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The relative importance of mangroves and seagrass beds as feeding areas for resident and transient fishes among different mangrove habitats in Florida and Belize: Evidence from dietary and stable-isotope analyses

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ABSTRACT

In the western Atlantic region, the contribution of mangrove food sources to fish diets has been considered of more limited importance than previously expected due to the proximity of mangroves to adjacent potential food sources such as those in seagrass beds. To investigate the influence of different types of mangrove habitats on the relative contribution of mangrove and seagrass food sources in fish diets, four mangrove habitats adjacent to seagrass beds were studied in Florida and Belize using gut-contents and stable-isotope analyses: mangrove fringe forests, basin mangrove, mangrove ponds and overwash mangrove islets. Carbon and nitrogen stable isotope compositions of 41 fish taxa and an array of potential primary (microphytobenthos, litter, seagrass leaves and their epiphytes, algae, plankton) and secondary (benthic invertebrates) prey were analyzed with SIAR mixing models to examine food source contributions in fish diets relative to habitat type. In all study sites, $\delta^{13}C$ values of mangrove prey were significantly depleted relative to those from seagrass beds, allowing stable isotopes to provide reliable insights about origins of fish food. Seagrass prey located near basin mangroves in the Indian River Lagoon (IRL, Florida) had more negative $\delta^{13}C$ signatures than seagrass prey adjacent to fringing mangroves of the Florida Keys, suggesting that seagrass from the IRL incorporated dissolved inorganic carbon from mangroves. Contributions of mangrove and seagrass prey to fish diets were influenced by type of mangrove habitat and fish residency status. Resident species significantly relied on mangrove prey, whereas only four transients foraged in mangroves. Most transient fishes occurring in basin and fringing mangroves actively foraged in nearby seagrass beds, thus reinforcing the limited role of mangroves as fish foraging habitat for transient species. However, a shift in fish diet was observed for transient species from mangrove ponds, in which they relied on mangrove prey. In overwash mangroves (Belize), the enriched carbon signatures of fishes and the generally higher contributions of seagrass prey to fish diets suggest that fishes derived most of their food from seagrass beds. This trend was particularly highlighted for juvenile reef fishes that shelter in mangroves but forage in nearby seagrass beds. These findings emphasize the importance of considering fish ecology (residency and life status) and type of mangrove habitat when assessing the contribution of mangrove prey to fish food webs in the western Atlantic region.

1. Introduction

Mangroves are important tropical and subtropical marine habitats that provide shelters and nursery grounds for an array of fish species. The complexity of mangrove prop roots, shallow shaded waters, and high food abundance are among the main factors suggested to explain the presence of diverse and abundant mangrove fish assemblages (e.g., Laegdsgaard and Johnson, 2001; Nagelkerken et al., 2008). Determining the importance of mangrove complexity and the influence of environmental factors have been the focus of many field and experimental studies (e.g., Faunce and Serafy, 2006; Nagelkerken et al., 2010; Vaslet et al., 2010), but the importance of mangroves as fish feeding grounds is still a subject of debate. In the 1970s Odum and Heald (1975) revealed the importance of mangrove litter as the foundation of a detrital food web that provides carbon sources for invertebrates and fishes in mangroves. This organic matter can also move out of mangroves with currents or invertebrate/fish migrations and contribute to secondary productivity in nearshore waters and coastal habitats. This export of mangrove carbon sources has been described as the "outwelling hypothesis." However, stable isotope studies have reported that leaves, detritus, and particulate and dissolved organic

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carbon from mangroves are exported to adjacent ecosystems to a much lesser extent than previously hypothesized (Guest and Connolly, 2004). Moreover, other primary producers, such as microphytobenthos and algae, have been identified as the main food sources in many studies of mangrove food webs due to their higher digestibility and nutritional quality than mangrove litter (e.g., Bouillon et al., 2008). In a study examining the outwelling of mangrove-derived organic matter in adjacent ecosystems, Granek et al. (2009) reported that the configuration of the area affects the degree of carbon outwelling and therefore the contribution of mangrove food sources in the coastal food webs.

Gilmore and Snedaker (1993) have described several different types of mangrove habitats: fringing mangrove forests, basin mangroves, mangrove ponds, or overwash mangrove islets. Mangroves are often interlinked with seagrass beds, and fish species move between these habitats through diurnal and tidal migrations (Nagelkerken et al., 2008). However, the accessibility of these coastal habitats depends on tidal influence and the geomorphology of the area (Lugendo et al., 2007; Nagelkerken et al., 2008). In the Indo-Pacific, mangroves are subject to large tidal amplitudes that drain all water from the intertidal habitats and constrain fish species to adjacent ecosystems or flooded creeks (Lugendo et al., 2007). In the western Atlantic region, basin mangrove forests and fringing mangroves are almost continuously flooded in the fall but can be exposed during low spring tides (e.g., December to April in Florida) (Provost, 1973; Gilmore G., personal communication). Even with some differences in tidal amplitudes, recent studies suggest an overall low dependence of fishes on mangrove-derived carbon sources in both Indo-Pacific (Benstead et al., 2006; Kruitwagen et al., 2010; Lin et al., 2007; Nyunja et al., 2009) and western Atlantic regions (Kieckbusch et al., 2004; Nagelkerken and van der Velde, 2004a). The extent of mangrove flooding is not the only factor to consider. Comparative studies in Tanzania and Kenya emphasized that fish dependence on mangrove food sources is correlated with mangrove configurations that define hydrological associations with adjacent waters, such as enclosed ponds or opened fringing mangroves (Lugendo et al., 2007; Nyunja et al., 2009). These studies suggested that fish dependence on mangrove food sources is higher in enclosed versus open mangrove systems. Effects of mangrove-habitat type on coastal food webs have not been sufficiently studied in the western Atlantic region where mangroves are either flooded or seasonally inundated. A number of studies reported low contributions of mangrove food sources to fish diets but have principally focused on fringing mangroves (Kieckbusch et al., 2004; Nagelkerken and van der Velde, 2004a, 2004b), or on specific fishes such as juvenile reef fishes and seagrass fishes (Nagelkerken and van der Velde, 2004a, 2004b). To understand coastal food webs and variability in mangrove outwelling, a diverse array of fishes needs to be studied to examine different trophic groups (Abrantes and Sheaves, 2009) and site-to-site differences (Lugendo et al., 2007). Determining the relative importance of mangrove-derived carbon sources for fishes in the western Atlantic region thus requires comparisons among different types of mangrove habitats (e.g., fringing forests, basin mangrove forests, ponds and overwash mangrove islet).

Gut-content analyses provide relatively high resolution of prey items ingested by a consumer but only reveal a snapshot of the consumer's diet within the last few hours (Hyslop, 1980). Stable-isotope analyses (SIA) of carbon and nitrogen provide insights into the food sources assimilated by a consumer in the preceding weeks to months (Gearing, 1991). By combining gut-content analyses and SIA, pathways of organic matter between primary producers and consumers can be traced, and the origins of food sources assimilated by consumers can be discriminated (Fry and Sherr, 1984; Nagelkerken and van der Velde, 2004a). Stepwise enrichment of stable isotopes occurs with trophic transfers and is, on average, about 0 to 1.3‰ for carbon and 2.0 to 3.5‰ for nitrogen (DeNiro and Epstein, 1978, 1981; McCutchan et al., 2003; Post, 2002). Signatures of carbon isotopes vary substantially among primary producers using different inorganic carbon sources and photosynthetic pathways, which explain the depleted carbon values of mangroves ($\delta^{13}C$ values between −30‰ and −24‰) compared to seagrasses ($\delta^{13}C$ values higher than −15‰) (Bouillon et al., 2008; Fry and Sherr, 1984; Hemminga and Mateo, 1996). Carbon signatures of animals reflect those of their diet; these values can thus be used to estimate the habitat from which a consumer predominantly derives its food. Consumers are typically enriched in ^{15}N relative to their diet, and nitrogen signatures give some insights into the trophic position of food sources and consumers in the food web (Post, 2002).

The objective of this study was to assess the relative importance of mangrove and seagrass food sources in fish diets, taking into consideration several types of mangrove habitats in the western Atlantic region. Gut contents and SIA of carbon and nitrogen were used (1) to determine the origin of carbon sources assimilated by fish species; and (2) to investigate the influence of mangrove habitat on the utilization of mangrove- and seagrass-derived carbon sources in coastal food webs.

2. Materials and methods

2.1. Description of the study sites

The study was conducted in mangrove ecosystems of Florida and Belize that encompass different types of mangrove habitats with different associations with adjacent seagrass beds (Table 1). According to Gilmore and Snedaker (1993), types of mangrove habitats refer to: mangrove fringe forests dominated by red mangroves along sheltered coastlines; basin mangroves that occur in inland topographic depressions and are influenced by tidal activity and freshwater runoff; mangrove ponds, represented by mangrove enclosed

Table 1
Location, mangrove habitats and association with seagrass beds of the three study sites in Florida and Belize: IRL = Indian River Lagoon, Keys = Florida Keys, Be = Belize, MB = basin mangrove, MF = fringing mangrove, MP = mangrove pond, MO = overwash mangrove islet, SG = seagrass beds near mangroves, and SGF = seagrass beds far from mangroves.

Location/habitats	Indian River Lagoon, Florida (Site 1)		Summerland Key, Florida Keys (Site 2)		Twin Cays, Belize (Site 3)	
	Mangroves	Seagrasses	Mangroves	Seagrasses	Mangroves	Seagrasses
Basin mangroves	IRL-MB	IRL-SG (within 2 m from mangroves)				
Mangrove pond	IRL-MP				BE-MP	
Fringing mangroves			Keys-MF	Keys-SG (within 2 m from mangroves)		
Overwash mangrove islet					Be-MO	Be-SG (within 2 m from mangroves) Be-SGF (2.3 km from mangroves)

creeks; and overwash mangrove islets, which are fringe forests completely overwashed by tidal waters. In this study, the term "habitat type" refers to fringing mangrove forests, basin mangroves, ponds or overwash mangrove islet, and "site" refers to the geographical location of the sampling stations.

Site 1 was located in Florida along the Indian River Lagoon (IRL, 27°33′N, 80°20′W), a 260 km long estuary separated from the Atlantic Ocean by a series of barrier islands (Fig. 1a). Water salinities in the IRL average 20–35, but can vary from brackish conditions (lower than 20) following rainfall and freshwater inputs to hypersaline maximum (up to 200) within ponds, impounded marshes and mangrove forests (Gilmore, 1995). Water depth within the lagoon varies between 0.5 and 3.0 m above a muddy and sandy substrate. The IRL is a microtidal lagoon, with semidiurnal tides varying between 0.1 m and 0.7 m near inlets (Smith, 1987). The IRL harbors 20% of the 202,000 ha of Florida's mangroves. Mangrove forests are of the basin type and were previously dominated by black mangroves, *Avicennia germinans* L., that have been replaced by red mangroves, *Rhizophora mangle* L., due to impounding and flooding (Gilmore, 1998). Site 1 consists of basin mangrove forests (IRL-MB, Fig. 1a) and mangrove ponds (IRL-MP, Fig. 1a) that are located inside the mangrove forests and connected to the IRL through a channel. Seagrass beds in the IRL are characterized by the species *Syringodium filiforme* (Kuetz) and *Halodule wrightii* (Ascherson) that colonize denuded sediment preceding the climax species *Thalassia testudinum* (Banks & Soland) in the natural successional sequence of western Atlantic and Caribbean seagrasses. Seagrass beds cover an area of 32,000 ha in the IRL and occupy about 16 ha in the vicinity of the basin mangroves in Site 1 (IRL-SG, Fig. 1a) (Saint Johns River Water Management District data).

Site 2 was located in the Florida Keys National Marine Sanctuary (FKNMS), a chain of limestone islands surrounded by marine waters. This site was located on Summerland Key, a fringing *R. mangle* mangrove forest (Keys-MF: 24°39′N, 81°26′W, Fig. 1b) associated with seagrass beds that are dominated by *T. testudinum* and *S. filiforme* (Keys-SG, Fig. 1b). Water salinity is circum-marine with average values of 35–36 (Johns et al., 2006).

Site 3 was located at Twin Cays, a peat-based, 92-ha overwash mangrove islet located 2 km from the barrier reef of central Belize (16°50′N, 88°06′W, Fig. 1c). This islet is located 12 km off shore and receives freshwater or terrigenous runoff from the mainland only during extreme climate events such as hurricanes (Koltes and Opishinski, 2009). An s-shaped Main Channel separates West and East Islands, which are characterized by a complex network of shallow channels that drain standing ponds (Fig. 1c, Rützler et al., 2004). The vegetation on Twin Cays is dominated by mangrove trees with a narrow seaward fringe of tall (5–6 m) *R. mangle* (Woodroffe, 1995). In the interior of the islet, mangrove ponds are dominated by dwarf (1–1.5 m) *R. mangle*, with *Laguncularia racemosa* (L.) Graetn.f. and *A. germinans* L. in scattered locations (Woodroffe, 1995). The sediment bottom around Twin Cays is mainly covered by the seagrass *T. testudinum*. Water salinity around Twin Cays is oceanic, 35–36 (Rützler et al., 2004). Several habitats were sampled at Twin Cays (Fig. 1c): overwash mangrove forests bordering the islet (Be-MO), seagrass beds located within 2 m of the mangrove forest (Be-SG) and seagrass beds located 5 m from the

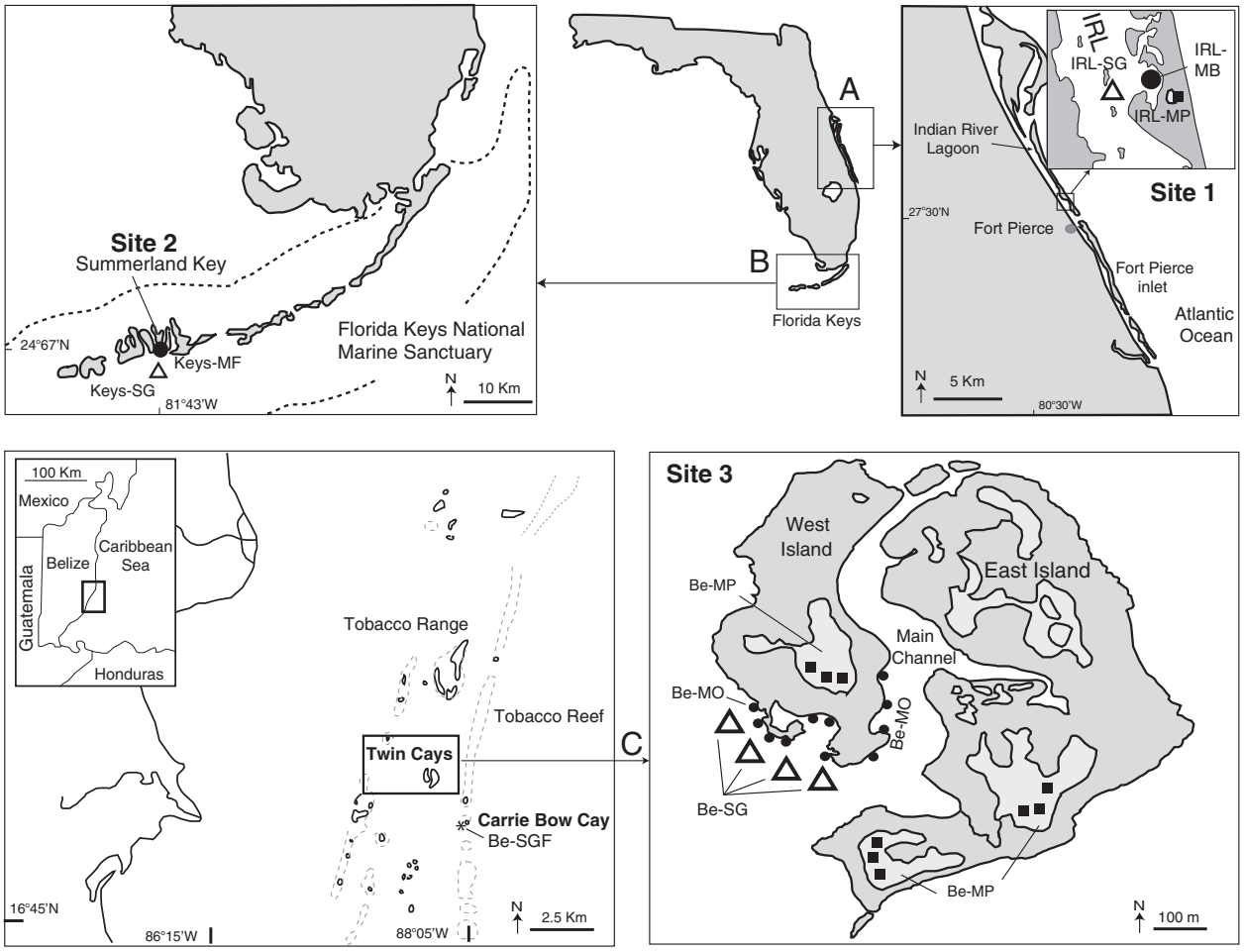

Fig. 1. Sampling locations in mangroves and seagrass beds of Florida (A: Indian River Lagoon, "IRL"; B: Summerland Keys, "Keys") and Belize (C, "Be"). Fishes were collected in mangrove ponds (MP: ■), fringing (MF: ●) or basin mangroves (MB: ●), and overwash mangrove islet (MO: ●). Food sources were sampled in mangroves and in seagrass beds within 2 m of mangrove fringe (SG: △) and seagrass beds located at 2.3 km from the mangroves of Twin Cays (SGF:*, Carrie Bow Cay).

shore of Carrie Bow Cay, an island without mangroves located approximately at 2.3 km from Twin Cays (Be-SGF). Two permanently inundated mangrove ponds (Be-MP) were also sampled at Site 3 (Fig. 1c): an enclosed pond on the western island and an open pond on the eastern island that is connected to the Main Channel.

2.2. Sample collection

Fish species were collected from multiple trophic levels of the food chain. From September 2009 to August 2010, 41 fish species were collected with repetitive samplings occurring during the same hydrological season in basin mangrove forests (Site 1), fringing mangroves (Site 2), mangrove ponds (Sites 1 and 3) and along continuous mangrove forests bordering the overwash mangrove islet (Site 3). Fishes were sampled using fish traps, light traps, fishing lines, beach seine nets (used in all mangrove sites except ponds due to shallow waters), hand nets and a fish anesthetic (quinaldine). Juveniles were distinguished from adults using information from data sets on fish maturity (Froese and Binohlan, 2000; Froese and Pauly, 2011). Fishes were further assigned to ecological categories based on their life history (Deegan and Day, 1984; Gilmore, 1995, 1998; Ley et al., 1999; Louis, 1985; Nordlie, 2003; Taylor et al., 2007): (1) estuarine residents (ER, fishes that complete their entire life cycle in estuaries); (2) estuarine transients (ET, species that spawn offshore and whose young remain in estuaries for varying periods of time for successful development); (3) marine transients (MT, marine fishes that are not developmentally tied to estuaries as nursery grounds but make regular seasonal visits to estuaries as adults); and (4) wetland residents (WR, species that use wetland habitats (such as mangroves) throughout their entire lifetime). Additional information on fish habitats was obtained from several extensive studies on mangrove and estuarine fish ecology (Gilmore, 1995, 1998; Lewis and Gilmore, 2007; Ley et al., 1999; Taylor et al., 2007). The main prey consumed by fishes were identified with gut-content analyses. When fewer than 15 specimens of a species were available for analysis, dietary data from the literature (Froese and Pauly, 2011; Gilmore, 1998; Harrington and Harrington, 1961), were consulted to ensure sufficient knowledge of a species' main prey items to enable classification into one of five trophic categories: herbivores, omnivores, planktivores, invertebrate feeders, and fish-invertebrate feeders.

Fish prey items were collected in mangroves and seagrass beds to assess fish feeding habits and habitats. Microphytobenthos (MPB), composed of benthic microalgae, was sampled following the method of Riera and Richard (1996): sediment with benthic microalgae was spread in trays under light during at least 24 h, and the top 2 mm surface layer of the sediment, into which motile microalgae had migrated, was gently scraped. Plankton samples were collected using a 0.1 mm mesh plankton net towed in the top 2 m of water, and zooplankton (mainly comprising copepods) was separated from tripton (inorganic particulate matter) in the laboratory. Particulate organic matter (POM), including suspended materials, phytoplankton and zooplankton, was sampled by filtering surface water on Whatman QM-A quartz-fiber filters following the method of Riera and Richard (1996). Plant materials consisting of mangrove litter, algae, seagrass leaves and their epiphytes were sampled in both mangrove and seagrass habitats. Benthic invertebrates (gastropods, annelids, crustaceans, echinoderms) were collected by hand net and light traps.

2.3. Stable-isotope analyses and mixing models

SIA of carbon and nitrogen were performed to identify the origin of carbon sources in fish diets and the trophic level of fish species. Isotopic analyses were performed on fish dorsal muscle, on soft tissue of larger prey (crabs, shrimps, molluscs) after dissection from their shell or exoskeleton and on the entire organism for small prey items. The samples were rinsed with distilled water and dried at 60 °C for at least 48 h. Carbon and nitrogen stable isotope compositions were measured with a Thermo Scientific Delta V Advantage mass spectrometer coupled to a C-N-S Costech ECS 4010 Elemental Analyser for combustion of organic material to CO_2 and N_2 gases. The analyses were performed at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Laboratory in Suitland, MD. Isotopic values are expressed in the delta notation as defined by the equation: $\delta = [(R_{sample} - R_{standard})/R_{standard}] * 1000$, where R is the ratio of heavy to light isotope (i.e. ^{13}C:^{12}C or ^{15}N:^{14}N). Standards were Vienna Pee Dee belemnite limestone carbonate for carbon and atmospheric air for nitrogen. Average reproducibilities were $\leq 0.2‰$ for $\delta^{13}C$ and $\delta^{15}N$.

Variation in lipid content in an organism can affect $\delta^{13}C$ values and thus ecological interpretations (Post et al., 2007). Thus prior to modeling and statistical analysis, carbon isotopic signatures of selected invertebrate prey items (gastropods, annelids, echinoderms) were normalized for lipid content following the mathematical normalization technique of Post et al. (2007). This normalization used a correction factor for $\delta^{13}C$ based on C:N values (i.e. C:N ratios >3.5 for lipid-rich tissue) and lipid content in animal samples. Additionally, prior to modeling, fish isotope signatures were adjusted for trophic enrichment using published values determined in previous studies (McCutchan et al., 2003; Vander Zanden and Rasmussen, 2001): $\Delta^{13}C$ of $1.0 \pm 0.3‰$ and $\Delta^{15}N$ of $2.2 \pm 0.3‰$ for planktivorous, herbivorous and omnivorous species; $\Delta^{13}C$ of $0.5 \pm 0.1‰$ and $\Delta^{15}N$ of $3.4 \pm 0.2‰$ for carnivorous species.

The Bayesian mixing model SIAR v4.0 (Stable Isotope Analysis in R) was used to determine the likely contribution of potential food sources from mangroves and seagrass beds to fish diets (Parnell et al., 2010). SIAR takes into account isotopic signatures, elemental concentrations, trophic enrichment factors (i.e., fractionation values) and the uncertainty associated with all these values throughout the modeling process. This Bayesian model assumes that variability associated with food sources is normally distributed (Parnell et al., 2010). Means and 95% Bayesian confidence intervals (95% BCI) characterize food source contributions to fish diets, with narrow estimated ranges of 95% BCI indicating more robust estimates of food source proportions in consumer diets. Food source estimates with large 95% BCI in consumer diets encompass too many possible contributions.

SIAR model is advantageous because it can (1) accommodate underdetermined systems, which occur when the number of food sources is greater than the number of isotopic values plus one (Phillips and Gregg, 2003), (2) provide a posteriori aggregation of food sources into two groups (i.e., mangrove prey, seagrass prey) to give more constrained and interpretable results (Phillips et al., 2005), and (3) consider concentration dependence factors. The incorporation of concentration factors is important when prey items have different elemental concentrations and therefore different digestibility. Indeed, plants have on average low [N] relative to [C], and these food sources may provide much lower proportions of N than C to consumer diets (Phillips and Koch, 2002; Vaslet et al., 2011). Concentration dependence factors were thus incorporated for mixing models performed on omnivorous fishes with diets consisting of both plants and animals. Assimilated [C] and [N] of potential prey were estimated following the methods of Koch and Phillips (2002), with source's digestibility reported in the literature (Benner and Hodson, 1985; Dawczynski et al., 2007; Dawes and Lawrence, 1980) and the elemental concentrations measured in this study.

2.4. Statistical analyses

Isotopic values of prey were normally distributed (Kolmogorov–Smirnov tests), and t-tests were performed to investigate differences in $\delta^{13}C$ signatures between habitats (mangroves, seagrass beds) and mangrove habitat types. T-tests were also used (1) to assess differences in $\delta^{13}C$ values between primary producers in the three sites;

(2) to test for effects of increasing distance from mangroves on $\delta^{13}C$ values of food sources from Site 3 (Be-MO, Be-SG, Be-SGF) and (3) to test differences in $\delta^{15}N$ values between primary producers and invertebrates. Non-parametric tests with post-hoc Bonferroni correction were used to determine differences among isotopic values of fishes, as these data were not normally distributed (Legendre and Legendre, 1998). Mann–Whitney U tests were performed to assess differences of $\delta^{13}C$ values of fish species collected inside and outside mangrove ponds in Site 1 (IRL-MB/IRL-MP) and Site 3 (Be-MO/Be-MP). Kruskal–Wallis tests were used to assess differences in $\delta^{13}C$ values of fishes from different mangrove habitat types and between $\delta^{15}N$ values among fish trophic categories. Statistical analyses were performed using R (R Development Core Team, 2010) with a significance level of $P<0.05$.

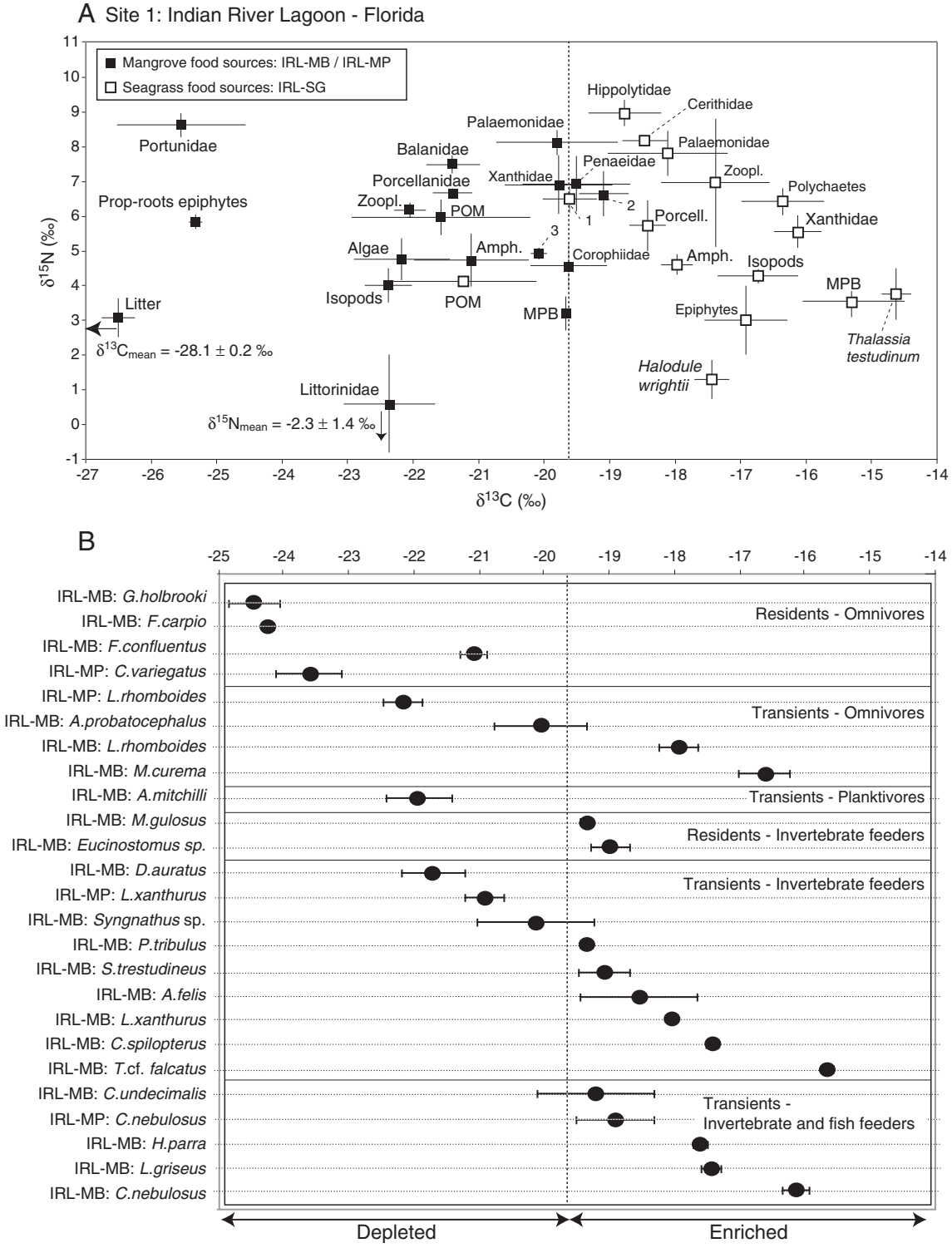

Fig. 2. (A) Mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of plant and invertebrate food sources from mangroves and seagrass beds of the IRL. Abbrev.: 1, Majidae; 2, Annelids Capitellidae; and 3, Grapsidae; MPB, microphytobenthos; POM, Particulate Organic Matter; Zoopl., zooplankton; Amph., amphipods; and Porcell., crabs Porcellanidae. Isotopic values of gastropods, annelids and echinoderms were adjusted for lipid content. (B) Mean $\delta^{13}C$ signatures (±SD) of fish species, corrected for trophic enrichment, from the IRL-MB and IRL-MP. Taxa are presented in order of increasing $\delta^{13}C$ mean values for each trophic category. The vertical dotted line is the median value of carbon isotopes for prey items.

3. Results

3.1. Stable isotope signatures of primary producers and animal prey items

Invertebrates from within basin and pond mangroves at IRL, and separately from within overwash and pond mangroves in Twin Cays had similar isotopic signatures and were merged as mangrove prey (t-tests, $P>0.05$, Figs. 2a, 3a, 4a). In all study sites, mangrove prey items were more ^{13}C depleted than those from seagrass beds (t-tests, $P<0.001$, Figs. 2a, 3a, 4a). In each study site, primary producers showed distinct carbon signatures, with lower values observed for mangrove litter (−28.9‰ to −27.1‰) and higher values for green seagrass leaves (−14.6‰ to −7.0‰) (t-tests, $P<0.001$, Figs. 2a, 3a, 4a). In Belize, an increasing $\delta^{13}C$ gradient was observed between primary producers from fringing mangroves bordering the overwash islet (Be-MO: −28.9‰ to −16.5‰), seagrass beds adjacent to mangroves (Be-SG: −16.0‰ to −13.0‰, t-tests, $P<0.001$) and seagrass beds far from mangroves (Be-SGF: −8.9‰ to −7.0‰, t-tests, $P<0.001$) (Fig. 4a). Microphytobenthos (MPB) had the most enriched $\delta^{13}C$ signatures of all mangrove primary producers, but there was still a good separation between MPB from mangroves (−19.8‰ to −16.4‰) and seagrass beds (−15.8‰ to −13.3‰) (t-tests, $P<0.001$, Figs. 2a, 3a, 4a). Even with some similar

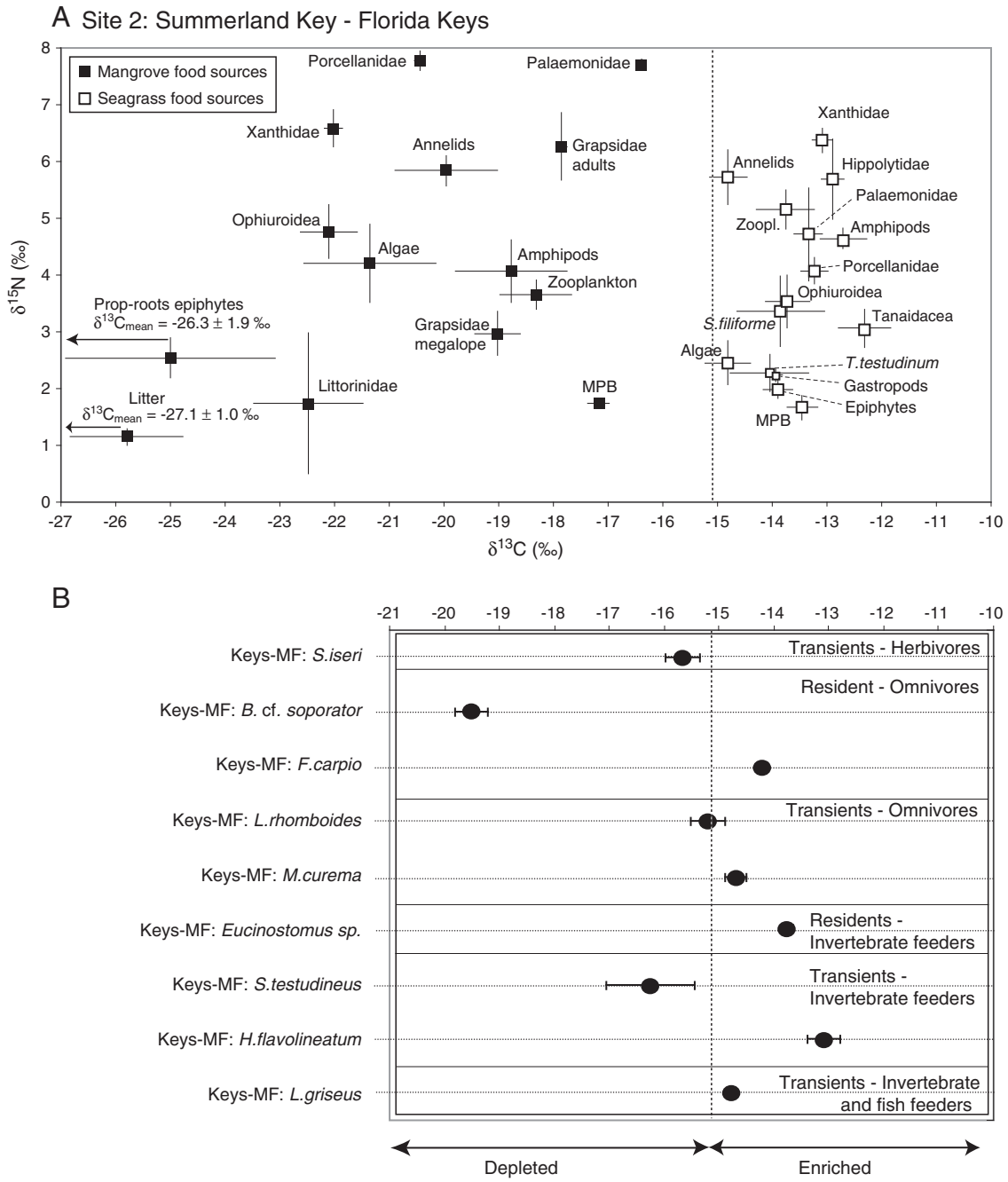

Fig. 3. (A) Mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of food sources from mangroves and seagrass beds of Summerland Key. Abbrev.: see Fig. 2 caption. Isotopic values of gastropods, annelids and echinoderms were adjusted for lipid content. (B) Mean $\delta^{13}C$ signatures (±SD) of fish species, corrected for trophic enrichment, from Keys-MF. See Fig. 2 caption for details.

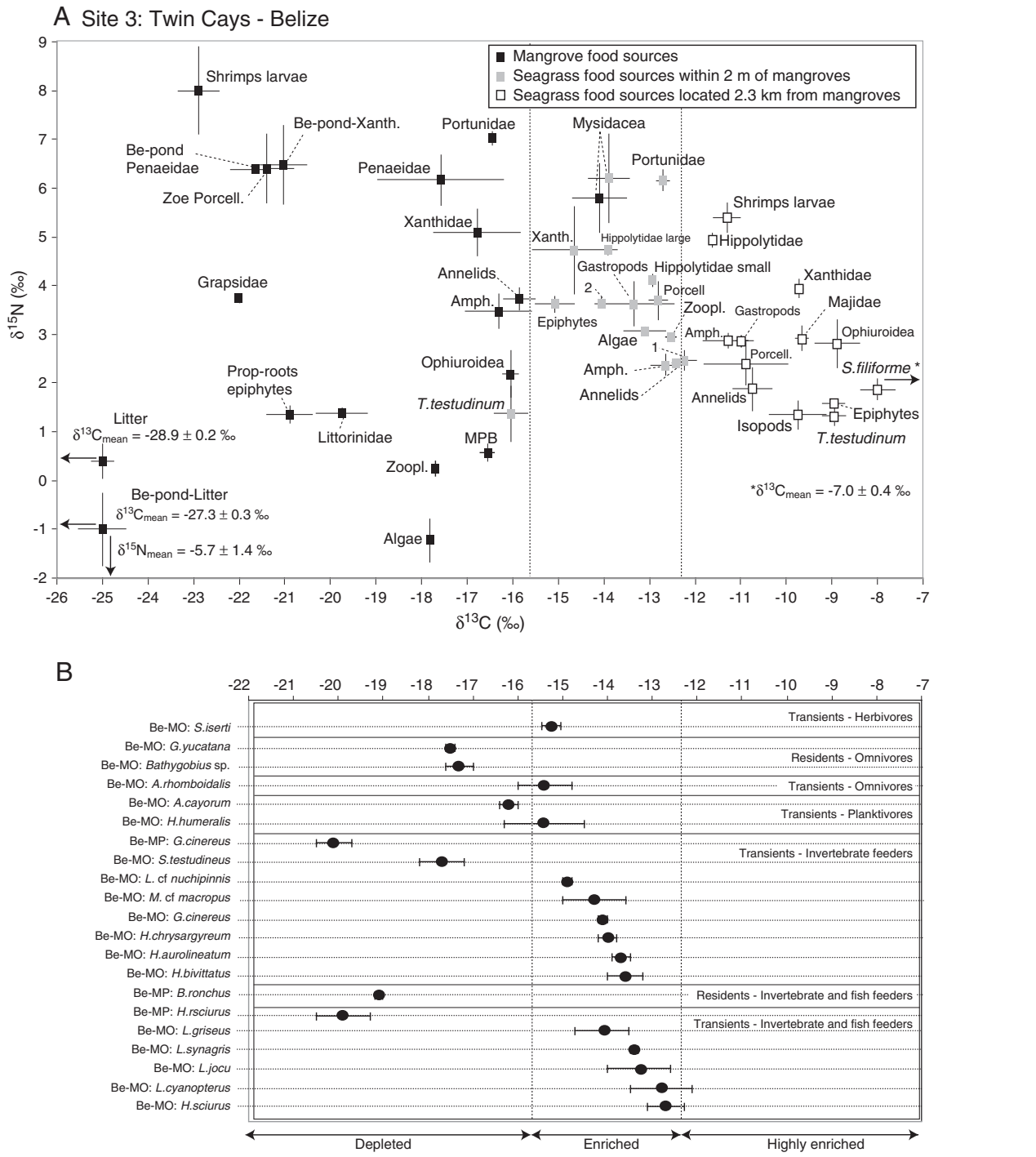

Fig. 4. (A) Mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of food sources from mangroves and seagrass beds of Twin Cays. Abbrev.: see Fig. 2 caption; 1, Ophiuroidea; and 2, Shrimps Penaeidae; Xanth., crabs Xanthidae. Isotopic values of gastropods, annelids and echinoderms were adjusted for lipid content. (B) Mean $\delta^{13}C$ signatures (±SD) of fish species, corrected for trophic enrichment, from Be-MO and Be-MP. See Fig. 2 caption for details.

carbon signatures between mangrove and seagrass motile prey items (i.e., Majidae crabs from IRL-SG and Mysidacea from Be-MO), invertebrates from mangroves had in general more depleted $\delta^{13}C$ values compared to those from seagrass beds (t-tests, $P<0.001$, Figs. 2a, 3a, 4a). Nitrogen signatures reflected the trophic level of the different food sources, with lower $\delta^{15}N$ values for primary producers (from −5.7 to +5.8‰) and higher $\delta^{15}N$ values for invertebrates (from −2.2 to +8.9‰) (t-tests, $P<0.01$) (Figs. 2a, 3a, 4a).

3.2. Composition of the fish assemblages

A total of forty-one fish species was collected in the mangroves of the IRL (IRL-MB: 21 species, IRL-MP: 4 species), Summerland Keys (Keys-MF: 9 species) and Twin Cays (Be-MO: 18 species, Be-MP: 3 species) and were separated into five trophic categories based on gut-content analyses (Table 2). Study sites in the IRL (IRL-MB, IRL-MP) were characterized by an estuarine fish assemblage, with 73% of individuals as estuarine transients and 27% estuarine residents

Table 2
Carbon and nitrogen stable isotope signatures (±SD) of fish species sampled in the mangroves of Florida and Belize. Isotopic values were not corrected according to trophic levels. Site labels are provided in Table 1. L_T, fish total length; stage (J, juvenile; A, adult); n, number of samples for isotopic analyses. Fish residency and habitats are provided (see footnotes). Main prey items identified in gut contents are indicated for each species: mi (microphytobenthos), pl (plant materials), zp (zooplankton), iv (benthic invertebrates), and fi (fish).

Fish species	Site	L_T (cm)	Stage	n	Residency[a]	Fish habitat[b]	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Herbivores								
Scarus iseri (pl)	Keys-MF	4–4.5	J	5	MT	R-SB	−14.8±0.3	5.3±0.1
	Be-MO	4–6	J	4	MT	R-SB	−14.4±0.1	4.5±0.1
Omnivores								
Mugil curema (mi, pl, iv)	IRL-MB	11–13	J	16	ET	W-SB	−15.6±0.5	6.9±0.5
	Keys-MF	10–13.4	J	12	MT	W-SB	−13.7±0.2	4.4±0.2
Fundulus confluentus (pl, iv)	IRL-MB	7.2–7.4	A	3	ER	W	−20.1±0.2	8.7±0.1
Cyprinodon variegatus (mi, pl, iv)	IRL-MP	5–6.5	J	15	ER	W	−22.6±0.5	5.8±0.2
Floridichthys carpio (mi, pl, zp, iv)	IRL-MB	9–11	A	4	ER	W-SB	−23.2±0.1	6.3±0.4
	Keys-MF	10–11.6	A	6	WR	W-SB	−13.2±0.1	7.7±0.2
Gambusia holbrooki (mi, pl, zp, iv)	IRL-MB	4.7–5.4	A	3	ER	W	−23.4±0.4	7.0±0.1
Gambusia yucatana (mi, pl, zp, iv)	Be-MO	5–6	A	6	WR	W	−16.5±0.1	4.8±0.2
Archosargus rhomboidalis (pl, iv)	Be-MO	6–8	J	15	MT	SB-R	−14.4±0.6	5.6±0.3
Archosargus probatocephalus (pl, iv)	IRL-MB	5.8–9.4	J	21	ET	W-SB	−19.0±0.7	7.9±0.2
Lagodon rhomboides (pl, iv)	IRL-MB	7–10	J/A	26	ET	SB	−16.9±0.3	7.5±0.3
	IRL-MP	5.8–8.4	J/A	15	ET	SB	−22.1±0.3	7.4±0.2
	Keys-MF	10–11	A	4	MT	SB	−14.2±0.3	4.2±0.5
Bathygobius cf. *soporator* (mi, pl, iv)	Keys-MF	6.3–7.4	J	4	WR	W-SB	−18.5±0.3	5.4±0.5
Bathygobius sp. (mi, pl, iv)	Be-MO	7	J	4	WR	W-SB	−16.3±0.3	6.3±0.4
Planktivores								
Anchoa mitchilli (zp)	IRL-MB	4.1–5.4	A	10	ET	SB-E-SMB	−20.9±0.5	10.5±0.2
Anchoa cayorum (zp)	Be-MO	6–8	A	4	MT	SB-E-SMB	−15.2±0.2	7.9±0.5
Harengula humeralis (zp)	Be-MO	12.7–13	A	3	MT	SB-E-SMB	−14.4±0.9	8.1±0.2
Carnivores (invertebrates feeders)								
Ariopsis felis (iv)	IRL-MB	20–25	A	7	ET	E-SMB	−18.0±0.9	10.2±0.1
Syngnathus sp. (iv)	IRL-MB	10	A	3	ET	SB	−19.6±0.9	7.9±0.5
Prionotus tribulus (iv)	IRL-MB	3–8.5	J	8	ET	E-SMB	−18.8±0.1	9.3±0.1
Trachinotus cf. *falcatus* (iv)	IRL-MB	3.4–4.8	J	3	ET	SB-E-SMB	−15.1±0.1	10.2±0.1
Eucinostomus sp. (iv)	IRL-MB	4–11	J	9	ER	W-E-SMB	−18.5±0.3	9.1±0.2
	Keys-MF	8.4–10	J	5	WR	W-SMB	−13.3±0.1	8.3±0.1
Diapterus auratus (iv)	IRL-MB	17–18	J	3	ET	W	−21.1±0.5	8.9±0.1
Gerres cinereus (iv)	Be-MO	8	J	3	MT	W-SB-E	−13.6±0.1	6.2±0.1
Haemulon aurolineatum (iv)	Be-MO	8–10	J	3	MT	SB-R-E	−13.2±0.2	7.8±0.3
Haemulon chrysargyreum (iv)	Be-MO	4–5	J	4	MT	SB-R-E	−13.5±0.2	7.5±0.2
Haemulon flavolineatum (iv)	Keys-MF	11–11.7	J	4	MT	SB-R-E	−12.6±0.3	6.5±0.2
Leiostomus xanthurus (iv)	IRL-MB	9.1–11.5	J	3	ET	W-E-SMB	−17.5±0.1	11.6±0.2
	IRL-MP	9–12	J	6	ET	W-E-SMB	−20.4±0.3	9.7±0.8
Halichoeres bivittatus (iv)	Be-MO	9.3–13.6	J	7	MT	SB-R-E	−13.1±0.4	7.5±0.1
Labrisomus cf. *nuchipinnis* (iv)	Be-MO	9–11	J	6	MT	SB-R-E	−14.4±0.1	8.1±0.1
Malacoctenus cf. *macropus* (iv)	Be-MO	5–6	A	4	MT	SB-R-E	−13.8±0.7	7.9±0.2
Microgobius gulosus (iv)	IRL-MB	2.7–4.8	J	6	ER	SB-E	−18.8±0.1	9.0±0.2
Citharichthys spilopterus (iv)	IRL-MB	7–9	J	3	ET	E-SMB	−16.9±0.1	9.0±0.1
Sphoeroides testudineus (iv)	IRL-MB	14.3–16	A	4	ET	W-SB	−18.5±0.4	8.0±0.2
	Keys-MF	14–15.5	A	6	MT	W-SB	−15.8±0.8	7.4±0.2
	Be-MO	9–13	J	4	MT	W-SB	−17.2±0.5	5.9±0.1
Carnivores (fish and invertebrates feeders)								
Centropomus undecimalis (fi, iv)	IRL-MB	26–41.8	J	12	ET	W-SB-E-SMB	−18.7±0.9	9.7±0.3
Lutjanus cyanopterus (fi, iv)	Be-MO	15–20	J	7	MT	W-R-SB	−12.3±0.7	7.3±0.3
Lutjanus jocu (fi, iv)	Be-MO	20–32	J	7	MT	W-R-SB	−12.8±0.7	8.4±0.4
Lutjanus griseus (fi, iv)	IRL-MB	15–18	J	8	ET	W-R-SB	−16.9±0.3	9.7±0.3
	Keys-MF	10–11	J	3	MT	W-R-SB	−14.3±0.1	8.4±0.2
	Be-MO	18–20	J	5	MT	W-R-SB	−13.6±0.7	8.8±0.3
Lutjanus synagris (fi, iv)	Be-MO	14	J	3	MT	W-R-SB	−12.9±0.	9.2±0.1
Haemulon parra (fi, iv)	IRL-MB	9–10	J	3	ET	W-R-SB	−17.1±0.1	9.5±0.1
Haemulon sciurus (fi, iv)	Be-MO	15–24	A	5	MT	W-R-SB	−12.2±0.4	7.6±0.1
	Be-MP	15–16	A	6	MT	W-R-SB	−19.4±0.6	7.5±0.1
Bairdiella ronchus (fi, iv)	Be-MP	14	J	3	WR	W	−18.6±0.1	6.4±0.5
Cynoscion nebulosus (fi, iv)	IRL-MB	30–35.5	A	11	ET	SB	−15.6±0.2	10.9±0.2
	IRL-MP	33.4–37	A	10	ET	SB	−18.4±0.6	11.2±0.2

[a] Residency of fishes in mangroves: ER = estuarine resident, ET = estuarine transient, MT = marine transient, and WR = wetland resident.
[b] Fish habitat (Gilmore, 1995, 1998; Lewis and Gilmore, 2007; Ley et al., 1999; Taylor et al., 2007): W = wetlands, SB = seagrass beds, R = coral reefs, E = open estuary, and SMB = sandy–muddy bottom.

that can tolerate variation of environmental conditions (i.e., salinity, temperature). Fish assemblages in Summerland Keys (Keys-MY) and Twin Cays (Be-MO, Be-MP) were dominated by reef-associated transient species, representing respectively 67% and 84% of all sampled species in these two sites. These reef species (e.g., Scaridae, Haemulidae, Lutjanidae, Labridae) were mainly present during their juvenile phase and used mangroves as nursery grounds (Table 2). Most of the fish species considered in this study (29 out of 41 species) were juveniles (Table 2).

3.3. Stable isotope signatures of fish species and isotopic mixing models

In the three study sites, fish species had a wide range of $\delta^{13}C$ signatures, with carbon values ranging between −23.4 and −15.1‰

in the IRL (IRL-MB and IRL-MP); −18.5 and −12.6‰ in Summerland Key (Keys-MF); and −19.6 and −12.2‰ in Twin Cays (Be-MO and Be-MP) (Table 2). The same wide variation in carbon signatures was observed while considering the different trophic categories of fishes (Table 2). Fish species from IRL had $\delta^{13}C$ values more depleted in ^{13}C (IRL-MB and IRL-MP: $\delta^{13}C_{mean} = -18.1 \pm 0.3‰$) than species from Summerland Key (Keys-MF: $\delta^{13}C_{mean} = -14.4 \pm 0.4‰$) and Twin Cays (Be-MO and Be-MP: $\delta^{13}C_{mean} = -14.1 \pm 0.7‰$) (Kruskal–Wallis tests, $P<0.05$) (Tables 2, 3).

Nitrogen isotopic signatures of fish ranged between +5.8 and +11.6‰ in IRL-MB and IRL-MP, +4.2 and +8.4‰ in Keys-MF, and +4.5 and +9.2‰ in Be-MO and Be-MP (Table 2). Significant differences in nitrogen signatures were observed between fish trophic categories, with lowest values for herbivores ($\delta^{15}N_{mean} = +5.0 \pm 0.3‰$) and omnivores ($\delta^{15}N_{mean} = +6.5 \pm 0.2‰$) and highest values for planktivores ($\delta^{15}N_{mean} = +9.5 \pm 0.6‰$) and carnivores ($\delta^{15}N_{mean}$ between +8.5 and 9.2‰) (Kruskal–Wallis tests performed separately between the four foraging guilds, $P<0.001$) (Table 2).

Resident fishes from Be-MO (*Bathygobius* sp., *Gambusia yucatana* Regan, 1914), Be-MP (*Bairdiella ronchus* [Cuvier, 1830]), IRL-MB (*Floridichthys carpio* [Günther, 1866], *Fundulus confluentus* Goode and Bean, 1879, *Gambusia holbrooki* Girard, 1859) and IRL-MP (*Cyprinodon variegatus* Lacepède, 1803), as well as *Bathygobius* cf. *soporator* (Valenciennes, 1837) from Keys-MF, had carbon signatures close to those of mangrove prey, with carbon values on average more depleted in ^{13}C than other resident and transient species (Figs. 2b, 3b, 4b). This trend was confirmed by higher mean contributions (95% BCI) of mangrove prey to resident diets, which varied between 41.6% (28.5–61.3%) for *Bairdiella ronchus* (Be-MP) and 71.1% (52.4–89.3%) for *Bathygobius* cf. *soporator* (Keys-MF, Table 4, Figs. 3b, 4b). Considering fish trophic categories, omnivores and invertebrate feeders from Florida (IRL-MB, IRL-MP, Keys-MF) and carnivorous species from Belize (Be-MO, Be-MP) showed significant variation in $\delta^{13}C$, indicating that these species relied on a variety of food sources (Figs. 2b, 3b, 4b). Five transient fishes in IRL-MB showed depleted carbon values similar to mangrove prey (i.e., IRL-MB: *Archosargus probatocephalus* [Walbaum, 1792], *Anchoa mitchilli* [Valenciennes, 1848], *Diapterus auratus* Ranzani, 1842, *Syngnathus* sp., *Centropomus undecimalis* [Bloch, 1792]), whereas only one and two species had lower $\delta^{13}C$ values in Keys-MF (*Sphoeroides testudineus* [Linnaeus, 1758]) and Be-MO (*S. testudineus*, *Anchoa cayorum* [Fowler, 1906]), respectively. Among the species listed above, only four actively

Table 3
P values from non-parametric tests performed on carbon isotope values of fish species between sites (Kruskal–Wallis tests) and between specimens within and outside mangrove ponds (Mann–Whitney tests). Abbreviations of sampling sites are provided in Table 1.

Comparisons between sites (Kruskal–Wallis tests)

	IRL-MP	IRL-MB	Keys-MF	Be-MP	Be-MO
IRL-MP	–	$P<0.001$	$P<0.001$	$P<0.001$	$P<0.001$
IRL-MB		–	$P<0.001$	$P<0.05$	$P<0.001$
Keys-MF			–	$P<0.001$	$P<0.126$
Be-MP				–	$P<0.001$
Be-MO					–

Comparisons outside and within ponds (Mann–Whitney tests)

	IRL-MP/IRL-MB	Be-MP/Be-MO
Leiostomus xanthurus	$P<0.05$	
Lagodon rhomboides	$P<0.001$	
Cynoscion nebulosus	$P<0.001$	
Gerres cinereus		$P<0.001$
Haemulon sciurus		$P<0.001$

Table 4
Mean biomass proportions (95% BCI, Bayesian confidence interval) of food sources in fish diets after a posteriori grouping of mangrove food sources (M sources), seagrass food sources close to mangroves (SG sources), seagrass food sources far from mangroves (SGF sources). Bold values in the "Food source contributions" column indicate high contributions from a single source. From the top to bottom, the three sections of the table correspond to high importance of mangrove prey, high importance of both mangrove and seagrass prey, and high importance of seagrass prey. Abbreviations of sampling sites and mangrove habitats are provided Table 1.

Sites	Fish species	Food source contributions		
		M sources	SG sources	SGF sources
Importance of mangrove prey: 95% BCI overlap with seagrass prey <15%				
IRL-MP	*L. rhomboides*	**97.9 (95.4–99.7)**	2.1 (0.2–4.3)	
	C. variegatus	**62.7 (44.1–81.3)**	37.3 (18.7–55.9)	
	L. xanthurus	**59.9 (43.9–75.9)**	40.0 (24.0–56.1)	
	C. nebulosus	**63.2 (54.8–70.7)**	36.8 (12.2–59.8)	
IRL-MB	*F. carpio*	**69.2 (52.6–85.8)**	30.7 (14.2–47.4)	
	M. gulosus	**68.6 (54.3–82.5)**	31.3 (17.4–45.7)	
	A. mitchilli	**83.2 (60.7–99.5)**	16.8 (0.4–39.3)	
	G. holbrooki	**67.2 (46.7–88.2)**	32.7 (11.7–53.2)	
	C. undecimalis	**66.5 (46.7–86.7)**	33.4 (13.3–53.2)	
Be-MP	*G. cinereus*	**86.5 (75.6–95.1)**	8.6 (1.3–17.2)	4.8 (0.2–10.7)
	H. sciurus	**51.4 (28.9–77.2)**	25.5 (7.4–42.7)	24.7 (6.2–42.0)
Be-MO	*Bathygobius* sp.	**60.1 (34.3–87.7)**	28.1 (6.6–48.9)	11.7 (0.3–27.9)
	A. cayorum	**44.5 (36.4–52.5)**	27.0 (6.2–47.5)	28.4 (13.2–43.7)
Keys-MF	*Bathygobius* cf. *soporator*	**71.1 (52.4–89.3)**	28.9 (10.7–47.5)	
Importance of mangrove and seagrass prey: 95% BCI overlap between 15% and 46%				
IRL-MB	*F. confluentus*	45.4 (20.9–70.4)	54.6 (29.6–79.0)	
	Eucinostomus sp.	43.4 (26.3–60.1)	56.6 (39.8–73.7)	
	D. auratus	59.1 (32.5–88.4)	40.8 (11.6–67.4)	
	A. probatocephalus	54.0 (34.8–73.5)	45.9 (26.5–65.2)	
	Syngnathus sp.	55.4 (35.8–74.7)	44.6 (25.3–64.3)	
	A. felis	55.6 (36.2–75.2)	44.4 (24.8–63.8)	
	S. testudineus	52.3 (27.1–76.8)	47.6 (23.1–72.8)	
	Trachinotus cf. *falcatus*	38.8 (14.6–62.1)	61.2 (37.9–85.4)	
Keys-MF	*S. iseri*	34.4 (24.2–44.7)	44.1 (22.7–65.8)	
	S. testudineus	51.6 (36.8–66.3)	48.4 (33.7–63.2)	
Be-MP	*B. ronchus*	41.6 (19.3–63.5)	29.5 (10.5–47.8)	28.8 (9.2–47.1)
Be-MO	*H. humeralis*	39.3 (26.1–53.4)	27.4 (6.5–47.6)	33.3 (15.6–51.1)
	G. cinereus	33.2 (22.2–43.9)	39.7 (19.4–60.3)	27.1 (11.0–43.4)
	A. rhomboidalis	41.3 (25.3–57.6)	42.9 (22.3–63.2)	15.8 (6.1–25.7)
	G. yucatana	44.8 (28.5–61.3)	36.5 (17.1–56.4)	18.6 (4.3–32.5)
	S. testudineus	48.3 (21.2–79.6)	25.9 (6.1–46.2)	25.7 (3.5–47.6)
	H. bivittatus	31.8 (18.8–44.6)	42.4 (18.7–66.4)	25.8 (10.8–40.6)
	Labrisomus cf. *nuchipinnis*	48.2 (34.6–62.0)	32.7 (12.4–53.0)	19.0 (6.7–31.3)
	Malacoctenus cf. *macropus*	33.6 (17.9–49.2)	46.0 (24.5–67.6)	20.4 (3.7–36.7)
	H. aurolineatum	32.7 (21.8–43.5)	38.9 (19.8–58.2)	28.3 (13.9–42.5)
	H. sciurus	22.2 (8.8–38.6)	27.5 (8.7–46.2)	50.3 (28.2–70.6)
	H. chrysargyreum	35.4 (23.4–47.4)	34.7 (15.0–54.4)	29.8 (16.9–42.7)
	L. cyanopterus	18.7 (6.1–31.6)	32.9 (11.8–53.6)	48.3 (32.2–64.6)
	L. jocu	27.6 (14.2–40.9)	42.7 (19.8–65.9)	29.6 (11.4–47.6)
	L. synagris	26.5 (11.2–41.7)	44.4 (21.8–67.0)	29.1 (13.6–43.8)
	L. griseus	29.0 (15.8–42.6)	34.1 (13.5–54.5)	36.8 (19.2–53.8)
Importance of seagrass prey: 95% BCI overlap with mangrove prey <15%				
IRL-MB	*M. curema*	26.2 (11.0–42.0)	**73.8 (57.9–88.9)**	
	C. spilopterus	31.3 (15.0–49.1)	**68.7 (50.9–84.9)**	
	L. rhomboides	37.0 (20.5–53.4)	**62.9 (46.5–79.5)**	
	L. xanthurus	29.3 (14.0–44.8)	**70.7 (55.1–85.9)**	
	P. tribulus	36.2 (21.6–51.3)	**63.8 (48.7–78.3)**	
	H. parra	33.7 (15.6–51.7)	**66.2 (48.2–84.3)**	
	L. griseus	41.4 (23.6–57.5)	**58.7 (42.4–82.7)**	
	C. nebulosus	22.3 (7.4–37.4)	**77.7 (62.6–92.6)**	
Keys-MF	*F. carpio*	14.8 (5.8–24.2)	**85.2 (75.8–94.2)**	
	M. curema	13.7 (5.1–24.3)	**86.2 (75.5–94.8)**	
	L. rhomboides	30.2 (16.9–44.0)	**69.7 (55.9–83.1)**	
	Eucinostomus sp.	13.0 (7.8–18.5)	**86.9 (81.4–92.2)**	
	H. flavolineatum	25.0 (3.1–49.3)	**74.9 (50.6–96.8)**	
	L. griseus	29.3 (19.0–40.3)	70.7 (55.1–83.8)	
Be-MO	*S. iseri*	28.8 (16.6–39.9)	56.6 (38.2–75.4)	14.6 (5.1–24.0)

foraged on mangrove food sources (i.e., *C. undecimalis*, *A. mitchilli*, *A. cayorum*, *D. auratus*). *D. auratus* had a higher mangrove prey contribution in its diet (95% BCI between 32.5 and 88.4%) than the others, which had a mixed diet comprising seagrass and mangrove prey (Table 4).

In the three sites, most transient species (22 out of 31 species) had intermediate or relatively enriched carbon values that are close to those of seagrass prey (Figs. 2b, 3b, 4b). Two resident species (Keys-MF: *F. carpio* [Günther, 1866], *Eucinostomus* sp.) and ten transient species showed higher contributions of seagrass prey in their diets, with mean proportions (95% BCI) varying between 56.5% (42.2–70.7%) for *Lutjanus griseus* (Linnaeus, 1758) (IRL-MB) and 86.9% (81.4–92.2%) for *Eucinostomus* sp. (Keys-MF, Table 4). The remaining transient fishes (i.e., 12 fish species) had a mixed diet comprising both mangrove and seagrass food sources, which explained high overlap in 95% BCI (Table 4).

Significant differences were observed between carbon isotope values of fish specimens collected within and outside mangrove ponds (Table 3). Transient species sampled in the ponds of IRL-MP (i.e., *Lagodon rhomboides* [Linnaeus, 1766], *Cynoscion nebulosus* [Cuvier, 1830], *Leiostomus xanthurus* Lacepède, 1802; $\delta^{13}C_{mean} = -20.6 \pm 0.6‰$) and Be-MP (i.e., *Gerres cinereus* [Walbaum, 1792], *Haemulon sciurus* [Shaw, 1803]; $\delta^{13}C_{mean} = -19.5 \pm 0.2‰$) showed more depleted $\delta^{13}C$ signatures compared with specimens of the same species from IRL-MB basin mangroves ($\delta^{13}C_{mean} = -16.6 \pm 0.3‰$) and Be-MO overwash mangroves ($\delta^{13}C_{mean} = -12.9 \pm 1.4‰$) (Kruskal–Wallis tests, $P<0.05$, Table 3). While in mangrove ponds, these fishes significantly foraged on mangrove prey (mean contributions between 50.4% and 97.9%), and shifted their diets in basin and overwash mangrove forests to feed in seagrass beds (mean prey contributions between 27.5% and 62.9%, Table 4).

Six fish species were common to two or three sampling sites, which enabled comparisons of their foraging habits and habitats between different types of mangroves. *F. carpio* and *Eucinostomus* sp. foraged to a larger extent on mangrove prey when these species occurred in IRL-MB compared to Keys-MF where they mainly feed on seagrass food sources (Table 4). This trend was not observed for *S. testudineus* which feed more on mangrove prey in Be-MO compared to the two other sites (Table 4). Finally, *Scarus iseri* (Bloch, 1789), *Mugil curema* Valenciennes, 1836 and *L. griseus* foraged in seagrass beds regardless of the sampling site and types of mangrove habitats (Table 4).

4. Discussion

4.1. Stable isotope composition of primary producers and POM

The carbon isotopic signatures observed in this study for primary producers were in the range of values reported in other studies conducted in Florida and Caribbean islands (Fry, 1984; Kieckbusch et al., 2004; Nagelkerken and van der Velde, 2004a). All of those studies noted more depleted carbon values for individual primary producers from mangroves compared with those collected in seagrass beds. The $\delta^{13}C$ values from seagrass beds in the IRL obtained in this study are in the lowermost part of the range of carbon signatures reported for seagrass plants (Bouillon et al., 2008; Hemminga and Mateo, 1996). These relatively depleted values are likely related to the incorporation of ^{13}C-depleted dissolved inorganic carbon (DIC) of mangrove origin (Lin et al., 1991). The incorporation of depleted DIC in seagrass leaves is consistent with previous findings (Bouillon et al., 2008; Lin et al., 1991), and may also explain the increasing $\delta^{13}C$ gradient observed in this study for seagrasses within 2 m of the fringing mangroves of Twin Cays and those located 2 km from mangroves. Other factors, such as seasonal variation of photosynthetic rates or fluctuation in solubility of CO_2 (Fourqurean et al., 2005), may also explain the patterns of $\delta^{13}C$ values of seagrass beds in the IRL, but further experiments are necessary to confirm these hypotheses.

In contrast to other primary producers, POM from mangroves and adjacent seagrass beds of the IRL exhibited similar carbon values. This is likely the result of water mixing and therefore of authochthonous and allochthonous POM in this estuarine basin mangrove system (Bouillon et al., 2008). Because POM is derived from the dominant primary producers (Harrigan et al., 1989), the low carbon signatures of POM observed in the IRL may reflect a mixture of phytoplankton, mangrove litter, and MPB (Abrantes and Sheaves, 2009; Rodelli et al., 1984).

4.2. Stable isotope composition of invertebrates

Invertebrates from mangroves and seagrass beds were well separated in $\delta^{13}C$ values and had on average more negative carbon values in mangroves than in seagrass beds (Kieckbusch et al., 2004; Lugendo et al., 2007). It has been reported that some of the invertebrate families considered in this study have narrow home ranges and derive most of their carbon sources from the habitat they occupy (Guest and Connolly, 2004). Invertebrates from IRL seagrass beds had relatively depleted $\delta^{13}C$ values (−22.0‰ to −14.1‰, Fry, 1984; present study) compared with benthic fauna from other seagrass meadows in Biscayne Bay (Florida) (−13.4‰ to −10.7‰, Kieckbusch et al., 2004) or Florida Keys (−14.8‰ to −12.3‰, present study). These lower carbon values likely reflect the negative $\delta^{13}C$ signatures of seagrass epiphytes, which apparently incorporate DIC from mangroves and support the IRL seagrass food web (Fry, 1984). The incorporation of mangrove DIC in epiphytic algae, and then in seagrass invertebrates foraging on these algae, may be explained by the mangrove basin system of the IRL. Specifically, mangrove-derived carbon may contribute more extensively to the seagrass food web in relatively 'closed' systems, such as the IRL, where mangrove production remains in residence due to limited exchange with adjacent ocean waters (Bouillon et al., 2004, 2008). In more open systems, such as fringing mangroves or overwash islets, the influence of tides or currents may affect the delivery rates of mangrove DIC, which is diluted during water mixing and therefore has more restricted influence — e.g., to only a few meters from the mangrove fringe (Guest and Connolly, 2004).

4.3. Relative importance of mangrove and seagrass food sources in fish diets

The ichthyofaunal diversity considered in this study reflects the biases and effectiveness of the collecting gear used. Few fishes were collected in mangrove ponds, and some fishes typically important in mangroves in terms of abundance and biomass were missing, such as *Mugil cephalus* Linnaeus 1758, *Poecilia latipinna* (Lesueur, 1821) (Lewis and Gilmore, 2007; Gilmore, personal communication). Including additional types of sampling methods such as fyke nets, throw-traps, breeder traps, hand spear or ichthyotoxic (rotenone), known to be effective in catching more species (Harrington and Harrington, 1961; Taylor et al., 2007), will allow more fish species to be included in future studies. Moreover, as not all mangrove habitat types occur in the three study sites (i.e., ponds and overwash mangrove islets lacking in the Florida Keys) caution should be taken when comparing fish foraging habitats between study sites.

Among the ichthyofaunal diversity sampled in this study, eight out of ten resident species relied on mangrove prey whereas only four transients actively foraged in mangroves. These transient species were zoobenthic feeders (*D. auratus*), water column feeders (*A. mitchilli*, *A. cayorum*) or large roving fishes (*C. undecimalis*) and were therefore indirectly supported by mangrove-derived carbon sources through the benthic and pelagic food web or secondary consumers (Nyunja et al., 2009). The *D. auratus* and *C. undecimalis* analyzed in this study were

juveniles, and it will be interesting to investigate whether those species exhibit ontogenetic changes in their diet and their foraging habitats. Previous studies showed that juveniles of *C. undecimalis* (<15 cm in standard length) are dependent on shallow mangrove tidal creeks and that larger ones undergo ontogenetic migrations due to limited tolerance to hypoxic conditions (Harrington and Harrington, 1961; Peterson and Gilmore, 1991). This habitat shift during their ontogeny would therefore influence their trophic dependence on mangrove food sources.

This study showed that most transient fishes (22 out of 31 species) from subtropical (IRL-MB, Keys-MF) and tropical mangroves (Be-MO) actively foraged in nearby seagrass beds, thus reinforcing the limited role of mangroves as fish foraging habitats for these species. These findings corroborate those from other studies showing that mangrove-derived food sources contribute to the diets of only a limited number of species (0 out of 9 species, Kieckbusch et al., 2004; 4 out of 23 species, Nagelkerken and van der Velde, 2004a; 7 out of 42 species, Nyunja et al., 2009). Mangrove food sources appear to be of secondary importance in the diets of most juvenile reef fishes, which shelter in mangrove prop roots but rely on seagrass food sources (Kieckbusch et al., 2004; Nagelkerken and van der Velde, 2004a, 2004b; this study). It has been shown that structural complexity of mangrove prop roots attract juvenile reef fishes, which use this habitat more as shelters and nursery grounds than as foraging areas (Laegdsgaard and Johnson, 2001; Nagelkerken et al., 2010). Moreover, the habitat surface area, complexity of habitat and sediment structure in seagrass beds may improve foraging conditions for zoobenthic feeders and large roving fishes by supporting a greater density of invertebrates compared to mangrove habitats (Nagelkerken and van der Velde, 2004a; Nyunja et al., 2009). Complementary studies of potential prey densities between mangroves and adjacent seagrass beds in multiple study sites are thus needed to test this hypothesis.

In this study, transient fishes from basin (IRL-MB) and overwash mangroves (Be-MO) foraged in seagrass beds, whereas specimens of the same species from mangrove ponds (IRL-MP, Be-MP) primarily relied on mangrove prey. These different carbon isotopic profiles of transient species suggest that their foraging habits were influenced by mangrove habitat types. This pattern has also been observed along the eastern African coast where fishes restricted to mangrove creeks at low tides appear to derive a substantial proportion of their diet from mangroves (Lugendo et al., 2007; Nyunja et al., 2009). These studies reinforce the necessity of considering mangrove-derived carbon sources in fish diets when food sources from other habitats are scarce or not accessible due to the influence of tide (Fry and Ewel, 2003; Lugendo et al., 2007). These findings differ from general statements of the relatively minor importance of mangrove-derived carbon sources to fish diets due to their low nutritional quality (Jennerjahn and Ittekko, 2002) or limited export to adjacent habitats (Guest and Connolly, 2004). This generalization should therefore be reconsidered in light of site-to-site variability to consider differences in mangrove habitat types (Lugendo et al., 2007; Nyunja et al., 2009; this study).

Some transient fishes from basin (IRL-MB), fringing (Keys-MF) and overwash mangroves (Be-MO) exhibited intermediate carbon values between mangroves and seagrass beds. This trend may be due to the consumption of prey with intermediate carbon values or the ingestion of a combination of food sources depleted and enriched in ^{13}C (Abrantes and Sheaves, 2009; Nagelkerken and van der Velde, 2004a). Another explanation may be recent ontogenetic or daily trophic migrations of fishes between mangroves and seagrass beds (Abrantes and Sheaves, 2009; Hobson, 1999; Nagelkerken and van der Velde, 2004a). Fishes can exhibit intermediate carbon signatures after migrating between isotopically distinct habitats (i.e., mangroves and seagrass beds), as it takes several weeks for muscle tissues to integrate isotopic signatures of assimilated diet (Hobson, 1999). During this period of time corresponding to muscle tissue turnover, fish species are not in equilibrium isotopically with their current environment and diet, and exhibit intermediate carbon values between these habitats (Hobson, 1999). This can explain the feeding habits of two transient species normally associated with seagrass beds but occurring in IRL mangrove ponds, *L. rhomboides* and *C. nebulosus*, which showed during their juvenile stage a dependence on mangrove food sources. Further studies including multiple size classes of fish species are therefore needed to explore the relationships between ontogenetic trophic patterns and foraging habitats of transient fishes in mangroves.

The SIAR Bayesian mixing model has been increasingly used in recent years as a tool for interpreting food webs derived using stable isotopes (Parnell et al., 2010; Vaslet et al., 2011). As noted, it has the main advantages of being able to incorporate variability of food source isotopic values, to include concentration dependence and to provide confidence intervals of estimated dietary composition of consumers (Parnell et al., 2010). However, for some fish species analyzed in this study, the SIAR model gave large confidence intervals of both mangrove and seagrass prey contributions, which were too wide to be informative on fish diets (Benstead et al., 2006). This outcome can be attributed to a mixed diet of fishes or to some overlap between isotopic values of mangrove and seagrass prey. Therefore, sulfur stable isotopes or fatty acid biomarkers can be used to improve discrimination of food sources in aquatic food webs (Connolly et al., 2004; Nagelkerken et al., 2008; Parnell et al., 2010).

In conclusion, this study emphasizes the importance of considering different mangrove habitat types when investigating fish foraging grounds. SIA facilitated tracing of mangrove and seagrass food-source contributions in fish diets and revealed that 8 out of 10 resident and only 4 out of 31 transient species from basin, ponds, fringing and overwash mangrove sites derived a substantial proportion of their diets from mangroves. In Florida and Belize, these species were large roving fishes, zoobenthic or water column feeders, that depend indirectly on organic matter from mangroves through the benthic–pelagic food web or secondary consumers. The remaining fish species, including juvenile reef fishes, occur in mangroves but appear to forage in adjacent seagrass habitats. Further investigations of fish feeding patterns are needed to take into account daily trophic migrations and species ontogenetic trophic migrations between habitats. The assessment of trophic relationships between fishes and mangroves is essential for fisheries and ecosystems management, and is of primary importance when examining the vulnerability of mangrove ecosystems to climatic and anthropogenic impacts (Valiela et al., 2001).

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Appendix 1. Mean carbon and nitrogen stable isotope values (±SD) of primary producers and invertebrates collected in mangroves and seagrass beds of Florida and Belize. Abbreviations of sampling sites are provided in Table 1; n, number of samples for isotopic analyses. Isotopic values of gastropods, annelids and echinoderms were adjusted for lipid content

Prey items	Site	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Mangroves				
Primary producers				
Microphytobenthos	IRL-MB	3	−19.7±0.05	3.0±0.4
	Keys-MF	3	−17.2±0.2	1.7±0.03
	Be-MO	3	−16.5±0.1	0.6±0.2
Litter — *Rhizophora mangle*	IRL-MB	4	−28.1±0.2	3.1±0.5
	Keys-MF	6	−27.1±1.0	1.1±0.1
	Be-MO, Be-MP	13	−28.0±0.5	−3.4±1.9
R. mangle prop-root epiphytes	IRL-MB	3	−25.3±0.1	5.8±0.2
	Keys-MF	3	−26.3±1.9	2.5±0.3
	Be-MO	5	−20.9±0.5	1.3±0.2
Algae	IRL-MB	3	−22.2±0.7	4.8±0.6
	Keys-MF	3	−21.3±1.2	4.2±0.7
	Be-MO	4	−17.8±0.05	−1.2±0.4
Particulate organic matter	IRL-MB	2	−21.6±1.3	5.9±0.5
Invertebrates				
Zooplankton	IRL-MB	4	−22.0±0.2	6.2±0.2
	Keys-MF	3	−18.3±0.6	3.6±0.3
	Be-MO	4	−17.7±0.1	0.2±0.1
Annelids Polychaetes	IRL-MB, IRL-MP	8	−19.2±0.2	6.4±0.4
	Keys-MF	5	−19.9±0.9	5.8±0.2
	Be-MO	3	−15.8±0.3	3.7±0.2
Gastropods Littorinidae	IRL-MB	5	−22.3±0.7	−2.3±1.4
	Keys-MF	4	−22.5±1.0	1.7±1.2
	Be-MO	5	−19.7±0.6	1.4±0.1
Balanidae	IRL-MB	3	−21.4±0.4	7.5±0.1
Amphipods/isopods	IRL-MB, IRL-MP	14	−21.1±0.6	4.5±0.3
Amphipods	Keys-MF	4	−18.8±1.0	4.1±0.5
	Be-MO	4	−16.3±0.7	3.5±0.3
Crabs Grapsidae	IRL-MB	6	−20.1±0.1	5.0±0.1
	Keys-MF	6	−18.2±0.5	5.2±1.4
	Be-MO	3	−21.9±0.1	3.7±0.1
Crabs Porcellanidae	IRL-MB	4	−21.4±0.3	6.7±0.1
	Keys-MF	4	−20.4±0.1	7.7±0.2
	Be-MO	3	−21.4±0.6	6.4±0.7
Crabs Portunidae	IRL-MBc	3	−25.5±0.9	8.6±0.3
	Be-MO	3	−16.4±0.0	7.0±0.1
Crabs Xanthidae	IRL-MB	5	−19.8±0.8	6.9±0.8
	Keys-MF	3	−22.1±0.2	6.6±0.3
	Be-MO, Be-MP	7	−18.6±1.8	5.7±0.7
Shrimps Palaemonidae	IRL-MB	5	−19.8±0.9	8.1±0.3
	Keys-MF	3	−16.4±0.0	7.7±0.1
Shrimps Penaeidae	IRL-MB	4	−19.5±0.8	6.9±0.8
	Be-MO, Be-MP	6	−20.0±2.0	6.3±0.2
Shrimps Mysidacea	Be-MO	2	−14.1±0.6	5.8±0.7
Shrimps larvae	Be-MO		−22.9±0.5	8.0±0.8
Ophiuroidea	Keys-MF	4	−22.1±0.5	4.7±0.5
	Be-MO	2	−16.1±0.2	2.2±0.5
Near seagrass beds				
Primary producers				
Microphytobenthos	IRL-SG	2	−15.3±0.8	3.5±0.2
	Keys-SG	2	−13.4±0.3	1.7±0.2
Thalassia testudinum	IRL-SG	3	−14.6±0.2	3.7±0.7
	Keys-SG	4	−14.0±0.7	2.3±0.3
	Be-SG	3	−16.0±0.3	1.4±0.5
Halodule wrightii	IRL-SG	4	−17.4±0.2	1.3±0.5
Syringodium filiforme	Keys-SG	3	−13.8±0.8	3.3±0.6
Seagrass leaves epiphytes	IRL-SG	3	−16.9±0.6	3.0±0.9
	Keys-SG	3	−13.9±0.3	1.9±0.2
	Be-SG	5	−15.1±0.4	3.6±0.1
Algae	Keys-SG	3	−14.8±0.4	2.4±0.4
	Be-SG	2	−13.1±0.4	3.1±0.1
Particulate organic matter	IRL-SG	2	−21.2±1.1	4.1±0.1
Near seagrass beds				
Primary producers				
Invertebrates				
Zooplankton	IRL-SG	3	−17.4±0.8	6.9±1.8
	Keys-SG	5	−13.7±0.3	5.1±0.8
	Be-SG	2	−12.5±0.1	2.9±0.1
Annelids	IRL-SG	3	−16.4±0.6	6.3±0.3
	Keys-SG	4	−14.8±0.3	5.7±0.5
	Be-SG	3	−12.6±0.3	2.4±0.2
Gastropods	IRL-SG	2	−18.4±0.3	8.2±0.05
	Keys-SG	3	−13.9±0.1	2.2±0.1
	Be-SG	3	−13.3±0.8	3.6±0.4
Amphipods/isopods/ Tanaidacae	IRL-SG	7	−17.3±0.6	4.4±0.2
	Keys-SG	8	−12.5±0.3	3.9±0.6
	Be-SG	5	−12.4±0.1	2.4±0.05
Crabs Majidae	IRL-SG	3	−19.6±0.4	6.8±0.4
Crabs Porcellanidae	IRL-SG	3	−18.4±0.3	5.7±0.7
	Keys-SG	5	−13.2±0.2	4.1±0.2
	Be-SG	4	−12.8±0.2	3.7±0.4
Crabs Xanthidae	IRL-SG	3	−16.1±0.3	5.5±0.4
	Keys-SG	3	−13.1±0.2	6.4±0.2
	Be-SG	4	−14.6±0.9	4.7±0.9
Crabs Portunidae	Be-SG	7	−12.7±0.1	6.1±0.2
Shrimps Hippolytidae	IRL-SG	3	−18.8±0.6	8.9±0.3
	Keys-SG	4	−12.9±0.2	5.6±0.7
	Be-SG	6	−13.4±0.4	4.4±0.3
Shrimps Palaemonidae	IRL-SG	3	−18.1±0.9	7.8±0.6
	Keys-SG	5	−13.7±0.5	4.8±0.3
Shrimps Penaeidae	Be-SG	3	−14.0±0.03	3.7±0.1
Shrimps Mysidacea	Be-SG	3	−13.9±0.4	6.2±0.9
Ophiuroidea	Keys-SG	3	−13.7±0.4	3.5±0.5
	Be-SG	3	−12.2±0.2	2.6±0.2
Far seagrass beds				
Primary producers				
Thalassia testudinum	Be-SGF	3	−8.9±0.2	1.3±0.2
Syringodium filiforme	Be-SGF	4	−7.0±0.4	1.8±0.2
Seagrass leaves epiphytes	Be-SGF	2	−8.9±0.2	1.6±0.1
Invertebrates				
Amphipods/Isopods	Be-SGF	9	−10.8±0.6	2.3±0.5
Annelids	Be-SGF	2	−10.7±0.4	1.9±0.4
Gastropods Neritidae	Be-SGF	3	−10.9±0.1	2.8±0.1
Crabs Majidae	Be-SGF	3	−9.6±0.1	2.9±0.2
Crabs Porcellanidae	Be-SGF	2	−10.9±0.9	2.4±0.4
Crabs Xanthidae	Be-SGF	3	−9.7±0.07	3.9±0.2
Shrimps Hippolytidae	Be-SGF	3	−11.6±0.01	4.9±0.1
Shrimps larvae	Be-SGF	2	−11.3±0.1	5.4±0.1
Ophiuroidea	Be-SGF	3	−8.9±0.5	2.8±0.5

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