Mangroves and Seagrass Beds as Feeding Areas for Fishes of Commercial Interest in a Caribbean Island

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ABSTRACT

Mangroves are considered as important source of organic matter for adjacent marine ecosystems due to their high primary production. Yet, there is still a debate on the contributions of mangrove carbon to food webs due to the influence of adjacent habitats, such as seagrass beds. To determine the importance of these two ecosystems as fish feeding grounds, stable isotopes of carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N) were performed on seven fish species of commercial interest and their potential food items in mangrove shoreline sites and adjacent seagrass beds in Guadeloupe. The IsoSource mixing model was used to determine the range of contributions of several potential food items in the consumers diet. On the basis of their $\delta^{13}C$, prey items collected in mangroves were more depleted in ^{13}C ($\delta^{13}C_{mean}$ = -20.7 ± 1.2‰) than those from seagrass beds ($\delta^{13}C_{mean}$ = -13.0 ± 0.5‰). The $\delta^{13}C$ signatures of most reef fishes from fringing mangroves were similar to those of prey items from seagrass beds, suggesting that these fish feed from seagrass habitats. Only two species, the carnivore *Ocyurus chrysurus* and the piscivore *Tylosurus crocodilus*, appeared to feed to a larger extent in mangrove habitat. Moreover, ontogenetic resource partitioning was observed for the carnivorous species *O. chrysurus*, with small juveniles feeding on zooplankton and invertebrates from mangrove habitat and larger specimens consuming invertebrates and fishes from seagrass beds. These findings show that seagrass beds represent important feeding grounds for juvenile reef fish species of commercial interest during their mangrove habitat phase.

KEY WORDS: Fish feeding areas, mangroves, seagrass beds, stable isotopes, Guadeloupe

Manglares y Praderas de Fanerógamas Marinas como Zonas de Alimentación de Peces de Interés Comercial en una Isla del Caribe

Los manglares son considerados como importante fuente de materia orgánica para los ecosistemas marinos adyacentes debido a su alta producción primaria. Sin embargo, todavía hay un debate sobre la contribución de manglares en los niveles tróficos debido a la influencia de los hábitats adyacentes, como las praderas de Fanerógamas marinas. Para determinar la importancia de estos dos ecosistemas en la alimentación de peces, los isótopos estables de carbono (^{13}C:^{12}C) y de nitrógeno (^{15}N: ^{14}N) fueron realizados sobre siete especies de peces de interés comercial y sobre sus alimentos posibles en estaciones localizadas en manglares y praderas en Guadeloupe. El modelo IsoSource fue utilizado para determinar las posibles contribuciones de varios alimentos en los hábitos alimenticios de los consumidores. Sobre la base de sus $\delta^{13}C$, alimentos que provienen de manglares son más pobre en ^{13}C ($\delta^{13}C_{mean}$ = -20,7 ± 1,2 ‰) que los de praderas de Fanerógamas marinas ($\delta^{13}C_{mean}$ = -13,0 ± 0.5 ‰). Las firmas en $\delta^{13}C$ de la mayoría de los peces de arrecifes cerca de manglares fueron similares a los de alimentos de praderas, lo que sugiere que estos peces se alimentan en las praderas marinas. Sólo dos especies, el carnívoro *Ocyurus chrysurus* y el piscivore *Tylosurus crocodilus*, parecen alimentarse más en manglares. Por otra parte, un cambio ontogenético de alimentación se observó para las especies carnívoras como *O. Chrysurus*; con los juveniles que se alimentan del zooplancton y de los invertebrados de manglares y los individuos más grandes que consumen invertebrados y peces de praderas. Estos resultados muestran que las praderas marinas representan zonas importantes de alimentación para los peces arrecifales de interés comercial durante su residencia en manglares.

PALABRAS CLAVES: Peces, zonas de alimentación, manglares, praderas marinas, isótopos estables, Guadeloupe

Les Mangroves et les Herbiers de Phanérogames Marines comme Zones D'Alimentation pour des Poissons D'Intérêt Commercial dans une Île de la Caraïbe

En raison d'une production primaire élevée, les mangroves sont considérées comme des sources importantes de matière organique pour les écosystèmes marins côtiers. Cependant, l'influence d'habitats adjacents, tels que les herbiers de Phanérogames marines, est à l'origine d'une controverse sur les contributions de la matière organique de mangrove dans la chaîne trophique. Afin de déterminer l'importance relative de ces deux écosystèmes en tant que zones d'alimentation pour l'ichtyofaune des analyses isotopiques du carbone (^{13}C:^{12}C) et de l'azote (^{15}N:^{14}N) ont été réalisées sur sept espèces de poissons d'intérêt commercial ainsi que sur leurs proies provenant des mangroves et des herbiers en Guadeloupe. Le modèle de mélange IsoSource a été utilisé pour déterminer les contributions des différentes proies dans le régime alimentaire des poissons. D'après les valeurs de $\delta^{13}C$, les proies collectées en mangrove sont plus appauvries en ^{13}C ($\delta^{13}C_{moyen}$ = -20,7 ± 1,2‰) par rapport à celles provenant des herbiers ($\delta^{13}C_{moyen}$ = -13,0 ± 0,5‰). Les signatures en $\delta^{13}C$ de la plupart des poissons récifaux collectés en mangrove sont similaires aux signatures des proies provenant des herbiers, suggérant que ces espèces s'alimentent dans les herbiers de Phanérogames marines. Seules deux espèces, le carnivore *Ocyurus chrysurus* et le piscivore *Tylosurus crocodilus* semblent s'alimenter en mangrove. De plus, une ségrégation ontogénétique des sources de nourriture a été observée pour l'espèce carnivore *O. chrysurus*, dont les juvéniles de petite taille s'alimentent de zooplancton et d'invertébrés présents en mangrove alors que les spécimens de plus grande taille consomment des invertébrés et des poissons provenant des herbiers. Ces résultats soulignent l'importance des herbiers en tant que zones d'alimentation pour des poissons récifaux d'intérêt commercial observés en mangrove au stade juvénile.

MOTS CLÉS**:** Ichtyofaune, zones d'alimentation, mangroves, herbiers, isotopes stables, Guadeloupe

INTRODUCTION

Mangroves are known to represent suitable habitats for fish species as nurseries, shelters, habitats for species of commercial interest, and fish feeding grounds. Early studies on mangrove food webs undergone in Florida by Odum and Heald in the 1970s emphasized the importance of mangrove litter via a detritus-based food web. Mangrove litter is degraded by microbial communities into a more palatable organic matter which is consumed by various organisms (annelids, crabs, shrimps…). These organisms can be consumed by second consumers such as fish. However, with the increasing use of stable isotopes in trophic studies, there is a debate upon the contribution of mangroves as fish feeding grounds and several researches pointed out the importance of adjacent habitats as fish foraging areas, such as seagrass beds (Kieckbusch *et al.* 2004, Marguillier *et al.* 1997, Nagelkerken and van der Velde 2004). Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in an organism reflect the isotope signatures of its diet, with an enrichment per trophic level of on average 1‰ for the carbon and 3 - 4‰ for nitrogen (DeNiro and Epstein 1978, Minagawa and Wada 1984). Thus, stable isotope ratios can be used as tracers of organic matter origin in aquatic trophic chain (Fry and Sherr 1984). Stable isotopes provide time-integrated assimilation over months of the organic matter assimilated by an organism (Gearing 1991). Due to different photosynthetic pathways, there is a natural variation of carbon isotope signatures between mangroves and seagrass beds, with mangroves characterized by isotopic ratios more depleted in ^{13}C compared to seagrass beds (Farquhar *et al.* 1989, Hemminga and Mateo 1996). Stable isotopes of carbon (^{13}C:^{12}C) can then be used to assess the contributions of sources from mangroves and seagrass beds in the food chain.

Thus, the objectives of the present study were to compare the relative importance of mangroves and seagrass beds habitats as fish feeding grounds and to focus on species of commercial interest sheltering in mangroves during their juvenile stages.

METHODS

Study Area

Guadeloupe island is located in the Lesser Antilles and is formed by two islands ("Grande-Terre" and "Basse-Terre") separated by a narrow channel named "Rivière Salée" (Figure 1). The study was carried out in the lagoon of the Grand Cul-de-Sac Marin (GCSM) located in the north part of Guadeloupe Island (Figure 1). This shallow lagoon of 11 000 ha is limited seaward by a 30 km long coral reef, one of the longest barrier reef of the Lesser Antilles (Bouchon and Laborel 1990), and landward by mangrove forests, dominated by *Rhizophora mangle* (Linnaeus), covering an area of 2 700 ha (Chauvaud *et al.* 2001) (Figure 1). The depth of the lagoon varies from a few decimetres on shallows and corals keys to 20 meters in the channels. Several of these cays (Fajou, Carénage, Christophe and Macou islets) are colonized by mangroves (Figure 1). The climate is typical of tropical areas and is characterized by a dry season (from December to April) and a wet season (from July to November).

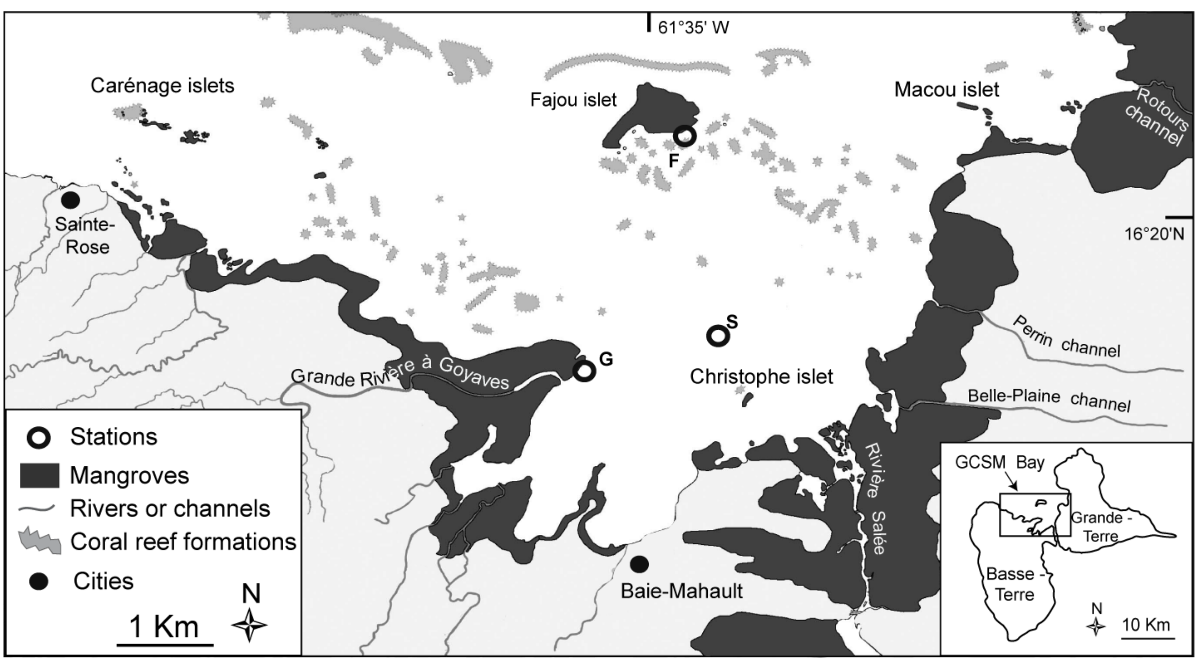

Figure 1. Map of the lagoon of the Grand Cul-de-Sac Marin in Guadeloupe showing the location of the mangroves (F-Fajou islet, G-Rivière à Goyaves) and seagrass beds (S) sites.

Study Design

To determine the relative importance of mangroves and seagrass beds as fish feeding grounds, two mangrove stations (F-Fajou islet, G-Grande Rivière à Goyaves) and one seagrass site (S) were sampled between September and December 2007 (Figure 1). Fishes were collected in mangrove sites using a net called "capéchade" (Figure 2a) and in seagrass beds with a seine-net (Figure 2b). Seven fish species of commercial importance were identified using FAO (Carpenter 2002ab) and FishBase data bases (Froese and Pauly 2006). Juveniles were separated from adults according to specific length at maturity reported in the literature (Cervigón 1994, Froese and Pauly 2006). In each station, various potential food items were collected by hand, such as mangrove litter, algae, seagrass leaves and their epiphytes, molluscs, gastropods, and crustaceans. Zooplankton samples were collected by towing a 100 µm net in the top 0.5 m of the water column during 5 minutes.

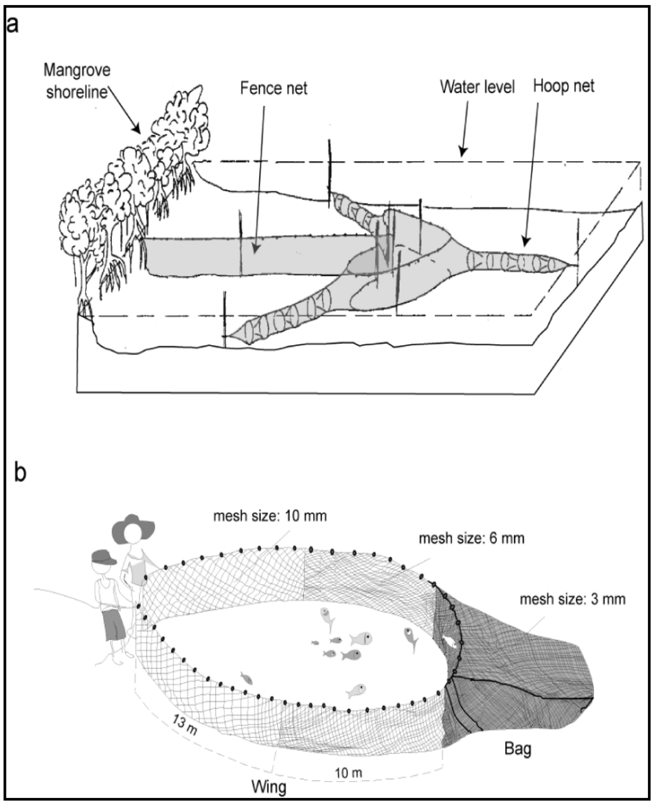

Figure 2. Capéchade (a) and seine-net (b) used to sample fish species in respectively mangrove and seagrass beds sites.

Data Analyses

The fish species collected were classified among six trophic categories as defined by Bouchon-Navaro *et al.* (1992) from data reported in the literature (Claro 1994, Randall 1967): planktivores, herbivores consuming algae and plants, carnivorous fishes ingesting fish and benthic invertebrates and piscivorous ones consuming more than 80% of fishes.

Fish dorsal muscle tissue was dissected and used for stable isotope analyses due to its slow turnover rate allowing to integrate food assimilation over months (Gearing 1991). Decapoda and mollusc muscles and entire other preys were oven dried at 50°C for at least 48 hours and then ground to a fine powder using a mortar and pestle. As the presence of calcium carbonates is known to interfere with carbon signatures, samples containing carbonates (i.e., amphipods, ophiuroids) were decalcified with 37% HCl (Bosley and Wainright 1999). Because lipids are depleted in ^{13}C, the variation of lipid content among organisms can affect $\delta^{13}C$ values and then ecological interpretations (Kling *et al.* 1992). Thus, the mathematical normalization technique of McConnaughey and McRoy (1979) was used to standardize lipid content for lipid-rich animal samples. A minimum of three replicates were sampled and prepared for each prey item and each fish species studied.

Carbon and nitrogen stable isotope compositions were measured with a mass spectrometer coupled to a C-N-S elemental analyser for combustion of organic material to CO_2 and N_2 gases. These analyses were performed at the University of Liege in Belgium. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) ratios were noted with "delta" and expressed as the relative per mil (‰) difference between the sample and conventional standards (i.e., Vienna PDB for carbon and atmospheric nitrogen). The IsoSource mixing model, developed by Phillips and Gregg (2003), was used to determine the relative contribution of mangrove and seagrass beds food items in fish species diet. IsoSource estimates combinations of food sources (from 0 - 100%) in defined increments (in this case 1%) to evaluate the sources contributions that sum the known isotopic ratios of the mixture (in this case, the fish muscles) within a small tolerance (in this study, ± 0.2‰) (Phillips and Gregg 2003).

RESULTS

Dual isotope plots of $\delta^{13}C$ versus $\delta^{15}N$ ratios were compared to identify sources of organic matter using $\delta^{13}C$ and the trophic linkages based on $\delta^{15}N$ (Figure 3). A clear separation was observed between mangrove and seagrass beds preys (Figure 3a). The $\delta^{13}C$ signatures of mangrove preys were more depleted in ^{13}C ($\delta^{13}C_{mean}$ = -20.7 ± 1.2‰) compared to preys collected in seagrass beds ($\delta^{13}C_{mean}$ = -13.0 ± 0.5‰; Figure 3a).

The range of $\delta^{13}C$ and $\delta^{15}N$ values among fish species were respectively -16.7‰ to -11.9‰ and 6.2‰ to 11.7‰ (Figure 3b). This wide range of isotopic values reflects that fishes consumed different sources and occupied different trophic levels. Thus, the depletion or enrichment in ^{13}C was also observed among the following trophic levels and three different groups of fish species were observed (Figure 3b).

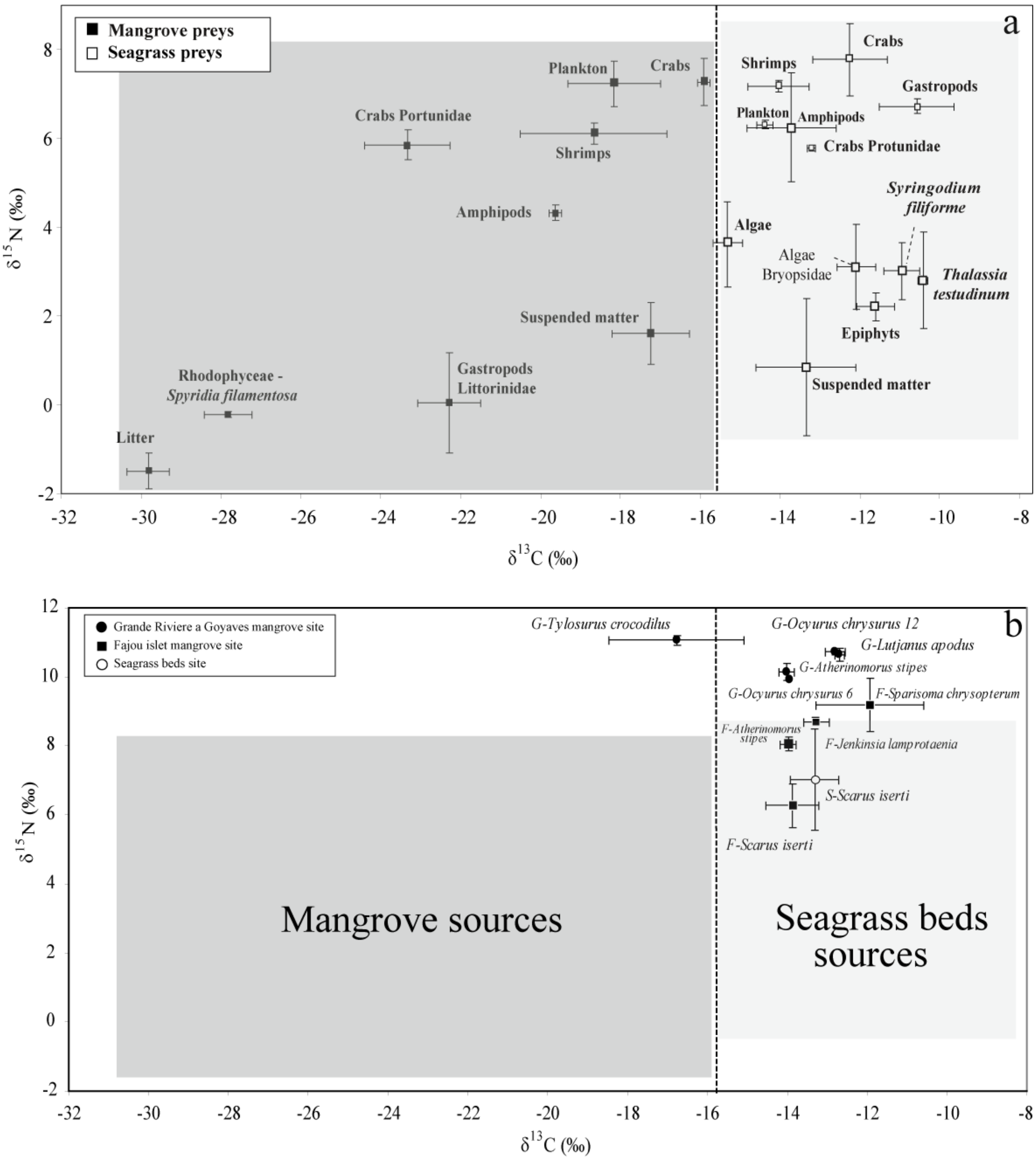

Figure 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values (± SD) of preys (a) and fish species (b) collected in seagrass beds (○-S), the mangroves of Fajou islet (■-F) and the Grande Rivière à Goyaves (●-G). The dark and light-grey boxes enclose isotopic values and 95% confidence limits of preys from mangroves and seagrass beds respectively.

The first group gathers planktivores (*Jenkinsia lamprotaenia*, *Atherinomorus stipes*), herbivores (*Scarus iserti, Sparisoma chrysopterum*) and the carnivore *Lutjanus apodus* which are characterized by enriched carbon ratios close to seagrass preys signatures. The IsoSource model suggests that these fishes appear to assimilate more seagrass preys 66 - 84% for planktivores, 82 - 97% for herbivores and 70% for the carnivore *Lutjanus apodus*) then mangrove prey items (Table 1).

A second group of fishes is represented by the species *Tylosurus crocodilus* which presented depleted carbon signatures which are close to mangrove preys isotopic values, suggesting that this species fed in this habitat. These observations are confirmed by the mixing model which found highest contributions of mangrove preys (90%) to this fish diet (Table 1).

The third group gathers the carnivore *Ocyurus chrysurus* for which different carbon signatures were observed according to the specimen total lengths. Small individuals (6 cm in total length) presented carbon signatures more depleted in ^{13}C compared to larger specimens (12 cm in total length). This difference is also observed with the mixing model showing that small specimens fed to a larger extent (34%) in mangrove whereas larger individuals appeared to consume preys from seagrass beds (30%; Table 1).

DISCUSSION

There is a good separation in carbon isotopic composition among mangrove and seagrass bed sources with mangrove preys more depleted in ^{13}C compared to seagrass sources. These mean isotopic values are in the range of the carbon ratios of mangrove (from -23.9 to -18.7‰) and seagrass beds (from -13.7 to -12.1‰) sources reported in previous studies (Kieckbusch *et al.* 2004, Lugendo *et al.* 2007). This segregation is due to different photosynthetic pathways between mangrove and seagrass plants during which photosynthetic enzymes use more or less the heavier carbon (^{13}C) (Farquhar *et al.* 1989). This enrichment or depletion in ^{13}C is noticed within the invertebrates and fishes collected in both habitats. Thus, three groups of fish species were observed in the present study according to their carbon isotopic signatures.

In the present research, the lowest δ^{13}C values were observed for the species *Tylosurus crocodilus* suggesting that mangrove-derived carbon represented an important part of their assimilated diet. This observation can be due to the fact that *T.crocodilus* specimens are mainly represented by juveniles which occurred in the mangrove to shelter and forage. In Curaçao, Nagelkerken and van der Velde (2004) also reported that the feeding behaviour of the piscivore *Sphyraena barracuda* is associated with the presence of mangroves where the juveniles shelter and forage on schools occurring at the interface mangroves-seagrass beds.

As observed by Nagelkerken and van der Velde (2004), juveniles of coral reef species (such as Scaridae and Lutjanidae in the present study) are characterized by enriched carbon ratios close to those of seagrass beds, indicating that sources from this habitat represent an important part of their diet.

A last group of fishes is represented by the species *Ocyurus chrysurus* characterized by intermediate carbon signatures between the sources from mangroves and seagrass beds, suggesting that this fish foraged in both habitats (Lugendo *et al.* 2007). Lugendo *et al.* (2006) also noticed this overlap of fish species carbon signatures between several bay habitats (mangroves, mudflats, seagrass beds) which can be due to ontogenetic migrations. This hypothesis can explain the segregation of resources

Table 1. Mean contributions (%) of the food sources from mangroves and seagrass beds in the fish diet.

Fish species	Sites	Mean contributions	
		Mangrove sources	Seagrass beds sources
		Planktivores	
Jenkinsia lamprotaenia	F	33.6	66.4
Atherinomorus stipes	F	15.6	84.4
Atherinomorus stipes	G	32.5	67.5
		Herbivores	
Scarus iserti	F	17.4	82.6
Scarus iserti	S	14.5	85.5
Sparisoma chrysopterum	F	2.3	97.7
		Carnivores	
Lutjanus apodus	G	29.7	70.3
Ocyurus chrysurus 12cm	G	34.0	67.0
Ocyurus chrysurus 6cm	G	30.9	69.1
		Piscivores	
Tylosurus crocodilus	G	90.0	10.0

observed in the present study for *O. chrysurus* between small and larger individuals.

This research pointed out the importance of seagrass beds as fish feeding grounds, particularly for juvenile reef species of commercial interest during their mangrove habitat phase.

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