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ORIGINAL ARTICLE

The bed and board services of crinoids to their associated fauna: a case study from the Great Reef of Toliara, SW Madagascar

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Abstract
Crinoids of the Order Comatulida are renowned for harboring a remarkable diversity of symbiotic organisms within echinoderms, including polychaetes, myzostomids, gastropods, crustaceans, brittle stars, or fish. Crinoids provide essential services to their symbionts, such as shelter, access to food resources, mating areas, nesting grounds, and nurseries. Symbionts within crinoids developed a variety of strategies, including foraging in the arm ambulacral grooves, preying upon other symbionts, living within galls, or accessing suspended food particles from the water column. In this work, we focused on the Great Reef of Toliara, where we collected specimens from seven crinoid species. Among the 84 crinoids examined, a total of 285 symbiotic organisms were retrieved. These symbionts were either moving freely on their host or found within cysts. Stable isotope analyses of carbon and nitrogen for both hosts and symbionts have shown that (a) all crinoids shared a common trophic niche; (b) a community-based approach indicated that crinoids initiated trophic networks primarily based on suspended particulate organic matter; (c) non-specific symbionts exhibited consistent dietary preferences regardless of their host; (d) myzostomids inhabiting cysts were found to feed on their host tissues; and (e) free-moving symbionts displayed divergent trophic niches linked to their predatory, kleptoparasitic, or filter-feeding behaviors. This research underscores the role of crinoids, particularly comatulid species, as key components of tropical ecosystems in the Western Indian Ocean, inhabited by a hidden biodiversity with complex trophic networks. Their intricate morphology accommodates a range of feeding strategies, supporting a diverse associated fauna.

Keywords Symbiosis · Trophic ecology · Crinoids · Stable isotopes · Echinoderms

Introduction

The order Comatulida, a group of echinoderms encompassing organisms called crinoids or feather stars, is known to harbor the highest diversity of associated fauna among echinoderms, including polychaetes, myzostomids, gastropods, crustaceans, brittle stars, and fish (Deheyn et al., 2006; Eeckhaut & Lanterbecq, 2005; Huang et al., 2005; Lanterbecq et al., 2010; Mekhova et al., 2015; Morton & Mladenov, 1992; Zmarzly, 1984). Numerous symbiotic species have developed a long evolutionary history with their host, and some associations are known as far as from the Paleozoic, with already highly specific symbioses that are visible through the presence of pits, secondary swellings, overgrowths, or galls in the fossil records (e.g., Baumiller, 1990; Lanterbecq et al., 2010; Thomka & Brett, 2021). Indo-Pacific shallow-water members of the Order Comatulida have been shown to host a diverse cryptofauna in the Red Sea (Fishelson, 1974), the Marshall Islands (Zmarzly, 1984), Vietnam (Mekhova & Britayev, 2012), Hong Kong (Morton & Mladenov, 1992), the Ryukyu Islands (Huang et al., 2005), the Great Barrier Reef (Fabricius & Dale, 1993; Potts, 1915), Papua-New-Guinea (Deheyn et al., 2006), and Indonesia (Virgili et al., 2020). In the Western Indian Ocean, only the crinoids from South Africa have been investigated (Hempson & Griffiths, 2008).

These close associations between crinoids and obligatory symbionts have driven the recognition of host-specific

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semiochemical or visual cues, as seen in crabs or snapping shrimps living with crinoids (Eeckhaut et al., 1998; Vanden-Spiegel et al., 1998; Caulier et al., 2022). These recognitions patterns have also been shown in other echinoderms, such as the snapping shrimps (Brasseur et al., 2018) or the pea crabs (Jossart et al., 2020) living with sea urchins or harlequin crabs living with sea cucumbers (Caulier et al., 2013).

Some of these symbionts closely live on their host during their whole adult life cycle while other non-specialized species may simply occur opportunistically (Britayev et al., 1999). In obligatory symbioses, multiple hosts switches can occur either between hosts from the same species or from different species (Caulier et al., 2012; Dgebuadze et al., 2012; Fishelson, 1974; Lanterbecq et al., 2010; Mekhova et al., 2015; Zmarzly, 1984). Benefits provided by the hosts to the symbionts are numerous and include a shelter and an access to food, as well as an access to mating areas, to nesting grounds or to nursery areas. Particularly, trophic advantages of the symbionts in crinoid-associated organisms are related to the specific morphology of the hosts, where food is gathered in the arm ambulacral grooves toward the mouth, allowing symbionts to divert a part of the food captured by the host. Other symbiotic species may not rely on the host as a food provider, but rather hide between the arms and prey on other symbiotic organisms living on the same host. On the other hand, some parasites also pass their life cycle in galls or cysts grown on crinoid tissues (Eeckhaut & Lanterbecq, 2005; Summers et al., 2014), while free-moving ectocommensals are often mimetic showing similar colors to the surface of the crinoid (Caulier et al., 2022; Eeckhaut & Lanterbecq, 2005; Virgili et al., 2020).

As a consequence of the symbiotic diversity and the respective trophic ecology of the symbionts, the food web associated to the crinoid host can be complex and involve different feeding strategies and interactions within the community. Such trophic relationships can be explored using a stable isotopes approach, which has a long history as a powerful tool allowing the assessment of trophic ecology of animals, and especially in symbiotic interactions (Ferrier-Pagès & Leal, 2019).

Crinoids from Madagascar are accounting for 26 species, out of which only six are known to occur in the Great Reef of Toliara (Humes & Ho, 1970; Lanterbecq & Eeckhaut, 2003; Marshall & Rowe, 1981). On this reef, crinoids belong to Comatulidae with *Capillaster multiradiatus* (Linnaeus, 1758), *Comanthus wahlbergii* (Müller, 1843), and *Phanogenia distincta* (Carpenter, 1888), Colobometridae with *Oligometra serripinna* (Carpenter, 1881), Tropiometridae with *Tropiometra carinata* (Lamarck, 1816), and Mariametridae with *Stephanometra indica* (Smith, 1876).

In this study, we explore the richness and the trophic diversity of the symbiotic fauna hosted by the crinoids found on the Great Reef of Toliara (GRT) in SW Madagascar. Specifically, we assess (a) the diversity of crinoids on the GRT, (b) the diversity of the symbiotic fauna at the scale of the reef compared to other Indo-Pacific areas, (c) the specificity of symbiotic communities for each crinoid specie , (d) the differentiation of trophic niches among symbionts in relation to their diversity and their trophic relationships with the host, and (e) the potential existence of a link between symbiotic diversity and trophic diversity with host characteristics (morphology, ecology, or behavior). The trophic diversity of the symbiotic fauna is assessed using the isotopic niche approach, considered as a proxy of the trophic niche (Newsome et al., 2007). Stable isotopes have already been used previously in ecological studies by our team on some host-symbiont associations in diverse taxa such as ophiuroids (Fourgon et al., 2006), holothurians (Caulier et al., 2014), scleractinian corals (Terrana et al., 2016), sea urchins (Brasseur et al., 2018), or antipatharian corals (Terrana et al., 2019).

Material and methods

Sampling

The study was carried out on the Great Reef of Toliara (GRT, SW Madagascar). The GRT is a barrier reef of around 18 km separated by the coast by two passes. It has the particularity to be bordered by the mouth of two rivers (the Fiherenana in the north, the Onilahy in the south) which are carrying loads of sediment particles during wet seasons (Andréfouët et al., 2013). The reef has been reported to have an average loss of 65% of coral habitat between 1962 and 2011, with a chronic pressure of fisherman gleaning on reef flats with destructive tools (Andréfouët et al., 2013). A total of 12 dives were performed on the external slopes of the northern and southern extremities of the reef, as well as in the lagoon, between 5 and 40 m depth (Fig. 1).

The crinoids were found either hidden in the rocky substrate with a few arms standing in the water, fully exposed or lying on top of whip black corals. Each crinoid was removed and placed in individual zipped plastic bags to avoid losing symbiotic organisms. Back in the laboratory, each crinoid was placed in an individual tank filled with sea water and the presence of ectosymbionts was carefully checked by eyes and under a stereomicroscope. To remove mimetic symbionts, each crinoid was quickly placed in a zipped bag filled with 30% ethanol and shaken for a few seconds. All the organisms were then immediately rinsed with sea water and separated. The endosymbiotic associated fauna was retrieved by dissecting the crinoids under a stereomicroscope. The presence of cysts containing myzostomids (Annelida: Myzostomida) was carefully checked in order to collect these symbionts. Suspended particulate organic

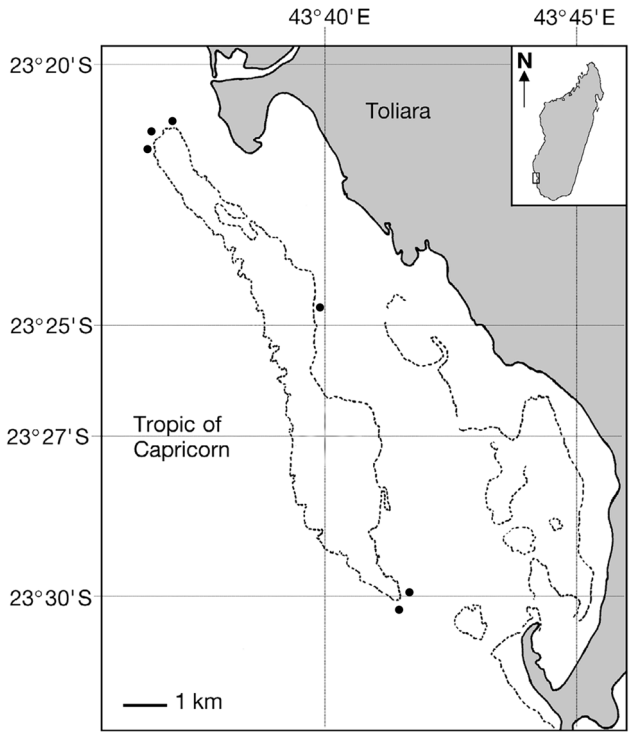

Fig. 1 Map of the study area showing the Great Reef of Toliara (dotted line) in SW Madagascar. Black dots represent the sampling areas

matter (SPOM) was accumulated by filtering 3 L of sea water on a pre-combusted 47 mm GF/F filter ($n = 10$).

Diversity, richness, and specificity assessments of crinoid and their symbiotic community

The symbionts were identified at various degrees of taxonomic levels based on the expertise of the authors about myzostomids, crustaceans, and echinoderms (see Fig. 2 for some examples). To assess the diversity and richness of the crinoid-associated fauna, two approaches were used. The first was to consider each host crinoid species and its symbiotic species as a whole single community. To characterize this single community, three parameters were calculated. The first is the overall species richness which represents the total number of host species and symbiotic species. To consider the frequency of the occurrence of each symbiotic species for all the hosts, the Shannon–Wiener index was calculated. This index, also called Shannon entropy, quantifies the uncertainty in predicting the species identity of an individual within a given community. It weighs each species according to its frequency and has the advantage of favoring neither rare nor common species disproportionately. The Gini–Simpson index was also calculated (Guiasu et al., 2012). This index represents an equitability: it is the probability that two individuals randomly chosen in a community belong to the same species and will reflect the dominance of a species within a community. The closer it is to 1, the higher is the chance to belong to the same species. Then, the second approach is to consider these three parameters for each host separately in order to compare the diversity of their associated fauna. Because the two indexes are nonlinear, differences between them cannot be directly compared as small differences in index values may result in high differences in terms of species number. Therefore, these indexes were converted in their respective effective number of species (Jost, 2006) which are obtained by calculating the exponential value of the Shannon–Wiener index for the latter, and by the formula $1/(1-x)$ for the Gini–Simpson index, where x represents the latter. This conversion allows to compare communities in terms of species richness.

Finally, the specificity of each symbiosis based on the density of the symbionts was assessed using the Rohde index (Rohde, 1980) for groups higher than six specimens. This index varies from 0 to 1; the degree of specificity increases as the index is close to 1. Species associated to only one host species will have an index of 1, while symbionts inhabiting several host species will have a lower index depending of host species number.

Stable isotope analysis

All the samples (crinoids and symbionts) were dried at 60 °C for at least 72 h. For the crinoids, only the arms were used, while symbionts were analyzed as a whole due to their minute size. Only the most numerous symbionts with a minimum size allowing the retrieval of a sufficient amount of material for an individual measure in the mass spectrometer were considered. They were ground into a homogenous powder using a mortar and pestle. Each sample was subdivided into two parts, of which one was acidified during 24–48 h in order to remove the carbonates, then rinsed with distilled water and re-dried. Crinoids were acidified by direct addition of single drops of HCl (37%) until the end of the effervescence reaction, rinsed and re-dried, while symbionts were exposed to fuming HCl (37%). The acidified samples were used for carbon stable isotope analysis, while the non-acidified samples were used for nitrogen stable isotope analysis. Isotopic and elemental measurements were performed in triplicates with an Optima mass spectrometer (Micromass, UK) coupled to a C–N–S elemental analyzer (Carlo Erba, Italy). Carbon and nitrogen isotope ratios were expressed as δ values (‰) using ammonium sulfate IAEA-N1 ($\delta^{15}N = 0.4 \pm 0.2$‰; mean ± SD) and sucrose IAEA-C6 ($\delta^{13}C = -10.8 \pm 0.3$‰; mean ± SD) as certified reference materials for nitrogen and carbon, respectively. These references are both calibrated against the international isotopic references Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. Standard deviations on multibatch


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◂**Fig. 2** Examples of crinoids and symbionts collected in this study: **a** *Cenometra bella*. **b** *Dichrometra flagellata* **c** *Comanthus wahlbergii* **d** *Dichrometra flagellata*. **e** Detailed view of a crinoid mouth, where symbionts often gather. **f** *Endomyzostoma* sp. **g** *Ceratocarcinus spinosus*. **h** *Synalpheus stimpsoni*. **i** *Allogalathea elegans.* **j** *Pontoniopsis comanthi*. **k** *Paradyte crinoidicola*. **l** *Myzostoma polycyclus.* Scales: a–d: 10 cm; e–l: 5 mm

replicate measurements were ± 0.2‰ for carbon and ± 0.1‰ for nitrogen.

Data treatment and statistics

Two approaches were used for data analyses. The first considers all the symbiotic fauna and the host crinoid species as a single community living on the reef. Means of the isotopic values of carbon and nitrogen were plotted with their standard deviations. Isotopic niches were assessed using the package SIBER v.2.1.5 (Stable Isotope Bayesian Ellipses in Jackson et al., 2011). Core isotopic niches, representing 40% of the data, were plotted, and the overlaps between each species' niche were calculated. Areas of the ellipses associated to each population were also estimated using Bayesian modeling (SEA_B; 10^5 iterations). The Bayesian analysis considers variability efficiently and provides a distribution of solutions rather than a single value, allowing that error estimates as well as pairwise comparisons. Model solutions were presented using credibility intervals of probability density function distributions. Direct pairwise comparisons were performed and were considered meaningful when probability of occurrence (i.e., number of model solution) exceeded 95%. The second approach considers each crinoid species with their own associated organisms as a unique community. This method allows to evaluate (a) if the trophic diversity associated with each crinoid is depending on the symbiotic diversity and (b) if symbionts are displaying different feeding strategies depending on the host species, as some of them are not species-specific. To evaluate these questions, mean isotopic values of each crinoid and symbiont are plotted for each community and convex-hull areas are evaluated, compared, and discussed. All the analyses and graphs were obtained in R software (R Development Core Team, 2022).

Results

Crinoid diversity and abundance

A total of 84 crinoids was collected during the survey. They belong to four families and seven species (Supplementary Information, Table 1), out of which the family Comatulidae was the most represented (67%, $n = 55$). *Phanogenia distincta* (Carpenter, 1888) was the most abundant crinoid (40%, $n = 33$), followed by *Cenometra bella* (Hartlaub, 1890) (17%, $n = 14$) and *Comanthus wahlbergii* (Müller, 1843) (16%, $n = 13$). Less than 10 individuals were collected for the remaining species *Capillaster multiradiatus* (Linnaeus, 1758), *Dichrometra flagellata* (Müller, 1843), *Dichrometra palmata* (Müller, 1843), and *Tropiometra carinata* (Lamarck, 1816) (Supplementary Information, Table 1). The overall Shannon–Wiener index for the crinoids was 1.66 with an effective number of species of 5.27. The overall Gini–Simpson index was 0.76 with an effective number of species of 4.21.

Associated fauna diversity and richness

A total of 285 symbiotic organisms was retrieved out of 76 crinoids from all the species, representing 90.5% of all the collected crinoids. For four species of crinoids, all the individuals were inhabited by at least one organism (*C. multiradiatus*, *C. wahlbergii*, *D. flagellata*, and *D. palmata*).

Among all the symbiotic organisms, crustaceans were the most represented (64.7%, $n = 185$), followed by annelids (32.2%, $n = 92$) and gastropods (2.8%, $n = 8$). More specifically, myzostomids and isopods were the most abundant (Supplementary Information, Table 2) and the most numerous on a single host: a maximum of six myzostomids *Endomyzostoma* sp. were recorded on a single specimen of *P. distincta* (Supplementary Information, Table 1). The maximum specific richness was observed for *C. wahlbergii* (Comatulidae) while the minimum was observed for *D. palmata* (Supplementary Information, Table 1).

The overall species richness of the symbiotic organisms was 16. The Shannon–Weaver index was 2.44, representing 11.47 effective species while the Gini–Simpson index was 0.90, representing 1.12 effective species. When considering the symbiont diversity for each crinoid species separately, *P. distincta* had the highest species richness with 14 symbiotic species while *D. palmata* had the smallest with three symbiotic species (Supplementary Information, Table 1). The Shannon–Wiener diversity index and the corresponding number of effective species was similar between *C. multiradiatus* (1.98 and 7.24, respectively), *C. wahlbergii* (2.01 and 7.46, respectively), and *P. distincta* (1.98 and 7.24, respectively). The index was the lowest for *D. flagellata* (1.16) and *D. palmata* (0.86) (Supplementary Information, Table 1). The Gini–Simpson index was the highest and lowest for the same crinoids as well (Supplementary Information, Table 1).

The specificity of the symbiosis was the highest in *Endomyzostoma* sp. and *Myzostoma polycyclus* ($S = 0.94$), *Synalpheus* sp. ($S = 0.93$), and *Synalpheus stimpsoni* ($S = 0.86$, Supplementary Information, Table 2). All these symbionts only inhabit the comatulidae *C. wahlbergii* and *P. distincta* (Supplementary Information, Table 2). The most opportunistic symbiont was *Paradyte crinoidicola* as it was found on all the crinoid species collected in this

study ($S = 0.45$). Among symbiotic species whose number was lower than six, *Ceratocarcinus spinosus* crabs were only found on comatulidae crinoids (a heterosexual pair on *P. distincta* and a single male on *C. multiradiatus*, Supplementary Information, Table 2). All the gastropods (*Mucronalia capillastericola*, *Mucronalia* sp. and *Melanella* sp.) were only found on comatulidae crinoids.

Symbionts localization on hosts

Only the myzostomids *Endomyzostoma* sp. were endosymbiotic: they were always found in cysts in the oral surface, next to the ambulacral grooves (Fig. 6). Among ectosymbiotic organisms, the myzostomids *M. nigromaculatum* and *M. polycyclus* were found free living on the host on the oral and aboral sides of the arms, and on the oral and proximal surfaces of the pinnules. Polychaete worms *P. crinoidicola* were found on every part of the crinoids on the oral and aboral sides of the calyx, cirri, arms, and pinnules (Fig. 6). Squat lobsters *Allogalathea elegans* were found on cirri or along the aboral side of the arm base, as well as the crabs *C. spinosus* (Fig. 6). The two species of *Synalpheus* shrimps were always located next to the center of the calyx or the oral side of the arm base, often hiding below the latter. In contrary, the two other mimetic shrimp species *Periclimenes* sp. and *Pontoniopsis comanthi* were found along the arms or pinnules. Copepods were either moving on the arms, pinnules, and calyx or attached by their antennae. Amphipods and isopods were free swimming on the arms and pinnules. Finally, gastropods were always found on the arms and pinnules with their proboscis inside the host tegument.

Stable isotopes analyses

Overall, values of $\delta^{13}C$ ranged between $-21‰$ and $-18.9‰$ for the symbionts and $-20.2‰$ and $-18.5‰$ for the crinoids (Fig. 3). Values of $\delta^{15}N‰$ ranged between 4.6 and 6.8‰ for the symbionts and 5.3‰ and 6.7‰ for the crinoids (Fig. 3). Means were significantly different for both stable isotopes between the groups (ANOVA, p-value < 0.001). Results of Tukey multiple comparisons are displayed as letters in Fig. 3b, c. Among the symbionts, the myzostomid *Endomyzostoma* sp. had a significantly different $\delta^{13}C$ mean from all the other symbionts, except for *Allogalathea elegans* (Fig. 3b); while its $\delta^{15}N$ mean was significantly different from all the other symbionts, except for *Pontoniopsis comanthi* (Fig. 3c). Among the crinoids, all the species had both similar $\delta^{13}C$ and $\delta^{15}N$ mean values. When comparing the symbionts with the hosts, all $\delta^{13}C$ mean values were not significantly different except for the myzostomids *Endomyzostoma* sp. that had a significantly different mean from *Dichrometra palmata* (Fig. 3a). Regarding $\delta^{13}C$ mean values, *Endomyzostoma* sp. mean value was similar to *D. palmata* and *D. flagellata* only (Fig. 3c).

For the isotopic niches represented by the ellipses (Fig. 4), all crinoids were considered as a single community since they share the same feeding behavior and did not show statistical differences in their isotopic values. The symbionts *Ceratocarcinus* were removed because of their sample size ($n = 3$). Isotopic niche areas of the crinoids and their symbionts ranged from 1.364 to 3.38‰^{2} (SEA, Table 1). The polychaetes *Paradyte crinoidicola* show the largest niche area, while the myzostomids *Endomyzostoma* sp. show the smallest one (Table 1). Ellipses overlaps of the core isotopic niches are given in Table 2. The largest overlap of the core isotopic niches occurs between *Synalpheus stimpsoni* and *Paradyte crinoidicola*, while the core isotopic niche of *Endomyzostoma* sp. does not overlap any other niche.

The community-based approach is considering seven different communities represented by every crinoid species (seven species) along with all their own symbionts, regardless of their taxonomic status. In the case of *Tropiometra carinata*, no isotopic values for symbiotic species were retrieved, but the values for the crinoid hosts are given. In this way, each community encompasses all the crinoid individuals with all the symbionts found on them for which stable isotope compositions were retrieved. Mean values (when several individuals were available for analysis) are shown in Fig. 5 along with centroids for each community. When considering the centroids of each of the community isotopic niches (Fig. 5), the variability in $\delta^{13}C$ was 1.4‰ (min. $-18.8‰$, max. $-20.2‰$) and the variability in $\delta^{15}N$ was 1.5‰ (min. 4.8‰, max. 6.3‰). Regarding $\delta^{13}C$, they all fall within the variation range of the SPOM (Fig. 5).

Discussion

Crinoid diversity and abundance

The four crinoid families collected here, namely Comatulidae, Colobometridae, Mariametridae, and Tropiometridae, were already collected in the past on the GRT (Lanterbecq & Eeckhaut, 2003; Marshall & Rowe, 1981). However, three species found in this study are new records for the GRT: *Dichrometra flagellata, Dichrometra palmata*, and *Cenometra bella,* the latter being a new record for Madagascar as well. On the other hand, *Oligometra serripinna* and *Stephanometra indica*, recorded, respectively, by Marshall and Rowe (1981) and Lanterbecq and Eeckhaut (2003), were not found during this study. Together, these data bring the known crinoid diversity found in Toliara to nine species from four families, and 27 species for Madagascar. However, it is not possible to establish the crinoid total species richness for the GRT based on the data of this

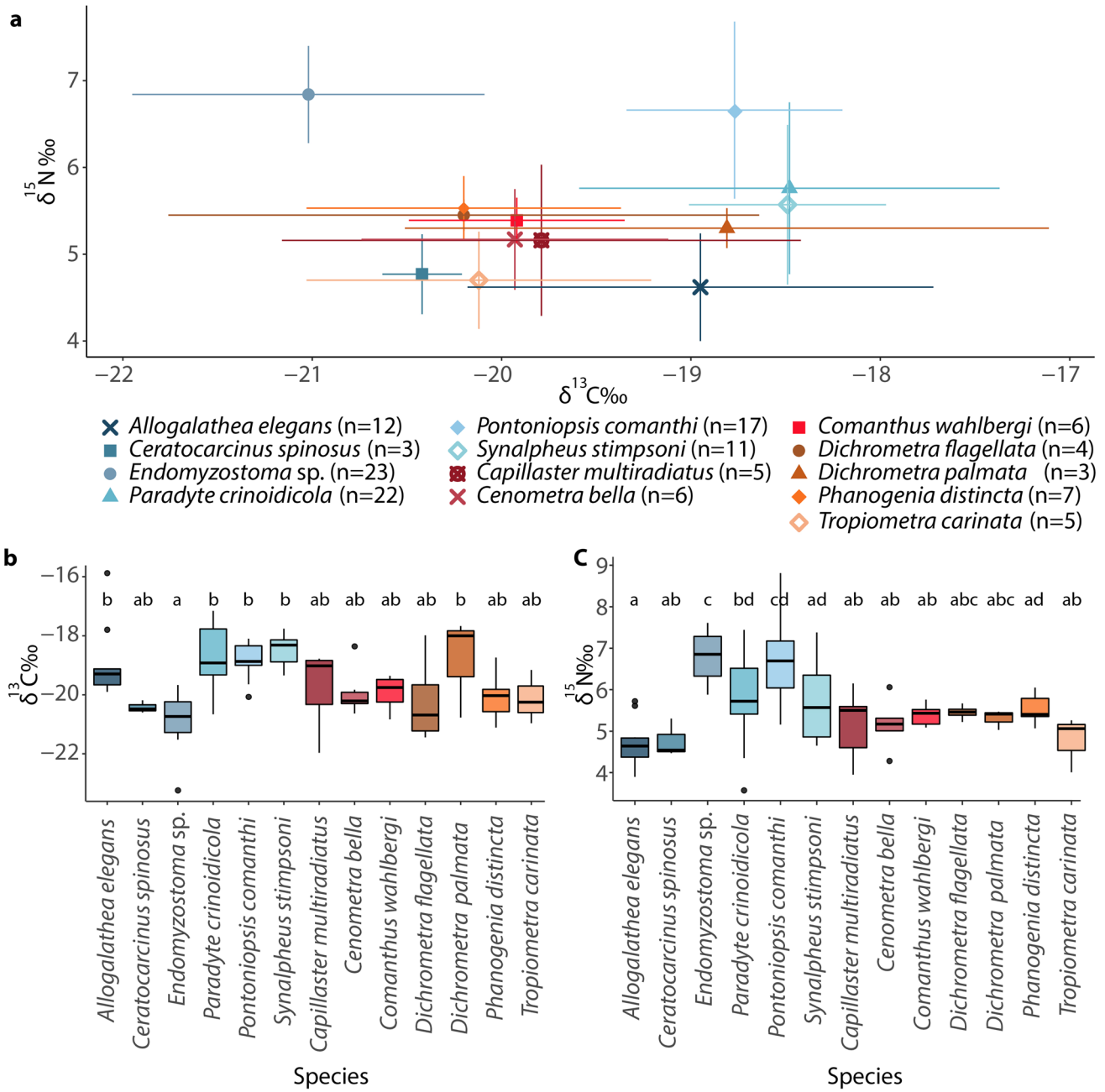

Fig. 3 **a** Mean values (±SD) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of the symbionts (in blue shades) and crinoid hosts (in red shades). **b** Boxplots of the $\delta^{13}C$ values (‰) for all the species with statistical pairwise comparisons displayed as letters. **c** Boxplots of the $\delta^{15}N$ values (‰) for all the species with statistical pairwise comparisons displayed as letters

study, as the methodology was not intended to collect a maximum of crinoid species. Still, the diversity is important when compared with the surrounding islands, as nine species of crinoids (out of which three are undetermined) have been recorded in the French Iles Eparses surrounding Madagascar (four species in Europa, SW Madagascar; six species in Juan de Nova, W Madagascar, and three species in the Glorieuses, NE Madagascar; Conand et al., 2016).

To make a thorough and significant comparison of species diversity and richness across locations, a standardized sampling protocol is mandatory. In addition, the intensity of sampling effort significantly impacts measures of richness and endemism (e.g., Cardoso et al., 2024), as this effort tends to be concentrated in areas easy to access, resulting in a skewed sampling of the environmental conditions where species occur (see for instance Table 3 for

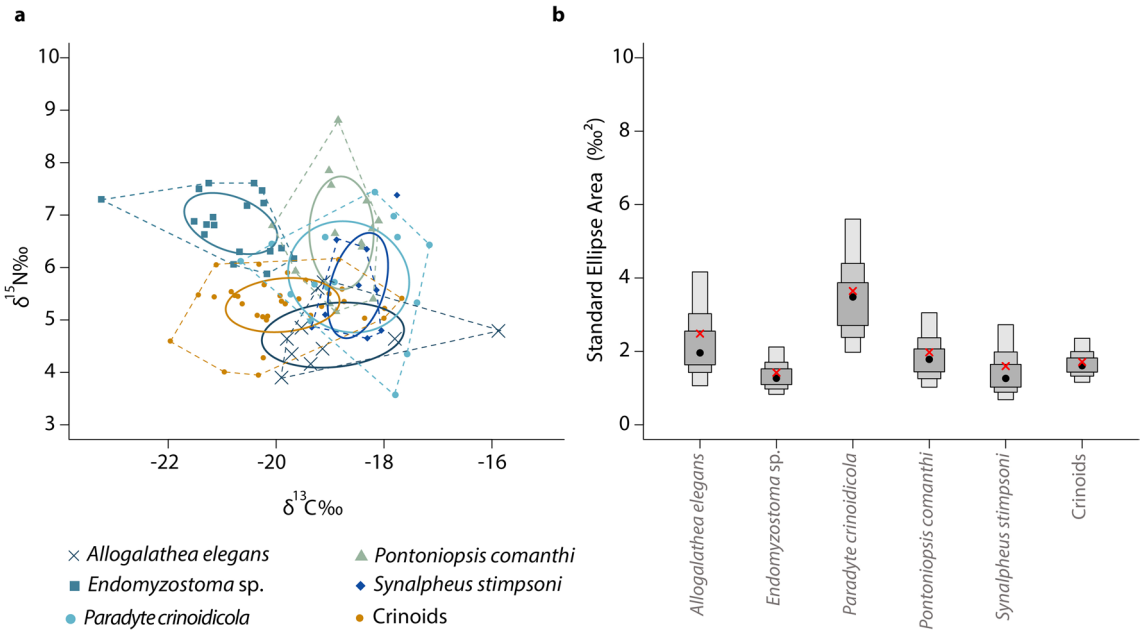

Fig. 4 **a** Core isotopic niches of the symbionts and the crinoid hosts represented by the standard ellipse areas (SEA,‰.^{2}). Each ellipse encompasses 40% of the data. All the ellipses are overlapping, except the one of the symbionts *Endomyzostoma* sp. **b** Estimates of the SEA for each species based on Bayesian inference. The boxplots represent the posterior probability distributions of model estimations of SEA (SEA_B). The boxes are the 50, 75, and 95% credibility interval. The mode of each distribution is shown by a black dot, while the red cross represents the SEA_C which is the value corrected for small sample size (n < 30)

Table 1 Areas of convex hulls (TA,‰^{2}) and the standard ellipses (SEA,‰^{2})

	Allogalathea elegans	*Endomyzostoma* sp.	*Paradyte crinoidicola*	*Pontoniopsis comanthi*	*Synalpheus stimpsoni*
TA	3.53	3.30	6.93	4.25	2.52
SEA	2.21	1.34	3.38	1.82	1.40

comparisons between number of crinoid species found and sampling sizes, and the number of symbiotic species associated with them). Therefore, some precautions are needed to minimize site-selection bias, such as the use of systematic site-selection schemes; maximizing sampling area; calculating biodiversity measures cumulatively across plots; and use of biodiversity measures that are less sensitive to rare species, such as the effective number of species (Mentges et al., 2021). It is even more difficult when aiming at specific clades where species can harbor a wide variety of behaviors, from nocturnal to diurnal, to cryptic or mimetic, such as crinoids, thus increasing the difficulty of the sampling efforts, since a significant proportion of crinoids is nocturnal and hide during the day under coral rubble or rocks (Zmarzly, 1984). Without such precautions, it is difficult to determine if a diversity gradient is existing across the Indian Ocean when looking at published data. To date, 20 species have been recorded along the South-east coast of Africa (Clark, 1911), 27 species in Madagascar (Lanterbecq & Eeckhaut, 2003; Marshall & Rowe, 1981 this study), and 39 species in India and its surroundings (Clark, 1909, 1912, 1932). In the Eastern Indo-Pacific, 54 crinoid species inhabit the

Table 2 Overlaps (‰^{2}) of the core isotopic niches of each species

	Allogalathea elegans	*Endomyzostoma* sp.	*Paradyte crinoidicola*	*Pontoniopsis comanthi*	*Synalpheus stimpsoni*	Crinoids
Allogalathea elegans	–	–	–	–	–	–
Endomyzostoma sp.	0.00	–	-	–	–	–
Paradyte crinoidicola	0.68	0.00	-	–	–	–
Pontoniopsis comanthi	0.00	0.00	1.20	–	–	–
Synalpheus stimpsoni	0.47	0.00	1.59	0.51	–	–
Crinoids	0.42	0.00	0.53	0.00	0.10	–

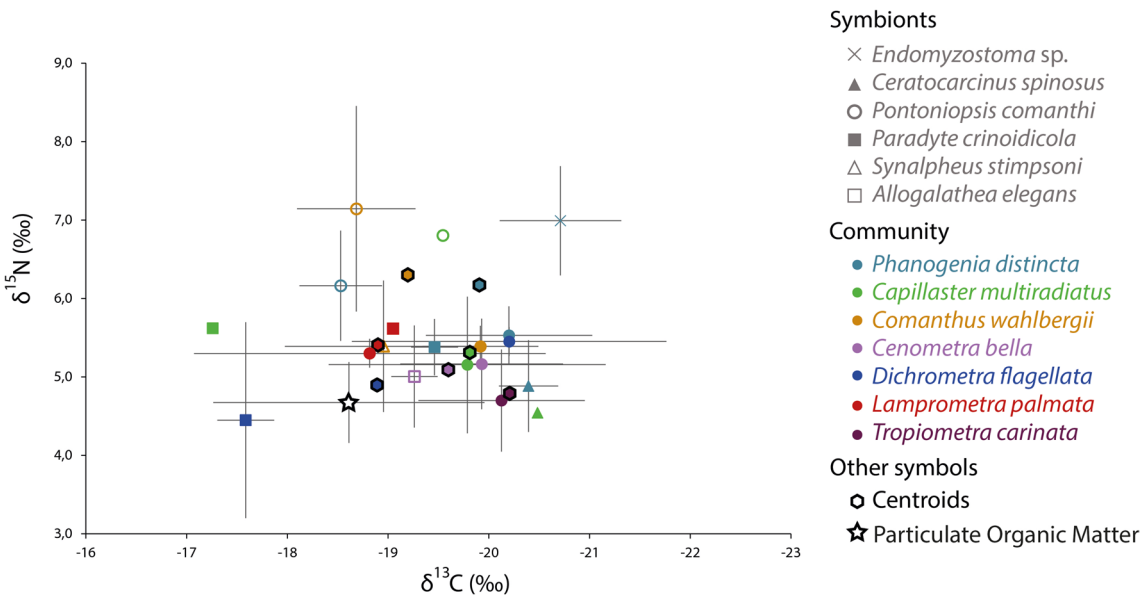

Fig. 5 Community-based approach of the host-symbiont complex between crinoids and their associated fauna. Each color represents a crinoid species with its associated fauna. The latter is composed of different species which are represented by a different symbol. Centroids of each communities (hexagons) are also plotted. Particulate organic matter is represented by the star. Mean values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) with standard deviation are given when available

Table 3 Number of symbiotic species found on comatulid crinoids previously recorded in the Indo-Pacific. Updated from Britayev and Mekhova (2011)

Number of crinoid species	Crinoid sample size	Number of symbiotic species	Location	Reference
4	97	18	Marshall Islands (Enewetak Atoll)	Zmarzly (1984)
1	23	7	Hong Kong, China	Morton and Mladenov (1992)
43	1114	46	Great Barrier Reef, Australia	Fabricius and Dale (1993)
1	42	11	Taiwan	Huang et al., (2005)
33	203	70	Nhatrang Bay, Vietnam	Britayev and Mekhova (2011)
2	25	14	Maldive Islands	Tchesunov (1989)
25	141	47	Papua New Guinea	Deheyn et al., (2006)
39	90	70	Bangka Islands, Indonesia	Virgili et al., (2020)
7	84	20–25	Great Reef of Toliara, Madagascar	This study

shallow-water reefs of Lizard Island, Australia (Messing, 1998); 44 species of crinoids were found in Papua New Guinea (Deheyn et al., 2006; Messing, 1998); 33 were collected in Nhatrang Bay, Vietnam (Britayev & Mekhova, 2011); 39 species belonging to six families were observed in Bangka Island in North Sulawesi, Indonesia (Virgili et al., 2020); and in the isolated Guam and the Commonwealth of the Northern Mariana Islands, a total of 21 species from six families have been recorded (Kirkendale & Messing, 2003). In any case, future studies on biodiversity assessments should emphasizes the need on standardized procedures.

Associated fauna

Fifteen taxa have been determined to specific level and four to higher taxonomic levels (amphipods, isopods, and copepods). Because it is likely that the latter taxa correspond to different species, it can be assumed that the total number of species associated as symbiont to the seven crinoid species collected in this study reach a minimum of 20–25 species. As highlighted by Britayev and Mekova (2011), the observed diversity of the symbionts is closely depending of the taxonomic expertise of the researchers, but also the coverage of host species, the adequate distribution of sampled specimens among species of hosts, and the sampling efforts

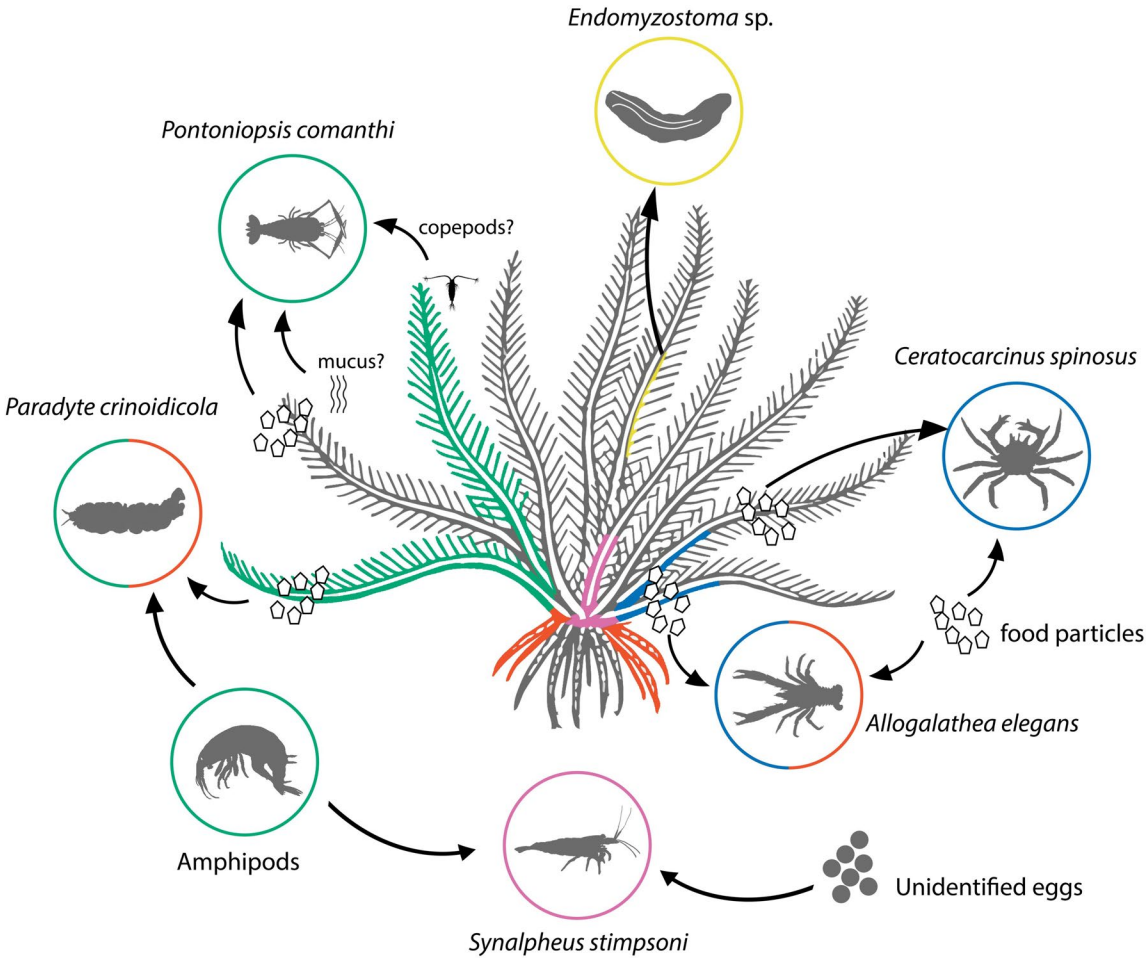

Fig. 6 Summary of the trophic relationships existing between comatulid crinoids and their associated fauna, along with the common positions of the symbionts on the host. The figure was constructed based on the isotopic results of this study as well as the position of the symbionts on their hosts when they were collected. The black arrows represent the food-consumer link and are interpreted as "*is eaten by*". Color legend: green – moving freely on arms; yellow – living on cysts next to ambulacral grooves; blue – living at the base of the arms on aboral side; pink – living next to the center of the calyx and the basal section of the arms on the oral side; orange – moving on the cirri

including a good location coverage. Given these considerations, the comparison with crinoid symbiotic species that have been previously listed in different locations in the Indo-Pacific is shown in Table 3. In our study, the diversity of the symbionts reached a number of species which is comparable to other locations where sampling size for crinoids has been similar (i.e., 18 symbionts species for 97 specimens of nine crinoid species, Marshall Islands, Zmarzly, 1984). To date, the highest diversity of crinoid-associated fauna described is in Nhatran Bay in Vietnam, which might even be higher as suggested by species accumulation curves that did not reach an asymptote (Britayev & Mekhova, 2011). This suggests that new symbiotic species or more diverse associations might still be found with crinoids.

Additionally, the probable existence of taxonomically cryptic species may also lead to the underestimation of the actual number of symbiont species, as some symbionts which are very similar morphologically can be highly specialized in specific ecological niches, such as *Crinotonia attenuatus* and *Crinotonia anastassiae* (Marin, 2008). On the other hand, in many studies, the identification until the species-level was not undertaken nor possible for all taxa (e.g., Deheyn et al., 2006; Fabricius & Dale, 1993; Morton & Mladenov, 1992) either because of the lack of documentation about local diversity, or the need of highly specialized taxonomists.

The crinoid *Phanogenia distincta* was the one with the highest symbiont diversity (14 different taxa), but the *H*-index was similar between all members of the Comatulidae, a family which have always been described as having a rich symbiont diversity species (e.g., Virgili et al., 2020). The host species of this study is generally cryptic during the day and is found under hard substrates. They crawl to prominent perches at dusk such as corals, sponges, or pinnacles,

where they extend their arms to feed. In addition, the arms and the pinnules, part of the feeding apparatus of the feather star, may become modified in response to local environmental parameters. In any case, host morphology may influence the availability for symbiotic species of nursery areas, access to food, ability to feed on host tissues, shelters from predators, or the ability to avoid intra- and inter-specific competition. For instance, in the genus *Comanthus,* some species are characterized by combs with a large spoon-like transverse proximal tooth (Taylor et al., 2017). These structures may retain more efficiently food particles, allowing symbionts to feed directly on them.

The high level of abundance of the symbionts on crinoids suggests that symbionts will have access to a limited set of resources provided by their host. Some authors (Deheyn et al., 2006; Fabricius & Dale, 1993) have sometimes suggested a low level of competition among crinoid symbionts. Indeed, the high abundance does not directly involve competition for space or food, as symbionts may be specialized on living on specific areas of their host. Crinoids have a complex morphology providing numerous spaces for symbionts, which may avoid each other by choosing a specific area on the host (Fig. 6). For instance, most myzostomid species move freely on their hosts, taking food from the ambulacral grooves, some others live in the digestive system where they divert the host's food as well and others live in coelomic cavities or the gonads of the host where they are supposed to eat on host's tissues or cells (Eeckhaut & Lanterbecq, 2005). In some cases, mutually exclusive competition for space can occur as in the case of the clingfish and synalpheid snapping shrimps (Huang et al., 2005) which both occur mainly on the calyx of crinoids.

In this study, myzostomids were among the most specific symbionts, occurring on only two host species. This is line with previous studies showing that myzostomids are highly specific symbiotic organisms, with rare host switch events or rare host diversity (e.g., Deheyn et al., 2006; Lanterbecq et al., 2010). This specificity was observed in the Red Sea (Fishelson, 1974), Hong Kong (Morton & Mladenov, 1992), and Vietnam (Britayev & Mekhova, 2011). The type of specificity might have been driven by geographically dependent evolutionary histories: for instance, Lanterbecq and Eeckhaut (2003) found that the crinoids *Capillaster multiradiatus* and *Tropiometra carinata* were not infested by myzostomids, although they are inhabited by these worms in other Indo-Pacific regions.

On the other hand, the most opportunistic symbiont was the polychaete *Paradyte crinoidicola*, found on all the species of crinoids investigated here. This is not surprising, since it has been demonstrated that this worm can have active host switch migration patterns (Britayev & Mekhova, 2014). Interestingly, amphipods and isopods were not found in Nhatrang Bay in Vietnam, which is one of the most extensive study on symbiotic associations of shallow-water crinoids to date (Britayev & Mekhova, 2011).

Trophic ecology

All the crinoid species of the Great Reef of Toliara shared similar $\delta^{13}C$ and $\delta^{15}N$ values, suggesting that they have similar feeding sources. Their values were consistent with animals feeding on particulate organic matter (see Frédérich et al., 2009 or Terrana et al., 2019 for isotopic surveys of organisms inhabiting the Great Reef of Toliara).

The community-based approach (Fig. 4) suggests that trophic networks of the crinoids and their associated fauna are all based on particulate organic matter at the basis, regardless of the host species, which is shown by centroids all encompassed in a variability of ~ 1‰ for both $\delta^{13}C$ and $\delta^{15}N$. This confirms that the crinoids investigated, feeding on SPOM, are starting a trophic network for symbiotic organisms (see Fig. 4). It is also showed that non-specific symbiotic organisms, found on different host species, share the same diet regardless of their host species and the associated fauna (e.g., the shrimps *S. stimpsoni* and *P. comanthi*, and the worms *P. crinoidicola*).

Nevertheless, the different symbionts showed significant different isotopic compositions for both $\delta^{13}C$ and $\delta^{15}N$ values. The myzostomids *Endomyzostoma* sp. are parasitic endosymbionts living in galls formed on crinoid arms, with dwarf males living on large females (Lanterbecq et al., 2010). They have a very limited moving capability as they spend their adult life totally enclosed in the galls (at least females). Galls have often openings allowing myzostomids to collect food particles in the ambulacral grooves of their hosts while other galls are closed suggesting that the inner myzostomids are eating host tissues. Their $\delta^{13}C$ values were not significantly different from those of their hosts; however, they showed an increase in $\delta^{15}N$ of around 2‰. It is generally considered that trophic shifts in the food chain are varying between 1.4‰ and 3.3‰ depending on the type of food (McCutchan et al., 2003). Parasites are not always enriched in nitrogen isotopes, and some studies have shown that both enriched and depleted isotopic compositions occur in parasites, depending on the life cycle and the type of tissue they feed on (see for instance Baillon et al., 2014). The myzostomids were also the symbionts with the lowest ellipse area, which was not superposed to any other. These results mean that their diet is very specific and different from other symbiotic species found on the same hosts and we assume that this species feeds on host tissues; otherwise, their ellipse area would be expected to be similar to their host.

The squat lobster *Allogalathea elegans* and the crab *Ceratocarcinus spinosus* presented similar $\delta^{15}N$ and $\delta^{13}C$ values which were not significantly different from their hosts. There was also an overlap between the trophic niche of the

squat lobsters and the one of the crinoids, suggesting similar food sources between hosts and symbionts. To date, there is no data available for the feeding behavior of the crab *C. spinosus*, while the squat lobster *A. elegans* has previously been presumed as feeding on the mucous secretions of the hosts and catching detritus particles in Fishelson (1974), but no detailed experiments were given. Both crustaceans were found on cirri or along the aboral side of the arm base, the last position suggesting that they are able to feed in the ambulacral grooves of the crinoids, therefore sharing the same food. The ingestion of host mucous might be an indirect consequence of stealing food on host's arms.

The shrimp *Synalpheus stimpsoni* and the polychaete worm *Paradyte crinoidicola* had similar $\delta^{13}C$ and $\delta^{15}N$ values, with the trophic niche of the shrimps almost entirely included in the one of the worms. The shrimps had a $\delta^{13}C$ composition shifted of around 1.5‰ compared to their host, and their trophic niche given by the standard ellipse was almost completely separated from the one of the crinoids, suggesting that they feed on different food sources. Indeed, the examination of the gut content of the shrimps showed the presence of unidentified eggs and entire amphipods, as well as bacteria (even if it is not possible to determine if the bacteria found are those living in the guts of the shrimps). This suggests that they are active predators feeding on other symbionts living on crinoid arms. This is consistent with Van Den Spiegel et al. (1998) who showed that snapping shrimps were grazing around the calyx, which is also the location were shrimps were mostly retrieved in this study. On the other hand, the worms had the highest standard ellipse area, partly overlapping the niche of the crinoids, and the mean $\delta^{13}C$ values were different from the values of the crinoids of around 1.5‰. Brought together, these results suggest that the polychaetes have a diversified diet that may include both preys found on the hosts and food gathered in the ambulacral grooves. An aggressive intra-specific behavior and competition cannot be excluded as well that would shape food availability for these predators (Britayev, 1991). Here, the worms were found on all parts of the crinoids, and they are known to be mobile symbionts with active host switch, which might also influence their isotopic ellipse area.

The shrimps *Pontoniopsis comanthi* showed slight enrichments of both isotopes compared to their hosts (~ 1‰ in $\delta^{13}C$ and ~ 1–1.5‰ in $\delta^{15}N$). In addition, their standard ellipse representing the trophic niche was completely separated from the one of the crinoids. These enrichments are not enough to consider a shift in trophic position, if using the traditional values used in trophic relationships studies (McCutchan et al., 2003). Both morphological features of *P. comanthi* and comatulid hosts support the hypothesis of a feeding strategy based on a food source from host ambulacral grooves. The shrimps possess chelae with spatulate dactylus that could help them in collecting food (Marin, 2006), while species from the Comatulidae are characterized by the inability to completely cover their ambulacral grooves due to the lack of ambulacral plates and reduced lappets, which may facilitate the access to the food for the shrimps (Fabricius & Dale, 1993). Virgili et al. (2020) mostly found *P. comanthi* on comatulid hosts in Bangka Islands, suggesting that these shrimps show a host preference facilitating their access to food sources. However, if the shrimps were strictly feeding on food coming from ambulacral grooves, then the same $\delta^{13}C$ and $\delta^{15}N$ values and trophic niches would be expected. The slight enrichments seen in this study could be explained by looking at the behavior of closely related species. Indeed, in the Red Sea, one relative of this species sharing the same hosts, *Periclimenes tenuis*, has been observed collecting food, feeding on mucus but also on copepods living on the host (Fishelson, 1974). It could then be assumed that *P. comanthi* is also opportunistic and feed on available preys, such as copepods. In this study, copepods were also found on same hosts than *P. comanthi*, suggesting that they could also be used as food source by the shrimps.

Conclusions

This study is a new demonstration that crinoids, and especially comatulid species, are major components of tropical ecosystems in the Western Indian Ocean that supports a hidden biodiversity and start trophic networks. They provide different food sources to their associated fauna, either through their ambulacral grooves where food is gathered, or by being inhabited by potential small preys such as amphipods. Crinoids are also used as shelter, where symbionts can safely graze, prey, and feed. The diversity of the symbionts found in comatulid hosts is also probably facilitated by the inability of these crinoids to completely close their ambulacral grooves, thus exposing themselves to kleptoparasitic species which find an easy access to food sources. Brought together, all these characteristics will start a complex trophic structure, based on particulate organic matter, but where trophic niches would be more diversified along with an increased symbiont diversity (*i.e.,* convex hulls increase but stay in the same isotopic space). The diversification of the associated fauna on a single host tends to increase and complexify the trophic structure associated with this host, through the presence of predators (Fig. 6). These different feeding habits and strategies allow the presence of a rich associated fauna, where competition and predation are important factors shaping species diversity and abundance.

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Author contributions All authors participated in the conception of this study. NL and IE collected samples, NL, GL and LT compiled the data; LT analyzed the data and wrote the manuscript; LT, GL and IE reviewed the analyses and the manuscript. All authors contributed to the draft and gave final approval for publication.

Data availability The isotopic datasets generated and/or analyzed during the current study are available online: https://doi.org/10.5281/zenodo.10972757.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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