# COMMUNITY ECOLOGY

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# Stable isotope analysis of production and trophic relationships in a tropical marine hard-bottom community

**Abstract** Seagrasses produce much of the organic carbon in the shallow waters of the Caribbean and it has long been assumed that a substantial portion of this carbon is exported to nearby habitats, contributing substantially to their food webs. In the shallow coastal waters of the Florida Keys (USA), seagrass intersperses with hard-bottom habitat where bushy, red macroalgae are the most prominent primary producers. However, the relative importance of seagrass-derived carbon versus autochthonous algal production or phytoplankton in supporting higher trophic levels within hard-bottom communities has never been investigated. We compared the carbon and nitrogen isotopic values of potential primary producers and representative higher trophic level taxa from hard-bottom sites on the bay-side and ocean-side of the Florida Keys. We also included in our study a set of bay-side sites that experienced significant ecological disturbances over the past decade (e.g., cyanobacteria blooms, seagrass die-off, and sponge die-offs) that may have altered trophic relationships in those regions. We did not detect any differences among regions in the trophic status of hard-bottom taxa that might be associated with ecosystem disturbance. However, our results suggest that autochthonous production of algal detritus is an important source of secondary production in these hard-bottom communities, with seagrass and phytoplankton contributing smaller fractions.

**Keywords** Benthic community · *Laurencia* · Macroalgae · Seagrass · Trophic structure

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## Introduction

Nearshore hard-bottom communities are a prevalent subtidal feature of the coastal Caribbean, yet little is known about the trophic structure or functional organization of these communities beyond a few general descriptions of their community structure (Croley and Dawes 1970; Opresko 1973; Holm 1978; Chiappone and Sullivan 1994a, b). In Florida, hard-bottom habitat—also referred to as live-bottom habitat, octocoral-dominated hardgrounds, exposed bedrock outcrops, alcyonarian-sponge communities, nearshore rock-bottom habitat, and algal-dominated hard-bottom (see Chiappone 1996)—occurs in shallow (<5 m) coastal waters and is characterized by low relief, limestone bedrock overlain by a thin (<10 cm) veneer of sediment. Sponges, octocorals, and scleractinian corals are the most conspicuous sessile fauna in these communities, which are inhabited by numerous motile species including some reef-dwelling species that use hard-bottom as a nursery (e.g., Caribbean spiny lobster, Nassau grouper and others; Butler and Herrnkind 2000; Eggleston et al. 1997). As the term "algal-dominated hard-bottom" (Chiappone and Sullivan 1994a) implies, a variety of red, green, and brown macroalgae occur in hard-bottom habitat. However, bushy, red macroalgae are the dominant producers, primarily species of the genus *Laurencia* (Fig. 1 inset). In the Florida Keys, *Laurencia* spp. typically occurs in extensive (ca. 40% bottom), bushy patches (15–25 cm tall and 1.5 m in diameter), but it may grow to >0.5 m in height and cover >90% of the bottom in some areas (Mathieson and Dawes 1975; Josselyn 1977; Field and Butler 1994; Butler et al. 1997; Herrnkind et al. 1997).

Hard-bottom is a major feature of the Florida Keys marine landscape, constituting ~30% of the shallow coastal zone (Zieman et al. 1989; Field and Butler 1994; Herrnkind et al. 1997), the remainder being a mosaic of sand or mud bottom and seagrass. Although production by seagrass (primarily *Thalassia testudinum* König, but

also *Syringodium filiforme* Kützing and *Halodule wrightii* Ascherson) and seagrass epiphytes is thought to dominate in these regions (Fry et al. 1982; Fry 1984; Harrigan et al. 1989; Kitting et al. 1984; Zieman et al. 1989, 1999; Fourqurean et al. 1992), the degree of inter-habitat connectance between seagrass and hard-bottom regions is unknown, as are the basics of energy flow within hard-bottom communities. The contribution of seagrass as a source of carbon to adjacent habitats varies among studies in which stable isotopes have been used. Fry et al. (1982) found that coral reefs and surrounding seagrass meadows are largely supported by seagrass carbon, which they attributed to the foraging activity of reef organisms within seagrass beds and the subsequent transport of seagrass-derived energy onto the reef. No difference was found in the values of consumers from seagrass beds or adjacent epilithic algal communities in the Mediterranean Sea, with seagrass epiphytes and epilithic algae forming the majority of support for consumers in both habitats (Lepoint et al. 2000). Both Loneragan et al. (1997) and Marguillier et al. (1997) found that seagrass-derived carbon rather than that from adjacent mangroves dominated the carbon signature in fish and invertebrates they sampled from these and nearby offshore habitats. Food web components sampled in eelgrass beds in the Newport River estuary, North Carolina, had carbon isotope values more similar to phytoplankton than seagrass (Thayer et al. 1978). The primary objective of our study was to identify the primary sources of production supporting higher trophic levels at representative hard-bottom sites in the Florida Keys, and to examine whether hard-bottom organisms are dependent on adjacent seagrass habitat for that carbon.

Since the late 1980s, the central portion of Florida Bay has also been subject to dramatic environmental change. The best known, although still insufficiently understood, change in the ecosystem is the death of thousands of hectares of the seagrass *T. testudinum* (Zieman et al. 1988; Robblee et al. 1991; Fourqurean et al. 1992; Fourqurean and Robblee 1999; Peterson and Fourqurean 2001). In the early 1990s, massive blooms of cyanobacteria (*Synechococcus* sp.) blanketed over 500 $km^2$ of the Florida Bay region for months at a time and were followed by a mass die-off of nearly the entire sponge assemblage and dramatic reductions in the recruitment of spiny lobster (Butler et al. 1995; Herrnkind et al. 1997). This same region, because of its hydrological linkage with the Everglades, experiences remarkable annual and intra-annual fluctuations in salinity, up to 50 psu a year (Fourqurean and Robblee 1999). Beyond the decimation of individual species, large-scale disturbances may also indirectly affect ecosystem function via shifts in trophic structure or changes in the nutritional condition of affected organisms (McClelland and Valiela 1998; Street et al. 1997; Isaksson et al. 1994). It is not known whether such impacts have occurred in the hard-bottom communities of Florida Bay.

In this study, we provide the first isotope-based description of trophic relationships in hard-bottom communities in the Caribbean and specifically, the Florida Keys. We also used stable isotope analyses to assess if ecosystem disturbance over the past decade has had a persistent effect on the trophic relationships within hard-bottom communities in Florida Bay, through changes in the dominant primary producer(s) or trophic position of select species.

## Materials and methods

### Background

One method of assessing trophic relationships and energy flow is through the use of stable isotope analysis (see reviews by Fry and Sherr 1984; Wada et al. 1991; Lajtha and Michener 1994). All organisms possess stable isotopes of common elements such as carbon and nitrogen. The abundance of these heavier isotopes in samples is expressed as a ratio (in delta ($\delta$) units or‰) by the equation:

$$\delta X = \left(\frac{R_{sample}}{R_{standard} - 1}\right)1000,$$

where $X$ is $^{13}C$ or $^{15}N$ and $R = {^{13}C}/{^{12}C}$ or $^{15}N/^{14}N$, respectively. The standard for carbon is Peedee belemnite limestone and for nitrogen is air.

Carbon stable isotope data are typically used in ecological research to determine which primary producer components are the ultimate carbon source assimilated by higher trophic level consumers (Fry and Sherr 1984; Peterson and Fry 1987). Organisms typically have $\delta^{13}C$ values similar to their food source (Michener and Schnell 1994) or only fractionate (i.e., shift toward the heavier isotope) between 1‰ (Wada et al. 1991; Fry and Sherr 1984) and 2‰ (DeNiro and Epstein 1978), yielding slightly more enriched values. Determining the source of carbon in a system can be confounded by the presence of multiple primary producers that possess similar isotopic carbon values (Fry et al. 1982; Fry and Sherr 1984; Hemminga and Mateo 1996; Phillips 2001). The use of additional isotope ratios, such as nitrogen and sulphur, and mixing models, help to better distinguish trophic interrelationships and relative importance of each component (Fry and Sherr 1984; Harrigan et al. 1989; Kwak and Zedler 1997; Phillips 2001; Kharlamenko et al. 2001).

Nitrogen stable isotopes are more often used to study trophic levels in communities (Wada et al. 1991). Organisms tend to fractionate nitrogen positively by ~3‰ (Michener and Schnell 1994; Wada et al. 1991) with each change in trophic level. Thus, higher trophic levels will have higher $\delta^{15}N$ values due to the discriminatory retention of the heavy isotope over the light one (Minagawa and Wada 1984; Peterson and Fry 1987).
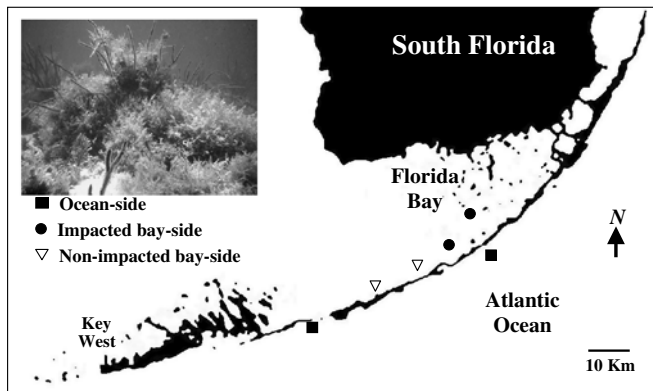
**Fig. 1** Locations of the sites sampled in the impacted bay-side, non-impacted bay-side, and ocean-side regions of the Florida Keys, Florida (USA). The inset picture shows how profuse the red macroalgae *Laurencia* spp often is in a typical hard-bottom area; here the algae is interspersed with octocorals

## Sample collection

In June–July of 1997, we sampled two hard-bottom sites in each of three regions in the middle and lower Florida Keys, Florida, USA (Fig. 1). The three regions are referred to as: (1) "ocean-side"—a shallow (< 3 m), nearshore region south of the Florida Keys, (2) "non-impacted bay-side"—a region in Florida Bay that has not experienced cyanobacteria blooms or sponge die-off, and (3) "impacted bay-side"—a region in Florida Bay that has experienced repeated blooms of cyanobacteria and incidents of sponge die-off from 1991 to 1995. Site locations were determined by consulting maps of bloom coverage created from weekly aerial surveys (T. Mathews, Florida Fish and Wildlife Conservation Commission, Marathon, Fla., unpublished data).

At each site, we hand-collected organisms representing different trophic levels from primary producers through secondary consumers. Composite samples suitable for stable isotope analysis were created by combining samples from 5 to 10 individuals for each type of organism from each site. Red macroalgae (*Laurencia* spp.) were collected from hard-bottom sites by selecting and combining small (250 ml), equal-sized samples from the top, center, and bottom of clumps of *Laurencia* spp. The macroalgae samples from Florida Bay were a mixture of *L. intricata* Lamouroux and *L. poitei* (Lamouroux) Howe, whereas ocean-side samples were dominated by *L. papillosa* (Agardh) Greville. Microalgal epiphytes were infrequently observed on any of the *Laurencia* spp. collected, possibly due to the antimicrobial properties of the numerous secondary metabolites produced by *Laurencia* spp. (Hay et al. 1987). The dominant seagrass in this portion of the Florida Keys is *T. testudinum*, and when collecting samples of this seagrass, we cut individual blades at the substratum. We obtained seagrass samples from meadows within 50 m of each hard-bottom area that we sampled. Particulate organic matter (POM) samples were obtained by pumping water from the middle of the

water column (ca. 1–2 m depth) through a filter apparatus with an in-line mounted pre-combusted glass fiber filter (0.45 μm pore size). A 200-μm screen was placed in-line immediately in front of the POM filter to eliminate most of the large zooplankton. It was not possible to isolate and analyze a pure phytoplankton sample. We obtained samples of sediment organic matter (SOM) by carefully removing the top 2 cm of sediment from the center of a 5×5 cm$^2$ area of open hard-bottom. The sponge *Ircinia stobilina* was subsampled by removing approximately 3 cm$^2$ of tissue from each sponge sampled at a site. At one impacted bay-side site (Old Dan Bank), *I. stobilina* was absent and a comparable substitute could not be found. All other organisms (i.e., gastropods, sea cucumbers, and spiny lobsters) were taken whole. We sampled only juvenile lobsters because adults are rarely found in shallow hard-bottom areas. All samples collected from the field were frozen at −20°C for later processing at Old Dominion University.

## Sample preparation/isotopic analysis

All samples were thawed and then rinsed with deionized water to remove seawater and foreign material. We obtained attached epibiont (i.e., epiphytes and epifauna) samples by scraping rinsed *T. testudinum* blades with the edge of a laboratory spatula. The entire scraping was used for analysis. Similarly, our water pump filters were scraped with a spatula to remove the POM. All of the internal tissues of the snail (*Lithopoma tectum*) were removed from their shell with forceps. Sponge samples were sliced into small pieces with a scalpel and kneaded to remove sediment and symbiotic organisms such as polychaete worms, amphipods and brittle stars. An unidentified sea cucumber (Holothuroidea) was cross-sectioned and the gut discarded prior to drying to exclude sediment and other debris that might confound the isotopic tissue analysis. All samples were dried at 52°C for 24 h or until dry. They were then ground to a powder in a mill (Wig-L-Bug; Crescent Dental) and stored in glass shell vials in a desiccator. With the exception of the spiny lobster muscle tissue sample, all samples were treated with HCl to eliminate inorganic carbon. Bosely and Wainright (1999) have demonstrated that neither freezing nor acidification has a significant influence on carbon or nitrogen stable isotopic compositions. Following acidification, re-drying and re-grinding, samples were analyzed at the Rutgers University Stable Isotope Laboratory using standard stable isotope analysis (for review see Ehleringer and Rundel 1989).

## Results

The mean ± 1 SD $\delta^{13}C$ and $\delta^{15}N$ isotope values (‰) for composite samples from each region are summarized in Table 1. A dual isotope plot was used to visualize

**Table 1** The mean $\delta^{13}C$ and $\delta^{15}N$ values (‰) ± 1 SD for composites (5–7 individuals/composite) created from impacted bay-side, non-impacted bay-side, and ocean-side hard-bottom habitats of the Florida Keys ($N = 2$ sites/region)

| Organism | Impacted bay-side | | Non-impacted bay-side | | Ocean-side | |
|---|---|---|---|---|---|---|
| | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{13}C$ | $\delta^{15}N$ |
| Particulate organic matter (POM)[a] | −18.0 | 1.8 | −18.0 | 1.8 | −17.2 | 0.1 |
| Sediment organic matter (SOM ) | −14.8 ± 0.7 | 0.6 ± 0.04 | −13.3 ± 0.8 | 0.09 ± 1.1 | −15.4 ± 0.3 | 0.7 ± 0.2 |
| *Laurencia* spp. (macroalgae) | −14.9 ± 1.1 | 4.3 ± 0.1 | −16.2 ± 3.4 | 2.3 ± 0.1 | −12.7 ± 0.7 | 2.6 ± 0.5 |
| Holothuroidea (sea cucumber) | −13.9 ± 0.9 | 4.1 ± 0.02 | −12.4 ± 0.2 | 4.3 ± 0.5 | −12.5 ± 0.04 | 5.0 ± 0.3 |
| *Panulirus argus* (lobster) | −11.8 ± 0.7 | 7.3 ± 0.1 | −12.0 ± 0.7 | 7.4 ± 0.2 | −12.6 ± 0.5 | 7.5 ± 0.2 |
| *Ircinia strobilina* (sponge)[b] | −10.8 | −1.6 | −10.6 ± 0.8 | 0.3 ± 0.6 | −10.8 ± 0.1 | 1.7 ± 0.1 |
| Epibiota (animals and algae) | −11.2 ± 1.3 | 4.2 ± 0.6 | −12.3 ± 1.6 | 4.1 ± 0.8 | −5.4 ± 0.2 | 3.6 ± 1.0 |
| *Lithopoma tectum* (gastropod) | −10.1 ± 1.8 | 4.9 ± 0.6 | −11.6 ± 1.2 | 4.2 ± 0.03 | −11.2 ± 0.1 | 4.3 ± 1.1 |
| *Thalassia testudinum* (seagrass) | −6.9 ± 0.3 | 2.9 ± 0.2 | −6.5 ± 0.7 | 2.8 ± 0.6 | −7.5 ± 0.5 | 3.2 ± 0.5 |

For regions in which only one composite was created a range is not reported
[a] Due to the homogeneity of water masses, only one composite was created from the bay-side and ocean-side areas
[b] *I. strobilina* was absent from one of the impacted bay-side sites

trophic relationships ($\delta^{15}N$) and primary production sources ($\delta^{13}C$) (Fig. 2). Three trophic levels were evident among the species we sampled, based on an enrichment of 3–5‰ per level. The spiny lobster is a secondary consumer in this system, solely occupying the third trophic level (TL). At TL2 lie a common gastropod, *L. tectum*, and a deposit-feeding holothuroidean. Epibiota, red macroalgae, and seagrass occupy TL1, with the epibiota intermediate between TL 1 and 2. Autotrophic epiphytes were not separated from attached invertebrates (e.g., hydroids), which explains this isotopic placement of the epibiota. Sponges, SOM, and POM had the lowest $\delta^{15}N$ values.

We found reasonable separation in $\delta^{13}C$ values among the potential sources of primary production in the hard-bottom community. POM collected from the water column had the most negative $\delta^{13}C$ values (−16 to −18‰), reflecting their phytoplankton constituent. The

$\delta^{13}C$ values of *Laurencia* and SOM were similar with $\delta^{13}C$ values between −13 and −16‰, suggesting that macroalgal detritus probably dominated SOM. We did not measure the isotope values for the benthic microalgal fraction separately from that of SOM in general because benthic microalgal mats are not a dominant feature of hard-bottom habitat in the Florida Keys, as they are in some marsh and estuarine habitats (Peterson et al. 1986; Kwak and Zedler 1997; Page 1997; Paterson and Whitfield 1997). In addition, our microscopic examination of the SOM showed only trace amounts of microalgae compared to the detrital load. The seagrass $\delta^{13}C$ signature was markedly different from the other producers, with $\delta^{13}C$ values of −6 to −7‰. With the exception of the highly enriched ocean-side $\delta^{13}C$ value (−5.4‰), seagrass epibionts had $\delta^{13}C$ values near −12‰ because these samples contained both epiphytes (e.g., microalgae and macroalgae) and epifauna (e.g., hydroids, bryozoans, etc.).

All animals sampled from hard-bottom sites had $\delta^{13}C$ values generally between −10 and −14‰, which are values enriched by 1–3‰ relative to macroalgae and SOM suggesting a trophic connection to these sources of primary production. The carbon and nitrogen isotope values for the animal taxa that we sampled did not differ among the ocean-side, non-impacted bay-side, and impacted bay-side regions (1-factor randomized block MANOVA; $df = 2$, Wilks' Lambda = 0.967; $P = 0.831$), although there were significant differences in $\delta^{13}C$ and $\delta^{15}N$ values among our selected species as one would expect.
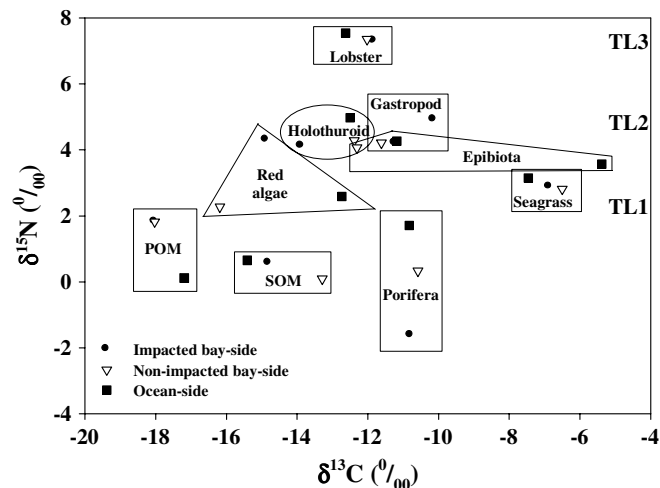


**Fig. 2** Dual isotope plot ($\delta^{13}C$ vs. $\delta^{15}N$) of values for primary producers and consumers of hard-bottom communities. Values for the same species or category are enclosed in *polygons*. Trophic levels (TL) were estimated based on an enrichment of ~3‰ per level

## Discussion

Our results suggest that the source of carbon supporting higher trophic levels in hard-bottom communities in south Florida is detritus available in SOM and derived largely from the highly prolific red macroalgae, with contributions from phytoplankton and adjacent seagrass beds. Based on stable isotope analysis alone, we also

cannot rule out the potential contributions of epiphytic algae on seagrass or sediment microalgae. *Laurencia* contains a suite of chemicals that deter direct herbivory (Fenical 1975; Erickson 1983; Paul and Hay 1986; Hay et al. 1987; Granado and Caballero 2001). The fate of these defensive compounds following decomposition has not been investigated, but the deterrent properties of many plant chemicals are lost following decay (Suren and Lake 1989; Baerlocher and Newell 1994). Thus, we suspect that most of the production attributable to *Laurencia* is consumed via a detrital pathway. However, several animals common in hard-bottom habitat (e.g., sea hares *Aplysia* spp., Rogers et al. 2002; Lapointe et al. 2004; the gastropod *Strombus gigas*, Hanisak 1992; LaPointe et al. 2004; and the spider crab *Mithrax sculptus*, Stachowicz and Hay 1996) graze *Laurencia* directly.

None of the animals we sampled had $\delta^{13}C$ values uniquely resembling seagrass, because $\delta^{13}C$ values of animals resemble their ultimate carbon source, or are only slightly (1–2‰) enriched (DeNiro and Epstein 1978; Fry et al. 1978; Petelle et al. 1979; Fry and Sherr 1984; Wada et al. 1991). The spiny lobster, which is a secondary consumer of mollusks, holothuroideans, and crustaceans (Andree 1981; Marx and Herrnkind 1985b; Herrnkind et al. 1988), had $\delta^{13}C$ values most resembling SOM, *Laurencia*, and epibiota. Although adult spiny lobsters are highly mobile and can move great distances (Herrnkind et al. 1975; MacDairmid et al. 1991; Cox et al. 1997; Kelly 2001), the absence of a dominant seagrass signal in their diet is evidence of the more restricted movement of juveniles within their hard-bottom nursery habitat. Surprisingly, the filter-feeding sponge *I. strobilina* that we sampled also had $\delta^{13}C$ values most similar to SOM and *Laurencia* spp., rather than POM as we expected. Sponges primarily filter bacteria- or smaller-sized particles (Reiswig 1971a; Ribes et al. 1999; Osinga et al. 2003). If the microbes are utilizing DOM derived primarily from the macroalgae that is so abundant on these sites, then they too would exhibit and transfer to the sponges a $\delta^{13}C$ signature most similar to macroalgae. The low nitrogen-based trophic placement of the sponge probably resulted from the presence of detrital particles, undigested microbes, and symbiotic microbes present within the sponge tissue that we processed (Wilkinson 1984; Corredor et al. 1988).

The trophic relationships, suggested from the representative hard-bottom organisms we selected in the Florida Keys, are strikingly different than those reported for seagrass communities, with which they intermingle. Harrigan et al. (1989) utilized isotope analysis and other techniques to investigate the source of nutritional support for the gray snapper in mangrove-dominated Whitewater Bay, Florida and at seagrass-dominated Schooner Bank in northwestern Florida Bay. The $\delta^{13}C$ values reported at Schooner Bank for *Laurencia* (−14.2‰) and epiphytes on the seagrass *Syringodium filiforme* (−11.7‰) were similar to values we obtained from the bay-side sites, whereas the POM value

(−15.3‰) was slightly more enriched (~2‰) than ours. $\delta^{13}C$ values reported by Harrigan et al. (1989) for the seagrass *T. testudinum* were considerably more negative (−13.6‰) than ours. This pattern is consistent with increased seagrass enrichment with decreasing latitude (Hemminga and Mateo 1996) and more oceanic-dominated waters, which typifies our sites south of Schooner Bank. Moreover, Evans (personal communication) found $\delta^{13}C$ values for *T. testudinum* ranged from −9 to −14‰ with a trend of increased enrichment from north to south in Florida Bay. The POM and SOM $\delta^{13}C$ values that we obtained from hard-bottom sites suggest that their source was primarily resuspended *Laurencia* detritus, rather than seagrass detritus, because *T. testudinum* had $\delta^{13}C$ values that were too enriched (−7‰) relative to most consumers to serve as their ultimate carbon source.

Stable isotope studies can yield equivocal results when primary producers have similar isotopic values (Fry et al. 1982), a problem we did not encounter. However, determining the relative contributions when multiple producers are present remains difficult, even when their isotope values vary. Our $\delta^{13}C$ values for seagrass (*T. testudinum*) were more enriched (−7‰) than most previously reported values (range: −7 to −16‰ for 12 studies reviewed; see Hemminga and Mateo 1996). The more depleted values for *Laurencia* (−13 to −16‰) allowed us to determine that it is a significant producer, though contributions from seagrass and phytoplankton are likely. Addressing the role of epiphytic algae in our study is difficult because the epiphyte load varied greatly in the regions sampled and was often mixed with other organisms (e.g., hydroids, tunicates, bryozoans, etc.) that we did not separate from the algae. The latter is one explanation for the exceptionally enriched $\delta^{13}C$ value observed for ocean-side epibiota (−5.4‰). Epiphyte loads are variable between seagrass beds in the Florida Keys, their biomass ranging from negligible to nearly equal that of the seagrass blade (LaPointe et al. 1994). Seagrass epiphytes can be important sources of energy for higher trophic levels, often eclipsing that of the seagrass (Fry 1984; Kitting et al. 1984; Yamamuro 1999; Moncreiff and Sullivan 2001; Vizzini et al. 2002). The $\delta^{13}C$ values for the epibiota from the bay-side sites suggests epiphytes may be contributing to primary production, but such is not the case on for ocean-side epibiota. Similarly, benthic microalgae may also contribute to the food web in hard-bottom and open sand communities, as it does in other systems (Peterson et al. 1986; Kwak and Zedler 1997; Page 1997; Moncreiff and Sullivan 2001). The $\delta^{13}C$ values for our SOM samples (−14‰) were similar to those for *Laurencia*, which dominates the vegetative biomass on hard-bottom sites in the Florida Keys. *T. testudinum* wrack is notably absent from hard-bottom areas (Behringer and Butler, personal observation), probably due to the nature of *T. testudinum* to sink, rather than be transported as occurs with more buoyant grasses (Zieman et al. 1979; Fry 1984; Fry and Virnstein 1988). Although the quantity of

microalgae available in the sediments of hard-bottom regions appeared, microscopically, to be inadequate to support production, the depleted $\delta^{15}N$ values of SOM relative to *Laurencia* spp. suggests another producer is present or a process is occurring to deplete the $\delta^{15}N$.

Isotopic mass balance equations are often used to estimate the range of possible contributions to the diet of an organism (Phillips 2001; Phillips and Gregg 2003). We used the Isosource program described by Phillips and Gregg (2003) to determine the feasible contribution ranges for the producers that support each of the hard-bottom consumers we sampled. Even after correcting for isotopic fractionation the number of potential sources and the geometry of their isotopic distribution yielded contribution ranges that were too broad to be useful. Further characterization of the primary producers in tropical hard-bottom communities would benefit from traditional or isotopic gut content analysis that could be used to constrain these ranges.

Our results also suggest that the cyanobacteria blooms, sponge mortalities, and seagrass die-offs that plagued the region over the past decade have not appreciably altered the general trophic relationships between hard-bottom organisms in the Florida Keys. Trophic relationships within the three hard-bottom regions (non-impacted bay-side, impacted bay-side, ocean-side) we sampled were isotopically indistinct, as reflected by statistically insignificant differences among regions and the isotopic similarity of like organisms. This is most likely due to similarities in the dominant primary producers and water quality of hard-bottom habitats in this area of western Florida Bay (Boyer et al. 1997). However, temporary alterations in trophic relationships within the affected hard-bottom sites would not have been detected by our sampling because of the time lapse between the last bloom (1995) and the inception of this study (1997).

Although red macroalgae is often profuse in hard-bottom areas (see inset, Fig. 1), it is notable that nearby seagrass beds contribute little to hard-bottom productivity. Dense, highly productive seagrass meadows, primarily the turtle grass *T. testudinum*, cover extensive areas of southwestern Florida Bay and the shallow coastal zone of the Florida Keys where macroalgae-covered hard-bottom habitat is also common (Zieman et al. 1989; Field and Butler 1994). The potential for transport of allochthonous seagrass-derived organic matter to adjacent hard-bottom habitats via detritus or animal movements is great. However, this potential varies among seagrass species and with local detrital transport dynamics. Large windrows of floating manatee grass, *S. filiforme*, can be transported long distances during wind events, whereas the detached blades of *T. testudinum* sink rapidly and are largely unavailable for mass transport (Zieman et al. 1979; Fry 1984; Fry and Virnstein 1988). Most seagrass in regions we sampled is *T. testudinum*, which may explain why we found little evidence of allochthonous, seagrass-based detritus in the hard-bottom areas we studied. It is possible that other hard-bottom areas receive more seagrass detritus, especially from *S. filiforme*, than those we sampled.

Seasonal changes in the environment can also affect the dominance of primary producers, as occurs, for example, between wet and dry seasons in an estuarine environment (Loneragan et al. 1997). Likewise, the ephemeral nature of *Laurencia may* create seasonal shifts in its influence on hard-bottom trophic structure. Seasonal sampling and collections of other representative taxa will be necessary to fully describe the trophic structure of shallow, hard-bottom communities. Although our study did not include a temporal component, the six hard-bottom sites we sampled were spread over a large area ($\sim$5,000 km$^2$) and we sampled a diverse, if somewhat numerically limited, taxonomic assemblage at each site. Nonetheless, our results offer intriguing evidence that hard-bottom communities are not solely dependent on allochthonous carbon import from nearby seagrass communities, but are probably supported by a mixture of producers including red macroalgae.

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