REPORT

# Evidence for trophic niche partitioning among three temperate gorgonian octocorals

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**Abstract** Trophic niche theory predicts that species in competition for a limiting resource will evolve adaptations allowing them to consume alternative resources and occupy new niche space. Trophic niche partitioning is often identified by differences in the morphology of feeding structures across species; however, these differences may not always be readily observable. Due to their constrained polyp morphology, octocorals are often viewed a single functional group that contributes to benthic-pelagic coupling by feeding opportunistically on available particles. To test the hypothesis that sympatric gorgonians share the same trophic niche, feeding selectivity of three gorgonian species (*Leptogorgia virgulata, Muricea pendula,* and *Thesea nivea)* was compared using a combination of flume experiments and stable isotope analysis. The tentacle length and polyp surface area of *L. virgulata* and *T. nivea* were also measured and compared. In flume experiments, clearance of rotifers ("typical" zooplankton) and a mixture of cultured phytoplankton indicated that *L. virgulata* and *T. nivea* fed on zooplankton and not phytoplankton. Stable isotope values for all three species are consistent with distinct trophic niches, with *M. pendula* occupying a lower trophic level. *Thesea nivea* was found to have significantly larger polyp surface area and tentacle length; however, this did not appear to explain observed trophic differences. The results of this study provide evidence for niche partitioning, but future work is required to better understand the mechanism behind this divergence.

**Keywords** Octocorals · Gorgonians · Clearance rate · Stable isotope analysis · SIBER analysis · South Atlantic Bight

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## Introduction

The niche is a central tenant of ecology that encompasses the conditions and resources required for species to survive and reproduce, and is often used to explain ecological and evolutionary patterns across ecosystems and environments (Strøm 1946; Hutchinson 1957; McGill et al. 2006). Hutchinson (1957) described this niche as a multi-dimensional hypervolume that could be visualized in Euclidian space with each axis representing a different niche component, such as a physical characteristic of the environment (e.g., temperature), a biotic resource (e.g., prey items), an abiotic resource (e.g., inorganic nutrients), or a biological interaction (e.g., competition; McGill et al. 2006; Soberón 2007). A major subset of the niche is the aggregate food resources that comprise the trophic niche of an organism. Competition for food can exert selective pressure that drives species to exploit new or different resources, leading to the evolution of new feeding traits that confer increased fitness (Grant 1968; Bridle and Jiggins 2000). Differences in the morphology of feeding structures (e.g., bird beaks) have therefore often

been used to identify trophic niche differences (Grant 1965; Gosler and Carruthers 1994).

In marine ecosystems, trophic niche partitioning is typically examined between disparate taxonomic groups that exhibit similar feeding modes, such as benthic suspension feeders. Benthic suspension feeders play an important ecological role in benthic pelagic coupling; by capturing seston, or suspended organic particles including phytoplankton, zooplankton, and detritus (a diverse mixture of non-living biological material; Duggins et al. 1989), they act as a major pathway for nutrients and energy to move from the water column to the seafloor (Dame et al. 2001; Wildish and Kristmanson 2005). Parallel to work in terrestrial habitats, morphological differences in the feeding apparatus of different benthic suspension feeders have been found to drive differences in particle capture, leading to resource partitioning among phyla (Riisgård and Larsen 2000; Coma et al. 2001; Lefebvre et al. 2009). For example, Wing and Jack (2012) found that three co-occurring mussel species with the same type of particle capture mechanism (cirral trapping) fed on similar diets, whereas species from other phyla with divergent feeding morphologies (a brachiopod, tubeworm, ascidian, and black coral) occupied different placements in the food web. Comparisons of the gross morphology of feeding structures, however, may miss critical differences in micromorphology or behavior (particle selection or rejection) that evolved to support niche partitioning within coarse morphological groupings. Few studies have looked for niche partitioning within established feeding guilds despite observed interspecific variation in food selectivity (Lefebvre et al. 2009; Wing and Jack 2012; Richoux et al. 2014). Specifically, octocorals, or soft corals, have been found to play a major role in benthic pelagic coupling (Rossi et al. 2017) and consume a variety of particle types (Ribes et al. 1998, 1999; Orejas et al. 2003; Tsounis et al. 2006), yet they are still often treated as a single functional group (Lewis 1982).

All octocorals have the same basic feeding apparatus consisting of eight pinnate tentacles used to intercept particulate food carried by ambient water flow (Lewis 1982), a trait that has led to the conclusion that most species have similar diets consisting predominantly of large (500–2000 μm) zooplankton (Leversee 1976; Lasker 1981; Lewis 1982; Sponaugle and LaBarbera 1991; Chang-Feng and Ming-Chao 1993; Gili and Coma 1998). More detailed investigations of octocoral nutrition, however, have identified other sources of food including symbiotic photosynthate (Baker et al. 2015), microzooplankton (ciliates; Orejas et al. 2003; Ribes et al. 2003; Sherwood et al. 2008), phytoplankton (diatoms, dinoflagellates; Sorokin 1991; Fabricius et al. 1995a; Ribes et al. 1999; Orejas et al. 2003; Gili et al. 2006; Tsounis et al. 2006), bacterioplankton (Farrant et al. 1987), and other POM (including detritus, mucous aggregates, and invertebrate eggs; Coffroth 1984; Ribes et al. 1999; Coma et al.

2001; Tsounis et al. 2006; Cocito et al. 2013). The consumption of these different particles is often thought to be the result of opportunistic rather than selective feeding (Ribes et al. 1999; Sherwood et al. 2008). For example, Coma et al. (2001) concluded that *Paramuricea clavata* is an opportunistic feeder even though gut content analysis showed a higher proportion of ciliates than present in the environment, suggesting a selective preference. Other studies have attributed variation in octocoral diets to differences in factors that influence particle availability, such as depth (Lasker et al. 1983; Gori et al. 2012) and substrate type (Sherwood et al. 2008). This explanation allows for observed differences in nutrition while still classifying octocorals as indiscriminatory suspension feeders.

Despite the propensity to view soft corals as opportunistic generalists, two aspects of polyp morphology have been identified as potentially playing a role in food selectivity: polyp size, and the distance between pinnules. In corals, polyp size is directly correlated with gape size; thus, differences in diet have been attributed to the ability of large-polyped corals to consume larger particles (Lewis 1982; Baker et al. 2015). Similarly, when pinnules are closer together, they can sieve smaller particles out of the water column, providing another explanation for nutritional divergence (Ribes et al. 2003; Grossowicz and Benayahu 2011). These morphological differences, however, cannot account for all observed variation in soft coral diet. Some species, for example, have been found to switch between particle types when preferred food is unavailable (Cocito et al. 2013; Leal et al. 2014). Further, three studies reported differences in the feeding of sympatric octocorals in the Indo-Pacific (Sorokin 1991), Antarctic (Orejas et al. 2003), and Mediterranean (Cocito et al. 2013) that are not explained by morphology. In these examples, octocorals inhabited environments where planktonic food was scarce, resulting in strong competition, or in nutrient rich, turbid waters where filter feeders could benefit from selective feeding by eliminating the energetic cost of regurgitating inedible or low-quality seston.

The South Atlantic Bight (SAB) off the coast of North Carolina is inhabited by 28 species of shallow water (< 40 m) octocorals, all of which lack photosynthetic symbionts and must rely solely on heterotrophy (Devictor and Morton 2010). Sixteen species contain a hard, central axis that allows substantial growth above the substratum (McFadden et al. 2010) and are thus grouped as gorgonians (a polyphyletic grouping of the suborders Halaxonia, Calaxonia, and Scleraxonia). Multi-species communities of gorgonians often dominate the hard bottom ledge habitats of the SAB, providing the potential for direct competition for particulate food; however, no previous studies have compared feeding across species in these communities (Wenner et al. 1984). We coupled controlled feeding experiments and stable isotope analysis (SIA) to investigate the ability of different

species to feed on phytoplankton and zooplankton, compare the relative size and placement of their isotopic niches, a proxy for trophic niche (Jackson et al. 2011), and assess the potential contribution of different size particles to their diet in situ.

## Materials and methods

### *Feeding experiments*

Five apical fragments, 10 cm in length, of the gorgonians *Leptogorgia virgulata* and *Thesea nivea* were collected using SCUBA for inclusion in captive feeding experiments. *Muricea pendula* was also collected; however, issues with standardized control treatments (detailed below) prevented inclusion in feeding experiments. Samples were collected from four sites off the coast of Wilmington, North Carolina (Alexander Ramsey, Dallas Rock, 23 Mile, and Dan's Spot; Online Resource 1) between November 2012 and April 2013. In the laboratory, each fragment was mounted on a ceramic tile using epoxy putty and allowed to acclimate under aquarium conditions for seven days (Sorokin 1991; Lin et al. 2002). Colony fragments were housed in a 60 L aquarium exposed to natural sunlight and equipped with a coarse filter and pump to provide circulation and aeration. Fragments were fed phytoplankton (*Chaetoceros muelleri, Isochrysis* sp. and *Tetraselmis* sp.) and rotifers (*Brachionus rotundiformis*) from culture twice a week and used in experiments within 90 days of collection. To compare feeding apparatus structure, average polyp surface area and tentacle length were estimated for both species used in the flume experiments by imaging five different colonies with a scale and tracing 10 polyps and tentacles per colony with the software ImageJ (Schneider et al. 2012). We were unable to measure polyp morphology for *M. pendula* because its polyps were obscured by large surface sclerites (Devictor and Morton 2010).

Feeding experiments were conducted in a unidirectional recirculating 20 L acrylic paddle-wheel flume with a $45 \times 10 \times 12$ cm (length x width x height) working channel. Flume speed was controlled by a Dayton gear motor (Model 2H577A) and Dart Micro-Drive II controller. Plastic inserts upstream and downstream of the paddle-wheel minimized turbulence and secondary flows within the flume (Robinson et al. 2007; Sumerel and Finelli 2014).

Two representative food sources maintained in culture were used to investigate gorgonian feeding preferences: (1) rotifers (*B. rotundiformis,* ~ 150 μm), representing active-swimming zooplankton, and (2) a mixture of three species of phytoplankton, including the diatom species *C. muelleri* (7–9 μm) and the two flagellates *Isochrysis* sp. (3–7.5 μm) and *Tetraselmis* sp. (10–14 μm). The use of cultured food sources allowed for control of the type and amount of food provided to each coral fragment across experiments, and all these plankton have been identified as food sources for gorgonians in previous studies (Sorokin 1991; Orejas et al. 2003; Ribes et al. 2003; Sun et al. 2010). Rotifers were obtained from cultures maintained by the University of North Carolina Wilmington (UNCW) Aquaculture facility in Wrightsville Beach, NC, and phytoplankton species were obtained from cultures maintained by the UNCW Shellfish Research Hatchery at the Center for Marine Science in Wilmington, NC. Rotifers were filtered through 125 μm mesh, caught on 90 μm mesh, and rinsed with sterile seawater, while phytoplankton were filtered through a 20 μm mesh to remove any larger debris (Sponaugle and LaBarbera 1991). Both food types were then re-suspended in filtered (1 μm), UV-sterilized seawater.

To determine the concentration of re-suspended rotifers and phytoplankton, two samples of each were measured using a LISST-Portable laser diffraction particle analyzer (Sequoia, Belleview, WA, USA). The average total concentration from these samples was used to calculate the volume of phytoplankton and rotifer suspension needed to reach final desired concentrations of 8 μl $L^{-1}$ for each food type, or 16 μl $L^{-1}$ total. These units (μl $L^{-1}$) were used because they account for particle size; a filter feeder has a greater chance of intercepting large particles than small particles if the same number of each is present in the water column; thus, standardizing the volume of each particle type is most appropriate. The concentration used was within the range of densities of phytoplankton and zooplankton measured in the SAB (Verity et al. 1996) and corresponds to ~ 11,000–12,000 phytoplankton cells $ml^{-1}$ and 3–5 rotifers $ml^{-1}$. Particle analyzer measurements at the beginning of each experiment confirmed that initial food concentrations were $16.88 \pm 0.99$ (mean $\pm$ SD) μl $L^{-1}$ for control treatments and $15.84 \pm 0.73$ μl $L^{-1}$ for experiment treatments.

For each experiment, the flume was filled with 20 L of filtered (1 μm), sterilized seawater that was circulated for 20 min. Prior to experimental trials, one colony fragment was starved in an isolation tank filled with aerated and filtered seawater for 24 h before being introduced to the flume system. Following fragment introduction, the water was filtered (1 μm) for another 20 min with a pump-driven system that could be added or removed from the working channel (Leversee 1976; Chang-Feng and Ming-Chao 1993). All feeding experiments were conducted using an average flow speed of 7.95 ($\pm 0.46$ std. dev.) cm $s^{-1}$, the optimal velocity for feeding of several gorgonian species (8-10 cm $s^{-1}$; (Leversee 1976; Sponaugle and LaBarbera 1991; Chang-Feng and Ming-Chao 1993; Lin et al. 2002). Flow speed was measured with an Acoustic Doppler Velocimeter (Sontek, San Diego, CA, USA). Salinity and temperature were maintained between 33 and 35 ppt and 18 and 21 °C.

Each fragment acclimated to the flow regime in the flume until its polyps were visibly extended and ready for feeding. A volume of flume water equivalent to that of the food suspensions was removed so that the total volume in the flume after adding the food mixtures would remain 20 L. The two food suspensions were slowly poured into the flume downstream of the colony and allowed to mix for five minutes before a 1 L water sample was collected. This sample was used to measure initial particle concentration in five replicate 200 ml subsamples using the particle analyzer. The colony was allowed to feed for two hours, during which time feeding was confirmed by direct observation and video recording of polyp feeding behavior (Lin et al. 2002). At the end of the experiment, another 1 L water sample was taken to determine the final food concentrations in five replicate 200 ml subsamples with the particle analyzer.

To account for particle deposition in the flume, control trials were performed for each colony. Briefly, each fragment was submerged in de-ionized water, dried overnight, covered in two layers of spray rubber coating (Plasti Dip, Blaine MN, USA), and used in a control trial. This replicated the flow regime in the flume during the experimental trial while preventing tissue sloughing from the colony. Attempts to dry and coat colonies of *M. pendula* resulted in the collapse of colony structure, preventing accurate control trials; thus, this species was excluded from flume experiments. The change in concentration of food during both the experimental and control trials was used to calculate a clearance rate (ml h$^{-1}$) for each colony, a metric which accounts for passive particle deposition and allows for comparisons between different suspension feeders and food types (Eq. 1).

$$Clearance\ rate = \left(\frac{Vol}{Time}\right) \ln \frac{(C_0)(C_{CF})}{(C_F)(C_{C0})} \tag{1}$$

*Vol* = flume volume (ml), *Time* = duration of experiment (h), $C_0$ = initial experimental particle concentration (µl L$^{-1}$), $C_{CF}$ = final control particle concentration (µl L$^{-1}$), $C_F$ = final experimental particle concentration (µl L$^{-1}$), $C_{C0}$ = initial control particle concentration (µl L$^{-1}$).

Clearance rates were standardized by the number of polyps in each colony as well as the total polyp surface area of each colony to facilitate comparisons between fragments. The total number of polyps in each colony was estimated by counting the polyps in five random 1 cm branch segments and multiplying the average of these counts by total colony length (Chang-Feng and Ming-Chao 1993). The total polyp surface area of each colony fragment was estimated by multiplying the total number of polyps in the colony by the average polyp surface area of that species.

A separate clearance rate was determined for each food type by estimating the total concentration of particles in the size classes corresponding to phytoplankton (diameter of 3.38–12.7 µm) and rotifers (diameter of 78.4–152 µm). Any initial or final concentration sub-replicate that was outside the range of 1.75 SD above or below the mean was considered an outlier and excluded from clearance rate calculations. This cut-off was arbitrarily determined and provided an objective method to remove outliers.

*Stable isotope analysis*

Gorgonian branch tips, small (1–28 µm) POM, and large (> 100 µm) POM were collected for SIA from nine subtidal sites in Onslow Bay off the coast of southern North Carolina between July and October 2013 (Online Resource 1). One apical fragment 2–3 cm in length was cut with scissors from up to five different colonies of each gorgonian species found at each site (Freeman et al. 2016). *T. nivea* and *M. pendula* were found at deeper sites (24–35 m), while *L. virgulata* was more abundant in shallower sites (12–20 m) and was rare (one individual observed) or absent at deeper sites. During each site visit, small POM was sampled by collecting between 15 and 18 L of bulk water at depth using one 20 L carboy. Large POM was collected with a 0.5 m diameter, hand-towed plankton net with 100 µm mesh that was pulled for five minutes at constant swimming speed. All samples were kept on ice during transport.

Gorgonian samples were rinsed with reverse osmosis water and stored at −20 °C. Small POM was extracted from bulk water samples by filtering them through a 20 µm sieve to remove larger seston and vacuumed filtered onto pre-combusted (450 °C for 5 h) 47 mm Pall type A/E glass fiber filters (1 µm particle retention; Kürten et al. 2014) before being stored at −20 °C. Large (> 1.41 mm) debris was removed from the large POM tows by pouring the sample through a 1 mm sieve and rinsing thoroughly with sterile seawater. The POM remaining (sized 141–1,410 µm) was collected on a 64 µm sieve and stored at −20 °C.

All frozen samples were freeze-dried for 72 h. The apical 1 cm, representing 4–24 months of growth, was subsampled from each gorgonian for isotope analysis (Cary 1914; Yoshioka and Yoshioka 1991; Mistri and Ceccherelli 1994; Sherwood and Edinger 2009; Baker et al. 2013). Gorgonian and large POM samples were homogenized with a mortar and pestle, and small POM filters were cut into quarters. In order to measure both $\delta^{15}$N and $\delta^{13}$C values accurately, two subsets of each sample were prepared for analysis: one un-acidified to measure the $\delta^{15}$N value and one acidified to remove inorganic carbonates and measure the $\delta^{13}$C value of organic carbon (Jacob et al. 2005). Between 0.3 and 1.8 mg of each sample was weighed into tin capsules for the un-acidified replicates, and 0.5–2.2 mg of each sample was weighed into silver cups before being fumigated with 12 M HCl (Redding et al. 2013). To ensure all carbonates had reacted during fumigation, four extra samples (2.2–2.5 mg)

were included in each batch and tested for the presence of carbonates by dripping 10% HCl onto them and visually confirming the absence of bubble formation (Redding et al. 2013).

$^{13}$C and $^{15}$N isotope composition was analyzed using an ECS 4010 Elemental Analyzer (Costech, Valencia CA, USA) coupled to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham MA, USA) at the Stable Isotope Geochemistry Laboratory at the UNCW Center for Marine Science, Wilmington NC. International reference materials (USGS40 and USGS41) were included in each run and used for calibration of results to the international standards Vienna PeeDee Belemnite and atmospheric $N_2$. Precision was determined by repeat analysis of reference materials and was better than $\pm 0.4$‰ for both $\delta^{13}$C and $\delta^{15}$N.

*Statistical analysis*

All statistics were performed with the statistical package R (v 3.5.2; The R Core Team 2018). Differences in tentacle length and polyp surface area were determined using one-way ANOVAs, while differences in clearance rates between gorgonian species and food types were determined using two-way ANOVAs. Residuals of these models were checked for normality visually with Q-Q plots and statistically using Shapiro–Wilk tests. Homogeneity of variance was assessed with Levene's Tests.

We assessed the effect of species and site on the distribution of samples in isotopic space by calculating a dissimilarity matrix using Euclidean distances between samples and fitting a permutational multivariate analysis of variance (PERMANOVA) model with the *adonis* function in the R package vegan (Oksanen et al. 2019; Freeman et al. 2020). We controlled for variation between sites by restricting shuffling within sites during permutations by including site as strata (Naman et al. 2016; Freeman et al. 2020). A nonparametric alternative to a multivariate analysis of variance, this analysis used permutations of the data (999) to return a pseudo-*F*-statistic and p-value, and provided an estimate of dissimilarity across samples that could be attributed to each included factor (species and site) via $R^2$ values. To determine if our data met the assumptions of a PERMANOVA, we assessed multivariate homogeneity of species dispersions with the *betadisper* function in vegan.

We visualized the core isotopic niche area of each gorgonian species by plotting the standard ellipse area corrected for sample size (SEA$_C$) on a $\delta^{13}$C and $\delta^{15}$N isotopic biplot using the R package SIBER (Jackson et al. 2011; The R Core Team 2018). SEA$_C$ captures $\sim 40\%$ of the variation of bivariate data and is minimally affected by outliers. Further, the size of each species' SEA$_C$ was estimated through Bayesian inference with SIBER, allowing for robust comparison

of groups with unequal sample size (Jackson et al. 2011; Syväranta et al. 2013; Freeman et al. 2020). Significant differences in the relative placement of each group in isotopic space were determined by calculating the Euclidean distances between the centroids (means) and applying a residual permeation procedure (RPP) and Hotelling's $T^2$ Test (Turner et al. 2010). Due to potential differences in the isotopic baseline across sites, we applied these analyses to a subset of samples found at a single site (Dan's Spot) where two species (*M. pendula* and *T. nivea*) co-occurred with suitable replication ($n = 10$). To compare the isotopic niches of all three species across sites despite potential differences in isotopic baselines, we examined $\delta^{13}$C and $\delta^{15}$N values for significant linear relationships with distance from shore. $\delta^{15}$N has been found to decrease from nearshore to offshore waters both in Onslow bay (Fogel et al. 1999), and across the northwestern Atlantic in general (Oczkowski et al. 2016). If significant, these relationships were used to standardize isotope values across sites prior to isotopic niche analyses; however, we do not discuss these results in depth due to unknown differences in isotopic baselines across sites.

To directly compare the isotope values of the gorgonians to that of their potential food sources, we separated all samples into three zones: nearshore (< 30 km from shore), midshore (30–50 km from shore) and offshore (> 50 km from shore). These delineations were based on previous work that found terrestrial influence on $\delta^{15}$N values up to 30 km offshore (Fogel et al. 1999) and intrusions of gulf stream waters from 50 to 100 km offshore on the seafloor in Onslow Bay (Blanton 1971). To account for trophic discrimination (predictable increases in $\delta^{13}$C and $\delta^{15}$N up each trophic level), we applied minimum (+ 0‰ for $\delta^{13}$C, + 2.5‰ for $\delta^{15}$N) and maximum (+ 1‰ for $\delta^{13}$C, + 3.5‰ for $\delta^{15}$N) published trophic discrimination factors (TDFs) (Parnell et al. 2010; Cocito et al. 2013) to the isotope values of each food source. Direct comparison of food source and consumer isotope values incorporating theoretical TDFs is an established alternative to mixing models when the assumptions of the models cannot be met (Cocito et al. 2013; Leal et al. 2014). Specifically, mixing models require sampling of all food sources (Stock et al. 2018), and thus are not robust when working with organisms such as filter feeders that may consume a large diversity of different particles that are challenging to separate and measure with SIA.

## Results

*Feeding experiments*

Mean tentacle length and polyp surface area were lower in *L. virgulata* ($1.2 \pm 0.0$ mm and $1.7 \pm 0.1$ mm$^2$) compared to *T. nivea* ($1.4 \pm 0.1$ mm and $2.4 \pm 0.1$ mm$^2$; $\pm$ SE). The residuals of tentacle length (Shapiro–Wilk Test, $W = 0.96$, p $= 0.82$)

and polyp surface area ($W = 0.96$, $p = 0.80$) models were normally distributed, and both datasets were homoscedastic (Levene's Test, tentacle length: $F = 0.26$, $p = 0.63$; surface area: $F = 1.95$, $p = 0.20$). ANOVA results indicated that *L. virgulata* had significantly shorter tentacles ($F = 9.917$; $p = 0.013$) and smaller polyp surface area ($F = 25.47$; $p = 0.001$) than *T. nivea*.

Mean clearance rates for zooplankton were positive when standardized by both number of polyps or total polyp surface area, with *L virgulata* clearing $2.3 \pm 0.9$ ml h$^{-1}$ polyp$^{-1}$ and $136.9 \pm 54.8$ ml h$^{-1}$ cm$^{-2}$ and *T. nivea* clearing $4.9 \pm 1.0$ ml h$^{-1}$ polyp$^{-1}$ and $208.0 \pm 44.1$ ml h$^{-1}$ cm$^{-2}$ ($\pm$ SE; Fig. 1). In contrast, phytoplankton clearance rates were negative, with *L. virgulata* clearing an average of $-0.2 \pm 0.2$ ml h$^{-1}$ polyp$^{-1}$ and $-10.2 \pm 9.6$ ml h$^{-1}$ cm$^{-2}$ and *T. nivea* clearing $-0.5 \pm 0.4$ ml h$^{-1}$ polyp$^{-1}$ and $-23.1 \pm 16.0$ ml h$^{-1}$ cm$^{-2}$ (Fig. 1). Negative clearance rates may occur if the final concentration of particles in the experimental treatments exceeds the initial concentration, possibly due to excretion of waste during the experiment. The residuals of clearance rate measurements were normally distributed (Shapiro–Wilk Test, $W = 0.94$, $p = 0.27$), and data were homoscedastic (Levene's Test, $F = 4.13$, $p = 0.06$). Both species fed significantly more on rotifers than phytoplankton
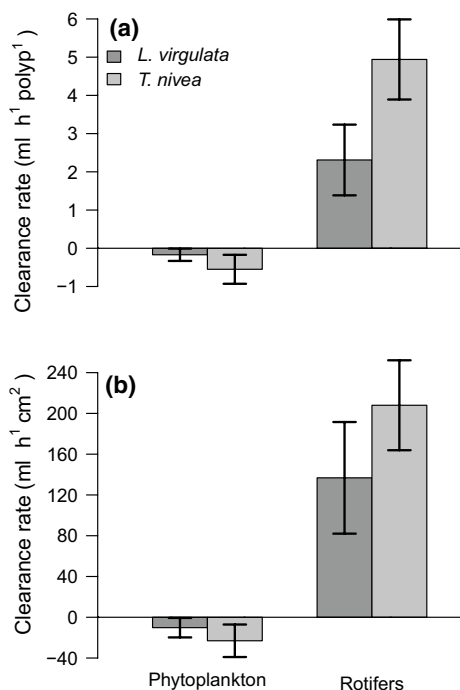


**Fig. 1** Clearance rates (mean ± SE) of phytoplankton and zooplankton in flume experiments by gorgonian corals *L. virgulata* (dark grey, n = 5) and *T. nivea* (light grey, n = 5) standardized by (**A**) number of polyps and (**B**) polyp surface area. Both species fed significantly more on rotifers than phytoplankton ($p < 0.001$), but there were no significant differences between species ($p > 0.13$)

when clearance rates were standardized by number of polyps (two-way ANOVA, $F = 29.93$, $p < 0.0001$; Fig. 1A) and polyp surface area (two-way ANOVA, $F = 27.02$, $p < 0.0001$; Fig. 1B); however, there was no significant difference between species (two-way ANOVA, polyp$^{-1}$: $F = 2.39$, $p = 0.14$; cm$^{-2}$: $F = 0.64$, $p = 0.43$) or the interaction term (two-way ANOVA, polyp$^{-1}$: $F = 4.25$; $p = 0.06$; cm$^{-2}$: $F = 1.34$, $p = 0.27$).

*Stable isotope analyses*

In total, 20 samples of *L. virgulata,* 15 of *M. pendula,* and 44 of *T. nivea* were collected for SIA (Online Resource 1). $\delta^{13}$C values were similar across all species, with means of -19.8 ± 0.4‰ for *L. virgulata*, −20.4 ± 0.4‰ for *M. pendula*, and −21.2 ± 0.6‰ for *T. nivea* (± SD). $\delta^{15}$N exhibited more variation with mean values of 8.2 ± 0.8‰ for *L. virgulata*, 4.9 ± 0.5‰ for *M. pendula*, and 6.3 ± 0.6‰ for *T. nivea* (± SD). Small and large POM had mean $\delta^{13}$C values of −23.3 ± 0.8‰ and −21.7 ± 0.9‰ and mean $\delta^{15}$N values of 4.2 ± 0.6‰ and 5.2 ± 1.6‰, respectively (± SD). Homogeneity of group dispersions was not significantly different across gorgonian species (df = 2, $F = 0.47$, $p = 0.63$). Isotope values varied significantly across species, which accounted for ~72% of dissimilarity across samples from all sites (PERMANOVA, df = 2, $F = 194.24$, $R^2 = 0.72$, $p = 0.001$). Site was not significant and accounted for ~16% of dissimilarity in isotope values across samples (PERMANOVA, df = 9, $F = 9.75$, $R^2 = 0.16$, $p = 0.743$).

$\delta^{15}$N values of all three gorgonian species decreased with distance from shore and linear regressions using data from *L. virgulata* and *T. nivea* showed this relationship was significant (GLM, $p = 0.015$ and 0.008 respectively; Table 1; Fig. 2A). *Muricea pendula* was collected from only two sites precluding a regression, but these data demonstrated a relationship with a similar slope (Table 1; Fig. 2A). There was no significant relationship between $\delta^{13}$C and distance from shore for either *L. virgulata* or *T. nivea* (GLM, $p = 0.91$ and 0.61, respectively; Table 1; Fig. 2C). There was also no significant relationship between distance from shore and the $\delta^{15}$N or $\delta^{13}$C values of the small (GLM, $p = 0.6118$ and 0.1405, respectively) and large POM (GLM, $p = 0.4176$ and 0.1413; Table 1; Fig. 2B and D).

Assessment of gorgonian isotopic niches resulted in similar results when analyzing Dan's Spot independently or all sites pooled; there was no overlap (0%) between the SEA$_C$s of different species (Fig. 3A and C) and the RPP and Hotelling's $T^2$ tests showed each species occupied unique isotopic space ($p < 0.0001$; Table 2). There were no significant differences in the sizes of isotopic niche areas of gorgonian species ($p > 0.05$) both within Dan's Spot (Fig. 3B) and across all sites (Fig. 3D).

**Table 1** Linear regressions between distance from shore and the carbon and nitrogen stable isotope values of each gorgonian species and size fraction of particulate organic matter (POM)

| Sample type | Isotope | | df | F | $R^2$ | p |
|---|---|---|---|---|---|---|
| *L. virgulata* | $\delta^{13}C$ | y = 0.00212x − 19.79 | 4 | 0.08 | − 0.23 | 0.796 |
| | $\delta^{15}N$ | y = − 0.03725x + 8.42 | 4 | 15.93 | 0.75 | 0.0162 |
| *M. pendula* | $\delta^{13}C$ | y = − 0.01676x − 19.40 | 0 | NA | NA | NA |
| | $\delta^{15}N$ | y = − 0.01983x + 6.06 | 0 | NA | NA | NA |
| *T. nivea* | $\delta^{13}C$ | y = − 0.00754x − 21.57 | 4 | 0.4773 | − 0.12 | 0.5277 |
| | $\delta^{15}N$ | y = − 0.02772x + 7.59 | 4 | 13.01 | 0.71 | 0.0226 |
| Small POM | $\delta^{13}C$ | y = − 0.01731x − 22.52 | 5 | 3.06 | 0.26 | 0.1405 |
| | $\delta^{15}N$ | y = − 0.00706x + 4.67 | 5 | 0.2925 | − 0.13 | 0.6118 |
| Large POM | $\delta^{13}C$ | y = 0.01771x − 22.39 | 7 | 2.749 | 0.18 | 0.1413 |
| | $\delta^{15}N$ | y = − 0.01759x + 5.60 | 7 | 0.7417 | − 0.03 | 0.4176 |



**Fig. 2** Relationships between distance from shore and the nitrogen (**A** and **B**) and carbon (**C** and **D**) stable isotope values (mean ± SE) of three gorgonian coral species: *L. virgulata* (circles), *M. pendula* (triangles), and *T. nivea* (crosshairs, **A** and **C**), as well as large (diamonds) and small (squares) particulate organic matter (POM; **B** and **D**). Regressions between distance from shore and $\delta^{15}N$ values were significant ($p < 0.015$)
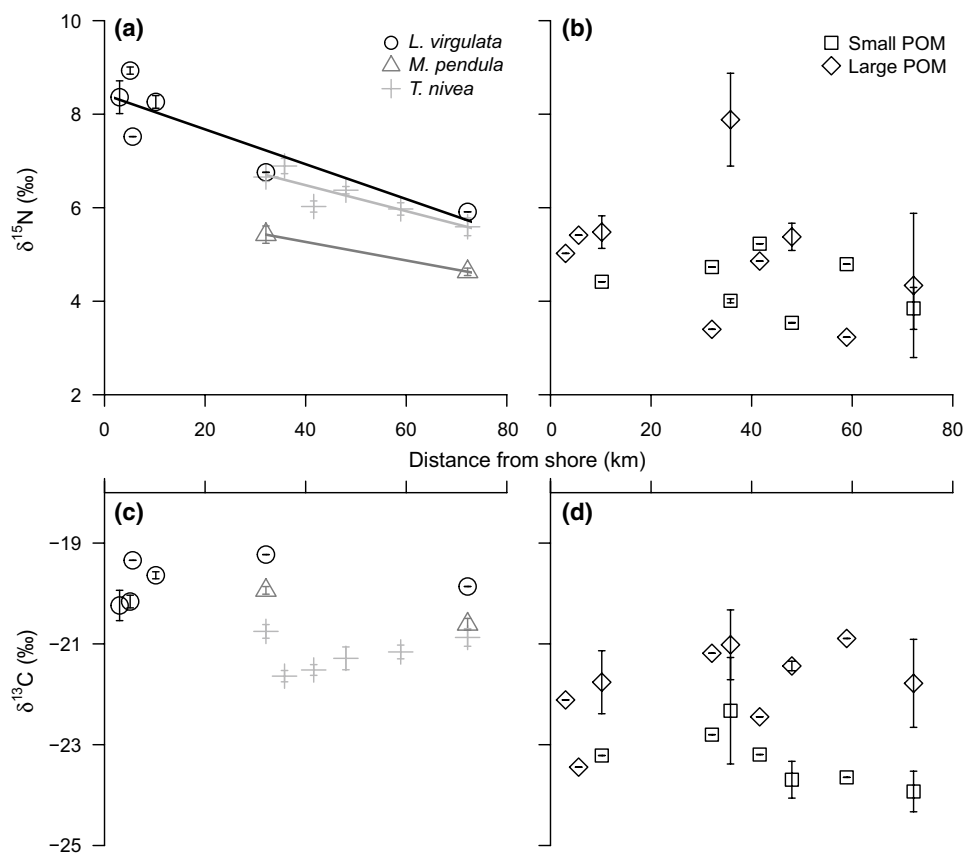
Comparison of gorgonian isotope values to that of large and small POM with minimum (+ 0.0 and + 2.5‰ for $\delta^{13}C$ and $\delta^{15}N$) and maximum (+ 1.0 and + 3.5‰ for $\delta^{13}C$ and $\delta^{15}N$) TDFs applied within each of three zones (nearshore, midshore, and offshore) shows that *L. virgulata* isotope values overlapped with maximally enriched large POM (Fig. 4A). In the midshore zone, *T. nivea* overlapped with small POM regardless of TDF as well as minimally enriched large POM (Fig. 4B); however, in the offshore zone, it only overlapped with large POM with either TDF applied (Fig. 4C). The isotopic values of *M. pendula* did not overlap

with any sampled food sources, although its $\delta^{15}N$ values most closely matched those of the minimally enriched small POM (Fig. 4B and C).

## Discussion

While distinct isotopic niches were found across all three gorgonian species, varying nitrogen isotope baselines limit the interpretation of these results. In particular, *L. virgulata* was rarely found at the same site as the other two
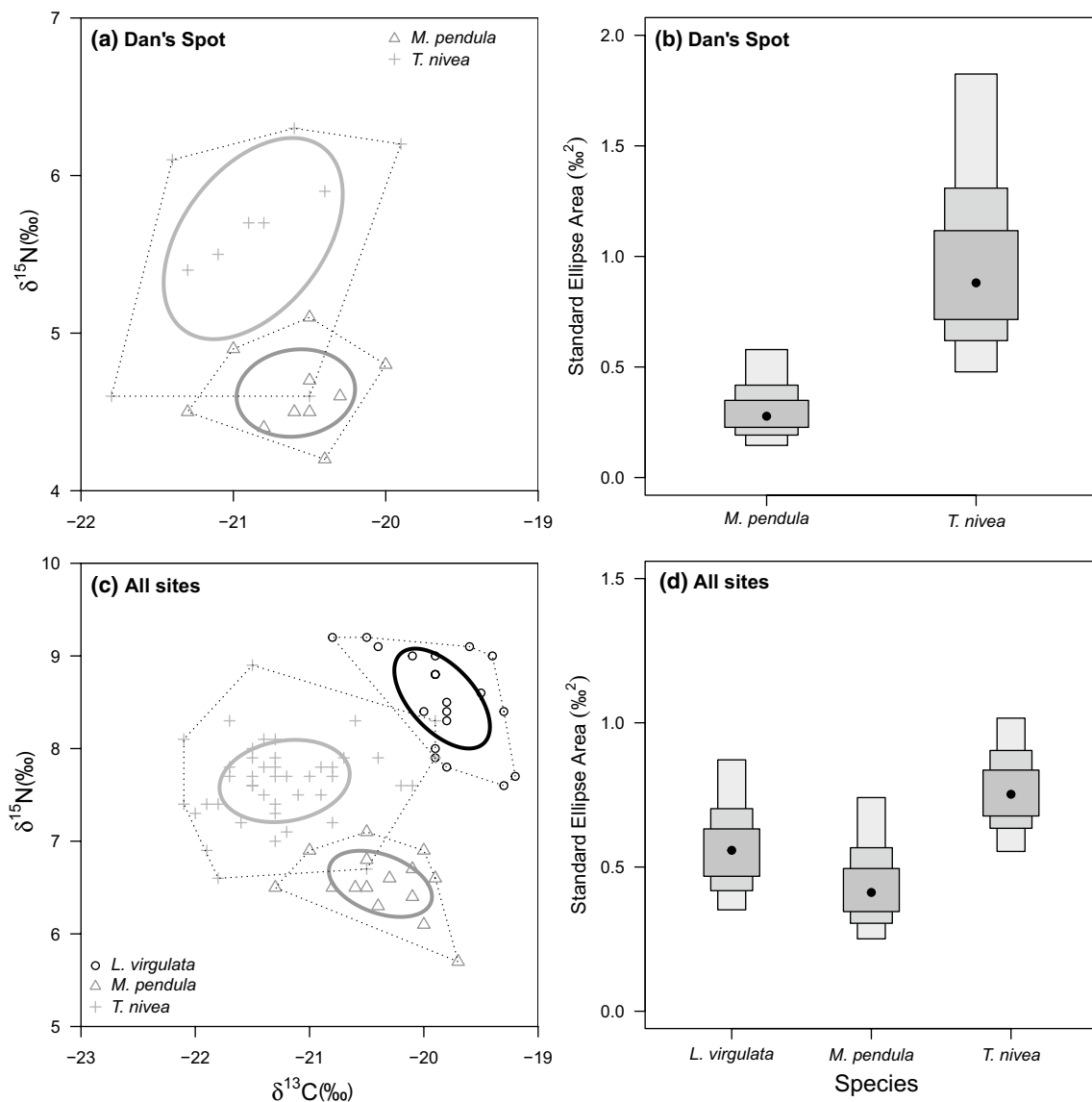
**Fig. 3** Carbon and nitrogen stable isotope values of three gorgonian corals (*L. virgulata*: black circles, $n = 20$; *M. pendula*: dark grey triangles, $n = 15$; *T. nivea*: light grey crosshairs, $n = 44$) collected from one site (Dan's Spot; **A**) and from all sites pooled with $\delta^{15}N$ values corrected for distance from shore (**C**). Solid lines represent standard ellipse area corrected for samples size (SEA$_C$), while dashed lines represent convex hulls. Each species occupied significantly different isotopic space (p < 0.0001). Distributions of SEA$_C$ estimates using Bayesian inference (mode, 50%, 75%, and 95% credible intervals) for each species again from Dan's Spot (**B**) and all sites pooled with $\delta^{15}N$ values corrected for distance from shore (**D**). There were no significant differences in size of species' SEA$_C$s ($p > 0.05$)

**Table 2** Results of the residual permutation procedures (RPP) and Hotelling's $T^2$ Tests for group comparisons among gorgonian samples both within the site Dan's Spot and across all sites where nitrogen isotope values have been corrected for distance from shore

| Group comparison | RPP | | Hotelling's $T^2$ Test | | |
|---|---|---|---|---|---|
| | Distance between centroids (‰) | $p$ | $T^2$ | $F$ | P |
| *Dan's Spot* | | | | | |
| *M. pendula* × *T. nivea* | 1.02 | 0.001 | 32.72 | 13.91 | 0.0001 |
| *All sites* | | | | | |
| *L. virgulata* × *M. pendula* | 2.07 | 0.001 | 189.29 | 86.53 | < 0.0001 |
| *L. virgulata* × *T. nivea* | 1.64 | 0.001 | 169.55 | 80.80 | < 0.0001 |
| *M. pendula* × *T. nivea* | 1.39 | 0.001 | 93.25 | 44.25 | < 0.0001 |

**Fig. 4** Carbon and nitrogen isotope values of three gorgonian corals (*L. virgulata*: circles, *M. pendula*: triangles, *T. nivea*: crosshairs) and mean values of small (diamonds) and large (squares) particulate organic matter (POM) from ten sights grouped into three zones: (**A**) nearshore, within 30 km of the shoreline, (**B**) midshore, between 30 and 50 km from the shoreline, and (**C**) offshore, greater than 50 km from the shoreline. Mean POM food sources are shown with low (+0‰ $\delta^{13}$C and +2.5‰ $\delta^{15}$N) and high (+1‰ $\delta^{13}$C and +3.5‰ $\delta^{15}$N) trophic discrimination factors applied for appropriate comparison to potential consumers. Error bars represent 1SD
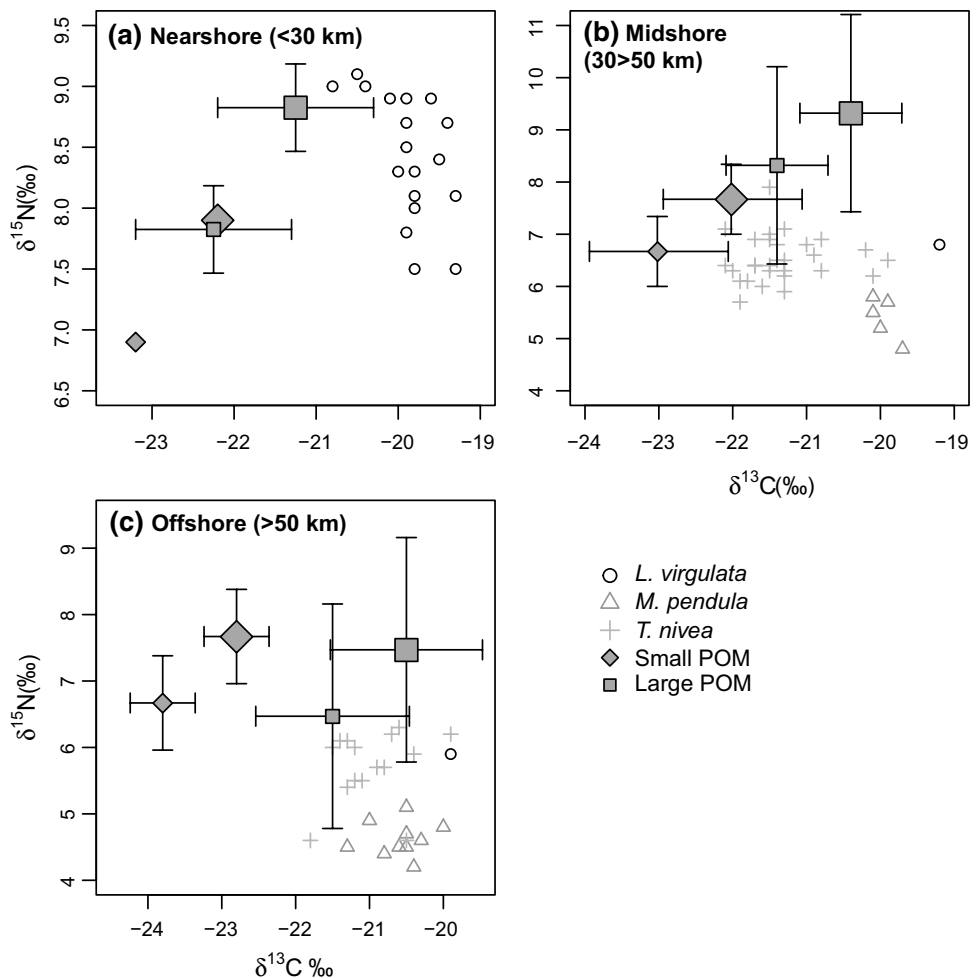


species, making comparisons challenging. To overcome this, $\delta^{15}$N values were corrected for distance from shore using the mean slope of this relationship for all three species (Fig. 2A); however, this generalized adjustment may not have captured the variation present at each site. Indeed, *L. virgulata* had the highest $\delta^{15}$N values when data across sites were pooled (Fig. 3C), yet the two individuals from locations where all species were present (Hyde and Dan's Spot) had $\delta^{15}$N values in the range of *T. nivea* (Fig. 4B and C). This suggests that the elevated isotopic niche of *L. virgulata* in the pooled dataset may be driven by higher $\delta^{15}$N baselines nearshore that were not fully accounted for in our correction. Further, *L. virgulata* and *T. nivea* both fed on rotifers but not phytoplankton in the flume experiments (Fig. 1), demonstrating clear fundamental niche overlap.

*Leptogorgia virgulata* and *T. nivea* may occupy the same trophic niche but avoid direct competition through spatial partitioning across nearshore and offshore habitats. Coexisting organisms often evolve to tolerate more extreme environmental conditions to occupy areas with fewer competitors (Connell 1961). *Leptogorgia virgulata* and *T. nivea*, which rarely occurred at the same site (Online Resource 1), may

have evolved different optimal temperature ranges, nutrient concentrations, or salinities, which all vary across Onslow Bay and the SAB (Atkinson et al. 1975; Singer et al. 1980; Fogel et al. 1999). Indeed, *L. virgulata*, has been found to tolerate extreme salinities as low as 17 and as high as 40 (Bayer 1961; Williamson et al. 2011). Spatial partitioning between these two species may also be linked to trophic partitioning. Sherwood et al. (2008) found that disparate diets in cold water octocorals from the Newfoundland continental slope were correlated with low vs. high flow environments, likely due to differing availability of large and small particles under divergent flow regimes. Distinct habitat specialization in *L. virgulata* may therefore result in trophic divergence if the concentrations of different particles change between nearshore and offshore sites. This could explain why this species exhibits niche overlap with *T. nivea* in feeding experiments and common sites, but niche divergence when sites are pooled. This may also explain differences in the overlap of their isotope values with prospective food sources; *L. virgulata* only overlapped with large POM, while *T. nivea* overlapped with both large and small POM (Fig. 4). This

pattern could arise if the particle composition of these size fractions varies nearshore to offshore.

The evidence supporting niche partitioning between *M. pendula* and *T. nivea* was more compelling. These two species had distinct isotopic niches both across all sites with a correction for distance from shore and within one site where they co-occurred (Fig. 3A and C). Further, site was not found to be a significant variable affecting isotope values, and species identity accounted for the majority (73%) of variance. The distinct isotopic niche of *M. pendula* was primarily driven by lower $\delta^{15}$N values, indicating it occupied a lower trophic level (Fig. 3A and C; Chisholm et al. 1982; Minagawa and Wada 1984). Given that *T. nivea* and *L. virgulata* both consumed zooplankton (rotifers) but not phytoplankton in flume experiments (Fig. 1), the diet of *M. pendula* likely consists of phytoplankton, which sit low in the food web. Diatoms and dinoflagellates are known to contribute to the diet of other gorgonians (Sorokin 1991; Ribes et al. 1999, 2003), and one species of octocoral has been identified as herbivorous, feeding nearly exclusively on phytoplankton (Fabricius et al. 1995a).

*Muricea pendula,* however, had very low overlap with either food source sampled from the SAB; only a few individuals offshore fell into the range of minimally enriched large POM (Fig. 4C). This may be due to the timing of POM sampling in our study, which was during summer and fall (July–October), with seven to 31 days between sampling dates (Online Resource 1). Planktonic organisms, particularly phytoplankton, have short tissue turnover times, so their isotope values reflect that of the nutrients they assimilated over recent days or weeks (Aberle and Malzahn 2007). Our sampling schedule may therefore have missed both inter and intra-seasonal variation in the values of the SAB plankton community. Gorgonians, on the other hand, exhibit growth rates between 0.5 and 2.7 cm per year, so our samples reflected the isotope values of 4–24 months of growth (Cary 1914; Yoshioka and Yoshioka 1991; Mistri and Ceccherelli 1994; Sherwood and Edinger 2009). The discrepancy between the stable isotope values of *M. pendula* and potential food sources could therefore be a result of the mis-matched time periods captured in their tissues. Alternatively, each size class of POM represented a coarse category consisting of many particle types potentially at different trophic levels, possibly obscuring variation in the isotope values of different seston within each sample. These limitations make it difficult to draw firm conclusions about the diet of *M. pendula*.

Despite being united in having eight pinnate tentacles, we found significant differences in the polyp morphology of *L. virgulata* and *T. nivea*, with *T. nivea* exhibiting significantly longer tentacles and larger polyp surface area. Larger polyps have been associated with faster feeding rates (Coates and Jackson 1985); however, this pattern did not hold in our study species, which did not have significantly different clearance rates (Fig. 1). Previous studies have speculated that larger polyps and tentacles allow corals to capture larger particles and zooplankton (Porter 1976); however, both flume experiments and SIA results suggested that *L. virgulata* feeds on zooplankton and large POM despite its smaller polyps (Figs. 1 and 4). Other morphological characters such as the number and type of nematocysts, number of ciliary structures on the tentacles (Mariscal and Bigger 1977), and distance between pinnules (Fabricius et al. 1995b; Grossowicz and Benayahu 2011) may be more important than polyp and tentacle size for particle selectivity.

Alternatively, differences in colony morphology may underlie trophic variation between species. *L. virgulata* has a whip-like morphology, with relatively reduced branching that predominately occurs at the base of the colony. In contrast, *M. pendula* exhibits extensive pinnate branching within one plane, resulting in a fan-like structure. Finally, *T. nivea* has moderate branching that can present in one plane or as clustered branches (Devictor and Morton 2010). Previous work suggests that the mechanism of particle capture in fan compared to bushy colonies is different. Leversee (1976) demonstrated that fan-shaped gorgonians have higher feeding rates when oriented perpendicular rather than parallel to prevailing currents, indicating this structure is an adaptation that increases contact area with food particles. Alternatively, polyps on downstream branches in bushy colonies may take advantage of the turbulence created by their upstream counterparts (Sebens et al. 1997). Particles can reside in these eddies for up to 20 s (Leversee 1976), resulting in seston concentrations an order of magnitude higher than the water column (Lee and Srinivasan 1978). Particles of various sizes may interact with microcurrents differently, thus potentially explaining particle selectivity across species with divergent colony structures.

Niche partitioning across similar filter feeders in the SAB might be surprising given the abundance of particulate food resources in this environment (Paffenhöfer et al. 1980; Paffenhöfer 1980). Ecological niche theory postulates that partitioning arises when organisms compete for limiting resources (Gause 1934; Lack 1947); if resources are plentiful, there is no evolutionary pressure for adaptive traits that circumvent this competition. One explanation is that these species diversified under past conditions that were more oligotrophic; indeed, there is evidence for nutrient limitation in the western Atlantic in prior evolutionarily relevant time periods (Allmon 2001). Alternatively, the conditions in the SAB may present alternative tradeoffs for filter feeding organisms. The ability to select high-quality particles out of a diversity of seston may save the energy required to capture, and in some cases expel, low-quality food items (Mariscal and Bigger 1977). Niche partitioning across sympatric gorgonians has previously been observed in another region with

a high particle load. In the Gulf of La Spezia in the Mediterranean, gorgonians were found to predominantly rely on either zooplankton or POM and SOM (sedimentary organic matter; Cocito et al. 2013). This region is subjected to large concentrations of particulates carried by discharge from the Magra River, and thus presents a similar environment to the SAB where diverse particles are abundant (Paffenhöfer et al. 1980; Paffenhöfer 1980). The hypothesis that corals in the Gulf of La Spezia conserve energy by selecting high-quality particles out of abundant, low-quality seston was supported by seasonal switching in two species that consumed zooplankton in the winter and POM in the summer when zooplankton were less available. Alternatively, in systems where food can be scarce, it may be beneficial for octocorals to consume any particles they capture. Elias-Piera et al. (2013) found similar broad diets across seven Antarctic gorgonian species that inhabit an environment with sparse planktonic communities. Partitioning of trophic resources in environments where food is abundant reveals that competition is not the only evolutionary pressure that can drive dietary divergence; energetic tradeoffs of different feeding strategies also select for trophic partitioning.

## Conclusions and future considerations

Our results counter the assumption that octocorals in the SAB act as a single functional group and instead support the hypothesis that these closely related suspension feeders have evolved mechanisms to exploit different food sources. Specifically, we found evidence that *M. pendula* selected lower trophic level seston than *T. nivea* and speculate that spatial partitioning exists between *T. nivea* and *L. virgulata*, which both fed on zooplankton. Future work should further investigate these findings with field surveys of the plankton available at inshore and offshore habitats as well as additional controlled feeding experiments to confirm whether *M. pendula* is herbivorous, and if *L. virgulata* and *T. nivea* can feed on other particles aside from rotifers. Differences in the ecological and trophic niches of these octocorals have implications for their contribution to benthic-pelagic coupling in the SAB, and full understanding of their feeding capacity will indicate whether they provide selective pathways for only some particles to pass from the water column to the seafloor. We also showed that significant differences in tentacle length and polyp surface area were not associated with trophic differences, and other morphological distinctions, including aspects of colony and tentacle morphology, should be investigated. While additional studies are necessary to have a complete picture of the trophic dynamics of these corals, our findings provide preliminary evidence for differences across species, suggesting they perform divergent ecosystem functions that support benthic communities.

**Declarations**

**Data availability** The stable isotope dataset generated during this study is available in the IsoBank repository [https://isobank-qa.tacc.utexas.edu/analyses/submitted_dataset_list/]. Clearance rate and morphology data are available in the supplementary information files.

**Ethics approval** No approval of research ethics committees was required for this study because experimental work was conducted with unregulated invertebrate species.

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