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A $^{13}\text{C}/^{12}\text{C}$ COMPARISON OF FOOD WEBS IN CARIBBEAN SEAGRASS MEADOWS AND CORAL REEFS

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ABSTRACT

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Stable carbon isotope analyses of more than 140 plant, animal, and sediment samples from the Miskito Banks, Nicaragua and St. Croix, U.S. Virgin Islands, were used to assess carbon flow in Caribbean seagrass meadows and coral reefs. Plants at the base of food webs had widely divergent $\delta^{13}\text{C}$ values, ranging from -4.0 (*Syringodium filiforme* Kütz) to -34.7‰ (an unidentified red alga). Isotopic values of 13 of 35 algal species ranged from -8.8 to -15.0‰ , and were similar to the -9.9 to -13.2‰ values of the dominant Caribbean seagrass, *Thalassia testudinum* Banks ex Koenig. This isotopic similarity prevented a clear assessment of the role that *Thalassia* plays in supporting Caribbean food webs. However, a $4\text{--}6\text{‰}$ ^{13}C enrichment was found among fish from seagrass meadows and coral reefs vs. fish collected offshore. This enrichment indicated that benthic algae and seagrasses together contribute at least 48–76% of the carbon found in fish from the former, shallow-water habitats.

INTRODUCTION

Surveys of the stable carbon isotope ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) composition of aquatic flora and fauna have delineated trophic relations in lakes, salt marshes and seagrass meadows (Thayer et al., 1978; Fry and Parker, 1979; Haines and Montague, 1979; McConnaughey and McRoy, 1979; Rau, 1980; Hackney and Haines, 1980). The $\delta^{13}\text{C}$ methodology traces which plants are important in sustaining the secondary production of food webs. This approach is based on two assumptions: that plant food sources differ in their isotopic compositions, and that animal consumers closely reflect the isotopic composition of their diets. Laboratory studies have confirmed that close isotopic similarity exists between animals and their diets, i.e., within $\pm 2\text{‰}$

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(DeNiro and Epstein, 1978), but in the sea, plants often show a continuous distribution of $\delta^{13}\text{C}$ values (see Fig. 1), rather than the distinct C_3 and C_4 groups found on land (Smith and Epstein, 1971). Although the lack of distinct isotopic groups among marine plants makes food web interpretations more difficult, the $\delta^{13}\text{C}$ approach is often still useful for analyzing the food-web importance of seagrasses, which form the ^{13}C -enriched end of the marine plant continuum (Smith and Epstein, 1971; Fry and Parker, 1979). Accordingly, and as part of a collaborative research cruise to the Miskito Banks, Nicaragua, we collected a variety of plant, animal and sediment samples to test the importance of seagrasses for Caribbean food webs. We present those results here, and for comparative purposes, also report on coral reef fish and a second Caribbean seagrass community at St. Croix, U.S. Virgin Islands.

METHODS

Samples were collected during March 1976, in several *Thalassia* seagrass beds in and around Tague Bay, St. Croix, and during October, 1977, at Cayos Miskitos, Nicaragua. The 1977 collections were made during a multi-disciplinary cruise on the RV Alpha Helix to investigate the large seagrass meadows on the Nicaraguan shelf. Bathypelagic fish and shrimp samples were collected off Nicaragua at 300–500 m depths with a midwater trawl.

All samples were individual rather than composite samples. For most animals, muscle tissue was analyzed; gonads and tube feet were removed from sea urchins and starfish, respectively, for analysis. Fish were usually ≥ 40 mm standard length, and most animals were adults.

Sample preparation, combustion and analysis followed the procedures given in Fry et al. (1977) and Fry and Parker (1979). Where necessary, samples were treated with acid for 24 h, or until bubbling stopped, to remove carbonates. Two algal species with $\delta^{13}\text{C}$ values between -8 and -10‰ were analyzed twice following mild acid treatment, (24 h, 1 M phosphoric acid) and again after extended acidification (concentrated phosphoric acid, one month). In both cases, $\delta^{13}\text{C}$ values were 0.8‰ more negative after a month and we report these more negative values. All results are expressed in $\delta^{13}\text{C}$ notation relative to the international Belemnite standard from the Pee Dee formation of South Carolina (Craig, 1957) where

$$\delta^{13}\text{C}_{\text{PDB}} = [({}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}})/({}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}) - 1] \times 10^3$$

Error in these measurements is routinely ± 0.3 or less.

RESULTS

Figure 1 shows the $\delta^{13}\text{C}$ values of plants, sediments and animals collected at Cayos Miskitos and St. Croix. The data for the two geographically separate sites appeared similar in their ranges and distribution of $\delta^{13}\text{C}$ values. Most samples had $\delta^{13}\text{C}$ values between -9 and -16‰ . Included in this range were

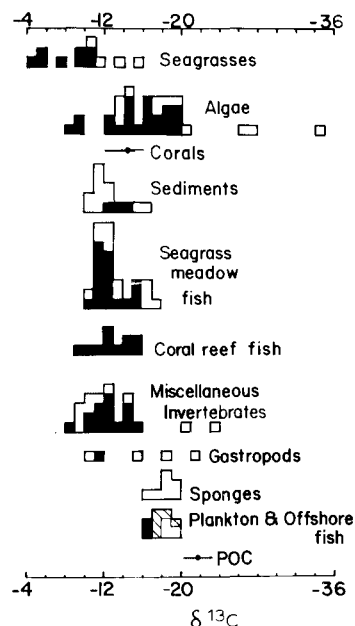


Fig. 1. $\delta^{13}\text{C}$ values of Caribbean flora and fauna. Symbols: diagram includes values from three areas: Nicaraguan (Cayos Miskitos) samples are white squares (\square), St. Croix samples are black squares (\blacksquare) and Jamaican samples (from Land et al., 1975 and Land et al., 1977) are cross-hatched squares or dotted lines (\boxtimes or \bullet). Mean values and range are shown for coral and POC samples; all other values are for individual organisms.

14 of 35 algae samples, 13 of 14 sediment samples, 40 of 43 fish samples and, excepting sponges, 24 of 30 invertebrate samples. A second major clustering of $\delta^{13}\text{C}$ values occurred between -16 and -21‰ . This cluster included about one-half of the algae samples, the sponges and the offshore and plankton samples. Plant samples gave the most extreme $\delta^{13}\text{C}$ values: -4‰ for a leaf of *Syringodium filiforme* Kütz. (Table I) and -34.7‰ for an unidentified red alga found growing on a mangrove root at Cayos Miskitos. The extreme animal $\delta^{13}\text{C}$ values were -8.5‰ for an *Ophiocoma* (brittlestar) and -23.3‰ for a *Cassiopea* (benthic jellyfish) (Table II).

Three fish species were collected at both Cayos Miskitos and St. Croix. *Diodon holocanthus* Linnaeus from Cayos Miskitos were approximately 5‰ more negative than at St. Croix, while the ballyhoo fish, *Hemiramphus brasiliensis* (Linnaeus), and the grunt, *Haemulon plumieri* (Lacépède), each had very similar $\delta^{13}\text{C}$ values at the two sites (Table III).

As a group, the brown algae were less negative than the red algae while the green algae did not show a consistent relation to the other groups (Table I).

At St. Croix, two fish collections were made to determine whether food webs reflected the stable isotope composition of the locally dominant plants. Seagrasses were enriched in ^{13}C , averaging about -9‰ , while coral and algal means were more depleted in ^{13}C , averaging -14 and -17‰ , respectively (Fig. 1).

TABLE I

 $\delta^{13}\text{C}$ values of Caribbean seagrasses and algae (Analyses shown are of individual plants)

| | St. Croix | Cayos Miskitos |
|------------------------------------------------------------|-------------------|----------------|
| A. Seagrasses | | |
| <i>Halophila decipiens</i> Ostenfeld | -9.8, -10.6, -7.5 | -10.3 |
| <i>Syringodium filiforme</i> Kütz. | -4.0, -5.1 | -6.8 |
| <i>Thalassia testudinum</i> Banks ex Koenig | -9.9, -10.0 | -13.2, -12.8 |
| <i>Halodule wrightii</i> Aschers. | | -11.1 |
| B. Algae | | |
| Cyanophyceae | | |
| <i>Hormothamnion</i> sp. | -9.4 | |
| Chlorophyceae | | |
| <i>Avrainvillea</i> (prob. <i>elliotti</i> A. & E.S. Gepp) | -16.4 | |
| <i>Avrainvillea nigricans</i> Decaisne | | -19.4 |
| <i>Batophora oerstedii</i> J. Ag. | | -17.5 |
| <i>Caulerpa paspaloides</i> (Bory) Grev. | | -26.8, -27.5 |
| <i>Caulerpa prolifera</i> (Forssk.) Lamour. | | -13.3 |
| <i>Caulerpa racemosa</i> (Forssk.) J. Ag. | | -13.9 |
| <i>Chaetomorpha linum</i> (Müll.) Kütz. | -17.9 | -20.6 |
| <i>Codium</i> sp. | | -13.3 |
| <i>Ernodesmis verticillata</i> (Kütz.) Boerg. | -16.6 | |
| <i>Halimeda monile</i> (Ell. & Soland.) Lamour. | -12.5 | |
| <i>Halimeda</i> sp. | | -14.9 |
| <i>Penicillus capitatus</i> Lam. | | -18.6 |
| <i>Penicillus dumetosus</i> (Lamour.) Blainv. | | -17.2 |
| Phaeophyceae | | |
| <i>Dictyota dentata</i> Lamour. | -14.1 | |
| <i>Dictyota dichotoma</i> (Huds.) Lamour. | -13.5 | |
| <i>Dictyota divaricata</i> Lamour. | -12.7 | |
| <i>Colpomenia sinuosa</i> (Roth) Derb. & Sol. | -8.8 | |
| <i>Padina sanctae-crucis</i> Boerg. | -9.5 | |
| <i>Sargassum polyceratum</i> Montagne | -14.8 | |
| Rhodophyceae | | |
| <i>Amphiroa fragilissima</i> (L.) Lamour. | -18.5 | |
| <i>Centroceras clavulatum</i> (C.Ag.) Montagne | -16.4, -16.7 | |
| <i>Ceramium</i> sp. | -19.4 | |
| <i>Galaxaura squalida</i> Kjellm. | -14.5 | |
| <i>Gelidiella acerosa</i> (Forssk.) Feldm. & Hamel | -15.9 | |
| <i>Gracilaria</i> sp. | -18.9 | |
| <i>Hypnea</i> sp. | -19.9 | |
| <i>Laurencia obtusa</i> (Huds.) Lamour. | -19.7 | |
| <i>Liagora ceranoides</i> Lamour. | -18.5 | |
| <i>Spyridia aculeata</i> (Schimper) Kütz. | -17.6 | |

TABLE II

 $\delta^{13}\text{C}$ values of sediments and individual invertebrates from *Thalassia* meadows

| | St. Croix | Cayos Miskitos |
|-----------------------------------------------------|------------------------------------------|-------------------------------------------|
| <i>Astrea</i> sp. (gastropod) | -10.6 | |
| <i>Callinectes</i> sp. (crab) | -10.4 | |
| <i>Cerithium litteratum</i> (Born) (gastropod) | -15.1 | |
| <i>Clibanarius</i> sp. (carb) | -14.0 | |
| <i>Diadema antillarum</i> (Philippi) (urchin) | -12.1, -12.9 | |
| <i>Echinometra lucunter</i> (Linnaeus) (urchin) | -14.5, -14.5 | |
| <i>Ophiocoma</i> sp. (brittlestar) | -8.5 | |
| Unidentified brittlestar | | -9.0 |
| <i>Oreaster reticulatus</i> (Linnaeus) (starfish) | -12.7 | -9.5, -20.1 |
| <i>Panulirus argus</i> (Latreille) (lobster) | -11.3 | |
| <i>Penaeus brasiliensis</i> Hay and Shore (shrimp) | -11.3 | |
| <i>Triploneustes ventricosus</i> (Lamarck) (urchin) | -11.5, -13.6 | |
| <i>Tegula fasciata</i> (Born) (gastropod) | -12.4 | |
| <i>Strombus gigas</i> Linné (conch) | -11.7 | -18.9 |
| <i>Strombus raninus</i> Gmelin (conch) | | -21.0 |
| Unidentified strombid conchs | | -10.7, -15.0 |
| <i>Cassiopea</i> sp. (jellyfish) | | -23.2 |
| Miscellaneous unidentified invertebrates | | |
| Polychaetes | | -9.3, -12.1, -14.4 |
| Sea cucumber | | -11.8 |
| Sand dollars | | -10.2, -10.8 |
| Sponges | | -18.1 \pm 1.0 (7)* (-16.0 to -19.2) |
| Organic matter in sediments | -13.7 \pm 1.1 (3)* (-12.7 to -14.9) | -12.2 \pm 1.9 (11)* (-10.7 to -16.3) |

*Values given are $\bar{x} \pm \text{S.D.}$, (N) and, below, the range for individual samples.

Fish collected from seagrass meadows did not, however, show a corresponding 5–8‰ shift relative to coral reef fish, and in fact $\delta^{13}\text{C}$ means of the coral reef fish and seagrass meadow fish were not significantly different ($P > 0.05$, t -test). Table IV shows a more detailed comparison of algivorous reef fish with fish that are known to consume large amounts of seagrass. Reef-dwelling algivores averaged 1.7‰ more negative than the seagrass consumers, but again this difference was not significant ($P > 0.05$, t -test).

While $\delta^{13}\text{C}$ values among fish of seagrass meadows and coral reefs were quite similar, their mean -12 to -14‰ values were enriched in ^{13}C relative to zooplankton and offshore fauna. Bathypelagic collections off Nicaragua yielded two -18.5 and -19.0 unidentified fish, and a -18.8‰ shrimp. At St. Croix, zooplankton collected at night over seagrass meadows measured -16.0‰, and a deep-sea lutjanid fish obtained from commercial fishermen was -16.9‰.

TABLE III

 $\delta^{13}\text{C}$ values of individual fish from seagrass meadows and coral reefs

| | St. Croix | Cayos Miskitos |
|-----------------------------------------------------------|---------------------|---------------------|
| A. Seagrass meadow fish | | |
| <i>Acanthurus chirurgus</i> (Bloch) | -15.9 | |
| <i>Atherinomorous stipes</i> (Müller and Troschel) | -15.0 | |
| <i>Diodon holocanthus</i> Linnaeus | -11.9, -12.2 | -16.6, -16.7, -17.6 |
| <i>Eupomacentrus leucostictus</i> (Müller and Troschel) | -12.4 | |
| <i>Haemulon chrysargyreum</i> Günther | -12.9 | |
| <i>Haemulon flavolineatum</i> (Desmarest) | -11.9 | |
| <i>Haemulon plumieri</i> (Lacépède) | -13.1 | -11.9 |
| <i>Haemulon sciurus</i> (Shaw) | -12.3 | |
| <i>Halichoceres bivittatus</i> (Bloch) | -11.8 | |
| <i>Hemiramphus brasiliensis</i> (Linnaeus) | -10.3, -11.1 | -10.6, -12.8 |
| <i>Monocanthus ciliatus</i> (Mitchill) | | -12.9 |
| <i>Ocyurus chrysurus</i> (Bloch) | | -12.4, -16.9 |
| <i>Opisthonema oglinum</i> (Le Sueur) | -15.8 | |
| <i>Pomacranthus paru</i> (Bloch) | | -13.3 |
| <i>Sparisoma chrysopterum</i> (Bloch and Schneider) | -11.6, -11.9 | |
| <i>Sparisoma radians</i> (Cuvier and Valenciennes) | -11.1, -12.5, -12.5 | |
| <i>Sparisoma rubripinne</i> (Cuvier and Valenciennes) | | -15.1 |
| <i>Sphyrna barracuda</i> (Walbaum) | -14.2 | |
| <i>Sphyrna tiburo</i> (Linnaeus) | | -11.9, -13.5 |
| B. Coral reef fish | | |
| <i>Abudefduf saxatilis</i> (Linnaeus) | -15.3 | |
| <i>Acanthurus coeruleus</i> Bloch and Schneider | -14.6 | |
| <i>Alutera schoepfi</i> (Walbaum) | -13.4 | |
| <i>Caranx ruber</i> (Bloch) | -11.5 | |
| <i>Chaetodon capistratus</i> Linnaeus | -12.4 | |
| <i>Eupomacentrus dorsopunicans</i> (Poey) | -12.8 | |
| <i>Eupomacentrus planifrons</i> (Cuvier and Valenciennes) | -14.2 | |
| <i>Holocentrus rufus</i> (Walbaum) | -12.3 | |
| <i>Microspathodon chrysurus</i> (Cuvier and Valenciennes) | -9.8 | |
| <i>Scarus vetula</i> Bloch and Schneider | -10.7 | |
| <i>Sparisoma viride</i> (Bonaterre) | -15.8 | |

DISCUSSION

The majority of the plant, animal and sediment samples fell in the -9 to -16‰ range at both St. Croix and Cayos Miskitos. These Caribbean values agree well with the results from tropical and subtropical seagrass meadows in Florida (Craig, 1953), Texas (Parker, 1964; Fry et al., 1977; Fry and Parker, 1979) and northern Australia (unpublished data, 1979). While based on only a few samples, the -17 to -19‰ Caribbean values for offshore fish and shrimp also agree well with $\delta^{13}\text{C}$ values observed in the Gulf of Mexico, where sampling has been more extensive (Gormly and Sackett, 1977; Fry and Parker, 1979).

TABLE IV

 $\delta^{13}\text{C}$ values of herbivorous fish from St. Croix, U.S. Virgin Islands

| Algivores | % Algae in diet* | $\delta^{13}\text{C}$ |
|---------------------------------|------------------------|----------------------------------|
| <i>Acanthurus coeruleus</i> | 93 | -14.6 |
| <i>Sparisoma viride</i> | 97 | -15.8 |
| <i>Scarus vetula</i> | 94 | -10.7 |
| <i>Sparisoma chrysopteron</i> | 83 | #1 -11.9 #2 -11.6 |
| <i>Acanthurus chirurgus</i> | 94 | -15.9 |
| | Average = | -13.4 |
| Seagrass consumers | % Seagrass* in diet | |
| <i>Alutera schoepfi</i> | 67 | -13.4 |
| <i>Hemiramphus brasiliensis</i> | 81 | #1 -11.1 #2 -10.3 |
| <i>Sparisoma radians</i> | 88 | #1 -11.1 #2 -12.5 #3 -12.5 |
| | Average = | -11.8 |

*From Randall, 1967.

This study slightly extends the $\delta^{13}\text{C}$ range reported for macroalgae. The previous extreme values are -11.3 and -32.4‰ (Black and Bender, 1976). Extreme values found in this study were -8.8‰ for *Colpomenia sinuosa* (Roth) Derbès and Solier at Boiler Bay, St. Croix, and -34.7‰ for an unidentified red alga collected on a mangrove root at Cayos Miskitos.

The $\delta^{13}\text{C}$ values in Tables II and III provide some clues to the diets of various animals. The scatter of $\delta^{13}\text{C}$ values among individuals indicates a diversity of diets for conchs, starfish, crabs and polychaetes. Little scatter of $\delta^{13}\text{C}$ values for the ballyhoo fish, *H. brasiliensis*, indicates isotopic similarity of diets among the four individuals sampled. The isotopic data also indicate which plants are important carbon sources for some animals. For animals near -10‰ , it is unlikely that plankton or the algae more negative than -16‰ provide a substantial portion of the dietary carbon. For animals which are intermediate in the -12 to -16‰ range, many combinations of plant diets could produce these values so that the $\delta^{13}\text{C}$ data need to be supplemented with observations on feeding behavior. Animals that seem more dependent on the -16 to -22‰ zooplankton and phytoplankton food sources include the -16 to -20‰ sponges, and probably the -16.6 to -17.6‰ *Diodon* fish collected off Nicaragua. These fish were year-0 specimens, and *Diodon*

is known to have a long larval life of up to 450 days in the plankton (Brothers, pers. comm., 1981; based on measurements of otolith rings). Larger adult specimens taken at St. Croix had -12‰ values typical of fish feeding on benthic plants and the shift from ~ -17 to -12‰ may reflect an ontogenetic switch from a planktivorous to a benthic plant diet.

Using the average values for the collected fish, we can estimate the carbon contributions that benthic plants make to the fish food webs of coral reefs and seagrass meadows. The offshore fish samples collected by midwater trawl or hook and line averaged -18‰ , while coral reef fish at St. Croix averaged -11.8‰ and fish from seagrass meadows averaged -12.6‰ (St. Croix) and -14.1‰ (Cayos Miskitos). As the -18.0 value represents fish entirely dependent on phytoplankton-derived carbon and the least negative fish $\delta^{13}\text{C}$ value, -9.8‰ , is representative of a 100% dependence on carbon derived from benthic plants, the -11.8 to -14.1 $\delta^{13}\text{C}$ averages suggest that benthic plants contribute 48–76% of the carbon in fish from the coral reef and seagrass meadow sites. These estimates are probably conservative for benthic plants since the -11.8 to -14.1‰ averages may result entirely from mixtures of various benthic algae and seagrasses.

The stable isotope data thus provide a means to broadly evaluate consumer diets, in this case showing that benthic plants are dominant food sources in these shallow Caribbean ecosystems. Attempts to define closely which benthic plants were the most important food sources largely failed, as fish consuming seagrasses at St. Croix did not significantly differ in $\delta^{13}\text{C}$ values from coral reef fish or from fish consuming macroalgae (Tables III and IV). The isotopic homogeneity among fish may reflect a close coupling between the reef and seagrass ecosystems which are juxtaposed at St. Croix. Mixing of carbon flows between the two habitats occurs as fish and invertebrates found on reefs during the day will forage at night in neighboring seagrass meadows (Ogden, 1980). Carbon flows between the two habitats may also be made via floating seagrasses. Seagrass leaves are regularly lost from grassbeds (Zieman et al., 1979) and, when trapped on a reef, these leaves may form a food source for reef-dwelling animals.

However, the case of the ballyhoo fish, *H. brasiliensis*, suggests another mechanism which could cause the observed isotopic uniformity. This fish consumes floating *Syringodium* seagrass leaves almost exclusively, but $\delta^{13}\text{C}$ values for two individual fish were -10.3 and -11.1‰ (Table III), while *Syringodium* leaves had $\delta^{13}\text{C}$ values of -4.0 to -5.1‰ . The discrepancy could be accounted for by digestion of epiphytic algae ($\delta^{13}\text{C} = -12.4\text{‰}$ for *Thalassia* epiphytes at St. Croix) rather than the seagrass leaf itself. Because microalgae are common both on coral reefs and on seagrass blades, consumption of these plants could account for the overall $\delta^{13}\text{C}$ similarity observed at all study sites. This explanation derives additional support from observations that epiphytic algae are often preferred fish foods (Lobel and Ogden, 1981).

In conclusion, the common occurrence of -9 to -15‰ $\delta^{13}\text{C}$ values among Caribbean algae strongly limits the power of the $\delta^{13}\text{C}$ technique to resolve

the specific food-web importance of the dominant Caribbean seagrass, *Thalassia testudinum* Banks ex Koenig ($\delta^{13}\text{C} = -10$ to -13‰). Because algal—seagrass differences are greater in the case of *Syringodium* seagrass ($\delta^{13}\text{C} = -4$ to -7‰), future laboratory and field investigations of this somewhat less common species may yield clearer definitions of the role seagrasses have as carbon sources in the nearshore Caribbean. The causes of the large 26‰ range among algae of the region are not known at present, but may involve complex isotope effects in both the diffusion and fixation steps of carbon uptake by the algae (Osmond et al., 1981). Clarifying the reasons for this isotopic variation among the algae will greatly enhance future $\delta^{13}\text{C}$ studies of carbon flow in the shallow Caribbean.

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