TROPHIC LINKAGES OF PRIMARY PRODUCERS AND CONSUMERS IN FRINGING MANGROVES OF TROPICAL LAGOONS

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Trophic linkages of primary producers and consumers in fringing mangroves of tropical lagoons

by

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A Thesis Submitted to the Faculty of

The Charles E. Schmidt College of Science

in Partial Fulfillment of the Requirements for the Degree of

Master of Science

Florida Atlantic University

Boca Raton, Florida

May 2001

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Marguerite S. Koch, Department of Biology, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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ACKNOWLEDGEMENTS

I would like to thank Dr. Bill Anderson at the Stable Isotope Laboratory at Florida International University for his assistance during the analysis of samples collected in Biscayne Bay, and Dr. Jeff Chanton at Florida State University for support during the analysis of the samples collected in the Bahamas. In addition, I would like to thank the Aquatic Plant Ecology Lab (Dr. Marguerite Koch, Amy Gras, Chelsea Donovan, Sam Evans and James Ersknie) for their endless support and input throughout the entire thesis process. A special thank you is extended to my wife, Ana.

ABSTRACT

Author: David K. Kieckbusch

Title: Trophic linkages of primary producers and consumers in fringing mangroves of tropical lagoons

Institution: Florida Atlantic University

Thesis Advisor: Dr. Marguerite S. Koch

Degree: Master of Science

Year: 2001

Stable carbon and nitrogen isotope ratios were analyzed to investigate the trophic linkages between primary producers and consumers in fringing mangrove ecosystems of The Bahamas and Biscayne Bay, Florida. The isotope ratios, in conjunction with stomach content analysis, were used to trace the flow of organic matter from the primary organic sources (mangroves, seagrass and macro-algae) to primary consumers and ultimately to the gray snapper (*Lutjanus griseus*). We found the mean $\delta^{13}C$ value of the primary consumers (-17.1‰) to be closely related to the mean values of the macro-algal material (-16.7‰) and the seagrass (-10.5‰) with very little correlation to the carbon signature of mangroves (mean = -27.4‰). Our results suggest the ultimate source of carbon for the primary and secondary consumers, located at our study sites, is algal and seagrass material, individually or possibly as a mixture, and that mangroves are not the sole source of carbon in these systems.

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INTRODUCTION

The focus of previous mangrove ecosystem studies has been on the role of mangroves as nursery habitat for fish and invertebrate populations (Robertson & Duke 1987, Thayer et al. 1987, Blaber et al. 1989, Robertson & Duke 1990, Sheridan 1992, Mullin 1995, Vance et al. 1996, Marguillier et al. 1997). Although this nursery role is well established, the intricate structure of the mangrove forest food web has not been thoroughly researched, partially the result of methodological limitations. Various methods, such as gut content analysis, have been employed by ecologists to trace food webs, as in the classical estuarine food web study by Odum and Heald (1975). Gut content analysis identifies the ingestion of a particular plant or animal, but does not unequivocally show that this ingested carbon is assimilated. Also, the mechanical and chemical processing that takes place along the length of an animal's gut complicates the identification of ingested materials. Thus, the actual contribution of a prey item to the nutrition and growth of the animal is not known.

To overcome the problems associated with gut content analysis, both radioactive and stable isotopes have been used to trace estuarine food webs (Marples 1966, Adams & Angelovic 1970). Working in natural settings with radioisotopes has distinct drawbacks, such as the difficulties in the retrieval of a significant number of labeled specimens and/or the legal restrictions that accompany the use of radioactive materials (Michener & Schell 1994). The use of stable isotopes has several distinct advantages, including the ability to sample a wide range of flora and fauna inexpensively and quickly and the how

the isotopic composition change is predictable as the elements cycle through the system (Peterson & Fry 1987).

The primary theoretical basis of using stable isotopes such as the $\delta^{13}C$ isotope as a tracer is that the characteristic isotopic ratio of different food sources are preserved as the isotope is cycled through organisms and detritus (Gearing 1991). The stable isotopic ratio of animals are largely determined by the carbon isotopic ratio of the food that has been assimilated over the past several weeks or months (Fry & Sherr 1984). These ratios have proven to be useful to ecologists in determining sources of nutrition for consumers. Nitrogen isotopic ratios ($\delta^{15}N$) have also been used for determining trophic relationships among organisms. Stable isotopes are being used from the Antarctic to tropical coastal estuarine systems to aid in the determination of feeding relationships between trophic groups (Fry & Parker 1979, Haines & Montague 1979, Fry et al. 1982, Thayer et al. 1987, Wada 1993, Gu et al. 1997).

Trophic relationships are defined by distinguishing between $\delta^{13}C$ signatures of marine, estuarine, and terrestrial plant organic matter. This $\delta^{13}C$ signature is defined by the ratio of ^{12}C to ^{13}C with approximately 98.9% of carbon existing naturally as ^{12}C, and the remainder as ^{13}C (Boutton 1991). The variation of carbon isotopic signatures in primary producers is a consequence of isotopic fractionation that occurs during photosynthesis. Mangroves and seagrasses, two dominant primary producers found in tropical estuarine and coastal ecosystems, have unique signatures (Figure 1). Mangroves are defined as C_3 plants, because the first product of CO_2 fixation is a three-carbon compound phosphoglycerate (PGA). Most C_3 plants are isotopically depleted

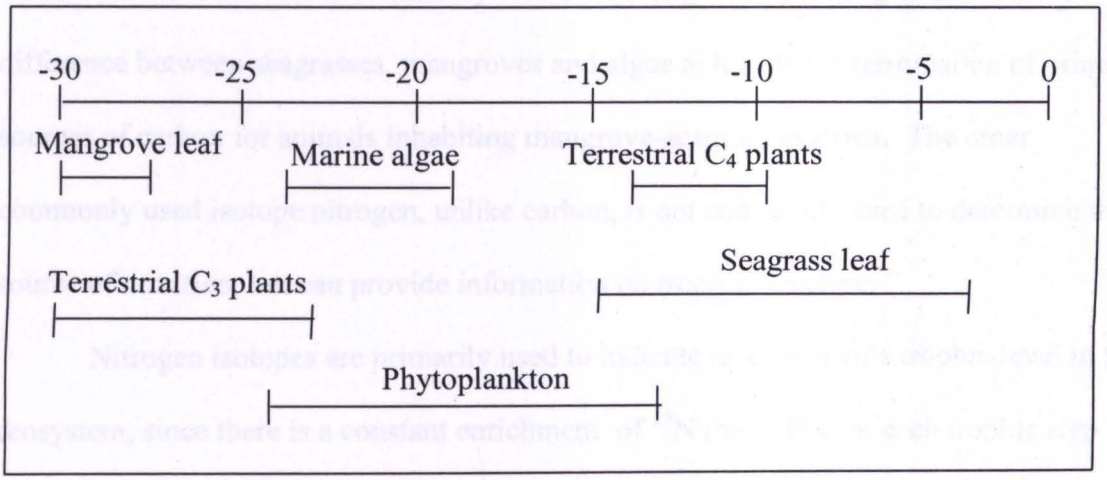

Figure 1. General range of $\delta^{13}C$ values of carbon sources in tropical coastal ecosystems compared to terrestrial C_4 and C_3 plants.

in ^{13}C compared to C_4 plants, and thus have a more negative signature. Seagrasses, such as the dominant tropical species *Thalassia testudinum,* although a C_3 plant, have a $\delta^{13}C$ value analogous to that of C_4 plants (Figure 1) that fix carbon dioxide into the four-carbon compound oxaloacetate. The $\delta^{13}C$ signature of marine algae, on average, is located between the values commonly found for mangroves and seagrasses. This difference between seagrasses, mangroves and algae aids in the determination of primary sources of carbon for animals inhabiting mangrove-seagrass systems. The other commonly used isotope nitrogen, unlike carbon, is not commonly used to determine the source of nutrition, but can provide information on trophic structure.

Nitrogen isotopes are primarily used to indicate an organism's trophic level in the ecosystem, since there is a constant enrichment of ^{15}N (by 3-4‰) at each trophic step (Fry & Sherr 1984). The enrichment of an animal relative to its food source, which is larger for $\delta^{15}N$ than for $\delta^{13}C$, is typically used to determine the trophic distance to the food source (Minagawa & Wada 1984). When enrichment occurs, preferential excretion of ^{14}N nitrogen, usually in the form of urea and ammonia (Minagawa & Wada 1984), causes a bio-magnification of ^{15}N up the food chain. Figure 2 illustrates how the ^{15}N isotope tends to increase in relation to ^{14}N with increasing trophic level (Peterson & Fry 1987). The trophic level of an organism, used in conjunction with the $\delta^{13}C$ value to determine the source of nutrition, can aid in establishing the contribution of primary producers to food webs.

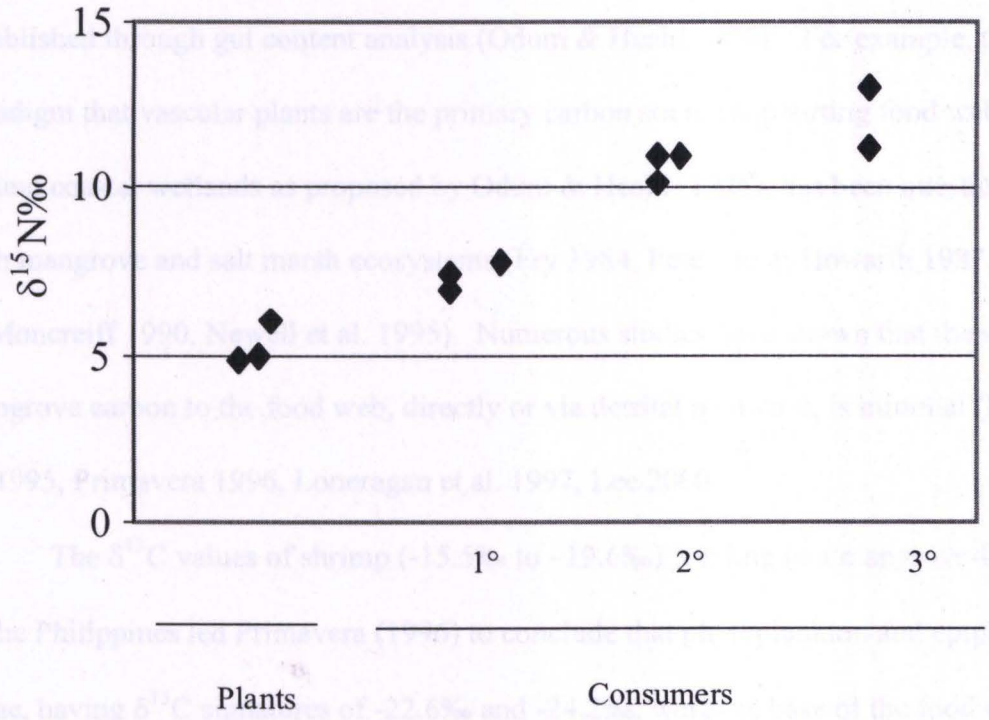

Figure 2. $\delta^{15}N$ for plants and primary, secondary and tertiary consumers illustrating the stepwise trophic enrichment of the ^{15}N isotopes (Deegan & Garritt 1997).

Stable isotope studies over the last few decades (Haines & Montague 1979, Fry 1984, Peterson & Howarth 1987, Sullivan & Moncreiff 1990, Newell et al. 1995, Primavera 1996, Lepoint et al. 2000) have brought into question food web paradigms established through gut content analysis (Odum & Heald 1975). For example, the paradigm that vascular plants are the primary carbon source supporting food webs in and around coastal wetlands as proposed by Odum & Heald (1975), has been questioned in both mangrove and salt marsh ecosystems (Fry 1984, Peterson & Howarth 1987, Sullivan & Moncreiff 1990, Newell et al. 1995). Numerous studies have shown that the input of mangrove carbon to the food web, directly or via detrital pathways, is minimal (Newell et al. 1995, Primavera 1996, Loneragan et al. 1997, Lee 2000).

The $\delta^{13}C$ values of shrimp (-15.5‰ to –19.6‰) residing in a mangrove-lined river in the Philippines led Primavera (1996) to conclude that phytoplankton and epiphytic algae, having $\delta^{13}C$ signatures of -22.6‰ and -24.2‰, were the base of the food web for shrimp rather than the mangroves (-28.6‰) or mangrove-based detritus (-27.3‰). In a mangrove-fringed estuary on the Pearl River of China, Lee (2000) showed the $\delta^{13}C$ signature of consumers (-20‰) to be more consistent with algal carbon ($\delta^{13}C$ range -21‰ to –19.3‰) than mangrove carbon (-28‰). Similarly, Newell et al. (1995) found in a Malaysian mangrove forest that overall; the amount of mangrove-based carbon ($\delta^{13}C$= -25.9‰) utilized by prawns ($\delta^{13}C$=-15.5‰) was small compared to benthic micro-algae ($\delta^{13}C$=-15.6‰). The exception to this pattern was seen in juvenile prawns ($\delta^{13}C$=-21.1‰) in tidal creeks, where mangrove based carbon was found to be important.

Similar to tropical mangrove forests, the carbon isotopic signature of estuarine and coastal invertebrates in temperate saltmarshes and seagrass beds tend to reflect the

$\delta^{13}C$ values of plankton and algae (-22‰ to -17‰), rather than the $\delta^{13}C$ values of *Spartina* (-13‰) or upland C_3 plants (-28‰) (Peterson & Fry 1987, Sullivan et al. 1990). Algae was found to be an important source of nutrition in *Syringodium filiforme* seagrass beds by Fry (1984) using stable isotopes in the Indian River Lagoon, Florida. Fry (1984) determined that local fauna ($\delta^{13}C$ range –16 to –22‰) possessed $\delta^{13}C$ isotope ratios more similar to benthic and epiphytic algae ($\delta^{13}C$ = -19.3‰) compared to seagrass detritus (-8‰).

While the above studies marginalize vascular plants as the source of carbon to coastal food webs, coastal wetland and estuarine fauna have also been shown to derive their carbon from multiple primary producers. This gives rise to a problem inherent to the stable isotope technique, which is a mixed signature. Mixture of two carbon sources occurs, giving a mixed $\delta^{13}C$ signature of the consumer. For example, the majority of the macrofauna collected by Peterson & Howarth (1987) in a salt marsh exhibited $\delta^{13}C$ values (-22‰ to -12‰) between those of plankton (-21‰) and *Spartina* (-13‰), and fall in the $\delta^{13}C$ range most commonly observed for macro-algae (-22‰ to -14‰, Sullivan & Moncreiff 1990). Although vascular plants still play an important role in coastal food webs, recent isotopic data lead to the hypothesis that plankton and algae can be equally or in some cases more important in the nutrition of fauna in coastal wetlands and estuaries.

This study was initiated to examine the relative importance of vascular versus nonvascular plants to the dominant primary and secondary consumers in high-clarity tropical and subtropical fringe mangrove ecosystems. The hypothesis was that algal-derived carbon in tropical fringe mangroves provides a major source of carbon to primary and secondary consumers in this ecosystem. Three objectives were established to test

this hypothesis. The first was to characterize the carbon and nitrogen isotopic signatures of dominant primary producers (mangroves, phytoplankton, seagrasses and macroalgae), primary consumers (herbivorous marine invertebrates and vertebrates) and secondary consumers (predatory fish) in the fringing mangrove-seagrass ecotone of a tropical lagoon in the Bahamas and a subtropical bay in South Florida. The second was to determine the percent contribution of macroalgae, seagrass and mangrove carbon to primary consumers using mixing equations. The third was to conduct stable isotope analysis of a dominant secondary consumer, gray snapper, and its associated gut contents, to determine which primary consumers were the dominant prey items of gray snapper, and on which primary producers they depend upon.

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), primary producers, primary consumers, and secondary consumers were sampled from the fringing mangroves adjacent to seagrass habitat (Figure 3). The Bahamas site provided a location to study the role of fringing mangroves to food webs, without the confounding effects of allochthonous material input from terrestrial sources. The Bahamas database was expanded to include data from two fringe mangrove sites on Elliot Key in Biscayne Bay, South Florida (Figure 3). Fringe mangroves on the Bay side of Elliot Key, similar in size and structure to the sites investigated in the Bahamas, were sampled from November 1999 to October 2000. Sampling in Biscayne Bay allowed a comparison isotopic data within the two geographical regions. Fish community studies (Faunce et al. in press) conducted by visual survey at the two Biscayne Bay sites facilitated the determination of the dominant secondary consumer, gray snapper (*Lutjanus griseus*).

Sample collection

Primary Producers

The dominant primary producers and primary and secondary consumers were collected at all fringe mangrove sites in the Bahamas and Biscayne Bay. Live and senescent (yellow) mangrove leaves were harvested from the trees and detrital leaves

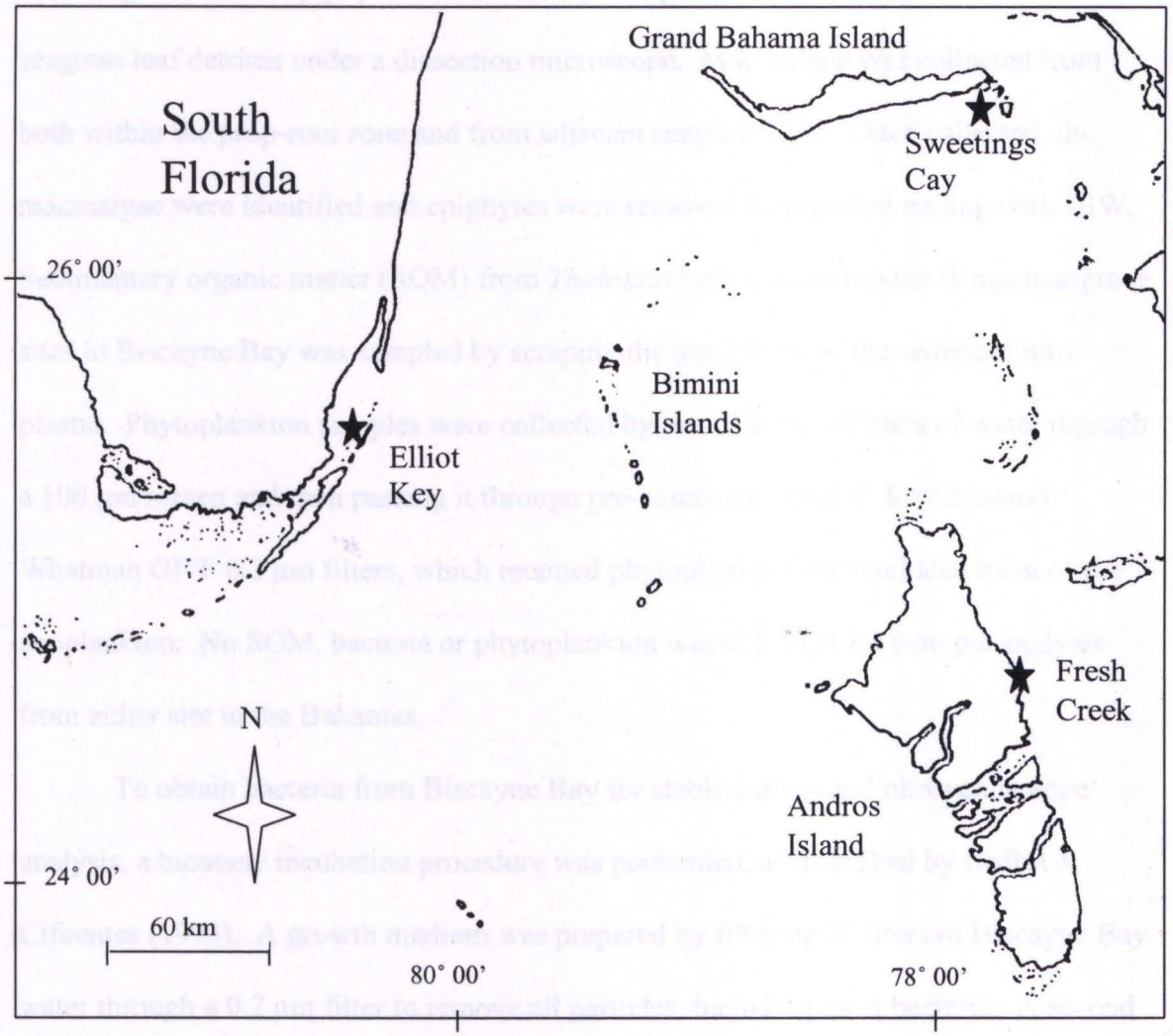

Figure 3. Location map of sampling sites: Sweetings Cay, Grand Bahama Island; Fresh Creek, Andros Island, The Bahamas; Elliot Key, Biscayne Bay, Florida.

were collected from the top layer of sediment under the canopy. All mangrove leaves were thoroughly rinsed with deionized water (DIW) aboard the ship (Bahamas cruises) or in the laboratory at Florida Atlantic University to remove all attached epibionts. Live (green) and detrital seagrass were sampled from *Thalassia*-dominated beds adjacent to the mangrove sites. Epiphytes were carefully scraped with a scalpel from freeze-dried seagrass leaf detritus under a dissection microscope. Macroalgae was 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) from *Thalassia* beds adjacent to the fringe mangrove sites in Biscayne Bay was sampled by scraping the top 2.0 cm of the sediment into plastic. Phytoplankton samples were collected by pre-filtering 30 liters of water through a 100 μm screen and then passing it through pre-combusted (500°C for 12 hours) Whatman GF/F 0.2 μm filters, which retained phytoplankton and excluded most of the zooplankton. No SOM, bacteria or phytoplankton was collected for isotopic analysis from either site in the Bahamas.

To obtain bacteria from Biscayne Bay for stable carbon and nitrogen isotope analysis, a bioassay incubation procedure was performed, as described by Coffin & Cifuentes (1993). A growth medium was prepared by filtering 20 liters 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% volume (200 ml) sample of the water that had been filtered with the 1.0 μm filter. The sample was then incubated

in the dark at room temperature 25°C for 24 hours. Bacteria was then concentrated by filtration on precombusted (500°C for 12 hours) GF/F 0.2 μm filters.

Primary consumers

Benthic consumers were collected by taking soil cores (20 cm diameter) to a depth of 40 cm in the mangroves and seagrass beds and separated by rinsing the sediment with filtered seawater through testing sieves with mesh sizes of 1.0 mm to 2.0 cm. Epiphytic animals were extracted from macroalgae on the mangrove prop roots and within the seagrass beds. All larger primary consumers (e.g. crabs, clams, oysters, etc.) were collected by hand. Once collected, consumers were placed in prefiltered (100 μm filters) seawater for 24 hours to allow purging of their digestive tracts. After purging, all consumers were identified, rinsed with DIW and frozen.

Secondary consumers

Most of the fish sampled in this study were from Biscayne Bay, because of time constraints on the Bahamas cruises. The numerically dominant fish were collected (when possible) from the fringe mangroves and adjacent seagrass areas using cast nets, pole spears, dip nets, and hook and line with artificial lures. Collected specimens were frozen immediately upon return to the laboratory. Based upon visual surveys (Faunce et al. in press, personal observations), the gray snapper (*Lutjanus griseus*) was determined to be the dominant upper level consumer in Biscayne Bay fringe mangroves and was selected as the target species.

The diet of the gray snapper from Biscayne Bay was determined by volumetric stomach content analysis of 18 fish. Stomach content is expressed as the ash free dry weight (AFDW) of a particular prey item as a percentage of the total prey AFDW.

Tissue preparation for isotopic analysis

All tissues collected from fish, primary producers, and consumers were kept cold and then 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 0.4 molar phosphoric acid (H_3PO_4) for 18 hours to remove any inorganic $CaCO_3$ (Showers and Angle 1986). Following acidification, samples were centrifuged and the acid decanted. The remaining sample was then rinsed with DIW four times and dried for 24 hours at 70°C. Dried samples were then analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Fry et al. 1977, Fry & 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 Stable Isotope Laboratory at Florida International University. All isotopic analyses were measured using standard elemental analyzer (EA) isotope ratio mass spectrometer (IRMS) procedures. The EA combusted

the organic material and reduced the formed gases into N_2 and CO_2. Isotopic compositions were subsequently determined on a Finnagin MAT Delta C IRMS in a continuous flow mode.

The ratios of heavy to light stable isotopes 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:

$$\delta^{N}E = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$$

where N is the heavy isotope of element E (carbon or nitrogen), 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 analysis performed at SERC and ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$ for analysis conducted at Los Alamos.

Data Analysis

Mixing Equation

$\delta^{13}C$ versus $\delta^{15}N$ values were compared graphically in dual isotope plots 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, algae and phytoplankton) to the primary and secondary consumers, mixing equations were used, in addition to gut content analysis. The carbon contributions to primary consumers were calculated with the

following two component mixing model from 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 from source A versus source B; and f = isotopic fractionation (‰). The isotopic fractionation (f) is the enrichment (~1‰) in the carbon isotope ratio that occurs in an animal relative to its diet. By factoring this isotopic shift out, we are able to more accurately compare the isotopic values of the primary producers and consumers. With a mixing model, we can calculate the contribution of each primary carbon source, assuming that only two sources are contributing to the isotope signature of the consumer (Figure 4). Although this approach has many obvious problems in interpretation, by using different end points, the range of possible contributions of different primary producers can be estimated (Loneragan et al. 1997).

Statistics

To determine if the differences that existed between the primary producers, primary consumers and secondary consumers and also between sites were significant, the stable carbon and nitrogen isotopic values were compared using Student's t-test. In cases where the underlying assumptions of equal variance between the two groups being compared were violated, the data was evaluated using Non-parametric Mann-Whitney Rank Sum tests. Significance is reported at the $P < 0.05$ level (Sigma Stat Version 2.03, 1997).

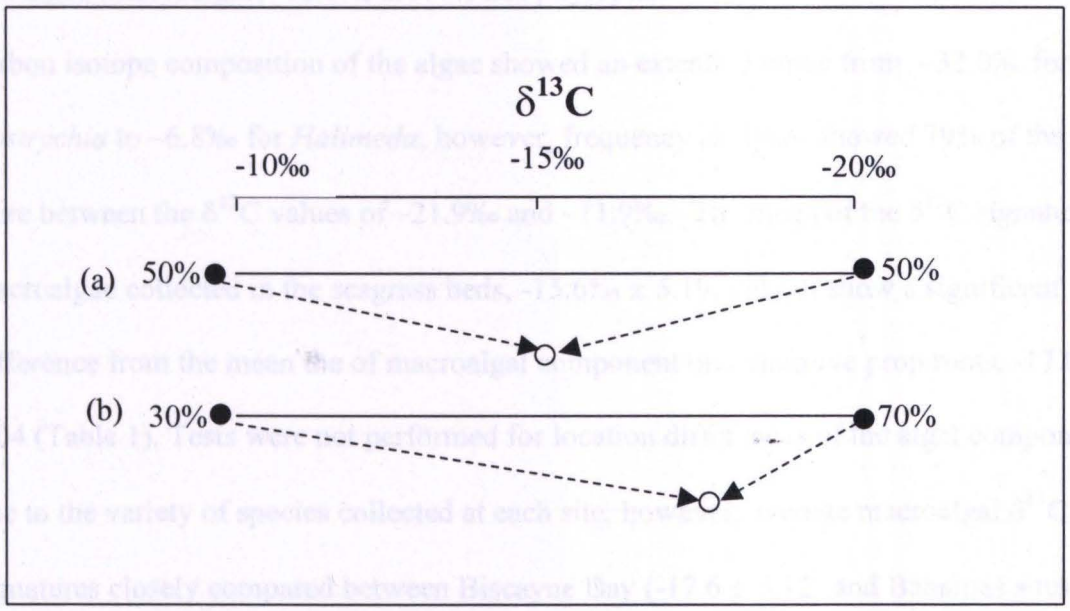

Figure 4. Isotopic mixing models used to determine the source of carbon. (a)Two end members (•) separated by a $\delta^{13}C$ value of 10‰ with the sample (o) having an intermediate isotopic value reflecting a simple 50/50 mixture of materials from the two sources, and (b) a two end member model with the isotopic composition of the sample suggesting a 70/30 mixture (b). (Modified from Fry & Sherr 1984)

RESULTS

Primary Producers

The mean $\delta^{13}C$ values of the dominant primary producers show distinct separation (Figure 5), particularly between red mangrove (–27.4‰ ± 0.83), seagrass (-10.5‰ ± 2.50), and algae (macroalgae, -18.0‰ ± 5.44; and phytoplankton, -18.4‰ ± 0.06). The stable carbon isotope composition of the algae showed an extended range from –32.0‰ for *Bostrychia* to –6.8‰ for *Halimeda*; however, frequency analyses showed 79% of the points were between the $\delta^{13}C$ values of –21.9‰ and –11.9‰. The mean of the $\delta^{13}C$ signatures of macroalgae collected in the seagrass beds, -15.6‰ ± 5.19, did not show a significant difference from the mean the of macroalgal component on mangrove prop roots, -17.0‰ ± 3.04 (Table 1). Tests were not performed for location differences of the algal component due to the variety of species collected at each site; however, average macroalgal $\delta^{13}C$ signatures closely compared between Biscayne Bay (-17.6 ± 3.12) and Bahamas sites (-14.4 ± 3.91).

The phytoplankton showed low variance in both the $\delta^{13}C$ values (-18.4‰ to –18.5‰, mean = –18.4‰) and the $\delta^{15}N$ values (4.8‰ to 5.2‰, mean = 4.9‰). The $\delta^{13}C$ values for phytoplankton (n =3), estuarine bacteria (-19.9‰, n =1) and sedimentary organic matter collected in the seagrass zone (-15.6‰, n =1) were similar to values determined for the combined macro-algae samples (Figure 5). The similarity in $\delta^{13}C$ values between the SOM and the algae suggest that the SOM is composed primarily of algal carbon. When comparisons were made between $\delta^{13}C$ values primary consumers and the algae,

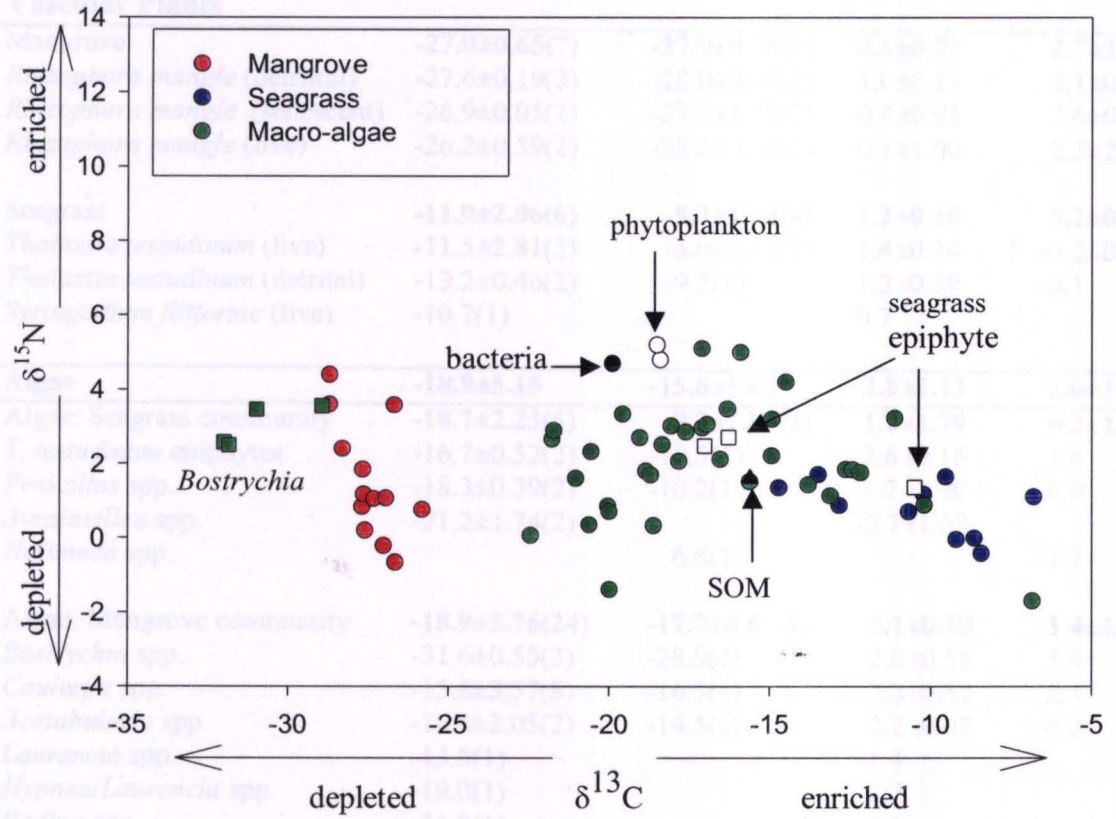

Figure 5. Carbon and nitrogen isotopic signatures of primary producers found in fringing mangrove ecosystems of Grand Bahama Island and Andros Island, The Bahamas, and Biscayne Bay, Florida.

Table 1. $\delta^{13}C$ and $\delta^{15}N$ isotope values for primary producers collected in The Bahamas and Biscayne Bay. All means represent the average of samples collected at the site indicated ± 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
Rhizophora mangle (senescent)	-26.9±0.05(2)	-27.7±1.42(2)	0.4±0.91	3.6±0.01
Rhizophora 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
Thalassia 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 spp.	-18.3±0.39(2)	-10.2(1)	1.7±1.90	0.9
Avrainvillea spp.	-21.2±1.74(2)		-0.7±1.03	
Halimeda spp.		-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 spp.	-31.6±0.55(3)	-28.9(1)	2.8±0.55	3.6
Caulerpa spp.	-15.8±3.57(8)	-16.5(1)	2.3±0.82	2.1
Acetabularia spp.	-16.4±2.05(2)	-14.5(1)	2.2±0.07	4.2
Laurencia spp.	-13.8(1)		1.4	
Hypnea/Laurencia spp.	-19.0(1)		2.7	
Padina spp.	-21.7(1)		2.9	
Dictyosphaeria spp.	-18.3(1)		2.5	
Valonia spp.	-16.9(1)		3.1	
Udotea spp.	-15.6(1)		1.5	
Halimeda spp.	-18.9±3.23(5)		1.0±0.76	
Dictyota spp.		-19.6(1)		3.3
Jania spp.		-17.1(1)		5.1
Dasycladus spp.		-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	

* Pooled sample of *Hypnea, Laurencia, Acetabularia, Batophora, and Dasycladus*

we were not able to differentiate the macro-algal sources of carbon from potential phytoplankton, bacteria and SOM sources. Because of this similarity, the phytoplankton, bacteria and SOM were omitted from analyses when determining sources of carbon for the primary consumers.

The $\delta^{13}C$ values of *Bostrychia* (-32.0‰ to –28.9‰), the highest intertidal algae collected on the mangrove prop roots, were significantly more depleted ($P < 0.01$) than the mean value of other species of macroalgae (-16.7‰ ± 3.62). In fact, the $\delta^{13}C$ signature of this algae was more similar to the red mangrove (*Rhizophora mangle)*, suggesting atmospheric CO_2 utilization during photosynthesis when exposed at low tide. The $\delta^{13}C$ signature of *Bostrychia* represented an anomalous value, and thus was not included when determining the potential trophic linkages.

The $\delta^{13}C$ values for *Rhizophora mangle* were, on average, the most depleted of all primary producers sampled, with the exception of *Bostrychia* (Figure 5). The mangroves did have a narrow range of $\delta^{13}C$ signatures (-25.8‰ to –28.7‰), which are within the published range of –24.3‰ to –30‰ for mangroves (Harrigan 1989, Fleming 1990, Newell 1995, Loneragan 1997, Marguiller 1997). The $\delta^{13}C$ values of the mangrove did not differ significantly between the Bahamas and Biscayne Bay sites nor among live, senescent and detrital leaves (Table 1).

The primary producers with the most enriched $\delta^{13}C$ values, on average, were the seagrasses *Thalassia* and *Syringodium* (Figure 5; mean = -10.5‰, range =-6.8‰ to –14.7‰). There was no significant difference found in $\delta^{13}C$ values between live and detrital *Thalassia* blades (Table 1). A comparison of $\delta^{15}N$ values for these samples also did not reveal any significant differences. Although there was a slight decrease in the mean $\delta^{13}C$

values of the Bahamas, relative to Biscayne Bay (Table 1), the seagrass collected in both locations had $\delta^{13}C$ values (-6.8‰ to –14.7‰) are similar to those reported in other studies, -4.0‰ to –15.3‰, (Fry et al. 1982, Fry 1984, Fry & Sherr 1984, Harrigan et al. 1989, Fleming et al. 1990). Since these samples from each location were collected in different seasons, the difference in $\delta^{13}C$ values, -8.3‰ during May 1998 and 1999 in the Bahamas, -9.9‰ during May 2000 and -12.9‰ November 1999 in Biscayne Bay, may be due to seasonal factors such as temperature and irradiance (Hemminga & Mateo 1996, Fourqurean et al. 1997). Despite these slight seasonal and geographic differences, all $\delta^{13}C$ values for the seagrasses collected were well within the published range, and thus were pooled when determining mean values in this study.

Primary Consumers

Invertebrate

The $\delta^{13}C$ signatures of the invertebrate primary consumers (-24.6‰ to –9.3‰, mean = -16.4‰ ± 0.50) spanned the mean and standard deviation of algae and seagrass $\delta^{13}C$ signatures (Figure 6, Table 2). Mean primary consumer $\delta^{13}C$ values were not significantly different from the $\delta^{13}C$ signatures of algae (-16.7‰ ± 0.58), or seagrass epiphytes (-17.0‰ to –10.5‰, mean =-14.6‰ ± 2.1). In comparison, the mean $\delta^{13}C$ value of the primary consumers differed significantly from the average $\delta^{13}C$ isotope signature of mangroves (-27.4‰), ruling out mangroves as a sole carbon source. The primary consumers that were most depleted in $\delta^{13}C$ signatures were the amphipods

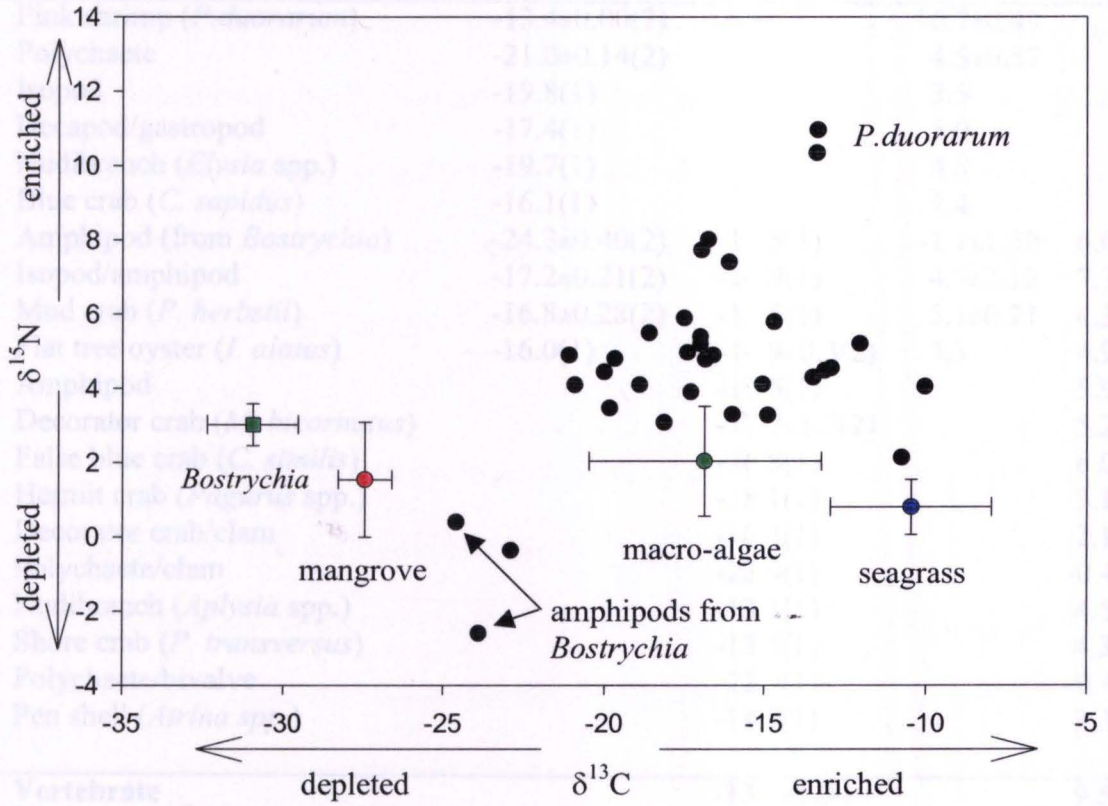

Figure 6. $\delta^{13}C$ and $\delta^{15}N$ isotopic values of primary consumers ( ) compared to the average values for dominant primary producers (± SD) in Grand Bahama Island and Andros Island, Bahamas and Biscayne Bay, Florida.

Table 2. $\delta^{13}C$ and $\delta^{15}N$ isotope values for primary and secondary consumers collected in The Bahamas and Biscayne Bay. All means represent the average of samples collected at the site indicated ± SD (n).

	$\delta^{13}C$(‰)		$\delta^{15}N$(‰)	
Sample	Biscayne Bay	Bahamas	Biscayne Bay	Bahamas
Primary Consumers				
Invertebrate	**-18.4±3.26**	**-15.9±3.08**	**4.7±3.22**	**4.5±2.01**
Pink shrimp (*P.duorarum*)	-13.4±0.00(2)		10.7±0.49	
Polychaete	-21.0±0.14(2)		4.5±0.57	
Isopod	-19.8(1)		3.5	
Decapod/gastropod	-17.4(1)		5.0	
Nudibranch (*Elysia* spp.)	-19.7(1)		4.8	
Blue crab (*C. sapidus*)	-16.1(1)		7.4	
Amphipod (from *Bostrychia*)	-24.3±0.40(2)	-17.5(1)	-1.1±1.50	6.0
Isopod/amphipod	-17.2±0.21(2)	-16.9(1)	4.7±2.12	7.7
Mud crab (*P. herbstii*)	-16.8±0.28(2)	-13.5(1)	5.1±0.21	4.3
Flat tree oyster (*I. alatus*)	-16.0(1)	-14.9±0.3(2)	3.3	4.9±1.2
Amphipod		-17.5(1)		5.9
Decorator crab (*M. bicornutus*)		-17.7±1.3(2)		5.2±0.5
False blue crab (*C. similis*)		-16.8(1)		8.0
Hermit crab (*Pagurus* spp.)		-18.1(1)		3.1
Decorator crab/clam		-10.8(1)		2.1
Polychaete/clam		-22.9(1)		-0.4
Nudibranch (*Aplysia* spp.)		-13.1(1)		4.5
Shore crab (*P. transversus*)		-13.5(1)		4.3
Polychaete/bivalve		-22.9(1)		-0.4
Pen shell (*Atrina spp.*)		-14.9(1)		3.3
Vertebrate		**-13.2±1.34**		**9.5±2.14**
Redear sardine (*H. humeralis)*		-14.6(1)		11.8
Parrotfish (*Scarus* spp.)		-11.7(1)		6.3
Damselfish (*Pomacentrus* spp.)		-13.9(1)		8.6
Sergeant major (*A.saxatilis*)		-14.2(1)		12.0
Yellowfin mojarra (*G. cinereus)*		-12.5±1.9(2)		9.3±2.05
Yellowtail snapper (*O. chrysurus)*		-12.7(1)		8.8
Pinfish (*L. rhomboides)*	-12.5(1)		9.5	
Secondary Consumers	**-10.2±1.39**		**10.9±0.51**	
Gray snapper (*L. griseus)*	-10.1±0.33 (19)	-10.1±0.6(3)	10.9±0.11	9.7±1.68
Bar Jack (*C. ruber*)	-10.5(1)		10.2	

(-24.6‰ and -23.9‰) that were sorted from samples of the algae *Bostrychia* (Figure 6). Coincidentally, this algae had the most depleted $\delta^{13}C$ value of all primary producers collected in Biscayne Bay and the Bahamas (Figure 6, Table 2). Since the outlying $\delta^{13}C$ values for the *Bostrychia* were not included in calculations for algae, the $\delta^{13}C$ values of the amphipods collected from the *Bostrychia* were not included when calculating the mean values for the primary consumers. The primary consumers with the most enriched $\delta^{13}C$ signatures (-10.5‰ to –9.3‰) were the prey items collected from the stomachs of the gray snapper (*Lutjanus griseus*) sampled in Biscayne Bay. This enrichment may be the result of the mixing of gray snapper carbon with prey items that occurs during the course of digestion.

The $\delta^{15}N$ values of the invertebrate primary consumers were enriched (2.9‰ to 11.0‰, mean = 5.2‰ ± 2.0) compared to the mean values of the three dominant primary producers collected (mangrove = 1.5‰ ± 1.55, seagrass = 0.8‰ ± 0.74, macroalgae = 2.1‰ ± 1.43) (Figure 6). This enrichment allowed the separation of the primary consumers into separate trophic levels, since the majority of primary consumers (89%) exhibited a greater enrichment of the $\delta^{15}N$ isotope, compared to the primary producers (2-3‰).

Vertebrate

The vertebrate primary consumers collected in the Bahamas had $\delta^{13}C$ values (-14.6‰ to –11.1‰, mean = -13.1 ± 1.27‰), (Figure 7 and Table 2) that were enriched in ^{13}C relative to the invertebrate primary consumers (Figure 6). The $\delta^{13}C$ values of these

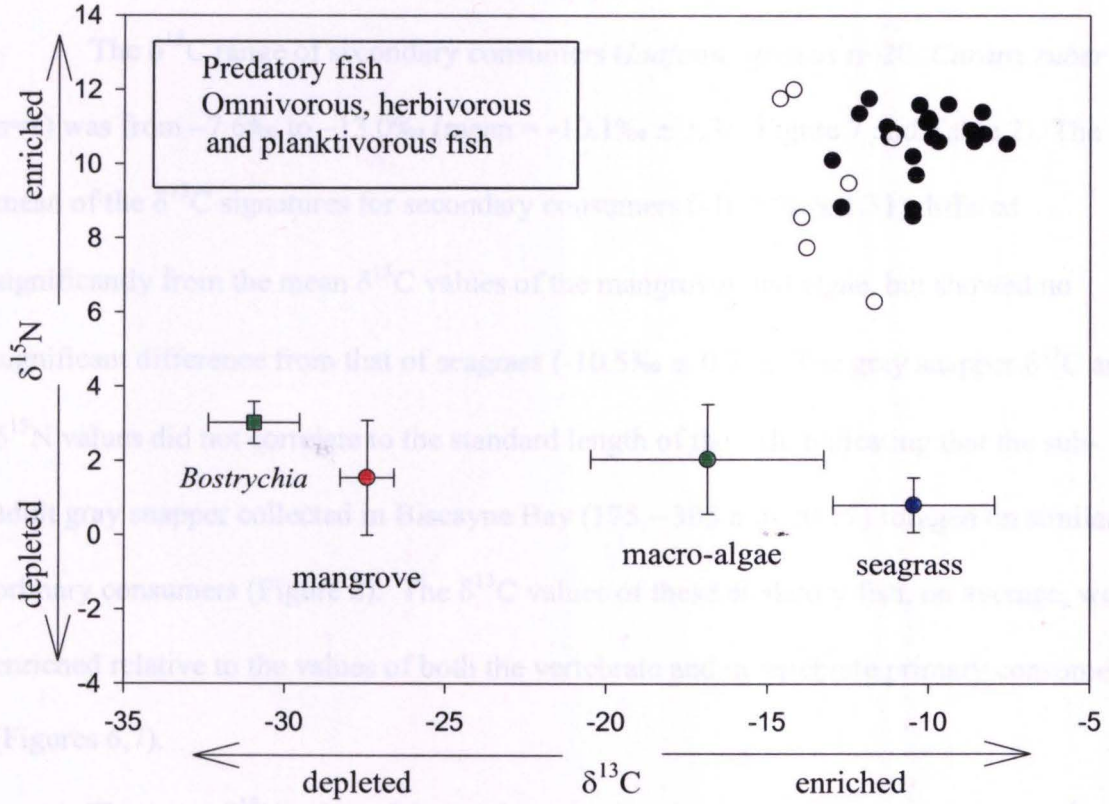

Figure 7. Isotopic signatures of predatory fish and vertebrate primary consumers (nonpredatory fish) compared to possible primary organic sources (± 1 SD) from Grand Bahama Island and Andros Island, Bahamas, and Biscayne Bay, Florida.

non-predatory fish were similar to the $\delta^{13}C$ signatures of both the algae and the seagrass, but differed significantly from the values determined for the mangroves (Figure 7). The wide range observed in $\delta^{15}N$ signatures (6.3‰to 12.0‰) of the herbivorous, planktivorous, and omnivorous fish suggest they do in fact at more than one trophic level.

Secondary Consumers

The $\delta^{13}C$ range of secondary consumers (*Lutjanus griseus* n=20, *Caranx ruber* n=1) was from –7.6‰ to –13.0‰ (mean = -10.1‰ ± 1.31, Figure 7 and Table 2). The mean of the $\delta^{13}C$ signatures for secondary consumers (-10.1 ‰ ± 1.31) differed significantly from the mean $\delta^{13}C$ values of the mangroves and algae, but showed no significant difference from that of seagrass (-10.5‰ ± 0.79). The gray snapper $\delta^{13}C$ and $\delta^{15}N$ values did not correlate to the standard length of the fish, indicating that the sub-adult gray snapper collected in Biscayne Bay (175 – 305 mm, n=17) foraged on similar primary consumers (Figure 8). The $\delta^{13}C$ values of these predatory fish, on average, were enriched relative to the values of both the vertebrate and invertebrate primary consumers (Figures 6,7).

The mean $\delta^{15}N$ value of the predatory fish (10.7‰ ± 0.81) was enriched in ^{15}N compared to the bulk of invertebrate (5.2‰ ± 2.0) and vertebrate (9.4 ± 1.98‰) primary consumers (Figures 6,7). The enrichment in $\delta^{15}N$ values observed confirm that the secondary consumers targeted in this study occupy the upper trophic levels in the mangrove/seagrass sites.

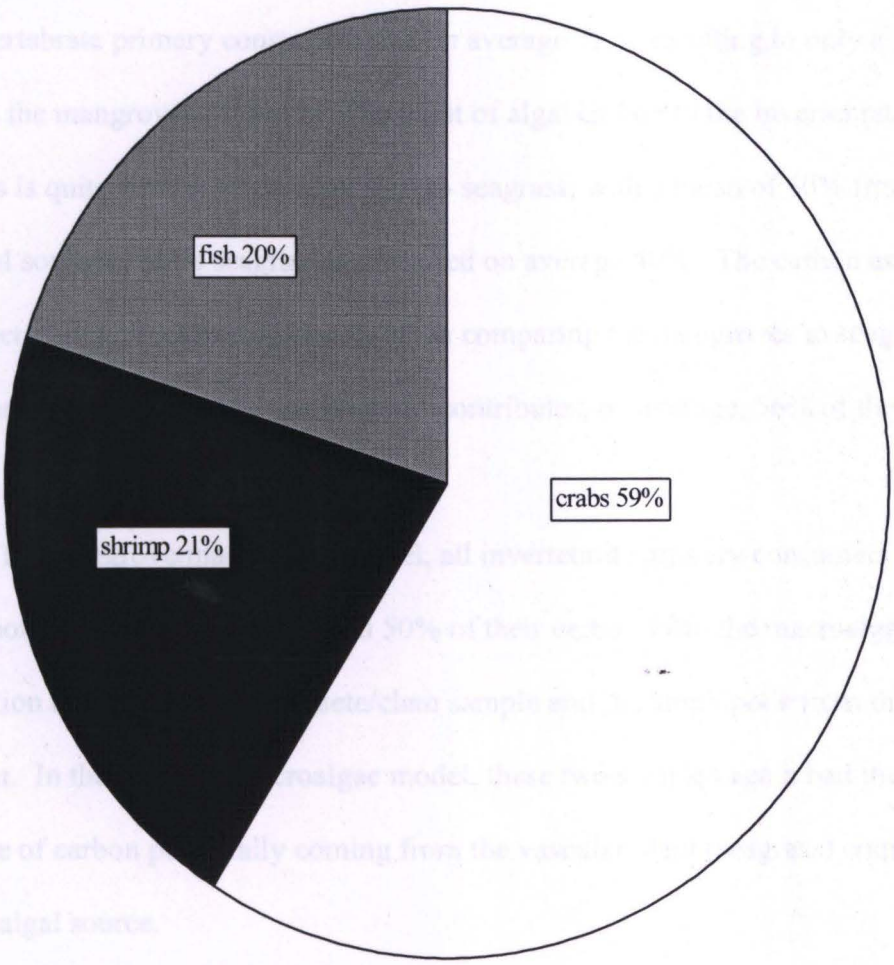

Figure 8. Volumetric stomach content of gray snapper (*Lutjanus griseus*) collected in Biscayne Bay, Florida. Values are expressed as percent of total volume.

Mixing Equations

A two-component mixing equation was used to quantitatively estimate the contribution of the different carbon sources to the primary consumers. When using mixing equations to compare mangroves to macroalgae, the contribution of algal carbon to the invertebrate primary consumers was on average 72%, resulting in only a potential 28% from the mangroves (Table 3). The input of algal carbon to the invertebrate primary consumers is quite similar when compared to seagrass, with a mean of 60% from macroalgal sources, while seagrass contributed on average 40%. The carbon assimilated by the invertebrate primary consumers, when comparing the mangroves to seagrass as the two primary sources, suggests that seagrass contributes, on average, 56% of the carbon compared to 44% from the mangroves.

In the mangrove/macroalgae model, all invertebrate primary consumers were found to potentially derive greater than 50% of their carbon from the macroalgae, with the exception of the pooled polychaete/clam sample and the amphipods from the *Bostrychia*. In the seagrass/macroalgae model, these two samples again had the highest percentage of carbon potentially coming from the vascular plant (seagrass) compared to the macroalgal source.

Table 3. Percentage (%) of diet potentially derived from mangrove (M), seagrass (S), phytoplankton (P), and macro-algae (A) carbon based on a 2-component mixing model. Blank spaces represent consumer values that fall outside the range of the two primary producers being considered.

1° Consumer	A vs. M	A vs. S	S vs. 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 & clam		21/79	92/08
Flat Tree oyster		94/06	66/34
Nudibranch (*Aplysia*)		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

DISCUSSION

Our isotope data suggest that algae is the strongest link between primary producers and primary consumers in fringe mangroves of Grand Bahama Island at Sweetings Cay, Fresh Creek on Andros Island, and Elliot Key in Biscayne Bay, Florida. The $\delta^{13}C$ values of the primary consumers, ranging from -21.1 to -12.1‰, were concentrated around the mean value of algae (-16.7‰ ± 3.62). The large differences found in mean $\delta^{13}C$ values of mangroves (-27.4‰) and primary consumers (-17.1‰) suggest that the input of carbon through the mangrove detrital pathway may be minimal when compared to the carbon input from algal ($\delta^{13}C$ =-16.7‰) and seagrass ($\delta^{13}C$ =-10.5‰) sources. No evidence was found to indicate that the carbon source was solely mangrove detritus, although the possibility still exists that primary consumers assimilate a mixture of carbon from algae, seagrass and mangrove sources. While the idea of a primary consumers' diet consisting of more than one primary producer has existed for more than thirty years (Teal 1962, Odum & Heald 1975), the dominant vascular plants were the primary producers most commonly thought to support estuarine food webs (Odum & Heald 1975). The importance of algae as a primary source of nutrition has grown as more research has been conducted with stable isotopes in estuarine ecosystems. Our results reflect the findings of the developing body of work that establishes the importance of algae in mangrove (Newell et al. 1995, Primavera 1996, Loneragan 1997, Hsieh et al. 2000), seagrass (Fry et al. 1982, Fry 1984, Lepoint et al. 2000), and salt

marsh food webs (Peterson & Howarth 1987, Sullivan & Moncreiff 1990, Dittel et al. 2000).

The linkages determined between the primary producers and primary consumers in the fringing mangrove food webs of the Bahamas and Biscayne Bay reflect those observed by Primavera (1996) in a Philippine riverine mangrove ecosystem where the $\delta^{13}C$ values of penaeid shrimp (-17.9‰) were more closely related to the values found for plankton (-22.6‰) and epiphytic algae (-24.2‰) than the values found for decomposing mangrove leaves (-27.3‰) and detritus (-28.0‰). These results are in agreement with a study on the diets of animals residing in the mangrove prop root habitat. Loneragan et al. (1997) used stable isotopes in conjunction with a two component mixing model, to determine the contribution of mangrove carbon, compared to seagrass and macroalgae, to the diets of penaeid shrimp residing in a riverine mangrove ecosystem located in Australia. The $\delta^{13}C$ values of the shrimp collected (-23.2 to –8.5‰), were more similar to those of plankton (-21.9 to -18.8‰) and seagrass (-15.4 to –9.7‰), showing little dependence on mangrove-based carbon (-28.8 to –27.0‰). Newell et al. (1995) reported in a multiple stable isotope study, investigating the source of nutrition of invertebrates inhabiting fringing mangroves in Peninsular Malaysia, the importance of mangrove carbon (-28.3‰) was shown to be limited to penaeid shrimp (-22.4‰) inhabiting tidal creeks draining the mangrove forests. However, these forests, unlike those in the Bahamas and Biscayne Bay, are associated with large contiguous mangrove forests and mangrove detritus was found to be a major component of the sedimentary organic matter located in the mangroves. Even in these tidal creeks rich in mangrove-based carbon, algae was found to contribute to the nutrition of the shrimp which is similar to our data

from the smaller fringe mangroves in the Caribbean and Florida. Away from the tidal creeks, Newell et al. (1995) found the shrimp (-15.5‰) to rely less on a mixture of algal and mangrove carbon and more upon algal and phytoplankton (-22.7 to –18.6‰) based carbon. Stoner & Zimmerman (1988), in a mangrove fringed lagoon in Puerto Rico, illustrated the importance of the benthic algae species, particularly the blue-green algae *Spirulina* ($\delta^{13}C$ = -14.4‰), rather than mangrove detritus ($\delta^{13}C$ = -25.0 to -22.9‰), in the diets of three species of penaeid shrimp ($\delta^{13}C$ = -18.1 to -15.0‰). These findings suggest that the linkage between primary producers and primary consumers in fringing mangrove food webs may not be based solely on mangrove carbon but a major input coming from algal-based carbon. In tropical/subtropical fringing mangroves found in the Caribbean, such as our study sites in the Bahamas and Biscayne Bay, high water clarity and less canopy cover and the resultant increased infiltration of light leads to a high abundance and production of edaphic algae and epiphytes (Robertson et al. 1992, Koch & Madden in press).

The predominance of algal-based carbon, in our study of the fringe mangroves, was shown in both the mangrove/algae and seagrass/algae two component mixing models. When using a mangrove/algae mixing model to estimate percent contribution of carbon to primary consumers in our study, algae was found to contribute, on average, 72% of the carbon. However, data based on a mangrove/seagrass two component-mixing model suggest that between these two dominant vascular plants, the mixed diet of the primary consumers is almost evenly divided between mangroves and seagrasses, 44% versus 56%, respectively. This output of the 2-component mixing model closely parallels the results from a stable isotope study in Biscayne Bay that investigated the contribution

of primary producers to fringing mangrove food webs also using a 2-component mixing model (Fleming et al. 1990). Considering only mangroves and seagrass as potential sources of carbon, Fleming et al. (1990) concluded that, on average, primary consumers (crabs, snails, fishes and oysters) derived 63% of their carbon from seagrass and the remaining 37% from mangrove-based sources. One limitation of the Fleming et al. (1990) study was the omission of a third spatially dominant primary producer, benthic macro-algae.

Although many species of primary consumers such as echinoids (Lawrence 1975) and crabs (Caine 1980) are known to feed directly on seagrass, algae (epiphytic and macro) are more likely to be a major food source for primary consumers because algal carbon is more labile than vascular plants due to the senescence and microbial decomposition that must occur before it is available for consumption making them less desirable to grazers and detritivores (Loneragan et al. 1997). Carbon isotopic signatures of primary consumers in Biscayne Bay and Bahamas fringe mangroves differed significantly from seagrasses; however, no significant difference in $\delta^{13}C$ signatures were found between primary consumers and seagrass epiphytes or algae ($P<0.01$). 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 epiflora growing upon the seagrass would potentially represent a key source of carbon, rather than the seagrass itself. Our findings concur with Fry (1984), who determined that the epiphytic algae ($\delta^{13}C$ = -19.3‰) associated with *Syringodium filiforme* seagrass beds were more important to the nutrition of the fauna ($\delta^{13}C$ ranging from -16‰ to -22‰) than the seagrass (-8‰) itself. In a study of *Posidonia oceanica* seagrass beds located in the Mediterranean, Lepoint et

al. (2000) also determined that the $\delta^{13}C$ values of crustacean primary consumers (-17.5 to 23.1‰) in seagrass beds were more similar to the $\delta^{13}C$ values of the epiflora (-18.6‰) and dominant epilithic macroalgae (-18.3‰) located in the seagrass beds than the $\delta^{13}C$ values determined for the seagrass (-13.9‰).

In temperate salt marshes, algae has also been shown to a major contributor of carbon to the food web. Peterson & Howarth (1987) found that the majority of the macrofauna collected in a *Spartina* salt marsh in Georgia exhibited $\delta^{13}C$ values (-22‰ to -12‰) between those of plankton (-21‰) and *Spartina* (-13‰), and fell in the $\delta^{13}C$ range most commonly observed for macro-algae (-22‰ to -14‰). Sullivan and Moncrief (1990), in their study of a salt marsh in Mississippi also found that the majority (88%) of $\delta^{13}C$ values of the consumers (-22.0 to –18.0‰) investigated were more similar to the values of edaphic algae (-20.6‰) and zooplankton (-23.3‰) than those determined for both *Juncus* (-25.5‰) and *Spartina* (-13.2‰).

The high nutritional value of algae, compared to mangrove and seagrass detritus (Tenore 1988), has been postulated as a reason for their increased importance in the diet of estuarine primary consumers, particularly direct grazers (Nicotri 1980), as well as the base of the food web for secondary consumers. Prey items consumed by secondary consumers, for example the gray snapper in fringe mangroves and seagrass communities, suggest that there is a linkage between algae and juvenile gray snapper (<80 mm) through invertebrates. Amphipods have been determined to be a major component of the diet of gray snapper less than 80 mm (Starck & Schroeder 1971). Of the possible primary organic sources we investigated, the isotope value of amphipods most closely resemble the algae. In contrast to juvenile snapper, the diet of sub-adult gray snapper in the size

range of 80 mm to 170 mm has been determined to consist largely of penaeid shrimp, cancroid crabs, and small demersal fish (Starck & Schroeder 1971). Based on carbon isotopic signatures, we determined that carbon assimilated by the pink shrimp, *Penaeus duorarum,* is primarily derived from seagrass epiphytes (100%) and/or other algae. The penaeid shrimp feeding behavior reinforces this conclusion. Being opportunistic omnivores (Newell et al. 1995), penaeid shrimp are known to consume polychaetes, amphipods, isopods, small crustaceans, molluscs and small fish (Zieman et al. 1984), which, our data suggest, feed primarily on algae including epiphytes. Our mixing model results indicate that cancroid crabs and small herbivorous fish obtain a greater part (>50%) of their carbon from seagrass-based sources, when comparing mangroves to seagrass, but the majority of their carbon from algal sources when contrasted to seagrass. Larger snapper (>170mm) tend to feed more upon fish and larger crustacea and our isotope data show that these prey items derive the majority of their carbon from seagrass (57% to 89%) in the seagrass/mangrove model. However, the algae/seagrass model indicates that over half (63%) of the prey diet comes from algal-based sources. In summary, prey items of the secondary consumers that inhabit the fringe mangrove/seagrass zone derive the majority of their carbon from algal sources.

The relationship between the gray snapper, the algae and the seagrass becomes more apparent after removing the fractionation (1‰, Peterson & Fry 1987) from $\delta^{13}C$ signatures (Figure 9). This is accomplished by using the difference in $\delta^{15}N$ values between the snapper and algae to determine the trophic distance from the primary producer and higher-level consumer. The consumers tend to be enriched in ^{15}N compared

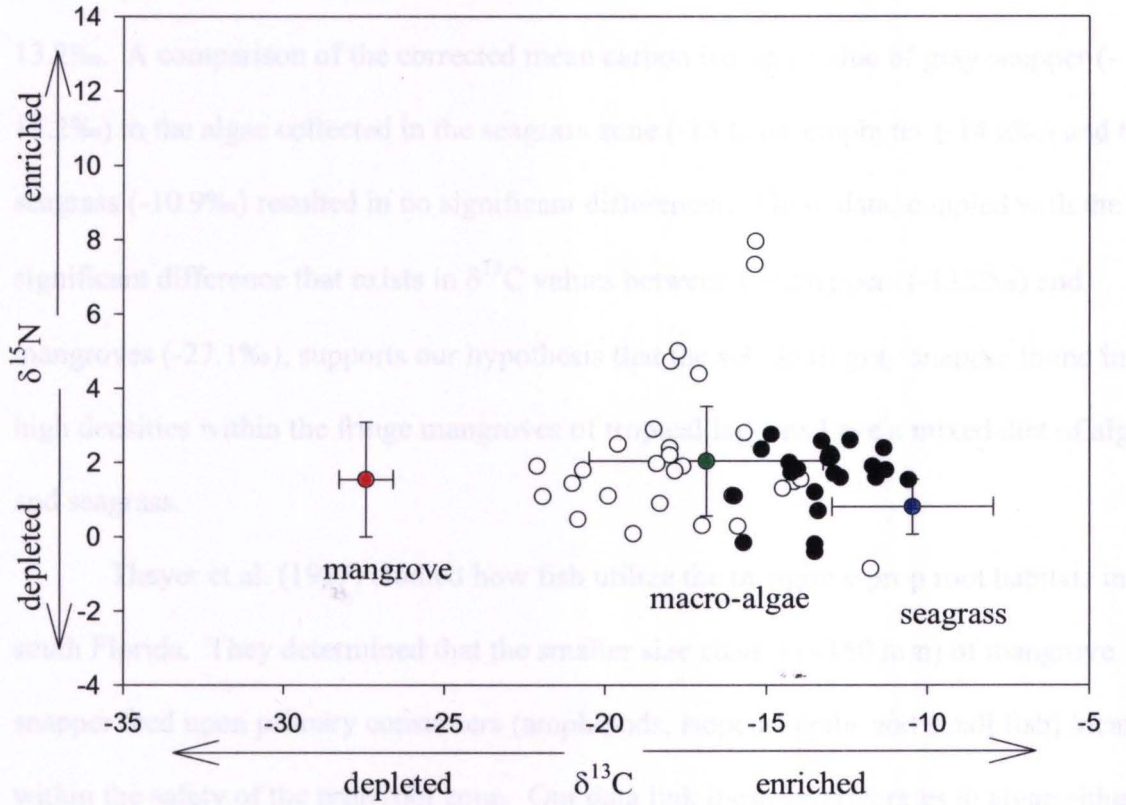

Figure 9. Isotopic signatures of predatory fish ( ) and primary consumers ( ), after corrected for fractionation, compared to possible primary organic sources (± 1 SD) from Grand Bahama Island and Andros Island, Bahamas, and Biscayne Bay, Florida.

to their food sources by as much as 2 to 4‰ per trophic level (Minagawa & Wada 1984). The difference in $\delta^{15}N$ values between the snapper (10.7‰± 0.169) and algae (2.1‰± 0.229) shows a possible separation of 3 trophic levels. Correction for the ^{13}C enrichment for the snapper, 3 trophic steps with each representing 1‰, results in a $\delta^{13}C$ value of -13.2‰. A comparison of the corrected mean carbon isotopic value of gray snapper (-13.2‰) to the algae collected in the seagrass zone (-15.6‰), epiphytes (-14.6‰) and the seagrass (-10.9‰) resulted in no significant differences. These data, coupled with the significant difference that exists in $\delta^{13}C$ values between the snappers (-13.2‰) and mangroves (-27.1‰), supports our hypothesis that the sub-adult gray snapper found in high densities within the fringe mangroves of tropical lagoons have a mixed diet of algae and seagrass.

Thayer et al. (1987) studied how fish utilize the mangrove prop root habitats in south Florida. They determined that the smaller size classes (<150 mm) of mangrove snapper feed upon primary consumers (amphipods, isopods, crabs and small fish) located within the safety of the prop root zone. Our data link these invertebrates to algae either within the mangrove prop roots or as epiphytes on adjacent seagrass beds. Thus, fringe mangroves may be providing a fish refuge during the day, as well as, hard substrate for benthic algal colonization and invertebrate and fish secondary production. Mangroves may also serve to trap and stabilize sediment, which can in turn enhance nutrients available to benthic and prop root associated primary producers (Koch & Madden in press) supporting this secondary production.

In conclusion, we determined the important role that algae plays in the food web associated with the fringe mangroves and that vascular plants, particularly mangroves,

don't appear to be the sole contributors of carbon to primary consumers. Also, primary consumers are not specialist feeders that rely solely upon a single source for carbon, but tend to preferentially consume carbon derived from algae and seagrass, quite possibly as a mixture. These data lead us to the conclusion that one of the most economically significant species inhabiting the fringe mangroves, gray snapper (Harrigan et al. 1989), is more trophically dependent upon seagrass and algae than on mangroves, but mangroves may be indirectly important for the gray snapper and other mobile fish species, particularly in tropical lagoons with high light and abundant algae. Because of the accelerating worldwide loss of coastal mangrove forests particularly in developing nations such as Thailand and the Philippines, which have lost more than half of their mangrove forests since 1960 (Mukerjee 1996), the role of the primary producers and the trophic linkages that exist in tropical lagoons with fringe mangroves is of critical importance.

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APPENDIX:

$\delta^{13}C$ and $\delta^{15}N$ values for individual primary producers, consumers and secondary consumers.

Sample	**Site**	$\delta^{13}C$	$\delta^{15}N$
Lutjanus griseus (gray snapper) 305mm	Biscayne Bay 7/00	-12.2	11.4
Lutjanus griseus 175mm	Biscayne Bay 7/00	-11.9	11.8
Lutjanus griseus 278mm	Biscayne Bay 7/00	-11.3	11.0
Lutjanus griseus 257mm	Biscayne Bay 7/00	-11.2	10.7
Lutjanus griseus 280mm	Biscayne Bay 7/00	-11.0	10.8
Lutjanus griseus 195mm	Biscayne Bay 7/00	-10.4	9.7
Lutjanus griseus 187mm	Biscayne Bay 7/00	-10.3	11.6
Lutjanus griseus 267mm	Biscayne Bay 7/00	-10.0	11.2
Lutjanus griseus 267mm (replicate)	Biscayne Bay 7/00	-10.1	11.1
Lutjanus griseus 210mm	Biscayne Bay 7/00	-10.0	11.2
Lutjanus griseus 212mm	Biscayne Bay 7/00	-10.0	11.2
Lutjanus griseus 266mm	Biscayne Bay 7/00	-9.9	10.7
Lutjanus griseus 180mm	Biscayne Bay 7/00	-9.7	10.6
Lutjanus griseus 263mm	Biscayne Bay 7/00	-8.7	10.9
Lutjanus griseus 270mm	Biscayne Bay 7/00	-8.6	10.6
Lutjanus griseus 204mm	Biscayne Bay 7/00	-8.3	11.4
Lutjanus griseus 226mm	Biscayne Bay 7/00	-8.3	10.8
Lutjanus griseus 225mm	Biscayne Bay 7/00	-7.6	10.5
Lutjanus griseus	Biscayne Bay 11/99	-13.0	10.1
Lutjanus griseus	Grand Bahamas 6/98	-10.5	8.8
Lutjanus griseus (replicate)	Grand Bahamas 6/98	-10.5	8.6
Lutjanus griseus	Andros Island 6/99	-9.4	11.6
Lagadon rhomboides (pinfish)	Biscayne Bay 11/99	-12.5	9.5
Caranx ruber (bar jack)	Biscayne Bay 7/00	-10.5	10.2
Ocyurus chrysurus (yellowtail snapper)	Grand Bahamas 6/98	-12.7	8.8
Harengula humeralis (redear sardine)	Grand Bahama 6/98	-14.6	11.8
Pomacentrus species (damselfish)	Grand Bahamas 6/98	-14.0	8.6
Gerres cinereus (yellowfin mojarra)	Grand Bahamas 6/98	-13.8	7.8
Gerres cinereus	Andros Island 6/99	-11.1	10.7
Abudefduf saxatilis (sergeant major)	Andros Island 6/99	-14.2	12.0
Scarus species (parrotfish)	Grand Bahamas 6/98	-11.7	6.3

APPENDIX con't.:

Sample	Site	$\delta^{13}C$	$\delta^{15}N$
Penaeus duorarum (pink shrimp)	Biscayne Bay 6/00	-13.4	11.0
Penaeus duorarum	Biscayne Bay 6/00	-13.4	10.3
Isognomon alatus (flat tree oyster)	Biscayne Bay 6/00	-16.0	3.3
Isognomon alatus	Grand Bahamas 6/98	-15.1	4.1
Isognomon alatus	Andros Island 6/99	-14.7	5.8
Callinectes similis (false blue crab)	Grand Bahamas 6/98	-16.8	8.0
Callinectes sapidus (blue crab)	Biscayne Bay 6/00	-16.1	7.4
Amphipod collected in *Bostrychia*	Biscayne Bay 6/00	-23.9	-2.6
Amphipod collected in *Bostrychia*	Biscayne Bay 6/00	-24.6	0.4
Amphipod	Andros Island 6/99	-17.5	5.9
Microphrys bicornutus (spotted decorator crab)	Andros Island 6/99	-18.6	5.5
Microphrys bicornutus	Grand Bahamas 6/98	-16.8	4.8
Panopeus herbstii (common mud crab)	Andros Island 6/99	-13.5	4.3
Panopeus herbstii	Biscayne Bay 6/00	-17.0	5.2
Panopeus herbstii (replicate)	Biscayne Bay 6/00	-16.6	4.9
Pachygrapsus transversus (common shore crab)	Andros Island 6/99	-18.9	4.1
Polychaete species	Biscayne Bay 6/00	-21.1	4.9
Polychaete species	Biscayne Bay 11/99	-20.9	4.1
Polychaete/bivalve *	Grand Bahamas 6/98	-22.9	-0.4
Isopod species	Biscayne Bay 11/99	-19.8	3.5
Isopod/amphipod *	Biscayne Bay 6/00	-17.3	3.9
Isopod/amphipod *	Biscayne Bay 6/00	-17.0	5.4
Isopod/amphipod *	Grand Bahamas 6/98	-17.0	7.7
Decapod/gastropod *	Biscayne Bay 6/00	-17.4	5.0
Atrina species (pen shell)	Grand Bahamas 6/98	-14.9	3.3
Fasciolaria tulipa (tulip snail)	Grand Bahamas 6/98	-12.1	5.2
Condylactis species (anemone)	Grand Bahamas 6/98	-12.9	4.6
Aplysia species (nudibranch)	Grand Bahamas 6/98	-13.1	4.5
Elysia species (nudibranch)	Biscayne Bay 6/00	-19.7	4.8
M. bicornutus/bivalve *	Grand Bahamas 6/98	-10.8	2.1
Tunicate species	Biscayne Bay 11/99	-20.0	4.4
Pagurus species (hermit crab)	Grand Bahamas 6/98	-18.1	3.1
prey fish	Biscayne Bay 6/00	-9.3	8.7
prey crab	Biscayne Bay 6/00	-10.0	4.0
prey shrimp	Biscayne Bay 6/00	-10.5	4.2
prey shrimp (replicate)	Biscayne Bay 6/00	-10.2	2.9

* indicates pooled sample

APPENDIX con't.:

Sample	Site	$\delta^{13}C$	$\delta^{15}N$
Thalassia testudinum-live	Biscayne Bay 6/00	-9.5	1.6
Thalassia testudinum-live	Biscayne Bay 6/00	-10.2	1.2
Thalassia testudinum-live	Biscayne Bay 11/99	-14.7	1.3
Thalassia testudinum-live	Grand Bahamas 6/98	-8.4	-0.4
Thalassia testudinum-live	Andros Island 6/99	-6.8	1.1
Thalassia testudinum-live (replicate)	Grand Bahamas 6/98	-8.7	0.0
Thalassia testudinum-detrital	Biscayne Bay 11/99	-13.5	1.7
Thalassia testudinum-detrital	Biscayne Bay 11/99	-12.8	0.9
Thalassia testudinum-detrital	Grand Bahamas 6/98	-9.2	-0.1
Syringodium filiforme-live	Biscayne Bay 11/99	-10.7	0.7
Rhizophora mangle-live	Biscayne Bay 11/99	-26.7	-0.7
Rhizophora mangle-live	Biscayne Bay 11/99	-25.8	0.8
Rhizophora mangle-live	Grand Bahamas 6/98	-27.6	0.2
Rhizophora mangle-live	Andros Island 6/99	-28.7	4.4
Rhizophora mangle-senescent	Biscayne Bay 11/99	-27.0	-0.2
Rhizophora mangle-senescent	Biscayne Bay 11/99	-27.0	1.1
Rhizophora mangle-senescent	Grand Bahamas 6/98	-26.7	3.6
Rhizophora mangle-senescent	Andros Island 6/99	-28.7	3.6
Rhizophora mangle-detrital	Biscayne Bay 11/99	-27.7	0.8
Rhizophora mangle-detrital	Biscayne Bay 11/99	-27.6	1.2
Rhizophora mangle-detrital	Biscayne Bay 11/99	-27.3	1.0
Rhizophora mangle-detrital	Andros Island 6/99	-28.3	2.4
Rhizophora mangle-detrital	Grand Bahamas 6/98	-27.7	1.8
Caulerpa prolifera	Biscayne Bay 6/00	-16.3	3.5
Caulerpa racemosa	Biscayne Bay 6/00	-14.9	3.2
Caulerpa racemosa	Biscayne Bay 6/00	-21.0	1.6
Caulerpa mexicana	Biscayne Bay 6/00	-12.6	1.8
Caulerpa mexicana	Biscayne Bay 6/00	-12.4	1.8
Caulerpa cupressoides	Biscayne Bay 6/00	-11.1	3.2
Caulerpa species	Biscayne Bay 11/99	-18.8	1.8
Caulerpa species	Biscayne Bay 11/99	-18.7	1.7
Caulerpa species	Grand Bahamas 6/98	-16.5	2.1
Halimeda incrassata	Biscayne Bay 6/00	-20.6	2.3
Halimeda incrassata	Biscayne Bay 6/00	-20.0	0.8
Halimeda incrassata	Biscayne Bay 6/00	-20.0	0.7
Halimeda opuntia	Biscayne Bay 6/00	-13.1	1.1
Halimeda species	Biscayne Bay 11/99	-20.6	0.3
Halimeda species	Grand Bahamas 6/98	-6.8	-1.7

APPENDIX con't.:

Sample	Site	$\delta^{13}C$	$\delta^{15}N$
Penicillus species	Biscayne Bay 6/00	-18.1	3.0
Penicillus species	Biscayne Bay 11/99	-18.6	0.3
Penicillus species	Grand Bahamas 6/98	-10.2	0.9
Acetabularia species	Biscayne Bay 6/00	-14.9	2.2
Acetabularia species	Biscayne Bay 11/99	-17.8	2.1
Acetabularia species	Andros Island 6/99	-14.5	4.2
Padina species	Biscayne Bay 6/00	-21.7	2.9
Dictyosphaeria species	Biscayne Bay 6/00	-18.3	2.5
Valonia species	Biscayne Bay 6/00	-16.9	3.1
Udotea species	Biscayne Bay 6/00	-15.6	1.5
Dictyota species	Grand Bahamas 6/98	-19.6	3.3
Laurencia species	Biscayne Bay 6/00	-13.8	1.4
Dasycladus species	Andros Island 6/99	-15.9	5.0
Jania species	Andros Island 6/99	-17.1	5.1
Epiphytes (*Thalassia*)	Biscayne Bay 11/99	-17.0	2.5
Epiphytes (*Thalassia*)	Biscayne Bay 11/99	-16.3	2.7
Epiphytes (*Thalassia*)	Grand Bahamas 6/98	-10.5	1.4
Unknown red filamentous algae	Biscayne Bay 11/99	-21.8	2.6
Hypnea/Laurencia *	Biscayne Bay 11/99	-19.0	2.7
Hypnea, Batophora, Laurencia *	Grand Bahamas 6/98	-17.6	2.9
Dasycladus, Acetabularia, Hypnea *	Grand Bahamas 6/98	-17.1	3.0
Hypnea, Batophora, Acetabularia *	Grand Bahamas 6/98	-12.2	1.8
Avrainvillea species	Biscayne Bay 11/99	-20.0	-1.4
Avrainvillea species	Biscayne Bay 6/00	-22.5	0.1
Bostrychia species	Biscayne Bay 6/00	-32.0	2.6
Bostrychia species	Biscayne Bay 6/00	-31.9	2.5
Bostrychia species	Biscayne Bay 6/00	-31.0	3.5
Bostrychia species	Grand Bahamas 6/98	-28.9	3.6
Phytoplankton	Biscayne Bay 8/00	-18.4	4.8
Phytoplankton	Biscayne Bay 8/00	-18.4	4.8
Phytoplankton	Biscayne Bay 8/00	-18.5	5.2
Sedimentary organic matter	Biscayne Bay 8/00	-15.6	1.6
Bacteria	Biscayne Bay 8/00	-19.9	4.7

* indicates pooled sample