



Dining on corals: stable isotope evidence for close trophic connection between gall crabs (Cryptochiridae) and their stony coral hosts

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Received: 6 April 2023 / Accepted: 7 November 2023
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Abstract

The exact nature of the relationship between symbiont fauna and their hosts is often unclear, but knowing more about these intricate ecological interactions is vital to understand the trophic positions of host-associated fauna, and can aid in accurate constructions of food-webs on coral reefs. Scleractinian corals are hosts to hundreds of symbiont taxa, including fish and many invertebrate species. Some of these associated fauna are beneficial to their coral host(s), whereas other taxa can have detrimental effects, yet their impact is often difficult to determine. Coral-dwelling gall crabs (Cryptochiridae) are obligate, often host-specific, symbionts of scleractinian corals but the nature of this relationship is still under debate. Three Atlantic gall crab species (*Kroppcarcinus siderastreicola*, *Opeccarcinus hypostegus* and *Troglocarcinus corallicola*) and their coral hosts' tissue/mucus were collected from reefs in Guadeloupe. Stable carbon and nitrogen isotope values were measured for 57 crabs inhabiting host coral colonies belonging to seven different coral species (although only 27 colonies from five coral species were collected), alongside other potential food sources (epilithic algal matrix, plankton and particulate organic matter). The carbon and nitrogen isotope values of gall crabs relative to those of their respective coral host(s) and other possible food sources showed that coral tissue/mucus was the main food source for the crabs. The results of the mixing models further supported this finding, suggesting that corals are responsible for 40–70% of the crabs' diet. In *T. corallicola*, the isotopic signature differed significantly between sexes, possibly caused by the high sexual dimorphism observed in this species. Here we showed that Atlantic gall crabs mainly dine on coral tissue and/or mucus excreted by their coral hosts, highlighting their nutritional dependence on their host. However, since coral mucus is continuously exuded by scleractinians, hence the energetic or metabolic drain for corals is expected to be minimal. Gall crabs depend on their coral hosts for settlement cues as larvae, for habitat as adults and - highlighted by this study - for food, essential for their subsistence. This obligate dependence on their hosts for all parts of their life makes them extremely vulnerable to reef degradation, and underlines the importance in understanding the exact nature of a relationship between symbiont and coral host.

Keywords Caribbean · Coral-associated fauna · Scleractinia · Symbiosis · Trophic food-web

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1 Introduction

Coral reefs are one of the most diverse, but also one of the most threatened, ecosystems on the planet. Many of the species inhabiting reefs are poorly known; scientific research at a global scale focuses on species with high economic value or on large and charismatic vertebrates (Clark and May 2002; Ressurreição et al. 2011; Wilson et al. 2007). Numerically, the most important species on reefs are invertebrates, particularly nematodes, crustaceans and molluscs, many of which await scientific description, or - based on species richness estimates - even await discovery. Hence, our current understanding of reef diversity is likely a gross underestimation (Fisher et al. 2015). Due to coral reef decline and lack of knowledge of marine invertebrates, many species are at risk of disappearing before we fully understand the impact and role they play in the ecosystem (Bravo et al. 2021; Stella et al. 2011). Of the currently described marine invertebrates that are known to inhabit stony corals, over half have an obligate symbiotic relationship with their hosts, meaning that their survival is dependent on their hosts' survival (Bravo et al. 2021). In addition, the nature of that relationship is often poorly understood (Boxshall and Hayes 2019; Stella et al. 2011), however, the necessity to derive nutrients from corals has been hypothesised to have been at the origin of the selection for coral-crustacean symbiotic relationships (Simon-Blecher et al. 1999).

Knowledge on the trophic ecology of symbiotic species can increase our understanding of these heterogeneous species interactions and elucidate the impact that the symbiont may have on its host (De Grave et al. 2021; González-Ortegón et al. 2022). Previous studies have shown that symbionts are able to: feed on the same or similar food source as their hosts (Kennedy et al. 2001); absorb different food sources (Caulier et al. 2014; Terrana et al. 2019), and even occupy a higher trophic level than their hosts due to food selection (Cabanellas-Reboredo et al. 2010); steal food from their hosts, *i.e.* kleptoparasitism (Ingram et al. 2017); feed on the host's tissues (D'Ambra et al. 2015; Goedknecht et al. 2018; Ross and Newman 1995); or even shift from one type of relationship with their host to another depending on the life stage of the symbiont (Gonçalves et al. 2021).

Information on the type of interaction between symbiont and host is also useful in the estimation of energy transfer from one trophic level to another. Cryptobenthic reef fishes, for example, were shown to contribute significantly to reef trophodynamics, due to having a broad range of dietary preferences and being a food source that many other fish species depend on, cycling energy from microscopic prey to larger consumers (Brandl et al. 2018;

Depczynski and Bellwood 2003). More insights into the trophic dynamics provided by small coral-associated invertebrate taxa could greatly enhance our understanding of complex coral reef food webs.

Coral-dwelling gall crabs (Cryptochiridae) are a prime example of obligate symbionts of stony corals, and the nature of said relationship is still under debate. Gall crabs have been classified as parasites (Simon-Blecher et al. 1999), commensals (Carricart-Ganivet et al. 2004; Kropp 1986), or with the neutral term symbionts (Castro 2015; van der Meij 2014). The designation as parasites stems from studies reporting that the crabs' nutrition consisted mainly of coral mucus, therefore contributing to the localised degradation of the host and impaired growth (Simon-Blecher and Achituv 1997; Simon-Blecher et al. 1999). Using *Kroppcarcinus siderastreicola* as model species, gall crabs have also been suggested to negatively impact the growth of the coral host, *Siderastrea stellata* (Nogueira et al. 2014). Other studies suggested a commensal relationship whereby gall crabs were described as filter feeders (Potts 1915) or deposit feeders (Abelson et al. 1991), taking advantage of the shape of their galls or chambers in the host coral and ingesting the particles that accumulate in them. Carricart-Ganivet et al. (2004) in turn suggested that gall crabs maintain pruned gardens of filamentous algae in the openings of their burrows to aid in their feeding.

Cryptochirids inhabit dwellings in their coral hosts. While males can also be found free-roaming on the surface of corals, females are thought to never leave their host after settlement. They are either physically trapped, not being able to leave their burrows, or their large egg pouches hamper their mobility. Some gall crabs inhabit shallow depressions (e.g. *Pseudocryptochirus viridis*), but the majority of the species inhabit pits, tunnels or galls in their coral host (van der Meij 2012; Wei et al. 2013, see Fig. S2). The galls inhabited by *Hapalocarcinus marsupialis* s.l. and *Pseudohapalocarcinus ransoni* enclose the crabs, effectively imprisoning them (Bähr et al. 2021). There is also a strong sexual dimorphism in cryptochirids, with females being considerably larger than males in most species (Kropp and Manning 1987). The mating system of cryptochirids has been dubbed as 'pure-search polygynandry of sedentary females' by Baeza and Thiel (2007), but it is more commonly referred to as 'visiting mating system' (Asakura 2009; van der Meij 2014). In this system, males visit females inhabiting separate dwellings for mating. Whilst males can be found inhabiting dwellings, they can also regularly be seen roaming around on corals (Fig. S3), which would allow access to more food sources compared to female crabs.

Three species of gall crabs are recognised in the Caribbean: *Troglocarcinus corallicola* Verrill, 1908; *Opecarcinus hypostegus* (Shaw and Hopkins 1977); and *Kroppcarcinus siderastreicola* Badaró, Neves, Castro & Johnsson, 2012.

These three species vary in size and degree of host-specificity (Kropp and Manning 1987; van der Meij 2014). *Opecarcinus hypostegus* shows strong host-specificity and is strictly associated with Agariciidae corals, just like *Kroppcarcinus siderastreicola* that solely associates with Siderastreidae and *Stephanocoenia intersepta* corals. *Troglocarcinus corallicola* is the only generalist species in the Cryptochiridae and associates with a wide range of coral families, but does not associate with the hosts of the other two Caribbean cryptochirid species (van der Meij 2014). A crescentic dwelling opening is characteristic for shallow-water Atlantic Cryptochiridae; however, in plate-forming Agariciidae tunnels or canopy-like dwellings, created by *O. hypostegus*, are often observed (Klompaker et al. 2016, Fig. S2).

In recent years numerous studies have explored various aspects of the natural history of these diminutive crabs (< 1 cm in size) (Bähr et al. 2021; Terrana et al. 2016; van der Meij 2022; van Tienderen and van der Meij 2016); however, their diet and the nature of the relationship with their hosts remain unclear. In order to have a more detailed insight into the relationship between crabs and corals, we decided to measure and compare the isotopic compositions of the crabs as well as that of all their potential food sources. A better understanding of the nature of the relationship between gall crabs and their coral hosts will allow us to infer the ecological role of gall crabs in the ecosystem, their fate in light of local and global coral reef threats, as well as the possible effects they may have on their coral hosts. It also contributes to a wider understanding of trophic dynamics in coral reef environments, and the estimation of more accurate coral reef food webs.

2 Material & methods

2.1 Field work

Samples were collected from a fringing reef off Port-Louis (Guadeloupe, Lesser Antilles, Caribbean; 16°24'37.76"N, 61°32'6.49"W) at a depth ranging from 7–9 m. A total of 57 gall crab specimens (23 males, 34 females, of which 15 were ovigerous), 27 coral pieces with tissue/mucus, plankton, and Epilithic Algal Matrix (EAM) (for an explanation on EAM see Wilson et al. 2003). Samples were collected whilst scuba-diving on two separate days (19th and 25th of May 2021) from the same location at approximately 11:00 AM, local time, on both days. Surface seawater (60 L) for Particulate Organic Matter (POM) was also sampled at the same time of sampling. We collected *K. siderastreicola* from *Siderastrea siderea* and *Stephanocoenia intersepta*; *O. hypostegus* from *Agaricia humilis* and *Agaricia lamarcki* (but no coral samples from *A. lamarcki* were obtained); and *T. corallicola* from *Montastraea cavernosa*, *Orbicella faveolata*,

and *Pseudodiploria strigosa* (but no coral samples from *O. faveolata* were obtained). Coral-crab pairs are linked in the data set. Corals were collected with hammer and chisel, and varied in size with the surface area ranging from 100 cm² to 250 cm². EAM was collected with an underwater vacuum pump by scraping rocks and dead coral with a metal spoon from the target corals or in their vicinity and the material pooled together. All samples were collected in zipper storage bags underwater, and subsequently stored in a cooling box, with cooling packs, for transportation to the laboratory. Plankton was collected with a 150 µm mesh attached to a rope with a collection tube at the end that was dragged from the boat at a depth of 1–2 m that performed a circular motion in the study area for a period of 10 min. Plankton material was pooled together for subsequent analysis.

2.2 Stable isotopic analysis

Samples were processed within 12 h of returning from the field. Gall crabs were removed from their coral hosts and cleared of debris before being put in individually labelled Eppendorf tubes without any medium. The surface of the coral specimens was scraped with a sterilised stainless steel knife in order to obtain coral tissue/mucus, which was then collected into a glass vial. Water collected from the surface was divided into six equal parts of 10 L each and then filtered using a vacuum pump system with Whatman GF/C filters (1.2 µm pore size), in order to collect POM. All samples, including EAM and plankton, were then stored in a freezer at -20 °C for a minimum of 48 h before being placed in a freeze-dryer for an additional period of 24 h.

Each sample of freeze-dried EAM, plankton, and scraped coral tissue/mucus was ground and homogenised with a pestle and mortar, which were thoroughly washed and disinfected in between samples. From the EAM and plankton material, five sub-samples from each were used for the determination of their respective stable isotope composition. Filters from the filtered seawater were soaked in 2 mol l⁻¹ of hydrochloric acid (HCl) and then fumed in an exicator with 12 mol l⁻¹ (37%) HCl in a cup to create the vapor. The decalcified filters were then cut in four equal parts, and one of these quarters was randomly chosen for the subsequent analyses and placed in tin cups. Samples of corals, crabs, EAM, and plankton also had to be decalcified prior to any further carbon measurement analyses (Jacob et al. 2005). For corals, given their naturally high concentration of carbonate material, approximately 0.1 g of the different ground-up samples was placed in glass vials and 2 mol l⁻¹ HCl was added until the reaction stopped, after which the samples were left in a shaker overnight to digest. The hydrochloric acid was then washed off the following day with deionised water and the samples were afterwards frozen and dried using a freeze-dryer for 24 h. EAM and

plankton powders were placed into pre-weighed silver cups and 2 mol l⁻¹ HCl was progressively added until it stopped reacting with the sample. Similar treatment was done for crab samples, with the difference that the extremely small crabs were not homogenised but placed in its entirety in pre-weighed silver cups. The silver cups were put in an oven dryer to dry for 24 h at a temperature of 55 °C. Decalcified coral samples for C measurements as well as non-acidified samples for N measurements were weighed into individual tin cups and folded.

Tin and silver capsules were analysed using a continuous-flow isotope-ratio mass spectrometry system (Thermo Scientific Delta V Advantage, Bremen, Germany), coupled to an elemental analyser (Thermo Scientific Flash EA2000, Bremen, Germany) at the Royal Netherlands Institute for Sea Research (NIOZ) at Texel. Isotopic ratios for our samples are reported in the 'δ' notation, expressed in ‰, relative to a reference standard (Vienna Pee Dee Belemnite (VPDB) for ¹³C and atmospheric air for ¹⁵N; noted as $R_{standard}$). The measured stable isotope values of the samples were calibrated using certified standard materials (Acetanilide, Urea and Casein) with known stable isotopic compositions analysed in the same analytical run. Every complete analytical sequence consisted of 94 analyses, 72 of which were samples, 3 blanks at the beginning and 19 certified standards distributed throughout the entire sequence. R_{sample} (¹³C/¹²C or ¹⁵N/¹⁴N ratios) was then used to infer the relative difference in isotope ratios (δ), expressed in ‰, using the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \quad (1)$$

2.3 Statistical analyses

A Multivariate Analysis of Variance (MANOVA) was used to test for differences in the isotopic signatures of δ¹³C and δ¹⁵N of the three species of gall crabs, as well as between males and females of the same species, and their supposed food sources (*i.e.* EAM, coral tissue/mucus, plankton and POM). When significant differences were found, a Tukey post-hoc test was used to determine exactly which comparisons were significant.

In order to further investigate the isotopic niche space occupied by males and females of the same gall crab species, and their potential overlap, standard ellipse areas corrected for small sample sizes (SEA_c) were used as a proxy. SEA_c (expressed in ‰²) corresponds to ellipses that encompass approximately 40% of the data. The overlap of ellipses (expressed in % of the total area occupied by both niches) was used as a proxy for niche overlap. This was inferred using Bayesian metrics implemented in the Stable Isotope Bayesian Ellipses in R (*SIBER*) package (v.2.1.7, Jackson et al. 2011).

To estimate the proportional contribution of the different food sources to the diet of the three cryptochirid species, a Bayesian mixing model implemented in the Stable Isotope Mixing Model R (*simmr*) package was used (v.0.4.5, Parnell 2021). Due to the lack of specific Trophic Discrimination Factors (TDFs) that are appropriate for symbiotic crustaceans in coral reef environments, we estimated our own TDF to use in the calculation of the mixing models. This TDF was calculated by subtracting the stable isotope values of corals from that of crabs using the specific coral-crab pairs. Separate TDFs were also inferred for the three species of gall crabs (Table S1) but for the mixing model analysis we used our generalised TDF estimated from all available data points (average ± SD: Δ¹³C = 1.5 ± 1.9‰; Δ¹⁵N = 1.6 ± 0.7‰). Moreover, we used two additional generalised TDFs for further comparison, one from McCutchan et al. (2003) (average ± SD: Δ¹³C = 0.5 ± 0.13‰; Δ¹⁵N = 2.3 ± 0.18‰) and one from Post (2002) (average ± SD: Δ¹³C = 0.4 ± 1.3‰; Δ¹⁵N = 3.4 ± 1.0‰). The models were run using paired data for crabs and corals, only taking into account the crabs that were found on that species of coral.

All of the analyses were conducted in R (v.4.0.3, R Core Team 2020) and the following R packages were used for data treatment and data visualisation: *dplyr* (v.1.0.2, Wickham et al. 2020), *ggplot2* (v.3.3.5, Wickham 2016) and *ggpubr* (v.0.4.0, Kassambara 2020).

3 Results

3.1 Isotopic ratios and niches

Isotopic signatures differed significantly amongst potential food sources of the different gall crab species (MANOVA: F = 30.72, df = 7, $p < 0.001$; Fig. 1 and Table 1), with these differences being also observed when considering δ¹³C and δ¹⁵N separately (ANOVA: F = 37.42, df = 7, $p < 0.001$, and F = 27.34, df = 7, $p < 0.01$, respectively). Of these potential food sources, POM had the lowest δ¹³C values (-21.34 ± 0.67‰) but a value of δ¹⁵N comparable to that of many species of corals (3.39 ± 0.76‰ for POM versus 2.75 to 3.51 ‰ for our studied corals) and higher than the mean δ¹⁵N for all coral species (3.10 ± 0.50‰; Fig. 2). Plankton had very low δ¹³C and δ¹⁵N values (-20.07 ± 0.21‰ and 1.66 ± 0.05‰, respectively). EAM on the other hand was found to have values of δ¹³C lower than that of our studied stony corals (-16.27 ± 0.06‰), with this difference ranging from 0.23–3.84‰ depending on the species of coral in question, but it had the lowest values of δ¹⁵N of all the sampled food sources (0.50 ± 0.20‰).

For the five different coral host species, there was a wide range of isotopic ratios, but with higher δ¹³C being usually correlated with higher δ¹⁵N ratios. For *S. intersepta* and *S.*

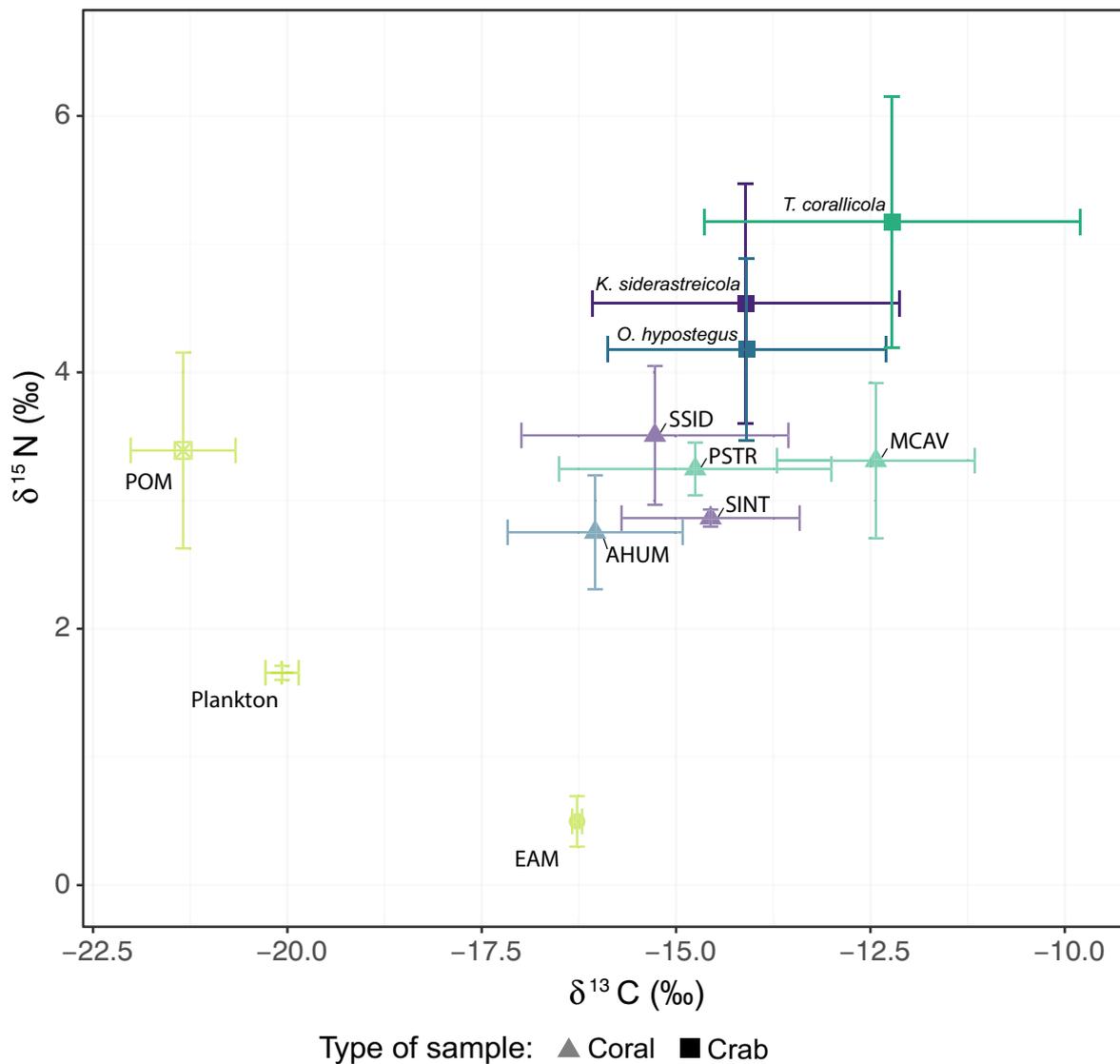


Fig. 1 Isotopic biplot of average values \pm SD (in ‰) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the three studied gall crab species (*K. siderastreicola*, *O. hypostegus* and *T. corallicola*) and their potential food sources. Gall crab spe-

cies (squares) and their associated coral hosts (triangles) are depicted with the same colour (abbreviations are listed in Table 1)

siderea, both hosts to *K. siderastreicola*, there was a significant difference in the $\delta^{15}\text{N}$ values (ANOVA: $F=6.99$, $df=1$, $p=0.03$), but not in $\delta^{13}\text{C}$ values. In the case of the two corals associated with *T. corallicola* (*M. cavernosa* and *P. strigosa*), the opposite was true, with the $\delta^{13}\text{C}$ values being significantly different (ANOVA: $F=6.51$, $df=1$, $p=0.03$), but not the $\delta^{15}\text{N}$ values (Fig. 2).

The isotopic ratios of the three species of crabs were significantly different from each other (MANOVA: $F=3.58$, $df=2$, $p<0.01$). *T. corallicola* had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the other two cryptochirids (-12.22 $\delta^{13}\text{C}$ and 5.17 $\delta^{15}\text{N}$, compared to -14.11 $\delta^{13}\text{C}$ and 4.54 $\delta^{15}\text{N}$ for *K. siderastreicola*, and -14.09 $\delta^{13}\text{C}$ and 4.18 $\delta^{15}\text{N}$ for *O. hypostegus*; Table 1). *Troglocarcinus corallicola* females showed higher isotopic values

than males (Fig. 3), but no clear differences were observed between ovigerous and non-ovigerous females (Fig. S4).

The stable carbon and nitrogen isotopic compositions of all species of crabs followed, to a certain extent, the isotopic ratios of their respective coral host species (Fig. 1, and S5-S7). This was true for most crabs for the $\delta^{15}\text{N}$ values that showed a slight increase in their stable isotope values if their hosts also had higher isotope values. For the $\delta^{13}\text{C}$ values there was also a slight increase for *K. siderastreicola* specimens and a significant increase for *T. corallicola* crabs that matched the isotopic values of their coral hosts (Fig. S6). There were no noteworthy differences in the stable isotopic composition between males and females in comparison with their coral hosts (Fig. S7).

Table 1 Isotopic values for gall crabs, their scleractinian coral hosts (and their respective abbreviations), and other potential food sources

Type of sample	Species name	N	$\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	$\delta^{15}\text{N} \pm \text{SD} (\text{‰})$
Gall crab	<i>Kroppcarcinus siderastreicola</i>	20	-14.11 ± 1.97	4.54 ± 0.93
Gall crab	<i>Opecarcinus hypostegus</i>	17	-14.09 ± 1.79	4.18 ± 0.71
Gall crab	<i>Troglocarcinus corallicola</i>	20	-12.22 ± 2.42	5.17 ± 0.98
Coral	<i>Agaricia humilis</i> (AHUM)	6	-16.04 ± 1.13	2.75 ± 0.44
Coral	<i>Montastraea cavernosa</i> (MCAV)	6	-12.43 ± 1.27	3.31 ± 0.61
Coral	<i>Pseudodiploria strigosa</i> (PSTR)	5	-14.75 ± 1.75	3.25 ± 0.21
Coral	<i>Siderastrea siderea</i> (SSID)	5	-15.27 ± 1.72	3.51 ± 0.54
Coral	<i>Stephanocoenia intersepta</i> (SINT)	5	-14.56 ± 1.15	2.86 ± 0.07
EAM	Epilithic Algal Matrix (EAM)	5*	-16.27 ± 0.06	0.50 ± 0.20
Plankton	Plankton	5*	-20.07 ± 0.21	1.66 ± 0.05
POM	Particulate Organic Matter (POM)	6	-21.34 ± 0.67	3.39 ± 0.76

N: number of samples. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are the means of all measured samples \pm Standard Deviation (in ‰)

* Each sample consisted of pooled individuals or matter

Differences in stable isotope values of males and females of the three gall crab species were only significantly different amongst specimens of *T. corallicola* for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (ANOVA: $F=9.71$, $df=1$, $p<0.01$, and $F=39.29$, $df=1$, $p<0.001$, respectively; Fig. 3).

The SEA_c allowed us to make further inferences into the differences in isotopic niches of males and females (Fig. 4). In all three species males had a larger SEA_c than their female counterparts, but this difference was only significant for *T. corallicola* ($p<0.01$; Table S2 and Fig. S8). The overlap in SEA_c was largest for specimens of *K. siderastreicola*, with males and females sharing 36% of their total niche area. Female and male specimens of *O. hypostegus* shared 17% of their niche area, but there was no overlap for specimens of

T. corallicola. Differences in isotopic niche areas occupied by males and females were mostly attributed to $\delta^{15}\text{N}$ values, but for *T. corallicola* $\delta^{13}\text{C}$ values also contributed to this separation of their SEA_c .

3.2 Mixing models

The results of the different stable isotope mixing models, based on the three different TDFs, were mostly consistent with each other, highlighting that stony corals are the main food source for their respective symbiotic crabs (Fig. 5, S9 and Table S3). Given the higher degree of uncertainty observed in the models using the generalised TDFs from literature, the reported values below concern only those

Fig. 2 Box plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the potential food sources of gall crabs (abbreviations are listed in Table 1). Each colour corresponds to a different gall crab species, except for the last three sources on the right-hand side in yellow, which signifies that all species potentially feed on those food sources

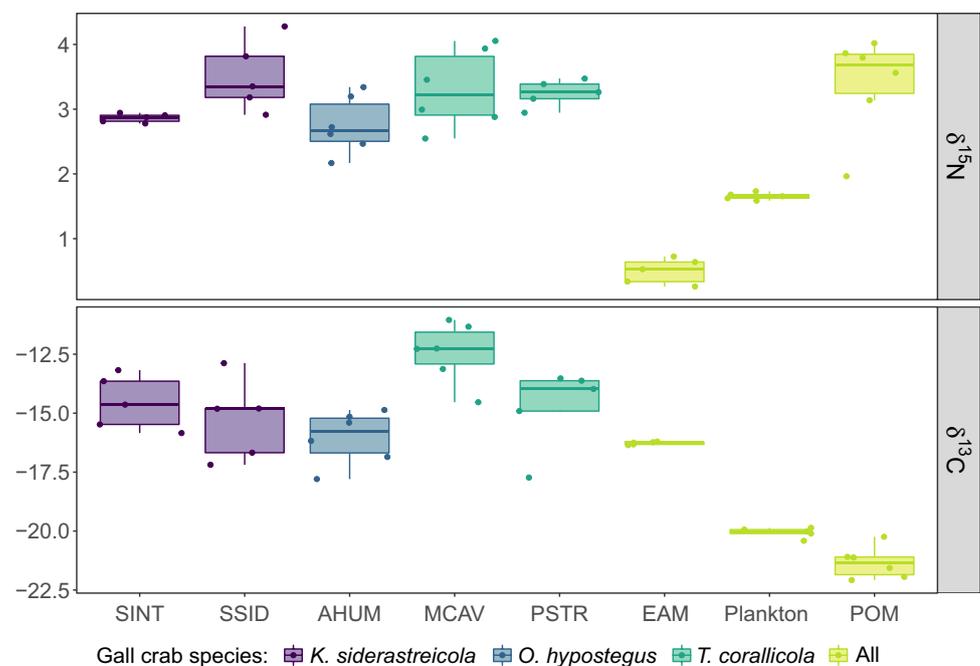
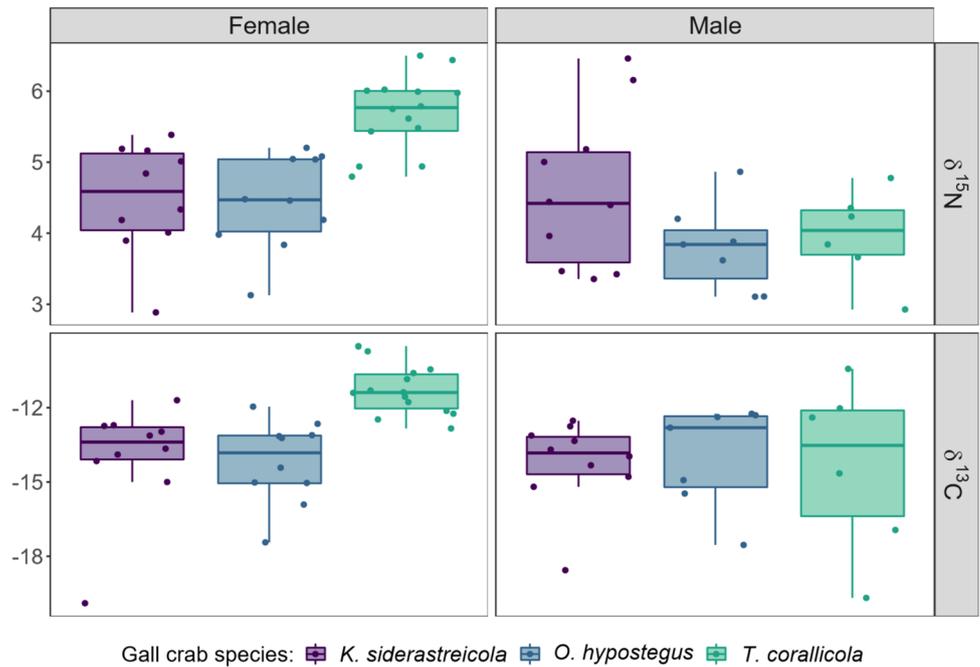


Fig. 3 Box plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the different gall crabs, divided by sex and colour coded by species



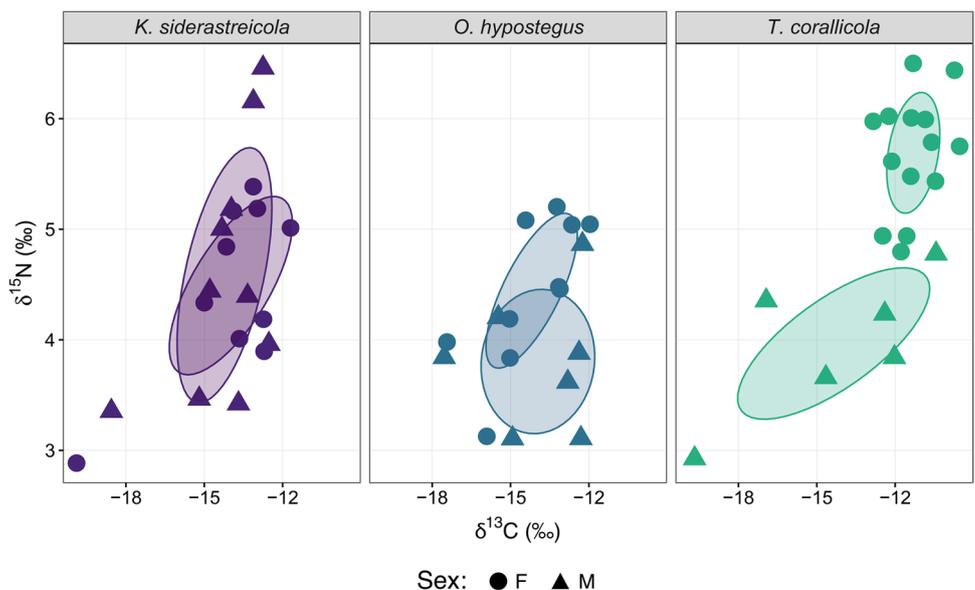
from the TDF determined in this study and based on the average difference between individual coral-crab pairs, with the remainder of the results being reported in Fig. S9 and Table S3.

Corals were estimated to be the main contributors to the diet of gall crabs, representing 41% or more of their diet (95% credibility interval, CI). The remaining food sources were also estimated to contribute to the diets of these crabs, but in more reduced quantities - below 20% each in most instances. The second most likely food source was POM, with slightly higher values than EAM (12–25% and 13–18%

CI respectively). Plankton was never suggested to contribute more than 11%.

The differences in the contributions of distinct coral species to the same gall crab species was evident for *K. siderastreicola*, where it was clear that *S. siderea* contributed a great proportion of the crab’s diet, whereas in *S. intersepta* the contribution was not as striking, with these two coral hosts differing in their contributions to the diet by as much as 9% (Fig. 5). The same was true for *T. corallicola*, where specimens associated with *M. cavernosa* and *P. strigosa* differed by 11% (Table S3).

Fig. 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots for the three studied gall crab species. Solid ellipse lines represent the corrected standard ellipse areas (SEA_c) and darker shaded areas correspond to the overlap between the isotopic niches of females (F; circles) and males (M; triangles). The plotted ellipses include 40% of the data points



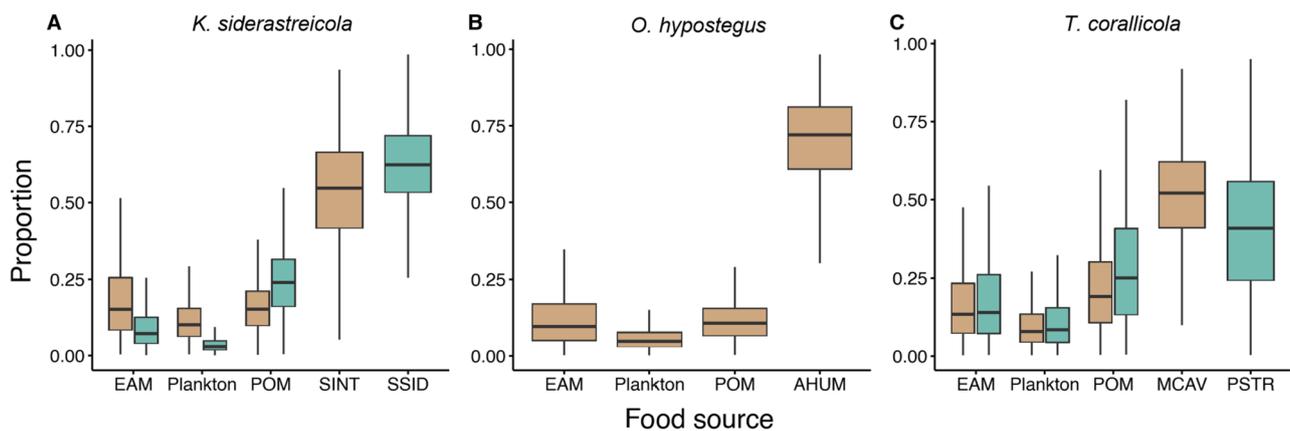


Fig. 5 Results of the estimated contribution of each potential food source, using the TDF values calculated in this study, to the diet of: **A** *K. siderastreicola*; **B** *O. hypostegus*; and **C** *T. corallicola*. The different colours on the same graph correspond to the model that was

run together with the coral of the same colour (i.e. separate models were run for the different coral species, using paired coral-crab data). Abbreviations can be found in Table 1

4 Discussion

Several studies tried to shed light on the nature of the relationship between gall crabs and their coral hosts, however the different approaches and findings have made it difficult to ascertain the exact nature of this relationship (e.g. Abelson et al. 1991; Kropp 1986; Simon-Blecher et al. 1999; Terrana et al. 2016). Using a stable isotope approach, we showed that the largest proportion of food sources contributing to the diet of three Atlantic gall crab species was coral tissue and/or mucus, corroborating that these crabs heavily rely on their coral host for sustenance. These results agree with the results of Simon-Blecher et al. (1999) who, based on carbon labelling, showed that cryptochirids inhabiting *Favites* corals in the Red Sea feed on coral mucus. The three species studied here all appear to have a very similar overall feeding strategy, despite being associated with different coral host species and showing variation in dwelling morphology (e.g. shallow dwellings *versus* long canopy-like tunnels). The observed differences in isotopic ratios across the three studied crab species were shown to be related to the different corals they settle on, which strongly suggests that they are feeding in great proportions on their particular coral hosts, as demonstrated by the results of the different mixing models.

The comparatively low contributions of POM as a food source in the mixing models suggests that the studied crabs are not filter feeders, which is in line with the findings of Kropp (1986), who demonstrated that three species of gall crabs (belonging to three separate genera), do not possess the appropriate mouth parts for filter feeding. Moreover, Scotto and Gore (1981) and Terrana et al. (2016) commented on the presence of live coral tissue in the dwellings of *T. corallicola* and galls of *Hapalocarcinus marsupialis* s.l., respectively, on which they can presumably feed. This is also

in agreement with our field observations of a male specimen of *T. corallicola* that was seen scooping coral mucus on the surface of *M. cavernosa* into a ball and then feeding on it using its chelipeds (Video S1), and previous similar observations by earlier authors (Abelson et al. 1991; Kropp 1986). According to our findings, apart from the large contribution of coral tissue/mucus to the diets of the crabs, cryptochirids potentially eat food that they can find in the vicinity of the burrows, or on the surface of their coral host (e.g. Dissolved Organic Matter (DOM), POM, detritus, microbes) to complement their diet. Moreover, gall crabs (especially free-living males) could be complementing their diet with other food sources in the vicinity of their coral hosts (e.g. EAM, plankton), also as suggested by the results of the mixing model. Simon-Blecher et al. (1999) suggested that the crabs encourage settlement of algae and fungi in their dwellings, which might serve as an additional food source, which is in line with the observations of Carricart-Ganivet et al. (2004). EAM was, however, rarely observed in the burrows, or their immediate vicinity, of the three species studied here.

We furthermore observed a significant difference between male and female specimens of *T. corallicola* in both their isotopic signatures and area of niche space occupied that was not as strongly observed in the other two species. This difference in isotopic ratios could possibly be explained by the sexual dimorphism in gall crabs, where females are bigger than their male counterparts (Kropp and Manning 1987). Whilst sexual dimorphism was observed for all three species, it was more apparent in *T. corallicola*. A positive correlation between carapace length and stable isotope values has been found in *Lissocarcinus orbicularis* Dana, 1852, Harlequin crabs, which was hypothesised to be due to a shift in food sources located at a higher trophic level as crabs grew larger (Caulier et al. 2014). It has also been shown in

species of trapeziid crabs that ovigerous females consume significantly more coral tissue/mucus (Rinkevich et al. 1991), suggesting that reproductive output can be responsible for a higher coral mucus consumption and/or a higher assimilation in the tissue due to greater metabolic needs. In a species of pinnotherid crab, *Afropinnotheres monodi* Manning, 1993, females have also exhibited a slightly higher trophic position, due to the specialised feeding on their mussel host, as opposed to the more generalist male counterparts (González-Ortegón et al. 2022). This could be observed in gall crab females of both *O. hypostegus* and *T. corallicola* and could also be an explanation for the larger niche areas occupied by males of all three species. Given the dimorphism observed in gall crabs and their high reproductive output (Bähr et al. 2021), the bigger size of these females allied to their forced confinement in the burrows, and therefore a restricted diet, can be the responsible factors for these higher isotopic values and smaller niche areas. However, no size data of the crab specimens used for the stable isotope data in this study were available. It is therefore possible that the significant differences observed in *T. corallicola*, and not in the other two species, are a result of female/male size differences (i.e. relatively large females, small males) in the specimens selected for the stable isotope analyses compared to the specimens selected for *O. hypostegus* and *K. siderastreicola* (e.g. relatively small females, large males). Overall, the observed values demonstrate that male and female crabs mostly rely on coral tissue and/or mucus for sustenance but males have a wider isotopic niche area, probably attributed to their free-roaming and access to other food sources. The number of males collected in this study was too low to run the mixing model separately on males and females to further investigate their food preferences.

Coral species can show a natural variation in stable isotope composition (Skinner et al. 2022), which might influence gall crab stable isotope compositions. Moreover, the stable isotope ratios of corals are mainly determined by their food sources; with most zooxanthellate corals capable of both auto- and heterotrophy. In scleractinian corals, ingestion of external food supplies (e.g. dissolved and particulate organic matter) represents an important source of nutrients (Houlbrèque and Ferrier-Pagès, 2009) and can be responsible for the natural variation in isotopic signatures. Here, we showed that the isotopic signatures of females and males of all three studied gall crab species tend to follow those of their coral hosts for both $\delta^{15}N$ and $\delta^{13}C$ (i.e. higher isotope values for corals results in higher values for crabs). It is important to note that these correlations were only significant (i.e. $p < 0.05$) for specimens of *T. corallicola* for $\delta^{13}C$, and that this trend was slightly negative for $\delta^{13}C$ values in both males and females of *O. hypostegus*, suggesting that the coral either supplies enough carbon to the crabs or that they obtain it elsewhere. The number of males in this study

compared to that of females was still low, so interpretations should be drawn carefully. The sometimes small number of specimens and the potential variation in chitin levels across individuals (due to having to use the entire specimens for isotopic analysis because of the small size of the crabs), which is naturally low in $\delta^{15}N$, could have resulted in some of the differences observed (Cherel et al. 2019).

Most crab species are known to be opportunistic omnivores (Lee 2015; Wang et al. 2020). It is unknown whether gall crabs could, if given the opportunity, or in the case of coral host die-off, change their food source. The now evident high nutritional dependence of gall crabs on their coral hosts highlights how vulnerable they are to coral die-off. A live specimen of *Lithoscaptus tri* was observed inhabiting a partially dead coral host in the Maldives (van der Meij 2022), and multiple live specimens of *T. corallicola* were also found in similar conditions on partially dead colonies of *M. cavernosa*, *O. faveolata* and *P. strigosa* in Guadeloupe during the course of sampling for this study (Fig. S1). These observations suggest that gall crabs might be able to complement or adjust their diet when confronted with a changing environment. However, it remains unclear how long cryptochirids are able to persist without access to their main food source of coral tissue/mucus. Moreover, their varying levels of host specificity impacts their vulnerability to reef degradation (van der Meij 2014, 2022).

Stony corals are an important source of nutrients for many different species on coral reefs. Coral mucus has been identified as an important energy carrier, capable of trapping carbon- and nitrogen-rich particles that are essential to consumers (Wild et al. 2004). The wide array of fauna that depends on them for food includes fish (Benson and Muscatine 1974), crabs (Rinkevich et al. 1991; Stimson 1990), shrimps (Patton 1994), barnacles (Achituv et al. 1997), bivalves (Goreau et al. 1970), zooplankton (Gottfried and Roman 1983; Richman et al. 1975) and even soft corals (Coffroth 1984). The isotope values obtained for the different crabs and their potential food sources, alongside the results of the mixing models, confirms that gall crabs also predominantly feed on their specific coral hosts. In this study, we could not distinguish whether the crabs feed on coral tissue or mucus, however the results of Simon-Blecher et al. (1999) revealed mucus as the most likely food source. Corals naturally produce surplus mucus as part of their sediment rejection mechanisms (Erftemeijer et al. 2012; Hubbard and Pocock 1972) and it has even been shown that this can be used to attract the presence of certain symbionts (Castro 1976; Glynn 1983; Stachowicz and Hay 1999; Stimson 1990). The ingestion of naturally produced coral mucus from the host's surface, does not necessarily result in a higher energetic cost for the host (Kropp 1986; Stimson 1990). Moreover, the presence of these gall crab symbionts, similarly to other mesograzers, can have a previously unknown positive effect, e.g. by

potentially aiding in the control of algal epibionts and algal overgrowth (Stachowicz and Hay 1999; Bravo and Tibbetts 2023), or by indirectly promoting coral host survivorship (Coen 1988). The presence of the pronounced dwellings of some species of gall crabs (e.g. the tunnels on *A. lamarcki*) can however alter the surface of the coral (Patton 1976), potentially affecting the surface flow on corals (Abelson et al. 1991; Boudier et al. 2022), but if and how much this negatively impacts the coral remains to be studied.

The feeding ecology of coral-associated invertebrates has received little attention in recent years and there is still much to be understood (Glynn and Enochs 2011). The stable isotopic analyses and mixing models used in this study have proven to be a useful tool in clarifying the diet of three Atlantic species of obligate coral-associated gall crabs. Indo-Pacific or deep-sea confamilials, however, might employ different feeding strategies, for example *H. marsupialis* s.l. creates dwellings in their coral host that completely enclose the crabs, which possibly influences their ability to feed on coral mucus (Abelson et al. 1991, but see Kropp 1986). Moreover, our increased understanding of the trophic dynamics involving gall crabs and stony corals will also allow for a more accurate calculation of trophic levels in coral reef ecosystems, with more meaningful inferences being made.

The results of the present study also highlight the need for TDFs tailored to the system/species being studied and that generalised TDFs may not provide the specificity required at non-ecosystem scale, leading to misinterpretations (Skinner et al. 2022). Our own estimated TDF and the isotopic values measured in this study can be used to infer further TDFs that could be used in similar host-symbiont systems. This does assume that the crabs are feeding almost exclusively on their coral hosts and nothing else. To our knowledge, there are only two records of fish feeding on these minute crabs (Kropp and Manning 1987; Leray et al. 2015), hence energy loops involving gall crabs appear to be (almost) closed. There are, however, gall crab byproducts (e.g. food discards, faeces, moults), which can be recycled into locally available nutrients, again highlighting the intrinsic nature of coral reef food webs.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13199-023-00968-y>.

Acknowledgements The authors are thankful to Sébastien Cordonnier for his help in the field. Further thanks goes to Irene Mognon for aiding in the transport of the material, and Ronald van Bommel and Jort Ossebaar for their help with stable isotope analyses at NIOZ. Sampling was authorised by the Direction de la Mer de Guadeloupe under Autorisation N°09/2021. Fieldwork by Henrique Bravo was funded by TREUB-maatschappij (Society for the Advancement of Research in the Tropics) and Flying Sharks. A final thank you to the three anonymous reviewers that provided comments on an earlier version of this manuscript.

Data Availability All the data used in this study are available in the supplementary material.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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