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TROPHIC LINKAGES AMONG PRIMARY PRODUCERS AND CONSUMERS IN FRINGING MANGROVES OF SUBTROPICAL LAGOONS

David K. Kieckbusch, Marguerite S. Koch, Joseph E. Serafy, and W. T. Anderson

ABSTRACT

Fringe mangroves associated with islands of the subtropical Atlantic/Caribbean region create extensive subtidal mangrove epibiont communities. While increasingly recognized as an important habitat, few studies have focused on the trophic structure of communities associated with mangrove prop-roots. We examined trophic linkages among primary producers (mangroves, seagrass, and algae) and consumers using stable carbon and nitrogen isotopes in fringe mangroves of the Bahamas and Biscayne Bay, Florida. The average $\delta^{13}C$ value of primary consumers (–16.4) was similar to macroalgae (–16.7) and seagrass epiphytes (–14.6) and highly distinguishable from mangroves (–27.4). Higher secondary consumers had enriched $\delta^{13}C$ values (–10.1) relative to primary consumers, and were similar to average seagrass $\delta^{13}C$ values (–10.5). The ranges of $\delta^{15}N$ signatures of vertebrate (6.3–12) and invertebrate (–0.4–10.7) consumers indicated a multi-trophic structure. Based on mixing equations, the majority of primary consumers diet was algal based, while secondary consumers depended on both algal and seagrass carbon. Mangroves do not appear to be the major source of carbon to consumers in fringe mangroves of subtropical lagoons. Rather, fringe island-associated mangroves constitute refugia for invertebrates and young reef fishes, and create substrate for a diversity of primary producers and consumers, thereby playing an important indirect role to the food web of these systems.

Over the last few decades, stable isotope studies (Haines and Montague, 1979; Fry, 1984; Peterson and Howarth, 1987; Sullivan and Moncreiff, 1990; Newell et al., 1995; Primavera, 1996; Lepoint et al., 2000; Chong et al., 2001; Bouillon et al., 2002a,b; Chanton and Lewis, 2002; Schwamborn et al., 2002) have questioned the paradigm that vascular plants are the primary carbon source supporting coastal wetland food webs (Odum and Heald, 1975). In the tropics and subtropics, mangrove ecosystems appear to be no exception. Most recent studies on the importance of mangrove carbon to primary consumers have focused on penaeid shrimp in Asia and Australia. In Malaysia (Newell et al., 1995), the Philippines (Primavera, 1996), China (Lee, 2000), and Australia (Loneragan et al., 1997) $\delta^{13}C$ isotopic signatures of shrimp (–8.5 to –20) from mangrove-associated estuaries more closely correspond to algae (–19.3 to –24.2), rather than mangroves (–28 to –29) or mangrove-based detritus (–27.3), with the exception of lighter carbon signatures of juvenile shrimp caught in some mangrove-lined tidal creeks (Newell et al., 1995). In contrast to Asia and Australia, few isotope food web studies have been conducted in fringing mangrove systems in the Atlantic/Caribbean region (Zieman et al., 1984; Stoner and Zimmerman 1988; Harrigan et al., 1989; Fleming et al., 1990). In the present study, we focus on the trophic relationship between primary producers and consumers within the submerged prop-root community of island-associated fringing mangroves of the Atlantic/Caribbean.

The Atlantic/Caribbean island-associated fringe mangrove systems are unique in that they are characterized by low tidal ranges and minimal runoff of terrestrial sediment. These conditions result in a high clarity subtidal mangrove fringe habitat with an extensive

prop-root epibiont community, primarily dominated by benthic algae and invertebrates. These prop-root communities also exhibit high fish densities, and are important habitats for juvenile and subadult reef fishes. We examined the relative importance of vascular and non-vascular plant carbon to dominant primary and secondary consumers in fringe mangroves of subtropical lagoons in the Bahamas (Grand Bahama and Andros Islands) and southeastern Florida (Biscayne Bay). We hypothesized that algal-derived carbon dominated by prop-root algae provides a major source of carbon to primary and secondary consumers in these fringe mangrove systems. We also hypothesized that adjacent seagrass beds, which frequently co-occur with fringe mangroves in Atlantic/Caribbean lagoons, are another major source of carbon. Three objectives were established to test these hypotheses. The first was to characterize the carbon and nitrogen isotopic signatures of the dominant primary producers (mangroves, phytoplankton, seagrasses, and macroalgae) and primary consumers (herbivorous and omnivorous marine invertebrates and vertebrates) within these epibiont fringing mangrove communities. The second was to compare the percent contribution of macroalgae, seagrass, and mangrove carbon to primary consumers using mixing equations. The third was to determine stable isotope signatures and gut content of an ecologically and economically dominant secondary consumer, the gray snapper, *Lutjanus griseus* (Linnaeus, 1758), in the fringe mangrove zone, and identify the primary consumers and producers upon which this target species depends.

Materials and Methods

Study Sites.—On two cruises to the Bahamas, one to Sweetings Cay on Grand Bahama Island (May 1998) and one to Fresh Creek on Andros Island (May 1999; Fig. 1), primary producers, primary consumers, and secondary consumers were sampled from fringing mangroves and adjacent seagrass beds. Stable isotope data from the Bahamas was expanded to include two fringe mangrove sites on Elliot Key in southeastern Florida (Fig. 1). Fringe mangroves on the bay side of Elliot Key were chosen because they were similar in size and structure to sites in the Bahamas. Biscayne Bay samples were collected from November 1999–October 2000. The Bahamas and Biscayne Bay sites allowed us to compare stable isotope data in fringing mangroves from two geographical regions.

Primary Producer Collection.—Live and senescent (yellow) mangrove leaves were harvested directly from the trees, while detrital leaves were collected from the top layer of sediment under the canopy. Mangrove leaves were thoroughly rinsed with deionized water (DIW) shipboard (Bahamas) or in the laboratory (Biscayne Bay) to remove all attached epibionts. Live (green) and detrital seagrass blades were sampled from *Thalassia testudinum* (Banks & Soland. ex Koenig) beds adjacent to the mangrove sites in both regions. Epiphytes were carefully scraped with a scalpel from freeze-dried seagrass leaves under a dissection microscope to remove epiphytic fauna. Macroalgae were collected from both within the prop-root zone and from adjacent seagrass beds. Once collected, the macroalgae were identified and epiphytes were removed by repeated rinsing with DIW. Sedimentary organic matter (SOM) was sampled from the top 2 cm of the sediment in *T. testudinum* beds adjacent to the fringe mangrove sites in Biscayne Bay. Phytoplankton samples were collected in Biscayne Bay by pre-filtering 30 L of water through a 100 μm mesh and passing it through pre-combusted (500ºC for 12 hrs) Whatman GF/F 0.2 μm filters. This process retained phytoplankton and excluded most of the zooplankton (Coffin and Cifuentes, 1993).

To obtain bacteria from Biscayne Bay for stable carbon and nitrogen isotope analysis, a bioassay incubation procedure was performed as described by Coffin and Cifuentes (1993). In summary, a growth medium was prepared by filtering 20 L of Biscayne Bay water through a 0.2 μm filter to remove all particles, including most bacteria. A second sample of water was filtered through a 1.0 μm filter to remove bactivores and particles >1.0 μm. The growth medium was then inoculated with a 1.0% by volume (200 ml) sample of the water that had been filtered with the 1.0 μm filter. The sample was incubated in darkness at room temperature (25ºC) for 24 hrs. Bacteria were then concentrated by filtration on pre-combusted (500ºC for 12 hrs) GF/F 0.2 μm filters.

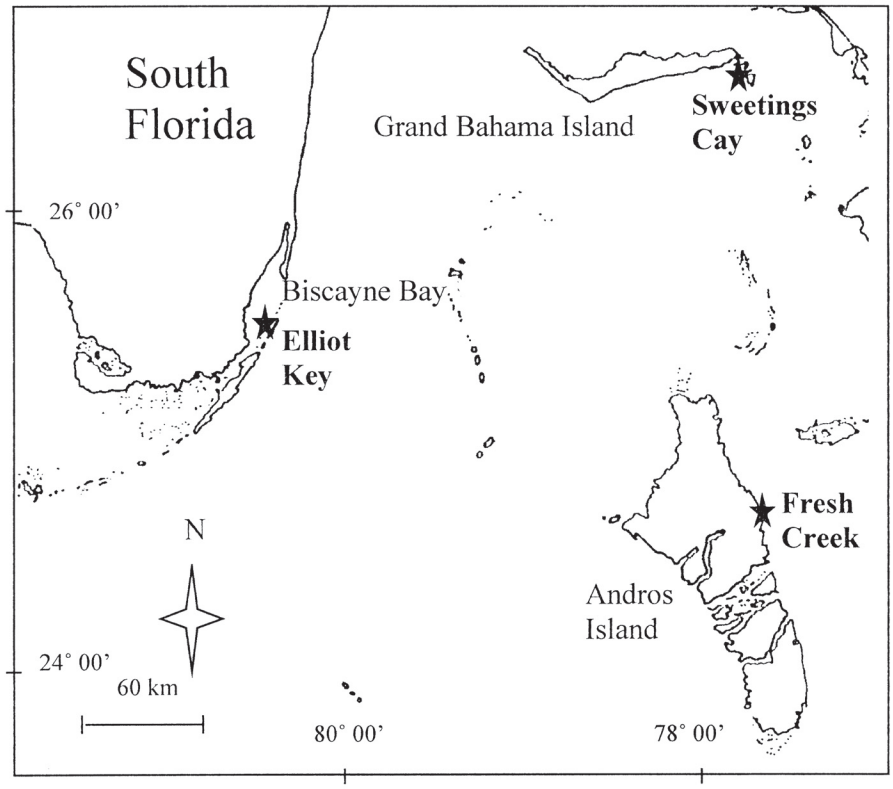

Figure 1. Map of sampling sites: Sweetings Cay, Grand Bahama Island; Fresh Creek, Andros Island, the Bahamas; and Elliot Key, Biscayne Bay, Florida.

Primary Consumer Collection.—Benthic consumers were collected by taking soil cores (20 cm diameter) to a depth of 40 cm in the mangroves and seagrass beds and were separated by rinsing the sediment with filtered seawater through sieves with mesh sizes from 1–20 mm. Epiphytic animals were manually extracted from macroalgae on the mangrove prop-roots and within the seagrass beds with the aid of a dissection microscope. All large primary consumers (e.g., crabs, clams, oysters, etc.) were collected by hand. Once collected, consumers were placed in pre-filtered (100 μm) seawater for 24 hrs to allow purging of their digestive tracts. After purging, all consumers were identified, rinsed with DIW, and frozen.

Secondary Consumer Collection.—Because of time constraints on the Bahamas cruises, the majority of fish analyzed in this study were from Biscayne Bay. Primary and secondary consumer fish were collected using cast nets, pole spears, dip nets, and hook-and-line baited with artificial lures. All fish collected were residing in the mangrove fringe, with the exception of the bar jack *Caranx rubber* (Bloch, 1793), yellowtail snapper *Ocyurus chrysurus* (Bloch, 1793), and yellowfin mojarra *Gerres cinereus* (Walbaum in Artedi, 1792), which were caught at the mangrove-seagrass transition zone. Collected specimens were placed on ice and frozen upon return to the laboratory. Based upon visual surveys, the gray snapper, *L. griseus,* was determined to be the dominant upper level consumer in fringe mangroves of Biscayne Bay (Serafy et al., 2003; pers. obs.) and the Bahamas (pers. obs.), and was selected as the secondary consumer target species in this study. In addition to isotope analyses, stomach contents of 18 gray snapper from Biscayne Bay were examined. These data are expressed as ash free dry weight (AFDW) of each prey item as a percentage of the total prey AFDW.

Tissue Preparation for Isotopic Analysis.—All plant and animal tissues collected were kept cold and immediately frozen upon return to the vessel or laboratory. Subsequently, tissues were freeze-dried and the dry weights recorded. Fish samples were prepared by filleting the dorsal muscle tissue to prevent contamination from the gut and bones (Gearing, 1991). All samples were ground using mortar and pestle followed by acidification with phosphoric acid (H_3PO_4, 0.4 M) for 18 hrs to remove inorganic $CaCO_3$ (Showers and Angle, 1986; Chanton and Lewis, 1999). Following acidification, samples were centrifuged and the acid decanted. The remaining sample was then rinsed with DIW four times and dried for 24 hrs at 70°C. Dried samples were then analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Fry et al., 1977; Fry and Parker, 1979).

Sample Analysis.—$\delta^{13}C$ and $\delta^{15}N$ isotopic composition of samples collected in the Bahamas were analyzed by Isotope Services, Los Alamos, New Mexico, while determination of stable $\delta^{13}C$ and $\delta^{15}N$ isotopic composition of samples collected in Biscayne Bay were run by the Southeast Environmental Research Center (SERC) Stable Isotope Laboratory at Florida International University. All analyses were measured using standard elemental analyzer (EA) isotope ratio mass spectrometer (IRMS) procedures. The EA is used to combust the organic material to form N_2 and CO_2 gases. Isotopic compositions of these gases were subsequently determined on a Finnagin MAT Delta C IRMS in a continuous flow mode.

The isotopic ratios are expressed in the δ notation which indicates the depletion (-) or the enrichment (+) of the heavy isotope, compared to the lighter isotope, relative to a standard according to the formula: $\delta^N E = [(R_{sample}/R_{standard}) - 1] \times 1000$, where N is the heavy isotope of element E (C or N), and R is the abundance ratio of the heavy to light isotope. The results are presented with respect to the international standards of atmospheric nitrogen (air, N_2) and Vienna PeeDee Belemnite (V-PDB) for carbon. Analytical reproducibility of this study based on sample replicates is better than ± 0.18 for $\delta^{13}C$ and ± 0.08 for $\delta^{15}N$ for analyses performed at SERC and ± 0.1 for $\delta^{13}C$ and ± 0.3 for $\delta^{15}N$ for analysis conducted at Los Alamos.

Data Analyses.—$\delta^{13}C$ versus $\delta^{15}N$ values were compared graphically to aid in the determination of trophic linkages based on $\delta^{15}N$ and to identify sources of nutrition using $\delta^{13}C$. To determine the potential relative contribution of carbon from each of the dominant primary producers (mangrove, seagrass, and macroalgae) to the primary and secondary consumers, mixing equations were used in addition to the gut content analysis. The carbon contributions to primary consumers were calculated with the following two-component mixing model based on Loneragan et al. (1997): $P_A = (\delta^{13}C_{consumer} - f - \delta^{13}C_{sourceB})/(\delta^{13}C_{sourceA} - \delta^{13}C_{sourceB})$, where P_A = proportion of consumers diet (assimilated carbon, C) from source A versus source B; and f = isotopic fractionation. The isotopic fractionation (f) is the enrichment (~1; Peterson and Fry, 1987; Michner and Schell, 1994; Cocheret de la Moriniere et al., 2003) in the carbon isotope ratio that occurs in an animal relative to its diet. By factoring out this isotopic shift, based on the ^{15}N data, we were able to more accurately compare the isotopic values of the primary producers to those of the consumers. Using the two-component mixing model, we calculated the contribution of each primary C source, assuming that only two sources are contributing to the isotope signature of the consumer. Although this approach has many obvious problems in interpretation, the range of possible contributions of different primary producers can be estimated (Loneragan et al., 1997). Mean differences among isotopic signatures of source and consumers and between Bahamas and Biscayne sites were tested using the Student's t-test. In cases where the underlying assumptions of normality and equal variance were violated, differences were examined using Non-parametric Mann-Whitney Rank Sum tests. Significance was declared at the $P < 0.05$ level.

Results

$\delta^{13}C$ Primary Producers.—On average, $\delta^{13}C$ signatures of the dominant primary producers were clearly distinguished (Fig. 2), specifically mangrove (–27.4 ± 0.8), seagrass (–10.5 ± 2.5) and algal (macroalgae –18.0 ± 5.4; phytoplankton –18.4 ± 0.1) signatures. While the stable carbon isotope composition of algae showed an extended range from

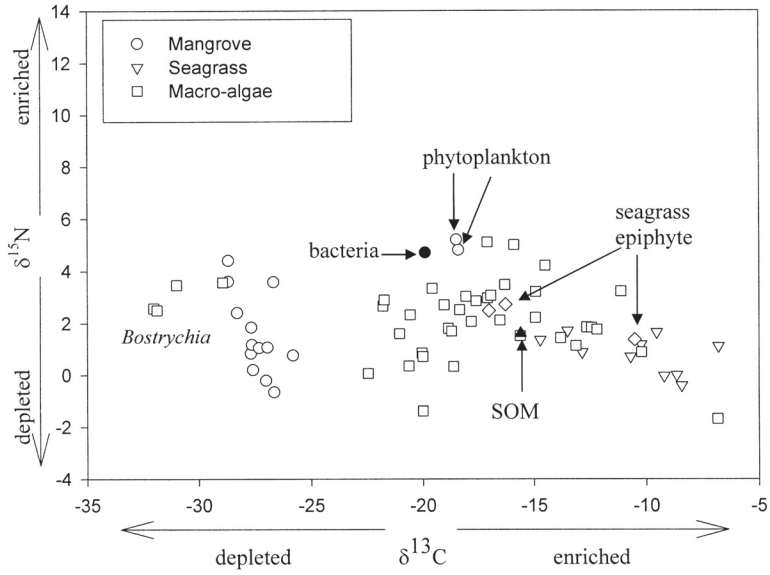

Figure 2. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of the three dominant primary producers (see key) and phytoplankton, seagrass epiphytes, bacteria, and sedimentary organic matter (SOM) (see arrows) collected from fringe mangroves in the Bahamas and Biscayne Bay, Florida.

–32.0 for *Bostrychia* to –6.8 for *Halimeda*, frequency analysis showed that 79% of the isotopic macroalgal values fell between –21.9 and –11.9. The mean $\delta^{13}C$ signature of macroalgae collected in the seagrass beds, –15.6 ± 5.2, was not significantly different from $\delta^{13}C$ of macroalgae associated with mangrove prop-roots, –17.0 ± 3.0 (Table 1). Macroalgal $\delta^{13}C$ signatures were similar between Biscayne Bay and Bahamas sites; however, they were slightly enriched in the Bahamas. Some of these differences may be accounted for by varying species collected from the two regions (Table 1).

Phytoplankton variability was low for both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 2; Table 1). The $\delta^{13}C$ signature for phytoplankton (–18.4 ± 0.1, n = 3) collected in Biscayne Bay adjacent to the fringe mangroves was slightly more enriched than an average of 56 literature values for marine phytoplankton (–21.3 ± 0.2, Peterson and Howarth, 1987). Bacteria in the water column, which had an enriched signature of –19.9, may have accounted for this difference. Both the phytoplankton and bacteria $\delta^{13}C$ signatures were within the range determined for macroalgae (Fig. 2) and thus indistinguishable from macroalgae. Therefore, when we define sources of carbon that contributed to primary consumers, the macroalgal source may also be attributable to phytoplankton or bacteria, recognizing that in these subtropical carbonate systems, phytoplankton biomass tends to be low. The similarity in $\delta^{13}C$ values between the SOM and the algae suggest that SOM is composed primarily of algal carbon or a mixture of algae and seagrass (Fig. 2). This algal component may be seagrass epiphytes and/or macroalgae, but the signature also reflects literature values for benthic microalgae (–14.9, Currin et al., 1995; and –15.6, Newell et al. 1995).

The $\delta^{13}C$ signature of *Bostrychia*, the highest intertidal alga collected from the mangrove prop roots, was significantly more depleted ($P < 0.01$) than the mean value of other macroalgal species (Table 1, Fig. 2). In fact, the $\delta^{13}C$ signature of *Bostrychia* was more similar to mangrove $\delta^{13}C$, suggesting that atmospheric CO_2 was utilized in photosynthe-

Table 1. $\delta^{13}C$ and $\delta^{15}N$ isotope signatures for dominant primary producers collected in the Bahamas and Biscayne Bay. Macroalgae (genus) are separated into collections from seagrass and mangrove communities. Mean ± SD (n).

	$\delta^{13}C$(‰)		$\delta^{15}N$(‰)	
Sample	Biscayne Bay	Bahamas	Biscayne Bay	Bahamas
Vascular Plants				
Mangrove	–27.0 ± 0.65(7)	–27.9 ± 0.78(6)	0.6 ± 0.72	2.7 ± 1.52
Rhizophora mangle (detritral)	–27.6 ± 0.19(3)	–28.0 ± 0.45(2)	1.0 ± 0.17	2.1 ± 0.39
R. mangle (senescent)	–26.9 ± 0.05(2)	–27.7 ± 1.42(2)	0.4 ± 0.91	3.6 ± 0.01
R. mangle (live)	–26.2 ± 0.59(2)	–28.2 ± 0.78(2)	0.1 ± 1.00	2.3 ± 2.97
Seagrass	–11.9 ± 2.06(6)	–8.3 ± 1.04(4)	1.2 ± 0.40	0.2 ± 0.66
Thalassia testudinum (live)	–11.5 ± 2.81(3)	–8.0 ± 1.01(3)	1.4 ± 0.24	–0.2 ± 0.79
T. testudinum (detrital)	–13.2 ± 0.46(2)	–9.2(1)	1.3 ± 0.59	–0.1
Syringodium filiforme (live)	–10.7(1)		0.7	
Algae	–18.9 ± 5.15	–15.6 ± 5.62	2.0 ± 1.13	2.6 ± 1.91
Algae: Seagrass community	–18.7 ± 2.23(6)	–9.2 ± 2.04(3)	1.2 ± 1.79	0.2 ± 1.65
T. testudinum epiphytes	–16.7 ± 0.52(2)	–10.5(1)	2.6 ± 0.16	1.4
Penicillus	–18.3 ± 0.39(2)	–10.2(1)	1.7 ± 1.90	0.9
Avrainvillea	–21.2 ± 1.74(2)		–0.7 ± 1.03	
Halimeda		–6.8(1)		–1.7
Algae: Mangrove community	–18.9 ± 5.76(24)	–17.7 ± 4.69(9)	2.1 ± 0.88	3.4 ± 1.17
Bostrychia	–31.6 ± 0.55(3)	–28.9(1)	2.8 ± 0.55	3.6
Caulerpa	–15.8 ± 3.57(8)	–16.5(1)	2.3 ± 0.82	2.1
Acetabularia	–16.4 ± 2.05(2)	–14.5(1)	2.2 ± 0.07	4.2
Laurencia	–13.8(1)		1.4	
Hypnea/Laurencia	–19.0(1)		2.7	
Padina	–21.7(1)		2.9	
Dictyosphaeria	–18.3(1)		2.5	
Valonia	–16.9(1)		3.1	
Udotea	–15.6(1)		1.5	
Halimeda	–18.9 ± 3.23(5)		1.0 ± 0.76	
Dictyota		–19.6(1)		3.3
Jania		–17.1(1)		5.1
Dasycladus		–15.9(1)		5.0
Algal composite*		–15.6 ± 2.99(3)		2.5 ± 0.67
Phytoplankton	–18.4 ± 0.06(3)		4.9 ± 0.23	
Sedimentary organic matter	–15.6(1)		1.6	
Bacteria	–19.9(1)		4.7	

sis when the prop-roots were exposed to air at low tide. Newell et al. (1995) observed depleted $\delta^{13}C$ signatures for *Gracilaria* (macroalgae) on creek banks of a Malaysian mangrove forest, and also attributed this anomalous signature to atmospheric CO_2 utilization at low tide. Because the $\delta^{13}C$ of *Bostrychia* represented an outlier for submerged macroalgae, *Bostrychia* data were not included when determining potential trophic linkages among the three dominant primary producers and primary consumers.

The mangrove $\delta^{13}C$ signatures were the most depleted of all primary producers sampled, with the exception of *Bostrychia* (Fig. 2). The $\delta^{13}C$ signatures for mangroves collected in Biscayne Bay and the Bahamas compared with ranges reported worldwide that encompass several genera (*Rhizophora, Sonneratia, Bruguiera, Avicennia;* –24.3 to –30; Rodelli et al., 1984; Harrigan et al., 1989; Fleming et al., 1990; Newell et al., 1995; Loneragan et al., 1997; Marguillier et al., 1997). These data show a wide geographic consistency of stable carbon isotopic signatures for mangroves. Analogous to this result, $\delta^{13}C$ of mangroves did not differ significantly between our Bahamas and Biscayne Bay sites or among live, senescent, and detrital leaves (Table 1).

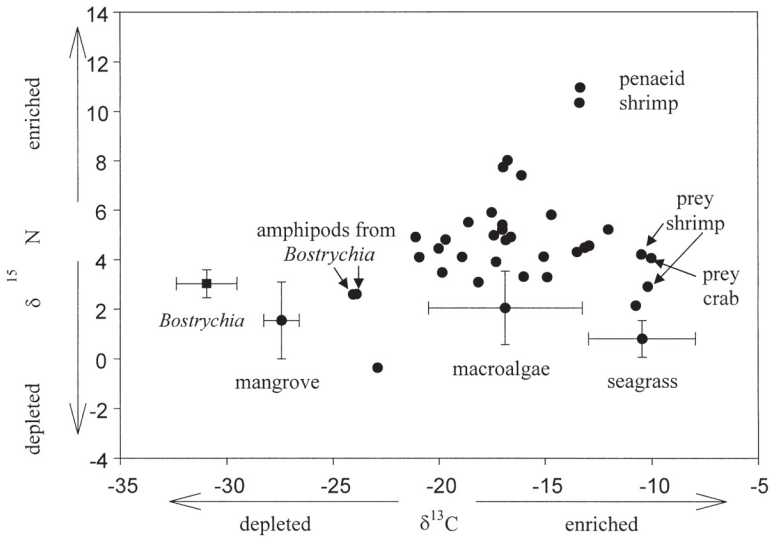

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of primary consumers (●) compared to the average values for dominant primary producers (± 1 SD) in the Bahamas and Biscayne Bay, Florida. Penaeid shrimp from the gut of the gray snapper and amphipods collected from *Bostrychia* on the mangrove prop-roots are identified.

The primary producers with the most enriched $\delta^{13}C$ signature were the seagrasses, *T. testudinum* and *Syringodium filiforme* Kuetz (Fig. 2; Table 1). Although there was a slight decrease in the mean $\delta^{13}C$ signature of *T. testudinum* tissue collected from the Bahamas relative to Biscayne Bay (Table 1), the range is within reported seagrasses values from other studies, –15.3 to –4.0 (Fry et al., 1982; Fry, 1984; Fry and Sherr, 1984; Harrigan et al., 1989; Fleming et al., 1990). No significant differences were found between live and detrital *T. testudinum* leaves (Table 1).

$\delta^{13}C$ Invertebrate Primary Consumers.—The $\delta^{13}C$ values of the invertebrate primary consumers spanned the mean and standard deviation of algae and seagrass carbon signatures (Fig. 3; Table 2). Mean primary consumer $\delta^{13}C$ values (16.4 ± 0.5) were not significantly different from the $\delta^{13}C$ signatures of algae (–16.7 ± 0.6) or seagrass epiphytes (–14.6 ± 2.1). In contrast, the mean $\delta^{13}C$ value of primary consumers differed significantly from mangroves (–27.4), ruling out mangroves as a sole carbon source. The primary consumers with the most depleted $\delta^{13}C$ signatures were the amphipods collected from *Bostrychia* on the mangrove prop-roots (Fig. 3), indicating their dependence on either *Bostrychia* and/or mangrove carbon. These amphipods were not included when calculating the mean $\delta^{13}C$ value for primary consumers (Table 2).

$\delta^{13}C$ Vertebrate Primary Consumers.—On average, the vertebrate primary consumers had enriched $\delta^{13}C$ signatures relative to the invertebrate primary consumers (Figs. 3,4; Table 2). However, these herbivorous, omnivorous, and planktivorous fishes were more depleted than the predatory fish (Fig. 4). The $\delta^{13}C$ values of non-predatory fishes were similar to the $\delta^{13}C$ signatures of algae and seagrass, but differed significantly from mangroves and *Bostrychia* (Fig. 4).

$\delta^{13}C$ Secondary Consumers.—Predatory fish $\delta^{13}C$ values were enriched relative to both the vertebrate and invertebrate primary consumers (Figs. 3,4). The raw $\delta^{13}C$ data of gray snapper, without isotopic adjustment for trophic level, differed significantly from

Table 2. $\delta^{13}C$ and $\delta^{15}N$ isotope signatures for primary and secondary consumers collected in The Bahamas and Biscayne Bay; Genus and species are given, when determined. Sample location for collections are in brackets: seagrass [SG], mangrove prop root [MPR], and mangrove fringe sediment [MSED]. Mean ± SD (n).

Sample	$\delta^{13}C$		$\delta^{15}N$	
	Biscayne Bay	Bahamas	Biscayne Bay	Bahamas
Primary Consumers				
Invertebrate	−17.4 ± 2.3	−16.5 ± 3.5	5.2±2.3	4.2±2.5
Polychaete [MPR]	−21.0 ± 0.1 (2)		4.5 ± 0.6	
Isopod [MPR]	−19.8 (1)		3.5	
Decapod/gastropod [MPR]	−17.4 (1)		5.0	
Nudibranch (*Elysia*) [MSED]	−19.7 (1)		4.8	
Blue crab (*Callinectes sapidus*) [MSED]	−16.1 (1)		7.4	
Pink shrimp (*Farfantepenaeus duorarum*) [SG]	−13.4 ± 0.0 (2)		10.7 ± 0.5	
Prey shrimp*	−10.4 ± 0.2 (2)		3.6 ± 0.9	
Prey crab*	−10.0 (1)		4.0	
Amphipod* (from *Bostrychia*) [MPR]	−24.0 ± 0.1 (2)	−17.5 (1)	2.6 ± 0.01	6.0
Isopod/amphipod [MPR]	−17.2 ± 0.2 (2)	−16.9 (1)	4.7 ± 2.1	7.7
Mud crab (*Panopeus herbstii*) [MPR]	−16.8 ± 0.3 (2)	−13.5 (1)	5.1 ± 0.2	4.3
Flat tree oyster (*Isognomon alatus*) [MPR]	−16.0 (1)	−14.9 ± 0.3 (2)	3.3	4.9 ± 1.2
Amphipod [MPR]		−17.5 (1)		5.9
Decorator crab (*Microphrys bicornutus*) [MPR]		−17.7 ± 1.3 (2)		5.2 ± 0.5
Shore crab (*Pachygrapsus transversus*) [MPR]		−13.5 (1)		4.3
Decorator crab/clam [MPR]		−10.8 (1)		2.1
Polychaete/bivalve [MPR]		−22.9 (1)		−0.4
Polychaete/clam [MPR]		−22.9 (1)		−0.4
Nudibranch (*Aplysia*) [SG]		−13.1 (1)		4.5
False blue crab (*Callinectes similis*) [SG]		−16.8 (1)		8.0
Hermit crab (*Pagurus*) [SG]		−18.1 (1)		3.1
Pen shell (*Atrina*) [SG]		−14.9 (1)		3.3
Vertebrate	−12.5	−13.3 ± 1.1	9.5	9.5 ± 2.2
Redear sardine (*Harengula humeralis)* [MPR]		−14.6 (1)		11.8
Parrotfish (*Scarus*) [MPR]		−11.7 (1)		6.3
Damselfish (*Pomacentrus*) [MPR]		−13.9 (1)		8.6
Sergeant major (*Abudefduf saxatilis*) [MPR]		−14.2 (1)		12.0
Yellowfin mojarra (*Gerres cinereus)* [SG]		−12.5 ± 1.9 (2)		9.3 ± 2.1
Yellowtail snapper (*Ocyurus chrysurus)* [SG]		−12.7 (1)		8.8
Pinfish (*Lagadon rhomboides)* [MPR]	−12.5(1)		9.5	
Prey fish*	−9.3(1)		8.7	
Secondary Consumers	−10.3±0.3	−10.1 ± 0.6	10.3 ± 0.6	9.7 ± 1.7
Gray snapper (*Lutjanus griseus)* [MPR]	−10.1±0.3 (19)	−10.1 ± 0.6 (3)	10.9 ± 0.1	9.7 ± 1.7
Bar Jack (*Caranx ruber*) [SG]	−10.5(1)		10.2	

*indicates sample not included in determination of means

those of mangroves and algae, but was not significantly different from seagrass. The $\delta^{13}C$ signature did not vary with fish size from 175–305 mm, total length (TL) (n = 18; Fig. 4), suggesting that the subadult gray snappers in Biscayne Bay forage on similar prey or prey with similar diets.

Gut Contents.—Out of the 18 gray snapper guts examined from Biscayne Bay, seven had indistinguishable stomach contents, seven had crabs, seven had shrimp, and five had small fish. On a weight by total volume basis, these prey items accounted for 59% crab, 20% fish, and 21% shrimp. While the gut contents provide an estimate of the major prey in the gut of this particular size class of gray snapper (175–305 mm TL), the isotope re-

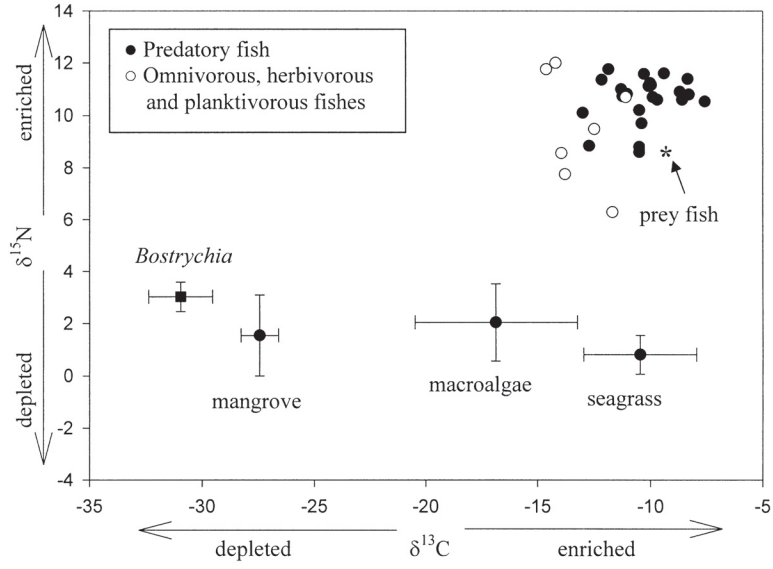

Figure 4. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of vertebrate primary consumers (nonpredatory fishes) and predatory fish compared to the average values for dominant primary organic sources (± 1 SD) in the Bahamas and Biscayne Bay, Florida.

sults of the prey may have been compromised. Invertebrate and vertebrate prey collected from the gut of the gray snapper had $\delta^{13}C$ signatures more enriched than any primary consumers collected from the fringe mangroves of the Bahamas or Biscayne Bay and reflect the same isotopic signatures as the gray snapper muscle tissue (Table 2; Figs. 3,4). It is assumed that this enrichment may have been the result of mixing with gray snapper carbon in the gut, or that the prey were captured at a location with different primary consumer signatures than sampled in this study.

Trophic Levels ($\delta^{15}N$).—The $\delta^{15}N$ values of the invertebrate consumers were enriched (range = 0.4–10.7, mean = 4.5 ± 2.4) relative to the mean values of the three dominant primary producers (Tables 1,2). The wide range of $\delta^{15}N$ signatures (6.3–12.0) of the herbivorous, planktivorous, and omnivorous fishes, as well as some of the invertebrates, suggest they feed at more than one trophic level (Figs. 3,4). The mean $\delta^{15}N$ value of the predatory fish (10.3 ± 0.6) was enriched in $\delta^{15}N$ compared to the majority of invertebrate (4.5 ± 2.4) and vertebrate (9.4 ± 1.8) primary consumers (Table 2; Figs. 3,4).

Mixing Equations.—The two-component mixing equation of algal versus mangrove carbon suggested that algae contributed 72% and mangroves 28% to invertebrate primary consumers (Table 3). Algae represented greater than 50% of the diet in the majority of invertebrate primary consumers sampled (79%). Amphipods collected on *Bostrychia*, as well as polychaetes and clams, appeared to rely on a lighter isotopic carbon source, potentially *Bostrychia* and/or mangrove carbon (Table 3). The importance of algal carbon in the diet of invertebrate primary consumers is slightly lower when compared to seagrass in the mixing equation. In this two-component model, algae represented 60% while seagrass accounted for 40% of the invertebrate diet (Table 3). The exception was the clam-crab aggregate sample, which was more closely aligned with seagrass (Table 3). Mixing model results comparing seagrass and mangrove carbon sources for invertebrates suggested a slightly stronger seagrass signature: 56% for seagrass carbon and

Table 3. Percentage of primary consumer diets potentially derived from mangrove (M), seagrass (S), and algal (A) carbon based on a 2-component mixing model. Blanks represent consumer values that fell outside the range of the two primary producers being modeled.

Primary consumer	Algae vs mangrove A/M	Algae vs seagrass A/S	Seagrass vs mangrove S/M
Invertebrate	72/28	60/40	56/44
Polychaete	50/50		32/68
Polychaete/clam	33/67		21/79
Isopod	62/38		39/61
Hermit crab	78/22		49/51
Decapod/gastropod	84/16		53/47
Spotted decorator crab	81/19		51/49
Amphipod	83/17		53/47
Amphipods from *Bostrychia*	20/80		12/88
Common Shore crab	70/30		44/56
Nudibranch (*Elysia*)	63/37		40/60
False blue crab	90/10		57/43
Blue crab	96/04		61/39
Isopod/amphipod	87/13		55/45
Mud crab (Biscayne)	90/10		57/43
Mud crab (Bahamas)		65/35	76/24
Pink shrimp		63/37	77/23
Decorator crab and clam		21/79	92/08
Flat Tree oyster		94/06	66/34
Nudibranch (A*plysia*)		58/42	79/21
Vertebrate		63/37	77/23
Parrotfish		35/65	87/13
Redear sardine		82/18	70/30
Damselfish		73/27	73/27
Sergeant major		76/24	72/28
Yellowfin mojarra		48/52	82/18

44% for mangrove carbon. These results are more difficult to interpret, because the algal carbon signature lies in between both the seagrass and mangrove signature. Nevertheless, the only invertebrates indicating a stronger mangrove than seagrass signature were the polychaetes, clams, and nudibranchs, as well as the amphipods from *Bostrychia*. Most of these invertebrates also indicated greater mangrove-based diets when compared to algae (Table 3). The vertebrate data for the algae-seagrass mixing model suggest the parrotfish (*Scarus* sp.) and yellowfin mojarra were utilizing seagrass in conjunction with algal carbon in their diets, while Redear sardines, *Harengula humeralis* (Cuvier, 1829), damselfish (*Pomacentrus* sp.), and sergeant major, *Abudefduf saxatilis* (Linnaeus, 1758), depend heavily on algal diets. Thus, in contrast to invertebrates, no vertebrates appeared to rely heavily on mangrove carbon (Table 3).

Discussion

Our stable isotope results suggest that algae are the strongest link between primary producers and primary consumers in island-associated fringing mangrove food webs of subtropical lagoons. We found the $\delta^{13}C$ values of the primary consumers were concentrated around the mean value of algae. The large differences between $\delta^{13}C$ values of

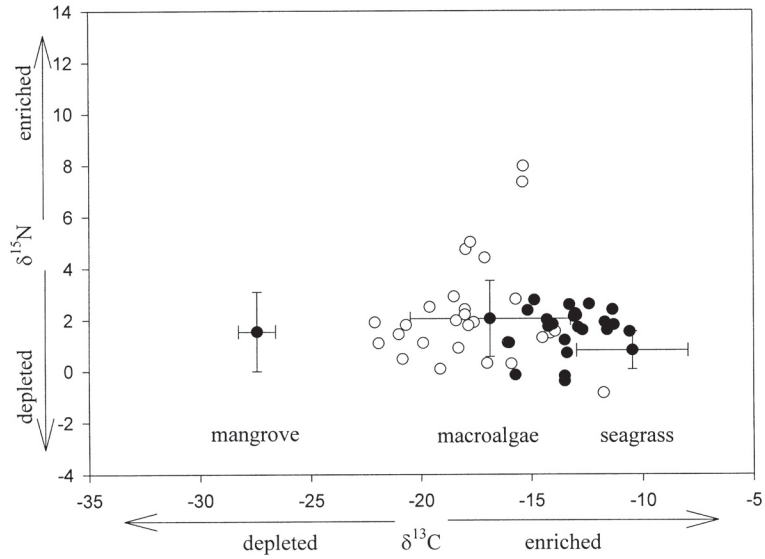

Figure 5. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of predatory fish (●) and primary consumers (o), after correcting for trophic fractionation.

mangroves and primary consumers suggest that the input of carbon through the mangrove detrital pathway may be minimal in comparison to input from algal and seagrass sources. These results add further support to the developing body of work indicating the importance of algae in mangrove (Newell et al., 1995; Primavera, 1996; Loneragan et al., 1997; Hsieh et al., 2000; Chong et al., 2001; Bouillon et al., 2002a,b; Schwamborn et al., 2002), seagrass (Fry et al., 1982; Fry, 1984; Lepoint et al., 2000), and salt marsh food webs (Peterson and Howarth, 1987; Sullivan and Moncreiff, 1990; Dittel et al., 2000).

Our two-component algae-seagrass mixing model results suggested that algae contributed the majority (60%) of the dietary carbon of primary consumers. In a comparative isotope study from Biscayne Bay, Fleming et al. (1990) indicated that primary consumers (crabs, snails, fishes, and oysters) derive 63% of their carbon from seagrass and the remaining 37% from mangroves. Our seagrass-mangrove mixing model indicated a similar apportionment of carbon for invertebrate (56% seagrass and 44% mangrove) and vertebrate (77% seagrass and 23% algae) primary consumers. In the Fleming et al. (1990) study, however, they did not consider two other dominant primary producers, benthic macroalgae, and phytoplankton. Our results suggest that this algal carbon may be the most important carbon source in fringing mangrove food webs of well-developed prop-root communities. The significance of this algal carbon may be attributed to the high physical digestibility and nutritional value of algae compared to vascular plants, which makes algae energetically desirable to grazers and detritivores (Nicotri, 1980; Tenore, 1988; Loneragan et al., 1997).

For this same reason, algal epiphytes on seagrass blades may also be significant. The similarity between the $\delta^{13}C$ values of the primary consumers (–16.4) and epiphytes collected in Biscayne Bay (–16.7) suggest that the seagrass epiflora potentially represent a key source of carbon. Both Fry (1984) and Lepoint et al. (2000) determined that epiphytic algae ($\delta^{13}C$ = –19.3) associated with *S. filiforme* seagrass beds were more important to faunal nutrition ($\delta^{13}C$ ranging from –16 to –22) than seagrass (–8). In the Mediterranean,

Lepoint et al. (2000) also determined that the $\delta^{13}C$ values of crustacean primary consumers (–17.5–23.1) in *Posidonia oceanica* (L.) Delile seagrass beds were more similar to the $\delta^{13}C$ values of the epiflora (–18.6) and dominant epilithic macroalgae (–18.3) than the $\delta^{13}C$ values of the seagrass (–13.9).

Based on carbon isotopic signatures, algal carbon may also be strongly linked to pink shrimp and other secondary consumers because they tend to be opportunistic omnivores and consume polychaetes, amphipods, isopods, small crustaceans, molluscs, and small fish (Zieman et al., 1984; Newell et al., 1995). Our data suggest that these primary consumers feed mostly on algae. Our mixing model results indicate that cancroid crabs and small herbivorous fish also obtain more than half of their carbon from seagrass-based sources, when comparing mangroves to seagrass, but obtain the majority of their carbon from algal sources when contrasted to seagrass.

There is also a link between algae and juvenile gray snapper (< 170 mm, TL) through invertebrates and vertebrates. While gray snapper examined in this study were all > 170 mm TL or subadult, juvenile snapper < 80 mm were found to primarily feed on amphipods (Starck and Schroeder, 1970). Of the possible primary carbon sources that we investigated, the isotope values for amphipods most closely resemble algae. The one exception was the more depleted carbon isotopic values for the *Bostrychia*-associated amphipods; however, our gray snapper carbon signatures did not reflect this depletion. The subadult gray snapper (80–170 mm, TL) diet consists largely of penaeid shrimp, cancroid crabs, and small demersal fish (Starck and Schroeder, 1970), and based on our data are linked to an algal or algal/seagrass diet. Larger subadults (> 170 mm, TL) feed primarily on fish and larger crustaceans (Starck and Schroeder, 1970), supported by the stomach contents found in gray snapper of this size class in Biscayne Bay: 59% crabs (*Panopeus* species), 21% shrimp, and 20% fish. The output from our seagrass-mangrove mixing model suggested that these prey items derive the majority (57–87%) of their carbon from seagrass. However, the algae-seagrass model estimates that almost two thirds of the prey diet comes from algal-based sources. Prey items of the gray snapper that we collected potentially derive the majority of their carbon from primarily algal and seagrass sources, while recognizing that we may not have encompassed all the prey base of this species in our sampling.

To better estimate the primary source of carbon to gray snapper, we corrected for trophic level and reexamined trophic relationships (Fig. 5). Consumers tend to be enriched in $\delta^{15}N$ by ~3.2 per trophic level (Minagawa and Wada, 1984; Peterson and Fry 1987). The difference in $\delta^{15}N$ between the gray snapper (10.7 ± 0.169) and the general primary producer signature, suggests a separation of approximately three trophic levels. The corrected snapper carbon signature was slightly more depleted (average = –13.2) and did not significantly differ from algae or seagrass. In contrast, $\delta^{13}C$ values between the gray snapper and mangroves remained significantly different after trophic adjustment. Thayer et al. (1987) examined fish utilization of the mangrove prop-root habitats in south Florida. They and others (Laegdsgaard and Johnson, 2001) determined that a smaller size class of fishes feeds upon primary consumers (amphipods, isopods, crabs, and small fish) located within the safety of mangrove prop-root zones. Our data link these invertebrates to algae either within the mangrove prop-roots or as epiphytes on adjacent seagrass beds. Thus, fringe mangroves likely serve as daytime refugia for fishes, as well as complex substrates for benthic algal colonization and secondary production of invertebrates and vertebrates, on which juvenile and subadult fish depend (Laegdsgaard and Johnson, 2001).

In conclusion, algae appear to play a significant role in the food web of island-associated fringing mangroves. While some invertebrate primary consumers (specifically crabs, polychaetes, and amphipods) associated with *Bostrychia* have a diet consisting of > 50% mangrove or other highly depleted carbon source, the majority of primary and secondary consumers, including pink shrimp and gray snapper utilize a heavier carbon source, and thus may be more dependent on algal/seagrass carbon. Subtropical lagoonal mangroves do not appear to be a major source of carbon in the diets of consumers. Rather, they constitute refugia for invertebrates and subadult reef fishes, as well as substrate for a diversity of primary producers and consumers that are important to the food web of these systems.

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Literature Cited

Bouillon, S., N. Koedam, A. V. Raman, and F. Dehairs. 2002a. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130: 441–448.

_____, A. V. Raman, P. Dauby, and F. Dehairs. 2002b. Carbon and nitrogen stable isotope ratios of subtidal benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India). Estuar. Coast Shelf Sci. 54: 901–913.

Chanton, J. P. and G. Lewis. 1999. Plankton and dissolved inorganic carbon isotopic composition in a river dominated estuary: Apalachicola Bay, Florida. Estuaries 22: 575–583.

_____ and _____. 2002. Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, USA. Limnol. Oceanogr. 47: 683–697.

Chong, V. C., C. B. Low, and T. Ichikawa. 2001. Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. Mar. Biol. 138: 77–86.

Cocheret de la Moriniere E., B. J. A. Pollux, I. Nagelkerken, M. A. Hemminga, A. H. L. Huiskes, and G. van der Velde. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotope and gut-content analysis. Mar. Ecol. Prog. Ser. 246: 279–289.

Coffin, R. B. and L. A. Cifuentes. 1993. Approaches for measuring stable carbon and nitrogen isotopes in bacteria. Pages 663–675 *in* P. Kemp, ed. Handbook of methods in aquatic ecology. Lewis Publishers, Boca Raton.

Currin, C. A., S. Y. Newell, and H. W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar. Ecol. Prog. Ser. 121: 99–116.

Dittel, A. I., C. E. Epifanio, S. M. Schwalm, M. S. Fantle, and M. L. Fogel. 2000. Carbon and nitrogen sources for juvenile blue crabs *Callinectes sapidus* in coastal wetlands. Mar. Ecol. Prog. Ser. 194: 103–112.

Fleming, M., G. Lin, and L. S. L. Sternberg. 1990. Influence of mangrove detritus in an estuarine ecosystem. Bull. Mar. Sci. 47: 663–669.

Fry, B. M. 1984. $^{13}C/^{12}C$ ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. Mar. Biol. 79: 11–19.

_____, R. Lutes, M. Northam, P. L. Parker, and J. Ogden. 1982. A $^{13}C/^{12}C$ comparison of food webs in Caribbean seagrass meadows and coral reefs. Aquat. Bot. 14: 389–398.

_____ and P. L. Parker. 1979. Animal diet in Texas seagrass meadows: ^{13}C evidence for the importance of benthic plants. Estuar. Coast. Mar. Sci. 8: 499–509.

_____, R. S. Scalan, and P. L. Parker. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. Geochim. Cosmochim. Acta. 41: 1875–1877.

_____ and E. B. Sherr. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27: 13–47.

Gearing, J. N. 1991. The study of diet and trophic relationships through natural abundance ^{13}C. Pages 201–218 *in* D. Coleman and B. Fry, eds. Carbon isotope techniques. Academic Press, London.

Haines, E. B. and C. L. Montague. 1979. Food sources of estuarine invertebrates analyzed using$^{13}C/^{12}C$ ratios. Ecology 60: 48–56.

Harrigan, P., J. C. Zieman, and S. A. Macko. 1989. The base of nutritional support for the gray snapper (*Lutjanus griseus*): an evaluation based on a combined stomach content and stable isotope analysis. Bull. Mar. Sci. 44: 65–77.

Hsieh, H. L., W. Y. Kao, C. P. Chen, and P. J. Liu. 2000. Detrital flows through the feeding pathway of the oyster (*Crassotrea gigas*) in a tropical shallow lagoon: $\delta^{13}C$ signals. Mar. Biol. 136: 677–684.

Laegdsgaard, P. and C. Johnson. 2001. Why do fish utilize mangrove habitats? J. Exp. Mar. Biol. Ecol. 257: 229–253.

Lee, S. Y. 2000. Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II: Trophic relationship based on carbon- and nitrogen-stable isotopes. Mar. Ecol. Prog. Ser. 205: 1–10.

Lepoint, G., F. Nyssen, S. Gobert, P. Dauby, and J. M. Bouquegneau. 2000. Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. Mar. Biol. 136: 513–518.

Loneragan, N. R., S. E. Bunn, and D. M. Kellaway. 1997. Are mangroves and seagrasses sources for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Mar. Biol. 130: 289–300.

Marguillier, S., G. van der Velde, F. Dehairs, M. A. Hemminga, and S. Rajagopal. 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by ^{13}C and ^{15}N. Mar. Ecol. Prog. Ser. 151: 115–121.

Michner, R. H. and D. M. Schell. 1994. Stable Isotope ratios as tracers in marine aquatic food webs. Pages 138–159 *in* K. Lajtha, and R. H. Michner eds. Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, Oxford.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta. 48: 1135–1140.

Newell, R. I., N. Marshall, A. Sasekumar, and V. Chong. 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Mar. Biol. 123: 595–606.

Nicotri, M. E. 1980. Factors involved in herbivore food preference. J. Exp. Mar. Biol. 42: 13–26.

Odum, W. E. and E. J. Heald. 1975. The detritus-based food web of an estuarine mangrove community. Pages 265–286 *in* L. Cronin, ed. Estuarine research. Academic Press, New York.

Peterson, B. J. and B. M. Fry. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18: 293–320.

_____ and R. W. Howarth. 1987. Sulfur, carbon and nitrogen isotopes used to trace organic matter flow in the saltmarsh estuaries of Sapelo Island, Georgia. Limnol. Oceanogr. 32: 1195–1213.

Primavera, J. H. 1996. Stable carbon and nitrogen isotope ratios of penaeid juveniles and primary producers in a riverine mangrove in Guimaras, Philippines. Bull. Mar. Sci. 58: 675–683.

Rodelli, M. R., J. N. Gearing, P. J. Gearing, N. Marshall, and A. Sasekumar. 1984. Stable isotope ratios as a tracer of mangrove carbon in Malaysian ecosystems. Oecologia 61: 326–333.

Schwamborn R., W. Ekau, M. Voss, and U. Saint-Paul. 2002. How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary? Mar. Ecol. Prog. Ser. 229: 195–205.

Serafy, J. E., C. H. Faunce, and J. J. Lorenz. 2003. Mangrove shoreline fishes of Biscayne Bay, Florida. Bull. Mar. Sci. 72: 161–180.

Showers, W. J. and D. G. Angle. 1986. Stable isotopic characterization of organic carbon accumulation on the Amazon Continental Shelf. Cont. Shelf. Res. 6: 227–244.

Starck, W. A. and R. E. Schroeder. 1970. Investigations on the Gray Snapper, *Lutjanus griseus*. Studies in tropical oceanography 10. University Miami Press, Miami. 224 p.

Stoner, A. W. and R. J. Zimmerman. 1988. Food pathways associated with penaeid shrimps in a mangrove-fringed estuary. Fish. Bull. 86: 543–551.

Sullivan, M. J. and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. Mar. Ecol. Prog. Ser. 62: 149–159.

Tenore, K. R. 1988. Nitrogen in benthic food chains. Pages 281–365 *in* T. Blackburn and J. Sorensen, eds. Nitrogen cycling in coastal marine environments. John Wiley & Sons, New York.

Thayer, G. W., D. R. Colby, and W. F. Hettler Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. Mar. Ecol. Prog. Ser. 35: 25–38.

Zieman, J. C., S. A. Macko, and A. L. Mills. 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bull. Mar. Sci. 35: 380–392.

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ADDRESSES: (D.K.K.) *Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149.* (J.E.S) *NOAA Fisheries, Southeast Science Center, 75 Virginia Beach Drive, Miami, Florida 33149* (W.T.A.) *Earth Sciences Department and Southeast Environmental Research Center, Florida International University, 11200 SW 8th St. University Park, Miami, Florida 33199.* CORRESPONDING AUTHOR: (M.S.K.) *Department of Biological Sciences, Aquatic Plant Ecology Lab, Florida Atlantic University, 777 Glades Road, Boca Raton, Florida 33431. E-mail: <mkoch@fau.edu>.*