

Plankton-benthos coupling on a Caribbean fringing reef

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ABSTRACT

Trophodynamic processes on coral reefs are complex and poorly understood. Near Discovery Bay, Jamaica, the nitrogen isotopic composition of diverse zooxanthellate cnidarians was depleted in ¹⁵N relative to other reef animals. ¹³C values for zooplanktivores, herbivores, and carnivores were generally explicable on the basis of their diet, as were ¹⁵N values for zooplanktivorous herring and herbivores. Demosponges (and perhaps other suspension-feeders) were more enriched than expected in ¹³C. Suspension-feeders, non-zooxanthellate scleractinians, and predatory barjacks were far less enriched in ¹⁵N than anticipated. Exudates from zooxanthellate cnidarians and/or cyanobacteria (or endosymbiotic cyanobacteria in some demosponges) are possible sources of ¹⁵N-depleted/¹³C-enriched organic materials for benthic suspension feeders. Benthic algae and zooxanthellate cnidarians on the fore reefs were depleted in ¹⁵N relative to congeners collected within Discovery Bay. Microbial reactions occurring within fine-grained Bay sediments can explain ¹⁵N enrichment as an alternative to imported anthropogenic nitrogen.

Keywords Stable isotopes, Carbon, Nitrogen, Jamaican reef organisms

Introduction

The generalization "You are what you eat, isotopically, plus a few per mil" summarizes the role of "stable isotopic ecology" in helping to elucidate the flow of carbon and nitrogen through food webs (DeNiro and Epstein 1978, 1981, Peters et al. 1978, Minagawa and Wada 1984, Peterson and Fry 1987). For example, the soft tissues of most zooxanthellate scleractinian corals and their contained microalgae (photosynthetic dino flagellates) are enriched in ¹³C relative to non-zooxanthellate scleractinians, particulate organic matter (POM) and zooplankton. Hence, external particulate foods are unlikely to be a major source of their dietary carbon (Land et al. 1975, 1977, Muscatine et al. 1989). Similar studies using ¹⁵N have reinforced the importance of dissolved inorganic nitrogen in the trophic budgets of zooxanthellate scleractinians (e.g. Muscatine and Kaplan 1994, Heikoop et al. 1998).

Fry et al. (1982), however, concluded that the ¹³C-enriched tissues of Caribbean reef corals was the result of uptake of carbon derived either from cyanobacteria or the seagrass, *Thalassia testudinum*, whereas Lorian et al. (1992) found ¹³C-isotopic evidence for significant input of POM from pelagic plankton to oligotrophic Israeli reefs via planktivores. Yamamuro et al. (1992, 1995) used ¹³C and ¹⁵N as dual tracers to suggest that corals in Japan and Palau do not depend on zooplankton as sources of carbon and nitrogen, but instead entire reef ecosystems are tied to nitrogen fixation. According to Risk et al. (1994) and Sammarco et al. (1999), inshore corals on the Great Barrier Reef (GBR) derive much of their nutrients from terrigenous sources which, for carbon, is measurable out to the edge of the continental shelf. Mid-shelf GBR corals may receive some nitrogen from nitrogen-fixation in cyanobacterial mats, and upwelled nitrogen may be important further offshore (Sammarco et al. 1999).

To help characterize the flow of carbon and nitrogen in fore-reef and lagoonal habitats near the small town of Discovery Bay, Jamaica (its population was 2,230 in 1991), we examined organisms representative of a broad range of trophic modes. Our initial sampling was in 1973-1974, when the narrow, north Jamaican fringing reefs

were dominated by zooxanthellate scleractinians, despite high levels of artisanal overfishing (Woodley 1979). The following decade brought massive perturbations: two major hurricanes in 1980 and 1988, the near-demise of a key herbivore *Diadema antillarum* in 1983, and the subsequent replacement of many stony corals by benthic macroalgae at shallow-intermediate reef depths (e.g. Hughes 1994). Collecting was resumed in 1993-1995 to help fill in earlier data gaps, and to test the hypothesis that anthropogenic nutrients in groundwater were enhancing algal growth at Discovery Bay (Goreau 1992).

No perennial surface streams enter Discovery Bay and its mangrove fringe is poorly developed (Gayle and Woodley 1998). Strong, nutrient-rich upwellings are not common along the Jamaican north coast (Leichter 2000), although tiny (<0.1° C) thermoclines are sometimes encountered during dives on fore-reef slopes (pers obs), and transient temperature decreases are induced by storms (Dustan 1975, J.D. Woodley pers comm).

Methods

Collections were made during summer months. About one-third of the samples were taken within 500 m of the shore inside Discovery Bay, at depths of 1-22 m. The remainder came from 1-43 m on fore-reefs located within 800 m of the coastline, mostly at Discovery Bay. A few, fore-reef samples were collected at Pear Tree Bottom and Rio Bueno, collectively spanning ~15 km of the coast.

Representative of the pelagos were POM (presumably a mixture of autotrophs and heterotrophs including both bacteria and protists, as well as other suspended organic matter), net zooplankton (collected during day and night tows) and herring (a zooplanktivorous fish). Demersal zooplankton were taken while diving with a light at night. Benthos-associated samples were more numerous and included various autotrophs (calcareous and fleshy algae, cyanobacteria, *Thalassia*), heterotrophs [e.g. several invertebrate suspension-feeders, including demosponges (many expected to contain heterotrophic endobacteria or endosymbiotic cyanobacteria), herbivorous echinoids and fishes, invertebrate corallivores, a carnivorous fish], and known mixotrophs [a zooxanthellate clionid demosponge, numerous zooxanthellate cnidarians, *Tridachia crispata* (a gastropod that sequesters siphonaceous green algal chloroplasts)]. Zooxanthella concentrates were obtained from half of the symbiotic cnidarian taxa. The extent of

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tissue inhomogeneity within individual organisms, or within populations, was not determined, nor were possible seasonal effects investigated.

Samples were prepared as outlined in Land et al. (1975). Decalcification was accomplished on dried, pulverized samples using 10% HCl. We detected no isotopic shifts of non-calcareous tissues resulting from the HCl treatment, whereas other acids (H₃PO₄, HAC, EDTA) definitely affected carbon isotopic values. Prior to 1993, samples were analyzed for $\delta^{13}\text{C}$ by combustion in a stream of oxygen (Craig 1953). Subsequent analyses were made by combustion at 850°C in quartz tubes (Lajtha and Michener 1994), so that carbon and nitrogen values could be obtained from the same sample. Initially, samples were analyzed for $\delta^{15}\text{N}$ by Kjeldhal digestion and gas purification (Kreitler 1975). It was found that many samples analyzed by this method not only yielded suspiciously-enriched values, but were not reproducible. Most of the early suspect data which could not be reproduced have been discarded, which is why more carbon than nitrogen values are reported. Nitrogen isotopic compositions have been normalized using the N-1 standard (+1.36‰), and are reported relative to atmospheric nitrogen. Carbon is reported relative to the PDB standard, and both isotopic compositions are reproducible to better than 0.3‰.

Results

The number of replicates per taxon varied from 1 to 19. Comparisons among taxa are given as taxon means. As organisms were not sampled on the basis of their relative abundance, it would be inappropriate to describe the reefs in any statistical sense with these data. The data will be archived at the Caribbean Coastal Data Center, Marine Science Center, University of the West Indies, Jamaica, WI, and are available by request from the senior author.

Carbon

The carbon isotopic analyses, which vary from -8.8‰ to -25.0‰ are summarized as histograms of trophic similarity in Fig. 1. Not shown are $\delta^{13}\text{C}$ values for two fresh-water plants, one from each mouth of the Pear Tree Bottom (-27.2‰) and Rio Bueno (-32.0‰) rivers. POM values averaged $-21.8 \pm 1.5\%$ (std dev, N = 10) on the fore reefs and $-21.5\% \pm 1.5\%$ (std dev, N=6) in the Bay. Fore-reef *Tridachia* were similarly depleted. Means for net zooplankton, benthic green macroalgae (fleshy as well as calcareous), algal turfs, *Madracis mirabilis* (a zooxanthellate scleractinian), and non-zooxanthellate scleractinians ranged from -17‰ to -20.5‰, as did the *Tridachia* and herring collected in the lagoon, and suspension feeders (a sabellid, a spirobid, an oyster, the crinoid *Nemaster* sp.) from the fore reefs. $\delta^{13}\text{C}$ values in fore-reef habitats averaged about -16.5‰ each for demosponges and the predatory barjack *Caranx ruber*, as did a sample of epibionts from *Thalassia* blades.

Averages for fore-reef brown algae and herbivorous fishes (damselfishes, parrotfishes) were about -16‰ and -15.0‰, respectively, while one echinoid, *Diadema antillarum* was -14.8‰ and a scavenging arrow crab,

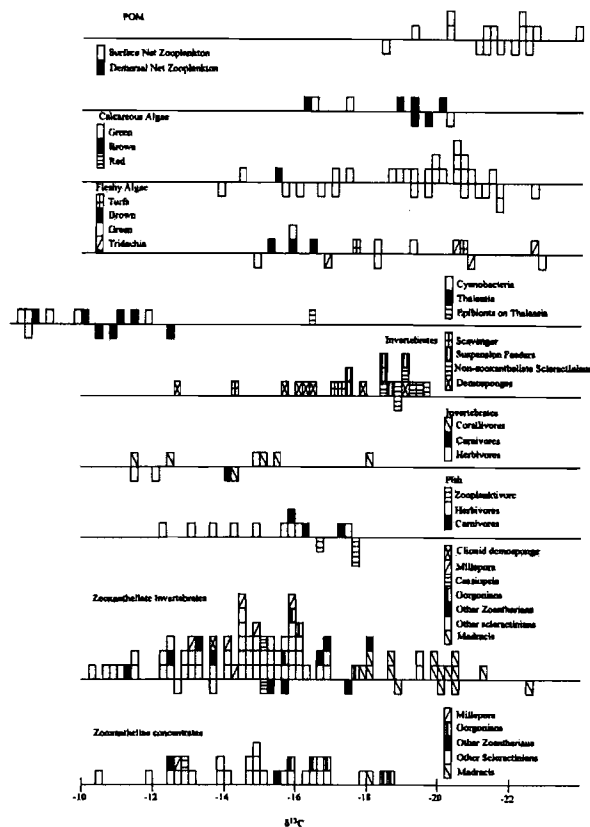


Fig. 1 Frequency histogram of carbon isotopic values, arranged according to trophic level (includes data from Land et al. 1975, 1977). Each rectangular box represents a single organism or sample, about 5% of which were duplicated, but not plotted. Boxes below the horizontal reference lines were collected inside Discovery Bay. N = 266.

Stenorhynchus seticornis, was -14.4‰. Mean $\delta^{13}\text{C}$ values were -11.5‰ for two echinoids (*Lytechinus variegatus*, *Tripneustes ventricosus*) collected as they were feeding on *Thalassia* in the Bay. *Thalassia* and cyanobacteria in both reef zones were the most ^{13}C -enriched of the sampled organisms, respectively averaging about -11‰ and 9.5‰. Although the bulk tissues of zooxanthellate organisms in both kinds of habitats spanned a wide range in $\delta^{13}\text{C}$ values (overall from -10.4‰ to -22.3‰), only *Madracis* (which has relatively few zooxanthellae—P.J. Edmunds, pers comm) was consistently more enriched than -18‰. Zooxanthella concentrates were very similar to the bulk tissues of the cnidarians from which they were separated, with a mean difference of $0 \pm 0.8\%$ (std dev, N = 20). Zooxanthellate scleractinians (and zooxanthella concentrates) generally became increasingly depleted in ^{13}C with increasing depth, at least to 20 meters (Fig. 2). The mean $\delta^{13}\text{C}$ value for corallivores (the polychaete *Hermodice carunculata* and the gastropods *Coralliophila abbreviata*, *Calliostoma javanicum*, *Cyphoma gibbosum*) was -14.7‰.

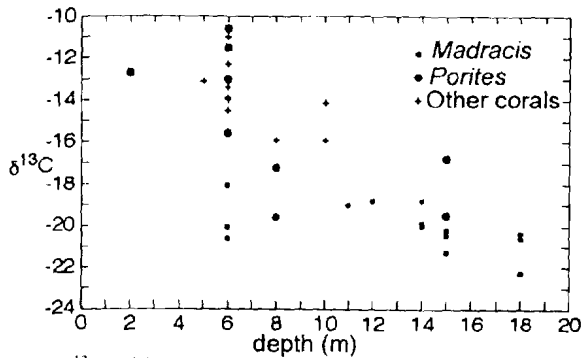


Fig. 2 $\delta^{13}\text{C}$ of bulk tissue of zooxanthellate scleractinians versus depth. Tissues tend to become depleted in ^{13}C with increasing depth within the upper 20 meters. The few corals collected deeper than 20 m (not plotted) do not continue the trend.

For taxa collected in both kinds of habitats, ^{13}C means from the Bay were depleted by about 1-2‰ relative to those from the fore reefs for *Penicillus capitatus* (a green calcareous alga) and two zooxanthellate cnidarians (the scleractinian *Montastraea cavernosa*, the actinian *Condylactis gigantea*), and by 2-3‰ in *Tridachia crispata* and the zooxanthellate scleractinian *Porites porites*. Corresponding values for POM and *Cassiopeia* sp. (a zooxanthellate scyphozoan) were essentially identical (<0.3‰ difference). Other samples from the Bay were enriched relative to conspecifics from fore-reef habitats: by about 1-2‰ for the demersal zooplankton, *Halimeda* spp. (green calcareous algae), *Thalassia*, two zooxanthellate cnidarians (*Madracis mirabilis*, the zoanthid *Zoanthus* sp.) and *Coralliophila*; by about 3‰ for surface zooplankton; and from about 4-7‰ for two green algae (the siphonaceous *Caulerpa* sp., the calcareous *Udotea* sp.) and for *Padina* sp., a fleshy brown alga.

Nitrogen

The nitrogen isotopic analyses range from 0.2‰ to 11.0‰ (Fig. 3). During analyses in the 1990's, no significant differences were found between recently collected samples and those stored below 0°C since the 1970's. The most $\delta^{15}\text{N}$ -depleted (<4.5‰) of the Bay samples were *Cassiopeia* sp., net zooplankton, and a cyanobacterial mat. $\delta^{15}\text{N}$ values for zooxanthellate cnidarians (scleractinians, *Condylactis gigantea*, *Zoanthus* sp.) *Tridachia*, and the fleshy green algae collected here varied between 4.5‰ and 6‰. POM, calcareous green algae, and a *Coralliophila* from the Bay, plus a sample of sewage from the Marine Laboratory's septic system, were all between 6.5‰ and 7‰, while the herring averaged 8‰. A predatory snail, and the echinoids (*Lytechinus*, *Tripneustes*) were the most ^{15}N -enriched (>9-11‰) of the Bay samples.

Most zooxanthellate organisms (the clionid demosponge, *Cassiopeia*, *Zoanthus*, the hydrozoan *Millepora* sp., many gorgonians and scleractinians) had mean $\delta^{15}\text{N}$ values of <4.5‰ on the fore reefs, as did benthic algae, cyanobacteria and the *Stenorhynchus*. Zooxanthella concentrates were similar to their corresponding bulk tissues (mean enrichment being $+0.3 \pm 1.4$ ‰ (std dev, $N = 12$). Average $\delta^{15}\text{N}$ values for the fore-reef demsponges, other suspension feeders (a serpulid, an oyster, *Nemaster*), the zooxanthellate corallimorph *Stoichactis helianthus*, *Thalassia*, POM, and the corallivores

(*Hermodice*, *Calliostoma*, *Cyphoma*) were all between 4.5‰ and 6.0‰. Somewhat more enriched at 6-7‰ were net zooplankton, non-zooxanthellate scleractinians, bar-jacks, and the echinoid *Diadema antillarum*. Herbivorous fishes were the most ^{15}N -enriched of the samples collected on the fore reef, with average values of 7.5‰.

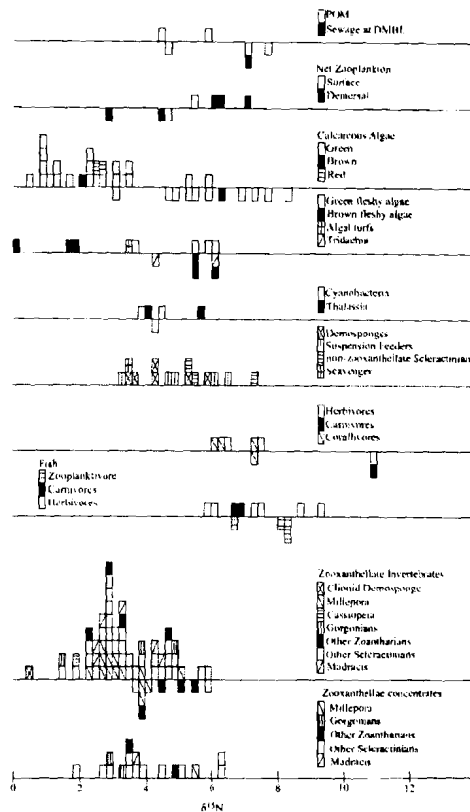


Fig. 3 Frequency histogram of nitrogen isotopic values, arranged by level and location, as in Figure 1. $N = 187$.

Zooplankton collected in the Bay averaged about 1-3‰ less enriched in ^{15}N than the fore-reef samples. $\delta^{15}\text{N}$ values for POM and the green alga *Caulerpa* sp. were virtually identical in both habitats. Zooxanthellate cnidarians (*Cassiopeia*, *Condylactis*, *Madracis mirabilis*, *Porites porites*, *Zoanthus*) and benthic algae (*Halimeda* spp., *Penicillus*, *Udotea*, *Padina*) sampled in both reef habitats showed average enrichments within the Bay of about 1-3‰ and of 3-4‰, respectively.

Discussion

Carbon

Dietary trophic shifts are typically less than +2‰ for $\delta^{13}\text{C}$ (Peterson and Fry 1987). Large-scale import of isotopically-depleted, terrigenous materials is unlikely to occur at Discovery Bay (see Introduction). Thus, suspended POM, averaging -21.7 ‰ and isotopically identical in the fore-reef and the Bay, is the most depleted food source routinely available to these north Jamaican ecosystems. In addition to feeding on plankton (Sebens et al. 1998, Ribes et al. 1998), some of the carbon ingested by the scleractinian *Madracis mirabilis*, and by the zooxanthellate gorgonians, may be derived from POM. However, carbon isotopic ratios of the zooplanktivorous herring, non-zooxanthellate scleractinians and suspension

feeders (a serpulid, a spirobid, an oyster and *Nemaster*) were consistent with a diet in which net zooplankton (or some other source of relatively-enriched carbon) contributes more than POM.

The mucus and dissolved organics released by zooxanthellate cnidarians (see Sorokin 1990, Muscatine and Weis 1992) or benthic cyanobacteria should be enriched in ^{13}C . Such exudates may contribute to the diet of the heterotrophic demosponges (and their contained bacteria), which averaged about 5.5‰ less depleted in ^{13}C than POM on fore reefs. Mixotrophic demosponges that host cyanobacteria (Wilkinson 1987) probably gain photosynthates that are similarly enriched in ^{13}C from their endosymbionts.

Fleshy and calcareous algae respectively averaged about 6 and 10‰ more depleted in ^{13}C than cyanobacteria and the seagrass *Thalassia*. ^{13}C values for herbivores are explicable with diets based primarily on *Thalassia* for echinoids inhabiting seagrass meadows in the Bay, and on algae (especially *Dictyota*) for *Diadema*, damselfishes and parrotfishes on the fore reefs. Similarly, the average carbon isotopic composition of the predatory barjacks was intermediate between those of the more depleted herrings and the more enriched herbivorous fishes, all of which are their potential prey (Randall 1967). The $\delta^{13}\text{C}$ values of carnivorous corallivores overlap those of the zooxanthellate cnidarians upon which they feed. In both kinds of habitat, the $\delta^{13}\text{C}$ values for *Tridachia* resembled those of *Caulerpa* sp., a possible source of its symbiotic chloroplasts (Trench 1975).

Excepting *M. mirabilis* and the zooxanthellate gorgonians, POM and net zooplankton were depleted in ^{13}C relative to zooxanthellate organisms. For example, sampled zooxanthellate scleractinians (excluding *Madracis*) on the fore reefs averaged about 4.0‰ and 7.0‰ more enriched than ambient demersal zooplankton and POM, respectively. Such large isotopic differences are unlikely to be due to dietary shifts. Symbiosis-created efficiencies of carbon cycling, which are evidenced by the close similarity between bulk animal tissues and their algal concentrates, probably reduce isotopic fractionation by the zooxanthellae during photosynthesis (Land et al. 1975, Muscatine et al. 1989). Zooxanthellate scleractinians from shallow water, where photosynthesis is presumably enhanced, displayed the most enriched $\delta^{13}\text{C}$ values (Fig. 2). Aside from the effects of depth, the wide range in the $\delta^{13}\text{C}$ values of most zooxanthellate cnidarians is not simply explained. Neither presumed symbiont clade (Baker and Rowan 1997), polyp size, colony morphology, growth rate, type of skeletal deposit (if any), nor higher taxonomic category of the animal host, was a good predictor of their stable carbon isotopic composition. More consistent patterns might have emerged had our samples been collected within a narrower range of depths and habitats.

Nitrogen

Heterotrophic organisms are generally 3-4‰ enriched in $\delta^{15}\text{N}$ relative to their primary sources of nutrition (Peterson and Fry 1987). The mean $\delta^{15}\text{N}$ values for herring were nearly 4‰ enriched relative to ambient zooplankton in Discovery Bay, as were herbivorous echinoids compared to *Thalassia*. Similarly, the $\delta^{15}\text{N}$ for *Diadema*, and mean values for herbivorous fishes, were enriched by about 3.5-4‰ relative to benthic algae in fore-reef habitats, while corallivores averaged <2.5‰ more enriched than their cnidarian prey.

Other expected feeding relationships were not realized. Means for nonzooxanthellate corals and net

zooplankton overlapped on fore reefs, and both were only about 1‰ more enriched than POM. Suspension feeders and demosponges, on average, were slightly (<1‰) less enriched than ambient POM and zooplankton. Predatory barjacks were slightly depleted relative to other fishes. Organic exudates from the ^{15}N -depleted zooxanthellate cnidarians and/or cyanobacteria may contribute to the nitrogen diet, at least for suspension feeders and (indirectly) for predators in this fringing reef system. Some demosponges may obtain photosynthates that we would expect to be depleted in ^{15}N from endosymbiotic cyanobacteria.

Although our samples were possibly contaminated by other organisms, benthic cyanobacteria did not show the minimal fractionation expected for nitrogen-fixers (Hoering and Ford 1960). The mean $\delta^{15}\text{N}$ values for *Madracis*, all other zooxanthellate organisms, and their zooxanthella concentrates resembled benthic algae and cyanobacteria. Furthermore, they were depleted relative to POM (both reef zones) and either depleted (fore reefs) or overlapped (Bay) with net zooplankton. Much of the dissolved inorganic nitrogen initially incorporated into organic compounds by the zooxanthellae and translocated to their animal hosts is presumably recycled back to the algae as ^{15}N -depleted ammonia before it can be excreted (e.g. Muscatine and Kaplan 1994, Heikoop et al. 1998), thereby eliminating the trophic shifts observed with other animals. Nocturnal expansion by cnidarian polyps to capture zooplankton may simultaneously increase the available surface area for uptake of dissolved inorganic nitrogen from seawater. As with carbon, the $\delta^{15}\text{N}$ of the zooxanthellate cnidarians (including *Madracis mirabilis*), bore no simple relationship to taxonomy, polyp size, colony morphology, growth rate, type of skeletal deposit (if present), higher taxonomy, or presumed zooxanthella clade identity; however, any such effects may have been masked by small, within-habitat sample sizes.

Two explanations seem possible for the observation that most benthic algae and diverse zooxanthellate cnidarians from inside Discovery Bay were enriched in ^{15}N relative to congeners collected on the fore reefs. Firstly, sediments within Discovery Bay overall are finer grained, and contain more organic matter, than those on the seaward reefs (Bonem 1988, Pigott and Laughlin 1988). Microbial degradation of organic matter in sediment involves the loss of ^{15}N -depleted products during denitrification, peptide bond hydrolysis, and/or deamination reactions (Sweeney and Kaplan 1980, Silver et al. 1992, Macko et al. 1993). Hence, the residual nitrogen remaining in the sediment, and potentially available for utilization by benthic algae and zooxanthellate organisms, will be enriched in ^{15}N . Alternatively, as proposed for coral reefs located close to considerably larger human populations (e.g. Mendes et al. 1997, Heikoop et al. 2000), the Bay could be "overfertilized" by ^{15}N -enriched nitrate in groundwater and sewage discharge. Nitrogen isotopic compositions overlap sufficiently so as to preclude an unequivocal distinction between these two explanations. However, given the close similarity in the $\delta^{15}\text{N}$ values of conspecific or congeneric organisms collected in the 1970's and resampled in the 1990's, we found no evidence that the fore reefs were being progressively impacted by anthropogenic nitrogen.

Acknowledgements The equipment program of the National Science Foundation provided partial funding for the instruments, and the Geology Foundation of the University of Texas contributed to travel and laboratory

expenses. The authors thank the Discovery Bay Marine Laboratory for providing the boats and diving equipment. Constructive comments from J. Erez, M. Estep, L. Muscatine, M. Risk, and J.-P. Torréton are gratefully acknowledged. DBML contribution No. 759.

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