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Use of isotopic signatures to assess the food web in a tropical shallow marine ecosystem of Southeastern Brazil

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Abstract

A dual isotope approach was used to assess the relative importance of terrestrial vegetation detritus and other primary producers in the trophic web of Flamengo Sound (Ubatuba, SP), SE Brazil, surrounded by the Atlantic Rain Forest. Primary producers showed distinct δ^{13}C signatures and the observed values suggest that little terrestrial (−29.4 ± 0.3‰) or bulk sediment organic matter (−21.1 ± 1.3‰) enter the food web of the sound. Suspended particulate organic matter (POM, −18.6 ± 0.5‰) supports the bulk of the consumers, with some contribution by macroalgae (−15.6 ± 1.8‰). Consumers δ^{13}C values ranged from −17.4 to −12.7‰. At least three trophic levels were detectable in the food web. The δ^{15}N value of POM was 7.5 ± 1.0‰, while that of sediment and detritus was 6.4 ± 0.7‰. The δ^{15}N values of suspension feeding benthic invertebrates were 8.2–8.6‰, deposit feeders 8.3–10.2‰, and carnivores 10.7–13.2‰. Values for fishes were 9.4‰ for detritivore, 11.4–13.3‰ for benthic feeders, 12.4–13.3‰ for zooplanktivores, and 13.2‰ for piscivores/benthic invertebrate feeders. Squid mean value was 12.8 ± 0.5‰. There is a reasonable agreement between feeding habits information from the literature and δ^{15}N values from this study. In the sound, the first and second trophic steps seem to be about 1–3‰ higher than those of similar organisms studied in temperate waters and this may reflect an input of allochtonous anthropogenic nitrogen enriched in ^{15}N from human activities.

Introduction

Isotopic signatures based on the ratio of different stable isotopes of elements have been broadly applied to investigate a variety of processes. In particular, the δ^{15}N and δ^{13}C have been used in environmental studies to understand the sources of nitrogen and carbon entering coastal ecosystems (McClelland and Valiela 1997; Heikoop et al. 2000; Costanzo et al. 2001; McKinney et al. 2001; Waldron et al. 2001) and to trace feeding relationships in food webs of coastal environments (Currin et al. 1995; Kwak and Zedler 1997; Peterson 1999; Griffin and Valiela 2001). The use of stable isotopes in food web studies is based on the assumption that the isotopic composition of a consumer is enriched by a factor of 3–4‰ and <1‰ for N and C, respectively, relative to its diet (Peterson and Fry 1987). Furthermore, there must be sufficient differences in the signatures of C and N of the different primary organic matter sources (terrestrial material, phytoplankton, benthic macro- and microalgae) to distinguish their contribution to the food web.

Many studies have used stable isotope ratios to distinguish the contribution of producers to particulate organic matter in tropical estuaries, mangroves and seagrass systems (Rezende et al. 1990; Lin et al. 1991; Rao et al. 1999; McKee et al. 2002; Barcellos et al. 2004). Other tropical and subtropical studies have considered the contribution of different primary producers in food webs of estuarine–mangrove systems (Ambler et al. 1994; Marguillier et al. 1997; Fry et al. 1999; Dehairs et al. 2000; Bouillon et al. 2002a, b; Fry and Smith 2002; Moriniere et al. 2003). The Southeastern coast of Brazil (between 23° S and 24° S) is characterized by the proximity of the Atlantic Rain Forest, which can contribute with terrestrial vegetation detritus to the coastal benthic system, mainly during the rainy season (Mahiques et al. 1998).

The purpose of the present study is to use a dual isotope approach ($\delta^{13}C$ and $\delta^{15}N$ analysis) to verify whether or not terrestrial vegetation detritus is actually incorporated into the shallow coastal food web in Flamengo Sound (SE Brazil), along with other primary sources of organic matter. The isotopic N and C content measurements of the fauna were also compared with information on feeding habits obtained from the literature to verify the trophic position of consumers found in the nearshore zone.

Material and methods

Study site

Sampling was carried out in Flamengo Sound (Ubatuba), southeastern Brazil (23°30′ S, 45°06′ W) (Figure 1), situated on the northern coast of São Paulo state, bordered by the Tropical Atlantic Forest. This area receives an average of 2100 mm of annual rainfall (Bencke and Morellato 2002, p. 238). The climate is typical of tropical rain forest, with a very rainy season between October and April (monthly mean rainfall of 285 mm) and a period (May to September) with monthly mean rainfall of 118 mm. Mean annual air temperature is 22 °C and, in general, February is the warmest month (mean temperature of 25.9 °C). The sound has a surface area of 18 km^2, mean width of 2.5 km and a maximum depth of 14 m. It is oriented N–S and subject to waves from E–NE, associated with trade winds, or S–SE, associated with the passage of cold fronts over the area (Mahiques et al. 1998). Muddy sediments are predominant, suggesting a low energy depositional environment characteristic of restricted circulation (Mahiques 1995). The Atlantic Tropical Forest surrounds the study site where there is no mangrove forest, and a poorly developed seagrass bed of *Halodule wrightii* is found in the very inner part of the sound (Oliveira et al. 1983). Water temperature ranges from 18.1 to 25.9 °C and salinity from 33.4 to 35.9 (Perazza 1982; Azevedo 2002). During the sampling period, the surface temperature in Flamengo Sound ranged from 28.9 to 30.1 °C and the salinity from 32.4 to 35.0. Lower salinity and higher temperature values are characteristically from Coastal Water (CW) in high summer in the northern coast of São Paulo state (Castro Filho et al. 1987). Local drainage from small rivers is not very important and continental sedimentary contributions take place during the summer rainy season, when transport of terrestrial macrophyte biomass represents a considerable organic matter contribution (Mahiques 1995; Mahiques et al. 1998). Oligotrophic conditions prevail during the year, and phytoplankton peaks occur in the spring–summer as a result of the enrichment of the euphotic layer (Sassi and Kutner 1982) by intermittent upwelling of deeper water (Castro Filho et al. 1987; Azevedo 2002). Additional contributions of nutrients are received from boats and marina activities, and from a small sewage outfall.

Methods

Samples were collected in February 1999, during the summer rainy season. Macroalgae, fishes and invertebrates were hand collected from intertidal boulders or with a beach seine towed along the shoreline of two beaches. Sublittoral benthic invertebrates, fishes, macroalgae, terrestrial plant

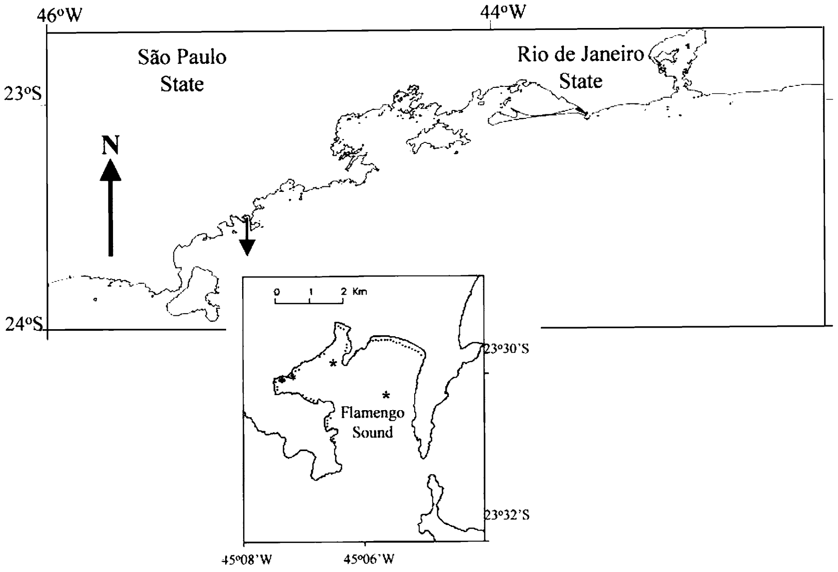

Figure 1. Southeastern coast of Brazil showing the four sampling sites (*) at Flamengo Sound.

leaves deposited on the bottom of the sound, and surface sediments were obtained on board of the R/B Velliger II, using a van Veen grab and an otter trawl, at two stations at 5 and 9 m depth (Figure 1).

Suspended particulate organic matter (POM) was obtained by filtering surface seawater onto GF/F glass fiber filters (nominal pore size 0.7 μm) and stored frozen. Macrobenthic infaunal invertebrates collected with the van Veen grab were washed on a 1 mm screen and sorted alive. Polychaetes, small molluscs and crustaceans were held in seawater overnight to allow gut clearance. Molluscs were removed from shells and their muscle tissue dissected. Barnacles, echinoderms and sediments were treated with 1 N HCl to remove inorganic carbonates before ^{13}C analysis. Before acidification, material for stable nitrogen isotope ratio analysis was separated. Muscle tissue samples were dissected from fishes, squids, and decapods. Macroalgae and macrophyte leaves were rinsed with distilled water and all visible incrustation was removed from their surface. Samples of individual macroproducers and macroconsumers were pooled to create representative composite samples.

Samples were dried at 60 °C and then grounded into powder with mortar and pestle. The dried samples were stored in sealed vials and kept in dessicator until packed for shipping.

The stable isotope measurements were performed by Boston University Stable Isotope Laboratory, using a Finnigan Delta-S isotope ratio mass spectrometer. Internal reference material (peptone and glycine) was analyzed after every ten samples to calibrate the system and compensate for drift with time.

Stable isotope ratios are expressed in δ notation as part per thousand (‰) according to the following relationship:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3,$$

where $X = {}^{13}C$ or ^{15}N, and $R = {}^{13C}/{}^{12}C$ or $^{15}N/{}^{14}N$ (Peterson and Fry 1987). The standard reference for carbon is Pee Dee Belemnite (PDB) and atmospheric N_2 for nitrogen. Precision of replicates analyses was ±0.2‰.

Results and discussion

Carbon and nitrogen signatures in primary producers and sediments

Macroalgae showed the highest values of $\delta^{13}C$ signatures among the primary producers ranging from −17.6 to −11.2‰, with a mean value of -15.6 ± 1.8‰ (Table 1). These values are within the range compiled from the literature (−32.8 to

Table 1. $\delta^{13}C$ and $\delta^{15}N$ (‰) (mean ± sd) of sediment, POM, primary producers and consumers in the coastal waters of Flamengo Sound, Ubatuba (SP).

Group/species		$\delta^{13}C$		$\delta^{15}N$		N	Length (mm)
		Mean	SD	Mean	SD		
Sediment		−21.1	1.3	6.4	0.7	3	
Producers							
C3 plant leaves		−29.4	0.3	3.7	0.0	2*	
POM		−18.6	0.5	7.5	1.0	4	
Macroalgae		−15.6	1.8	7.3	0.7	18	
Brown algae	*Dyctiopteris delicatula*	−17.0	0.2	8.1	0.5	2	
	Sargassum filipendula	−15.1	0.5	7.7	0.1	2	
	Padina vickersiae	−13.6	0.9	7.6	1.1	2	
Green algae	*Enteromorpha* sp.	−17.0		7.4		1	
	Ulva fasciata	−17.2	2.1	6.4	1.1	3	
Red algae	*Chondracanthus acicularis*	−17.6		7.5		1	
	Hypnea spinella	−17.0		7.3		1	
	Pterocladiella capilacea	−16.4		7.4		1	
	Acantophora spicifera	−15.6		7.3		1	
	Agardhiella subulata	−15.2		7.1		1	
	Hypnea musciformis	−15.2		7.7		1	
	Gelidium floridanum	−15.0		6.6		1	
	Galaxaura frutescens	−11.2		6.2		1	
Invertebrates							
Suspensivore		−16.9	0.2	8.4	0.2	2	
Crustaceans	*Chthamalus bisinuatus*	−17.0		8.2		1*	
Bivalves	*Chione* sp., *Anomalocardia* sp., *Pitar* sp.	−16.7		8.6		1*	
Depositivore		−15.9	2.2	9.5	1.0	5	
Polychaetes	*Spiochaetopterus nonatoi*	−16.4	2.2	10.2	0.5	2*	
Ophiuroids	*Hemipholis elongata*	−16.7		10.2		1*	
Bivalves	*Tellina* sp., *Abra* sp., *Solen* sp. Diplodontidae	−17.4		8.3		1*	
Gastropods	*Strombus pugilis*	−12.7		8.5		1*	
Carnivore		−14.9	1.1	11.3	0.8	7	
Asteroids	*Luidia* sp.	−13.5	0.3	10.9	0.1	2*	
Crustaceans	*Xiphopenaeus kroyeri*	−15.6		11.6		1*	
	Callinectes danae	−14.4		11.0		1*	
	Callinectes ornatus	−15.4		10.7		1*	
Gastropods	*Stramonita haemastoma*	−15.2		10.9		1*	
Polychaetes	*Goniada* sp., *Glycinde* sp., *Nereis* sp. *Parandalia* sp.	−16.3		13.2		1*	
Piscivore/invertebrate feeder							
Squids	*Loligo* sp.	−16.4	0.8	12.8	0.5	2*	
Fish							
Detritivore	*Mugil* sp.	−17.2		9.4		1*	32–37
Benthic feeder		−14.4	1.1	12.0	0.9	16	
	Diapterus rhombeus	−14.6	0.7	12.4	0.3	3*	69–122
	Ctenosciaena gracilicirrhus	−15.7		12.8		1*	97–114
	Etropus crossotus	−16.4		11.4		1*	112–124
	Eucinostomus argenteus	−12.8	0.5	11.7	1.0	3*	35–130
	Eucinostomus gula	−15.5		13.3		1*	141–147
	Micropogonias furnieri	−14.3		12.0		1	172
	Lutjanus synagris	−14.2	0.5	11.7	1.4	5*	52–248
	Trachinotus carolinus	−15.6		11.7		1*	60–89

Table 1. Continued.

Group/species		$\delta^{13}C$		$\delta^{15}N$		N	Length (mm)
		Mean	SD	Mean	SD		
Zooplanktivore		−16.8	0.4	12.8	0.5	5	
	Cynoscion jamaicensis	−16.5		12.7		1*	121–128
	Pellona harroweri	−17.2	0.1	13.3	0.6	2*	77–149
	Chirocentrodon bleekerianus	−16.6	0.4	12.4	0.3	2*	61–95
Piscivore/invertebrate feeder							
	Centropomus undecimalis	−16.2		13.2		1	219

N = number of samples, (*) composite samples.

−4.9‰) by Fry and Sherr (1984) and Currin et al. (1995).

POM and terrestrial plant leaves had values of −18.6 ± 0.5‰ and −29.4 ± 0.3‰, respectively (Table 1). The low $\delta^{13}C$ values of plant leaves were in agreement with results from elsewhere (Currin et al. 1995; Deegan and Garritt 1997; Kwak and Zedler 1997; Loneragan et al. 1997) and with the $\delta^{13}C$ values of tree leaves from the Tropical Atlantic Forest but lower than that observed from the sea bottom (−26.1‰) at the entrance of Flamengo Sound (Matsuura and Wada 1994). Our values for isotopic ratios in POM were higher than those found in the coastal shelf zone (−21.7 to −20.5‰) of Ubatuba region (Matsuura and Wada 1994). Microphytobenthos biomass is high in the sound (Corbisier et al. 1997). Although its isotopic signature was not analyzed, data from the literature were higher than those for macroalgae (mean of −14.9‰, references in Currin et al. 1995).

Nitrogen stable isotope ratios of producers in Flamengo Sound varied from 3.7‰ (C3 plant leaves) to 8.1‰ (brown algae). POM had value of 7.5 ± 1.0‰ (Table 1 and Figure 2), which was in the range of those for phyto- and microzooplankton (6.9–9.6‰) from the coastal shelf zone (Matsuura and Wada 1994). The different values found by these authors for the tree leaves (7.9‰) could reflect degradation of organic material (Zieman et al. 1984).

Nitrogen isotopic signatures of macroalgae collected in Flamengo Sound (7.3 ± 0.7‰) were higher than those measured in oligotrophic estuaries of the northeastern United States (McClelland and Valiela 1997), and were in the range of algae values from an estuary with N loading from wastewater (McClelland and Valiela 1998a, b). This high signature might be a result of input from the sewage treatment plant outfall as verified elsewhere by Costanzo et al. (2001), Savage and Elmgren (2004) and Cole et al. (2005), or from the possibly heavy NO_3 that enters Flamengo Sound during intermittent upwelling (Aidar et al. 1993). Reports of $\delta^{15}N$ values from deeper waters, however, suggest that upwelled water may hold nitrate with average $\delta^{15}N$ of about 4.8‰, perhaps as high as 6‰ (Sigman et al. 2000). These relatively low values seem unlikely to serve as the sources that create the higher values in POM and macroalgae $\delta^{15}N$ evident in Figure 2. The source of the relatively higher signatures therefore seems more likely to be associated with wastewater input to the sound.

The $\delta^{13}C$ of sediment organic matter in Flamengo Sound (−21.1 ± 1.3‰) was clearly dominated by marine sources, with values in the range of continental shelf sediments (−21.9 to −20.3‰) between 40 and 124 m depth along the southeastern coast of Brazil (Matsuura and Wada 1994; Mahiques et al. 1999). This finding contrasts with the gradient from −27.2 (continental influence) to −23.1‰ (marine influence) that was observed in a lagoonal estuarine system surrounded by extensive mangroves in the south of São Paulo state (Barcellos et al. 2005).

The $\delta^{15}N$ of sediment was 6.4 ± 0.7‰ (Table 1), a value somewhat higher than found by Matsuura and Wada (1994) in the coastal shelf zone (4.1–6.0‰) and by Mahiques et al. (1999) in the outer shelf (4.9–6.1‰). The slight increase might be another indication of wastewater inputs.

Food web

The overall distribution of $\delta^{13}C$ values for consumers shows that, considering a trophic enrichment of ~1‰, they did not rely substantially on

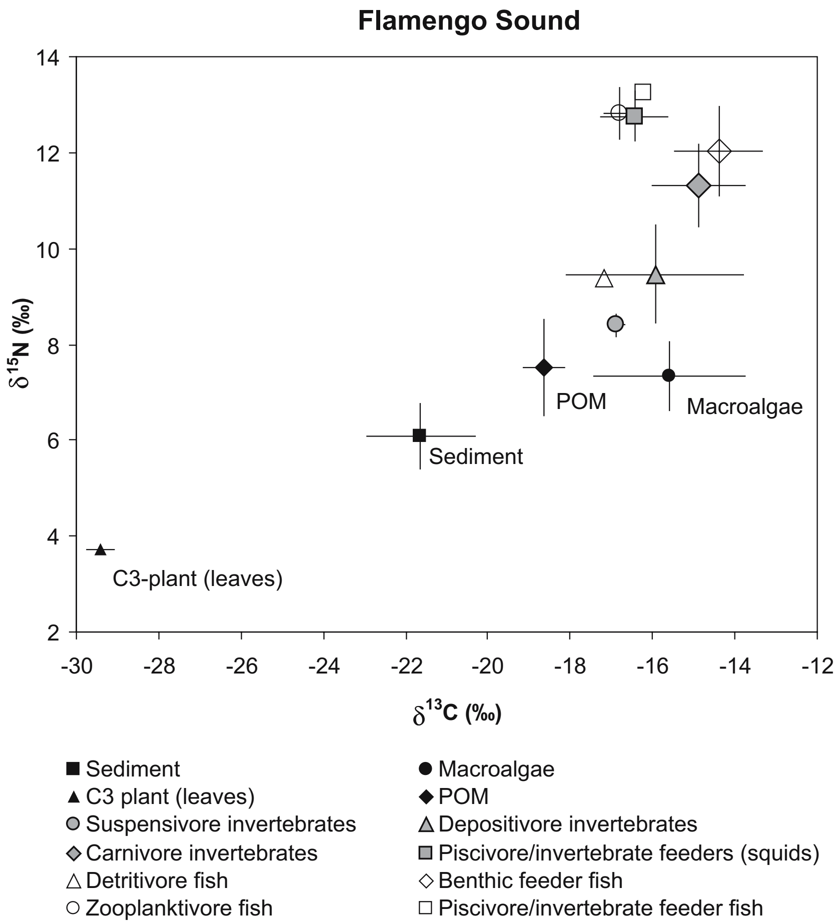

Figure 2. δ^{13}C and δ^{15}N (‰) (mean ± sd) of sediment, producers and consumers of Flamengo Sound.

the terrestrial carbon source (-29.4 ± 0.3‰) during the summer rainy period. In fact, the δ^{13}C values of the fauna are typical of marine phytoplankton-based food webs (Table 1 and Figure 2), with some of the more ^{13}C-enriched values (> -15‰) also suggestive of inputs such as benthic macroalgae or microalgae (Currin et al. 1995). Microphytobenthos could also be an important source of carbon for depositivore organisms, although its biomass in the sound is represented mainly by phaeopigments (Corbisier et al. 1997) produced during degradation of photosynthetic organisms.

Suspensivore and depositivore invertebrates showed δ^{13}C values between POM and macroalgae, suggesting contribution of these primary sources of carbon to both feeding groups (Figure 2). Another potential carbon source could be the microphytobenthos. These two group of invertebrates are slightly distinct in δ^{15}N values (δ^{15}N = 8.4 and 9.5‰, respectively) and the two potential primary sources of organic nitrogen exhibited similar δ^{15}N values: POM 7.5 ± 1.0‰ and macroalgae 7.3 ± 0.7‰. The trophic classification of bivalves into suspensivore and depositivore is not always easy and accurate, because both groups can feed directly on deposits and also take up a good deal of suspended matter with the inhalant flow (Arruda et al. 2003). These facts tend to make interpretation of δ^{15}N data in the first steps of the food web more difficult. There can be substantial variation in consumer-diet δ^{15}N enrichment throughout trophic webs: detritivores yield lower estimates of enrichment than carnivores, as well as mollusks and crustaceans in relation to other groups, partly due to the excretion of ammonia (Vanderklift and Ponsard 2003). The high $\delta^{13}C$ value of *Strombus pugilis*, that feed on algae and/or detritus (Rios 1994), would be explained if this gastropod was feeding on some enriched macroalgae.

Carnivore invertebrates had average $\delta^{13}C$ of -14.9 ± 1.1‰. Similar $\delta^{13}C$ values of *Xiphopenaeus kroyeri* and *Callinectes ornatus* were found in Ubatuba Bay (Mantellato et al. 2002), an area near the sampling site. Shrimps, crabs and sea stars make up the main megabenthic group of the inner shelf of Ubatuba in terms of density and biomass (Pires 1992), and are active predators that exploit a broad range of food items like polychaetes, mollusks and crustaceans (Tararam 1993; Petti 1997). Among the invertebrates, they presented the highest $\delta^{15}N$ signatures.

The $\delta^{13}C$ of fish collected in the Flamengo Sound ranged from -17.2‰ to -12.8‰ (Table 1). The lowest signatures of $\delta^{13}C$ and $\delta^{15}N$ were found on the detrivore fish (*Mugil* sp.). This is in agreement with their food habits since mugillids use detritus and microphytobenthos as a food source (Oliveira and Soares 1996). Zooplanktivore fishes showed $\delta^{13}C$ values closer to the POM. However, their $\delta^{15}N$ signatures showed that they were not feeding directly on POM, but probably on zooplankton as verified by Gasalla and Oliveira (1997) and Soares et al. (in press).

The piscivore and invertebrate feeder fish and squids had similar $\delta^{13}C$ signatures, an indication of the same primary carbon source. The similarity of $\delta^{15}N$ signatures of these groups may be due to the small size of squids and *C. undecimalis* sampled in this study, which feed mainly on zooplankton (Andriguetto and Haimovici 1997; Teixeira 1997).

The more enriched $\delta^{13}C$ of benthic feeder fishes could be associated to their diet since most of the species in this group feed mainly on polychaetes, represented here by the depositivore invertebrates (Table 1).

There was little evidence that bulk sediment or terrestrial organic matter substantively entered the food web of Flamengo Sound (Figure 2). Matsuura and Wada (1994) also concluded that the terrestrial plant leaves have no direct relationship with the food web of the coastal shelf ecosystem in this area. In a tropical estuarine mangrove ecosystem, carbon stable isotope ratios also suggested that mangrove-derived and other terrestrial carbon are not a significant food source for subtidal benthic invertebrates (Bouillon et al. 2002a), as well as for most intertidal benthic invertebrates (Bouillon et al. 2002b), where mangrove carbon is only assimilated by a limited number of invertebrate groups (sesarmid crabs, and some gastropods). Similar results were found in temperate salt marsh ecosystems (Currin et al. 1995; Deegan and Garritt 1997).

Primary producers create organic matter in Flamengo Sound with $\delta^{15}N$ values between 3 and 8‰ (Table 1 and Figure 2). The lowest trophic position of consumers ($\delta^{15}N = 8.4$–9.5‰) in the Flamengo Sound food web included suspensivore and depositivore invertebrate species, and detritivore fish (Figure 2). A second tier ($\delta^{15}N = 11.3$–12.0‰) is composed of invertebrates and fish that feed on bottom-dwelling species. Zooplanktivores, and piscivore and invertebrate feeders appeared in the highest trophic position ($\delta^{15}N = 12.8$–13.2‰).

The range of $\delta^{15}N$ of consumers (Table 1) seems to reasonably match feeding type assignments done on the basis of gut contents and feeding morphology information from literature (Table 2). A comparison of the range of species pooled into trophic groups (Figure 2) shows increasing $\delta^{15}N$ values in groups of species that were placed higher up in the food web on the basis of feeding habits information.

In summary, the stable isotope data helped to identify not only the main primary sources of carbon (POM and macroalgae) entering the Flamengo Sound food web, but also to dissect the trophic relationships in this ecosystem. The first and second trophic steps seem about 1–3‰ higher than those of similar organisms studied in temperate waters (McClelland and Valiela 1998; Martinetto et al. 2006). These results may reflect an input of allochtonous anthropogenic nitrogen enriched in ^{15}N from human activities. Costanzo et al. (2001) detected high $\delta^{15}N$ levels in macroalgae near sewage outfalls in a semi-enclosed bay receiving multiple sewage inputs, in Australia. Further studies assessing temporal variations in Flamengo Sound $\delta^{15}N$ values, and comparison with similar tropical pristine areas must be done in order to confirm the cause of the high $\delta^{15}N$ signatures of primary producers (mainly macroalgae).

Table 2. Feeding habits of the analyzed species based on the literature data.

Species	Food habits	References
Fish		
Mugil sp.	Bacillariophyceae and detritus	Oliveira and Soares (1996)
Chirocentrodum bleekerianus	Zooplanktivore (fish larvae)	Gasalla and Oliveira (1997)
Pellona harroweri	Zooplanktivore (fish larvae)	Soares et al. (in press)
Cynoscion jamaicensis	Piscivore and zooplanktivore	Soares et al. (in press)
Diapterus rhombeus	Benthic invertebrate feeder (polychaetes and infaunal crustaceans)	Soares et al. (in press)
Etropus crossotus	Benthic invertebrate feeder (polychaetes and infaunal crustaceans)	Soares et al. (in press)
Eucinostomus argenteus	Benthic invertebrate feeder (polychaetes and infaunal crustaceans)	Soares et al. (in press)
Eucinostomus gula	Benthic invertebrate feeder (polychaetes and infaunal crustaceans)	Soares et al. (in press)
Lutjanus synagris	Benthic invertebrate (crustacean) and fish feeder	Rodrigues (1974)
Micropogonias furnieri	Benthic invertebrate feeder (polychaetes) and piscivore	Soares et al. (in press)
Trachinotus falcatus	Benthic invertebrate feeder (molluscs, polychaetes, amphipods, mysids)	Helmer and Teixeira (1995)
Ctenosciaena gracilicirrhus	Piscivore and benthic invertebrate feeder (shrimps)	Soares et al. (in press)
Centropomus undecimalis	Piscivore and crustacean feeder	Vasconcelos-Filho et al. (1980); Teixeira (1997)
Invertebrates		
Anomalocardia sp., *Chione* sp.	Suspensivore	Arruda et al. (2003)
Chthamalus bisinuatus	Suspensivore	Navarrete and Wieters (2000)
Abra sp., *Tellina* sp.	Deposit feeder	Arruda et al. (2003)
Spiochaetopterus sp.	Surface deposit feeder	Fauchald and Jumars (1979)
Strombus pugilis	Feeding on algae or detritus	Rios (1994)
Callinectes ornatus	Carnivore: shrimp/polychaetes/crabs/fish/molluscs	Petti (1997)
Luidia sp.	Carnivore: polychates,crustaceans, molluscs	Tararam et al. (1993)
Stramonita haemastoma	Carnivore: mussels, oysters, barnacles, molluscs	Rios (1994)
Callinectes danae	Carnivore: molluscs, polychaetes, crustaceans	Branco and Verani (1997)
Xiphopenaeus kroyeri	Carnivore: mainly on Gammaridea; omnivore (crustacean/algae/polychaetes)	Branco and Moritz (2001); Tararam et al (1993)
Loligo sanpaulensis	Carnivore: fish, crustaceans, squids	Andriguetto and Haimovici (1997)

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