corals and a mixed plankton sample, were collected from the study area. The proportion of each biological category collected in the study area organisms are presented in Fig.2. Notably, among the macroalgae collected, 4 types of CCA were identified (Fig.2a). The invertebrate group consisted of 17 species of Gastropoda, 4 species of Bivalvia, 2 species of Malacostraca, 1 species of Demospongiae, Holothuroidea, Asteroidea, and Hydrozo (Fig.2c). Among the 58 fish species, there were 49 species of Perciformes, 4 species of Tetraodontiformes, 2 species of Anguilliformes, and 3 species of Beryciformes (Fig.2d). The fish collected from the study area ranged in size from 65 to 492 mm, with *Gymnothorax margaritophorus* being the largest and *Stegastes fasciolatus* the smallest.

3.2 Carbon and nitrogen stable isotopic characteristics of marine organisms collected from the coral reef ecosystem in the southern SCS

SIA revealed that the $\delta^{13}C$ value of marine fauna in the study area ranged from -21.72‰ (plankton) to -3.26‰ (sea sponge), with an average of -15.61‰. The $\delta^{15}N$ values ranged from 2.42‰ (*Cerithium* sp.) to 10.97‰ (*Cephalopholis leopardus*), averaging 7.39‰. Specifically, fish exhibited $\delta^{13}C$ values ranging from -19.64‰ to -10.56‰ (average: -16.15‰) and $\delta^{15}N$ values from 4.72‰ to 10.97‰ (average: 8.66‰). Invertebrates showed $\delta^{13}C$ values spanning from -19.68‰ to -3.26‰ (average: -14.50‰) and the $\delta^{15}N$ values ranging from 2.42‰ to 8.59‰ (average: 5.10‰).

We also analyzed the potential food sources in the study area, including macroalgae, OMCs, and plankton. Specifically, SIA revealed that the $\delta^{13}C$ values of macroalgae in this coral reef ecosystem varied between -21.72‰ and -7.19‰, averaging -13.25‰, while $\delta^{15}N$ values ranged from 1.40‰ to 2.73‰, averaging 2.16‰. The OMCs exhibited $\delta^{13}C$ value ranging from -19.55‰ to -9.92‰ (average: -14.99‰) and $\delta^{15}N$ values from 1.49‰ to 9.35‰ (average: 4.70‰). Additionally, to reduce the spatial and temporal variability of planktonic isotopic signatures, plankton samples from the study area were mixed as an individual food source for analysis. The $\delta^{13}C$ and $\delta^{15}N$ values of this mixed plankton sample were -21.54‰ and 5.74‰, respectively (Fig.3).

3.3 TL of marine organisms from the coral reef ecosystem in the southern SCS

The $\delta^{15}N$ range of main organisms in the study area corresponded to TLs ranging from 1.08 to 3.35

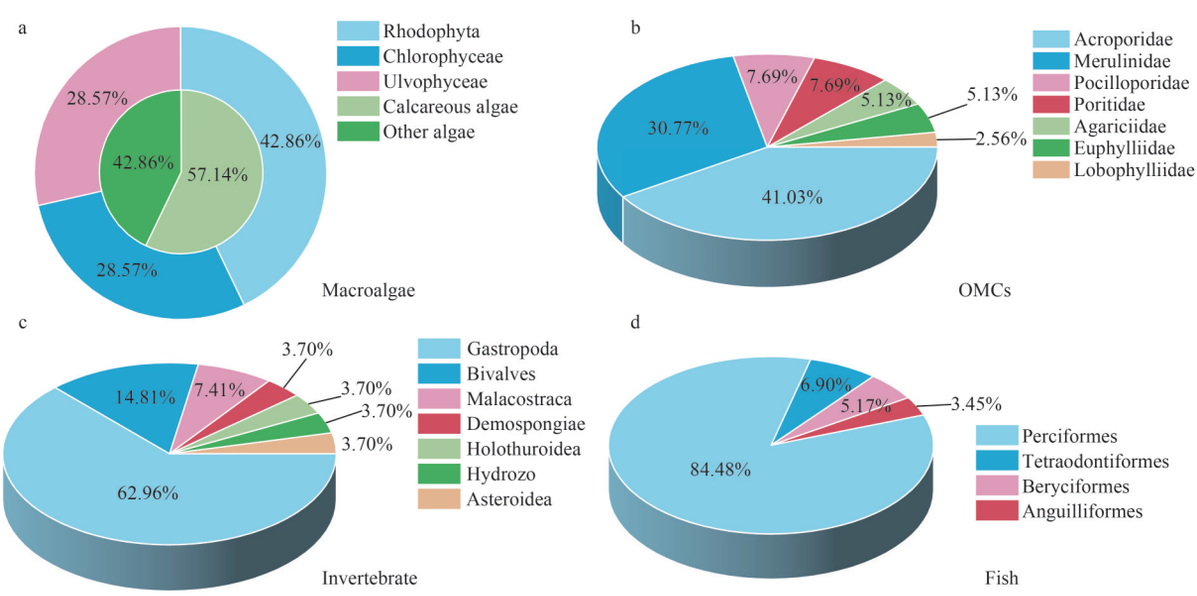

Fig.2 Composition of biological samples collected from the study area

Each proportion is based on the number of species.

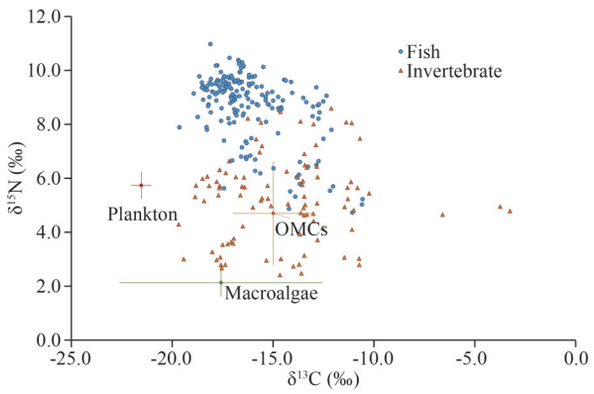

Fig.3 Distribution of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values among fish, invertebrates, and key food resources in the coral reef ecosystem of the study area

(Fig.4). Specifically, the TL of fish varied between 1.80 (*Acanthurus nigrofuscus*) and 3.35 (*Heniochus acuminatus*), with an average of 2.83. As shown in Fig.4, the fish community in the study area mainly consisted of Perciformes, Tetraodontiformes, Anguilliformes, and Beryciformes. The TL distribution patterns differed significantly among these groups. Among them, Perciformes had the largest species count and the broadest TL range (Figs.2 & 4). Specifically, their TL values were distributed within the range of 1.80–3.35. Of the 49 Perciformes species identified in this study, four species—*A. nigrofuscus* (1.80), *Stegastes fasciolatus* (1.90), *Scarus niger* (1.93), and *Chlorurus japanensis* (1.99)—exhibited TLs below 2 and were classified as representative low-level consumers. Additionally, 27 species, including *Zebrasoma veliferum* (2.02) and *Heniochus varius* (2.81), fell within the TL range of 2–3. Furthermore, 18 species, such as *Cheilinus fasciatus* (3.01), exhibited TLs above 3. The wide trophic distribution and high species richness of Perciformes highlighted their diverse ecological roles within the food web structure of the southern SCS. The TL values of Tetraodontiformes ranged from 2.40 to 3.16, indicating a relatively dispersed distribution and Anguilliformes had fewer species but showed a more concentrated TL range. Among all groups analyzed, Beryciformes exhibited relatively higher TL values, including *Myripristis violaceus* (2.77), *Myripristis berndti* (3.10), and *Sargocentron punctatissimum* (3.16).

For invertebrates, 14 species—such as *Trochus niloticus* (1.17) and *Tridacna crocea* (1.21)—were characterized by TLs below 2 and primarily function as prey within the coral reef food web. Another 13 species, including *Leucozonia smaragdula* (2.03) and *Phyllidia nobilis* (2.55), displayed TLs above 2. These results indicate a well-structured food web in the coral reef of the study area, where fish occupy higher and more diverse trophic positions compared to invertebrates.

3.4 Contribution of key food sources for marine fauna in the coral reef ecosystem

There are various food sources in the coral reef ecosystem of southern SCS, primarily including macroalgae, plankton, and OMCs, which sustain a diverse community of marine fauna. Using MixSIAR software and $\delta^{13}C$ values, we calculated the relative contributions of these food sources and classified marine organisms into five trophic groups: carnivores, corallivores, planktivores, macroalgae-consuming herbivores and omnivores.

Among these groups, carnivores, consisting of 25 fish species, likely serve as the top predators in the study area (Fig.5a). Specifically, there were 12 corallivores, with only 3 invertebrate species feeding on OMCs, compared to 9 fish species, whose OMC contributions ranging from 38.0% to 55.0% (Fig.5b). Corallivores are defined as marine organisms that primarily rely on OMCs as their food source. Typical corallivorous taxa included members of Scaridae such as *Chlorurus sordidus* and *Chlorurus capistratoides*, and Chaetodontidae such as *Heniochus varius*, all of which exhibited high levels of coral-derived nutrition.

In total, 16 species were classified as planktivores, including 8 fish and 8 invertebrate species (Fig.5c). Planktivores are defined as organisms with a pronounced preference for plankton. Among them, *Plumularia* sp. exhibited the highest reliance on plankton (74.0%), while *Tridacna squamosa* and *Pomacanthus imperator* had the lowest within this group (40.0%). Classic planktivorous fish such as *Naso vlamingii*, *Trapezia tigrina*, and *Chromis weberi* showed consistently high plankton contributions (above 50.0%). The presence of a substantial number of planktivores underscores the ecological importance of plankton as a primary energy source for mid-to-upper TLs in the southern SCS.

There were 9 macroalgae-consuming herbivores, comprising 4 invertebrates and 5 fish species, whose macroalgae contributions ranged from 40.4% to 74.7% (Fig.5d), with the lowest in *Cypraea tigris* (40.4%) and the highest in *Leucozonia smaragdula* (74.7%). Macroalgae-consuming herbivores are defined

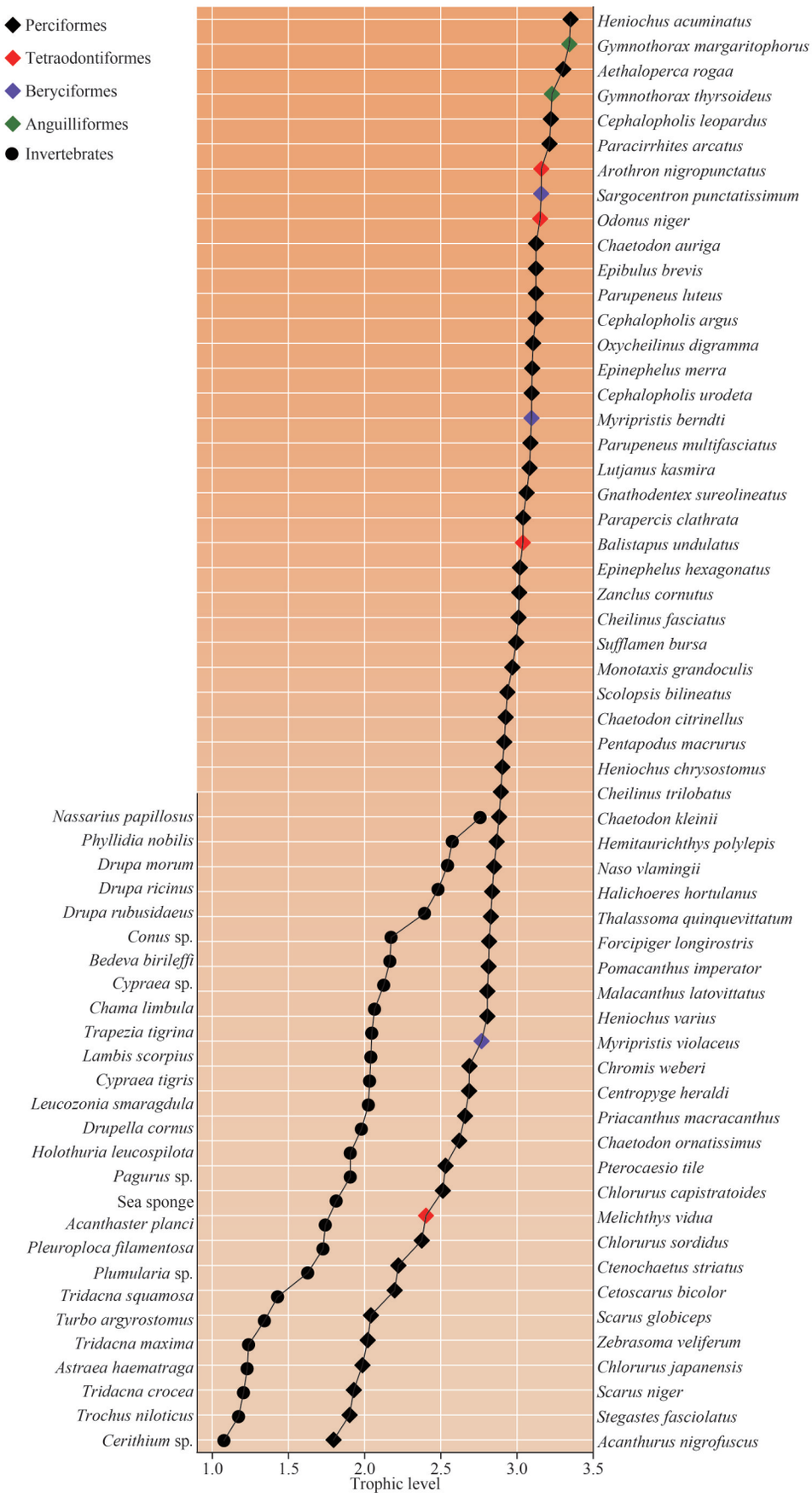

Fig.4 The TL distribution of fish and invertebrates in the study area

as marine organisms that preferentially consume macroalgae. Notably, typical herbivorous fish such as *Acanthurus nigrofuscus*, *Scarus niger*, and *Chlorurus japanensis* exhibited macroalgae contributions above 60.0%.

Additionally, there were 9 omnivores exhibiting mixed feeding strategies with relatively balanced contributions from macroalgae, OMCs, and plankton, including 4 invertebrate species and 5 fish species (Fig.5e). Representative species included *Melichthys vidua*, *Hemitaurichthys polylepis*, and *Astraea haematraga*.

4 DISCUSSION

4.1 Stable isotope characteristic of carbon and nitrogen for marine fauna in the southern SCS

In this study, during the spring in the southern SCS, the $\delta^{13}C$ values of macroalgae and OMCs largely encompassed those of most fish and invertebrates (Fig.3). Primary producers were comparatively comprehensively sampled, including CCA, such as *Halimeda macroloba*, *Tricleocarpa fragilis*, *Amphiroa foliaceae*, *Amphiroa fragilissima*, as well as other macroalgae species, such as *Ulva Lactuca*, *Cauleroa serrulate*, and *Caulerpa mexicana*. Additionally, the diet of some planktivores was primarily composed of plankton (Fig.5c). Therefore, the main potential food sources in the coral reef ecosystem of the study area were identified as macroalgae, OMCs and plankton. Compared with other studies on the marginal seas of the western Pacific Ocean (Ning et al., 2016; Zhang et al., 2019), the consumers collected in this study exhibited a wider range of $\delta^{13}C$ (18.46‰). This range reflects the diversity of food source within the food web. A larger carbon range value indicates a broader spectrum of initial carbon sources and dietary options, suggesting a more complex the food web structure in the coral reef ecosystem of western Pacific Ocean (Bos et al., 2013). According to literature research, the food sources of the southern tropical marine ecosystems generally include plankton, particulate organic matters, macroalgae, and other primary producers (Chen et al., 2012), which aligns with the findings of our study. In some coral reef studies, corals are not considered as a major source of organic matter due to the limited number of coral-feeding fishes in the study area (Yin et al., 2023). However, we collected a large number of coral-feeding fish in our study area, such as members of the family Chaetodontidae—

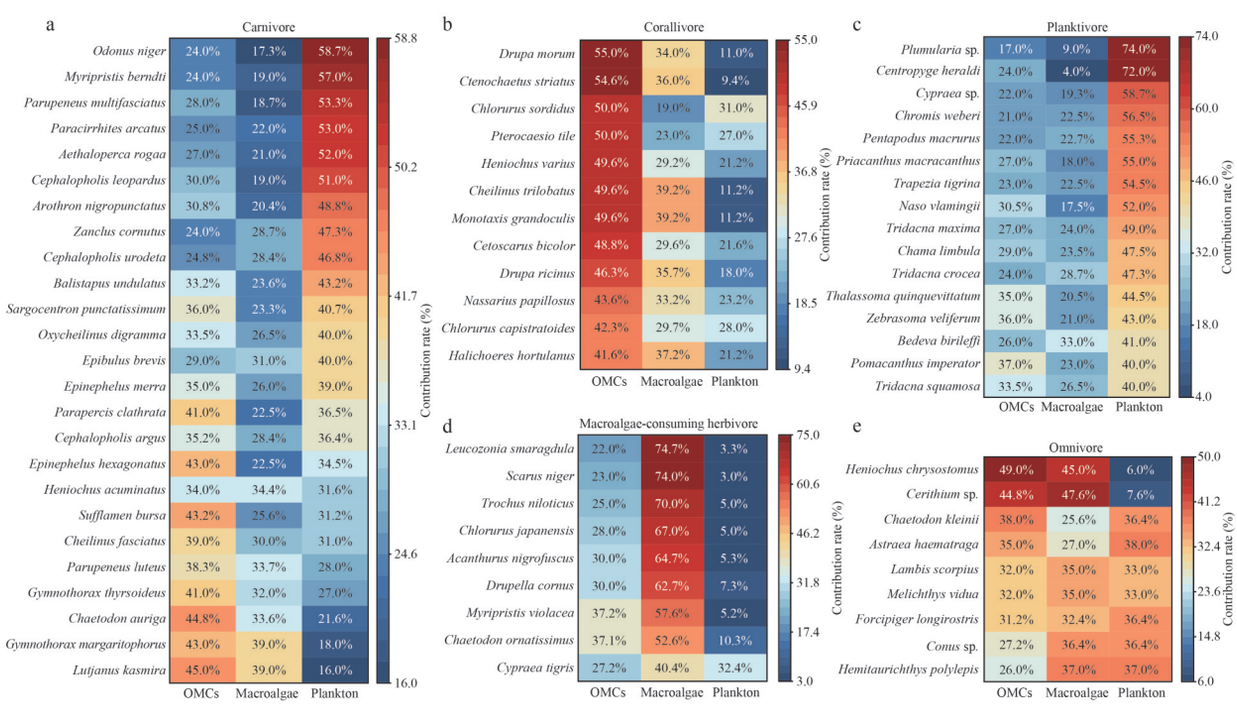

Fig.5 Mean contributions of macroalgae, organic matter on coral surfaces (OMCs), and plankton to fish and invertebrates in the southern South China Sea (SCS), estimated by the MixSIAR model with surrounding 95% credibility intervals (Supplementary Table S5)

including *Chaetodon kleinii*, *Chaetodon citrinellus*, and *Chaetodon Auriga*—indicating that coral-associated organic matter is an important potential food source. Therefore, OMCs were considered as the primary source of organic matter in the carol reef ecosystem of the southern SCS. The broader $\delta^{13}C$ range observed among consumers (spanning 18.46‰) implies a high diversity of food sources and feeding strategies, which is characteristic of a structurally complex and functionally rich coral reef system.

Studies have also shown that the $\delta^{13}C$ values of consumers closely reflect those of their food sources. Among consumers, fish and invertebrates exhibited $\delta^{13}C$ and $\delta^{15}N$ values that largely overlapped with those of macroalgae and OMCs, indicating that these two food sources form the dominant energy base in the benthic food web. Plankton generally exhibited lower $\delta^{13}C$ values (-21.54‰) compared to macroalgae and OMC. In the coral reef ecosystem, plankton represents a distinct pelagic feeding pathway, originating from the water column and being largely independent of benthic substrates (Fry, 2006; Layman et al., 2012; Yin et al., 2023). Therefore, consumers that rely heavily on plankton incorporate isotopic signals from the pelagic zone, reflecting a trophic linkage between reef-associated species and broader oceanic nutrient cycles. In contrast, macroalgae-consuming herbivores and corallivores primarily reflect local benthic primary production pathways. This distinction highlights the ecological heterogeneity within the southern SCS coral reef food web and emphasizes the role of planktivory in maintaining pelagic-benthic coupling.

The $\delta^{13}C$ values of marine organic matter indicate that the primary food sources for marine fauna are phytoplankton (-22‰–-20‰) and marine benthic algae (-20‰–-10‰) (Christianen et al., 2017). In the coral reef ecosystem of the southern SCS, the $\delta^{13}C$ values of macroalgae ranged from -21.72‰ to -7.19‰. Notably, most of the macroalgae collected in the study area were CCA, including *Halimeda macroloba*, *Tricleocarpa fragilis*, *Amphiroa foliaceae*, and *Amphiroa fragilissima*. These CCA species exhibited an average $\delta^{15}N$ value of 2.18‰ and a mean $\delta^{13}C$ value of -10.01‰, whereas other macroalgae showed an average $\delta^{15}N$ value of 2.13‰ and a mean $\delta^{13}C$ value of -17.58‰. Importantly, the $\delta^{13}C$ value of CCA was significantly higher than that of other macroalgae (Fig.6), reflecting distinct carbon acquisition mechanisms. CCA are calcifying macroalgae that deposits calcium carbonate ($CaCO_3$) both intracellularly and extracellularly. Through the process of calcification, they form rigid structures such as shells, scales, or skeletons, which contribute to long-term carbon sequestration (Prathep et al., 2018). The elevated $\delta^{13}C$ values in CCA can be attributed to the following factors:

(1) Carbon source preference: CCA predominantly utilize bicarbonate (HCO_3^-) rather than dissolved CO_2 during photosynthesis. Since HCO_3^- has a higher $\delta^{13}C$ value and undergoes less isotopic fractionation, this leads to enriched $\delta^{13}C$ signatures in algal tissues (Bilan and Usov, 2001).

(2) High pH environment: Ocean acidification (OA) can elevate seawater pH, shifting the speciation of dissolved inorganic carbon toward HCO_3^- while reducing CO_2 concentrations. Under these conditions, CCA actively take up HCO_3^-, further minimizing isotope fractionation (De Barros Marangoni et al., 2017).

(3) Calcified structure: The calcareous cell walls of CCA may restrict CO_2 diffusion, thereby increasing their reliance on HCO_3^- transport and contributing to higher $\delta^{13}C$ values (Prathep et al., 2018).

These physiological and environmental mechanisms collectively contribute to the isotopic distinctiveness of CCA. The sample size of macroalgae collected in this study was sufficient to differentiate CCA from other common macroalgal species, revealing preliminary but significant differences in their roles

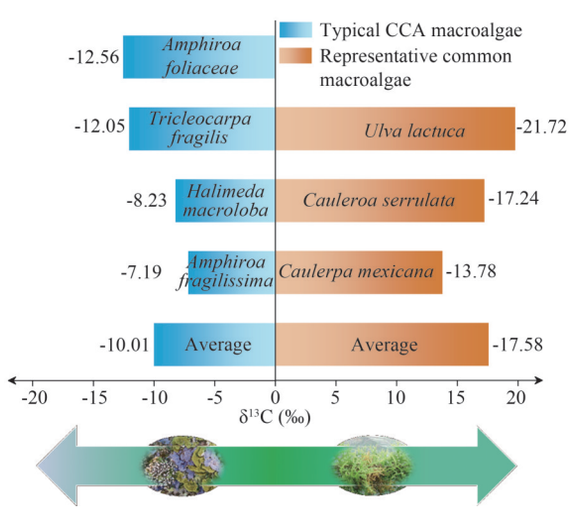

Fig.6 Comparison of $\delta^{13}C$ values between typical crustose coralline algae (CCA) and representative macroalgae in the southern South China Sea (SCS)

as primary producers during spring (Fig.6). As a result, we conducted a preliminary classification and observed notable differences in $\delta^{13}C$ values between CCA and non-CCA macroalgae, as well as in their respective contributions to the diets of local consumers in spring. This divergence prompted a focused analysis of the phenomenon. To fully validate and refine these findings, more systematic and comprehensive investigations are warranted in future studies.

Additionally, previous studies have demonstrated that elevated CO_2 concentrations in atmosphere and reduced seawater pH can lower calcification rates and impede the growth and reproduction of CCA (Anthony et al., 2008; Johnson and Carpenter, 2012; Roleda et al., 2015). Therefore, the impacts of future OA on the carbon physiological processes of CCA may be even more prominent, representing a crucial issue that requires focused attention in future research.

4.2 Functional group and their ecological role in southern SCS coral reef ecosystem

In this study, a structured triangular ecosystem was established in the coral reef ecosystem of the southern SCS during the spring. This ecosystem primarily involves organisms at low to mid-TLs, while the number of apex consumers is relatively small (Fig.3). Based on the food source contribution calculations, TLs, and findings from previous studies (Liu et al., 2021), organisms in the study area were categorized into five trophic groups: carnivores, corallivores, planktivores, macroalgae-consuming herbivores and omnivores (Fig.7). Carnivores in the southern SCS coral reef ecosystem were defined as organisms with TLs exceeding 3.00. Corallivores were species that depend on OMCs for nutrition. Planktivores were organisms whose diets are predominantly supported by plankton. Macroalgae-consuming herbivores were those that rely primarily on macroalgae as their main food source. Omnivores were classified as those exhibiting relatively balanced consumption of all three basal resources.

In this study, herbivorous fish did not dominate the study area in spring. Actually, they play essential roles in key ecological processes such as the carbon cycle and biological erosion of coral reefs (Bruggemann et al., 1994). According to previous studies (Polunin et al., 1995; Ferreira et al., 1998), herbivorous fish, particularly those from the Scaridae and Acanthuridae families, make significant contributions to the maintenance of the ecological balance within coral reef ecosystem in the western Pacific Ocean. A reduction in the functional contribution of herbivores—whether resulting from a lower proportion, reduced diversity, or altered feeding behavior—may weaken the top-down control on algae and increase the probability of a shift towards algal dominance (Hughes et al., 2007;

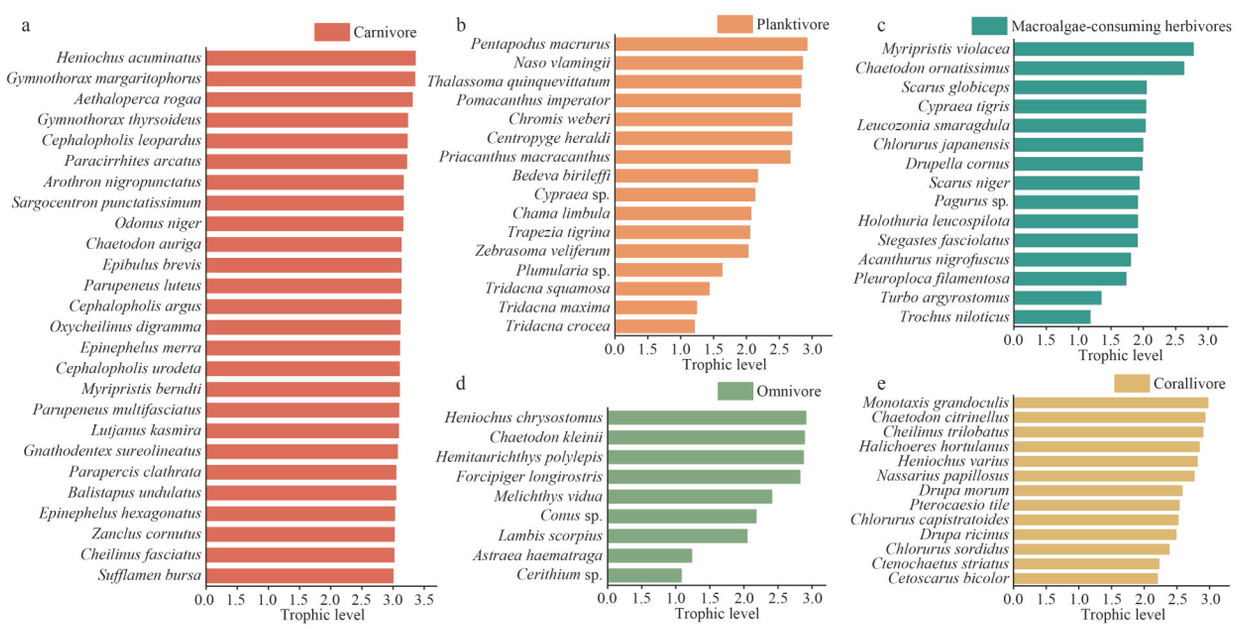

Fig.7 The trophic spectrum of marine fauna grouped due to their food source

Smith et al., 2010). Therefore, changes in the representation of herbivorous organisms, such as a reduced proportion or lower abundance, can be considered as a potential indicator of decreased stability in coral reef ecosystems. In future efforts to conserve and preserve the ecological balance of coral reef ecosystems, particular attention could be paid to changes in the abundance or feeding behavior of herbivorous fishes, as this may enable more effective monitoring of coral reef ecosystems.

Meanwhile, coral-feeding fish also play vital roles in coral reef ecosystem and are similarly affected by coral degradation. Typical corallivore include members of the Chaetodontidae and Labridae families. Coral-feeding fish serve as important conduits for the transfer of energy and nutrients from primary producers (i.e., corals) to higher TLs. Consequently, these species exhibit strong dependence on coral health. The loss of coral dominance can lead to rapid declines in the species richness and abundance of corallivores or force them to alter their feeding strategies. Fish that rely exclusively on coral as a food source are particularly vulnerable to coral degradation (Pratchett et al., 2011). In this study, *Chaetodon ornatissimus*, a coral-feeding fish, exhibited the highest dietary contribution from algae, with algae accounting for up to 52.6% (Fig.5d). Similarly, *Heniochus chrysostomus*, another coral-feeding species, showed nearly equal contributions of algae and OMCs in its diet (Fig.5e). These findings suggest that corals are no longer the primary food source for either *C. ornatissimus* or *H. chrysostomus* during spring in the study area. Both species appear to have shifted from corallivores to herbivores under influence of the increasing algal dominance in coral reef habitats. Corallivorous fish may serve as potential indicator species for assessing the health status of coral reefs.

This study concentrates on the spring food-web within coral reef ecosystem in the southern SCS, while minimizing the impact of seasonal environmental variability. In fact, within coral reef ecosystems of the SCS, seasonal environmental variability, such as temperature fluctuations, upwelling, and tropical cyclones, can serve as significant drivers of changes in trophic community composition (Yin et al., 2023). Future research can conduct more systematic and thorough analyses to further validate and strengthen these findings.

4.3 Degradation of coral reefs indicated by food source analysis of *A. planci*

Among marine organisms within coral reef ecosystem, *A. planci* exhibits distinct feeding behaviors and dietary preferences across its developmental stages—larval, juvenile, and adult. During its early life stage, *A. planci* primarily consumes detritus from CCA and plankton. CCA plays particularly crucial role in larval settlement and early survival (Jensen et al., 2025). In the juvenile stage, a significant dietary shift occurs: young juveniles continue to feed on CCA (Deaker et al., 2020), but as they grow, they gradually begin consuming small to medium-sized branching corals (Wilmes et al., 2020). This transitional phase is characterized by a mixed diet consisting of CCA and coral, reflecting a significant shift in dietary patterns from herbivory to corallivory. $\delta^{13}C$ values reflect long-term dietary sources, highlighting the importance of considering stage-specific diets when applying mixing models such as MixSIAR to accurately estimate source contributions and ensure representative model inputs. Throughout its developmental stages, *A. planci* does not feed on macroalgae; therefore, we excluded macroalgae as a potential food source. Consequently, we conducted a separate analysis of the food sources for *A. planci*, categorizing the potential food sources o into three types in our model: CCA, plankton, and OMCs. Using SIA with the MixSIAR model, we found that CCA contributed an average of 49.2% (95% credibility interval: 21.8%–74.4%), OMCs contributed an average of 33.1% (95% credibility interval: 2.0%–76.0%), and plankton contributed an average of 17.7% (95% credibility interval: 0.9%–33.1%). These results indicate that CCA is the dominant food source, with a significantly higher contribution than the other two (Fig.8).

Due to the 2020 outbreak of *A. planci*, coral reefs in the SCS have not yet returned to an ecologically stable state (Han et al., 2024). Moreover, influenced by multiple interfering factors previously outlined, the coral reef has experienced a significant decline in coral cover. This has led to the rampant growth of macroalgae, including CCA, which now occupies the dominant ecological niche within the coral reef ecosystem of the SCS. Previous studies have reported notable variations in the $\delta^{13}C$ values of

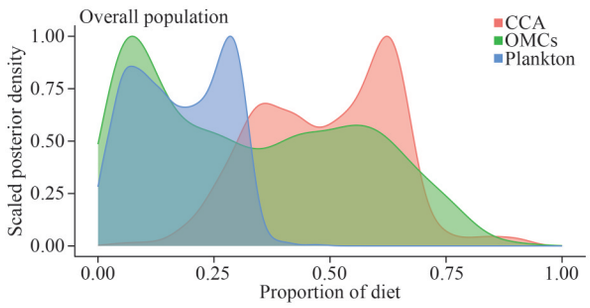

Fig.8 Contributions of crustose coralline algae (CCA), organic matter on coral surfaces (OMCs) and plankton to *Acanthaster planci* in southern South China Sea (SCS) estimated using the MixSIAR model with 95% surrounding credibility intervals

A. planci across different life stages, indicating fundamental shifts in dietary sources as the organism matures (Ma et al., 2024). These findings not only highlight the dynamic nature of diet transitions in *A. planci*, but also suggest that the species exhibits stage-specific responses to food source availability within the coral reef ecosystem. The increased abundance of CCA provides an accessible alternative food source for *A. planci*. Under such conditions, the juvenile phase may be prolonged by several months or even years (Deaker and Byrne, 2022; Patel et al., 2024). Extended feeding on CCA can delay development, result in reduced body sizes, and lead to a high proportion of juveniles within the population (Wolfe et al., 2015; Wilmes et al., 2020). Consequently, the specimens collected in this study were predominantly juveniles whose feeding behavior primarily relied on CCA, thereby explaining the relatively high contribution of CCA observed in this study.

Moreover, the long-term scarcity of live coral may subject adult *A. planci* to prolonged periods of starvation. Echinoderms, including sea stars and sea urchins, are known to reduce energy consumption through various physiological mechanisms under starvation conditions, such as gonadal regression and degeneration of muscular and connective tissues in the arms (Caballes et al., 2016; Wilkie and Carnevali, 2023). In the study area, where coral coverage has undergone a significant decline, adult *A. planci* have experienced chronic food deprivation, leading to atrophy and deterioration of the digestive system, thereby limiting their ability to consume large quantities of coral tissue at once. During prolonged starvation, starfish may autotomize their arms, while connective tissues undergo severe degeneration to conserve energy. These physiological changes impair the ability of *A. planci* to effectively prey on extensive coral surfaces. As a result, these adaptations significantly reduce its capacity to feed on live corals, forcing individuals to rely on more accessible CCA or algal-associated substrates as alternative nutrient sources. The heavy reliance on CCA as a food source by *A. planci* individuals confirmed for the first time that, in the study area, most *A. planci* individuals were juveniles exhibiting growth stagnation or adults experiencing prolonged starvation. These *A. planci* juveniles or starved adults may survive during the gradual recovery of coral reefs and await the next large-scale outbreaks as they mature. Therefore, analyzing the food source of *A. planci* is helpful for future monitoring and management of its population outbreaks.

5 CONCLUSION

In summary, the $\delta^{13}C$ and $\delta^{15}N$ values indicate a diverse and structured trophic relationship within the coral reef ecosystem of the southern SCS in the western Pacific Ocean. There is a continuous trophic spectrum spanning from low-level to higher-level consumers, with primary food sources including macroalgae, plankton, and OMCs. Results indicated that some corallivorous species, such as *C. ornatissimus* and *H. chrysostomus* in the study area, had altered their feeding strategies, shifting from corallivory to herbivory, highlighting their potential as indicator species for reef health monitoring. Additionally, CCA made the highest contribution as a food source for *A. planci* in this study, which indicated the first time that most of the *A. planci* in the study area were juveniles exhibiting growth stagnation or adults experiencing prolonged starvation, largely due to the replacement of coral reefs by algal dominance. Therefore, food availability may be a crucial factor in determining the incubation period of *A. planci* and plays a vital role in monitoring and managing population outbreaks. This study aims to provide fundamental isotopic evidence for characterizing trophic relationships in coral reef ecosystems of the southern SCS during the spring season, and offer new insights to support conservation and sustainable management efforts for coral reefs in the western Pacific Ocean. In this study, a mixed plankton sample was collected from the study area to analyze the food source contribution for high-TL consumers. Future studies can collect additional

plankton samples from different sites or depths to enhance the inputs of the MixSIAR model, and conduct seasonal or inter-annual sampling to verify the stability of the observed food-web patterns in the coral reef ecosystems of the SCS.

6 DATA AVAILABILITY STATEMENT

Data will be made available on request.

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Electronic supplementary material

Supplementary material (Supplementary Tables S1–S5) is available in the online version of this article at https://doi.org/10.1007/s00343-026-5389-9.