



# Mangrove carbon sustains artisanal fish and other estuarine consumers in a major mangrove area of the southern Caribbean Sea

Luis Alejandro Sandoval<sup>1,2,\*</sup>, José Ernesto Mancera-Pineda<sup>3</sup>,  
Jenny Leal-Flórez<sup>1</sup>, Juan F. Blanco-Libreros<sup>2</sup>, Antonio Delgado-Huertas<sup>4</sup>

<sup>1</sup>Universidad de Antioquia, Corporación Académica Ambiental, Research Group for Marine and Coastal Systems, 057860 Turbo, Colombia

<sup>2</sup>Universidad de Antioquia, Facultad de Ciencias Exactas y Naturales, Research Group for Lotic Ecology, Islands, Coasts and Estuaries, 050010 Medellín, Colombia

<sup>3</sup>Universidad Nacional de Colombia, Departamento de Biología, Facultad de Ciencias, 111321 Sede Bogotá, Colombia

<sup>4</sup>Instituto Andaluz de Ciencias de la Tierra (CSIC-UGR), 18100 Armilla, Granada, Spain

**ABSTRACT:** Estuaries are highly productive habitats that support fisheries production. However, the importance of mangrove carbon to estuarine consumers can differ considerably among systems. In this study, we used stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) to investigate the importance of mangrove carbon as an energy source to estuarine consumers in the Atrato River Delta, Colombia, an area where fringing mangroves dominate the coastline and where other productive coastal habitats that may otherwise support the food web are absent. Basal resources and consumers were collected from mangrove and nearshore habitats during the rainy season. Results revealed a food web with a maximum length of 4.6 trophic positions. Bayesian mixing models indicated that most consumers used a mixture of basal sources, which suggests intertwined energetic pathways. However, mixing models also indicated that some species relied more heavily on some basal sources than others and revealed trophic pathways (food chains). Mangrove carbon directly supported herbivorous crabs (Sesarmidae) and indirectly supported planktivorous fish (Engraulidae) and piscivorous fish. Mangrove carbon also contributed significantly to the diet of 2 of the most common fish species in the local artisanal fishery: *Centropomus undecimalis* (mean: 46%; credibility interval [CI]: 1–80%) and *C. pectinatus* (mean: 33%; CI: 1–78%). Our findings highlight that mangrove carbon can be an important food source in areas without other productive coastal habitats and can play an important role in sustaining the production of fisheries.

**KEY WORDS:** Colombia · Gulf of Urabá · Atrato River Delta · Carbon · Nitrogen · Stable isotope analysis · Pathway · MixSIAR

Resale or republication not permitted without written consent of the publisher

## 1. INTRODUCTION

Much of the research on marine food webs is aimed at understanding how different pathways of energy and elements move from the resource base to top consumers (Bukovinszky et al. 2008). In addition, food web studies often seek to understand the sources of nutrition and habitats supporting fisheries production (Bouillon et al. 2011). Knowing the structure

of food webs and the trophic flow of energy provides insights into how ecosystems function and may help us predict the resilience of coastal ecosystems to human disturbance (Gascuel et al. 2008). For example, knowing the loss or disturbance of key basal resources, density or composition of predators or prey, or food web connectivity may help us to predict population collapses (Link 2002, Abrantes et al. 2015a). Although estuarine ecosystems are highly produc-

tive and may contribute substantially to the recruitment of important marine species, such as certain commercial fisheries (Blaber 2013), food web studies that trace the energy sources of the community are surprisingly scarce. Better knowledge of energy sources should contribute to the conservation and restoration of coastal ecosystems (Abrantes et al. 2015a, Qu et al. 2019).

Describing pathways of organic matter in estuarine food webs can be difficult due to a variety of potential energy sources. For instance, organic matter can arrive from upstream (i.e. the riverine environment) or the downstream oceanic environment (Bouillon et al. 2011). It can also arise from within the estuary itself, e.g. seagrass, microalgae, or from lateral habitats, such as mangroves and salt marshes (Bouillon et al. 2011). Nevertheless, the use of stable isotopes in such a setting potentially allows characterization of the origins and movements of organic and inorganic matter (Peterson & Fry 1987, Bouillon et al. 2011, Duarte et al. 2018). Stable isotopes, mainly carbon ( $^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ ), have been useful to identify the primary sources that support fish production in estuarine food webs and to understand habitat use by diverse fish species in mangrove ecosystems (Fry & Ewel 2003, Layman 2007, Layman et al. 2012). For invertebrate consumers, stable isotope studies have also been instrumental in pointing out the surprising diversity of food sources and specialization in mangrove ecosystems (Bouillon et al. 2011).

The mangrove outwelling hypothesis states that the export of primary production from trees supports much of the secondary production of estuaries and nearshore waters (Odum & Heald 1975). However, the importance of mangrove carbon in estuarine and near-coastal environments is variable. Some studies have found that mangrove carbon is important for both benthic and pelagic consumers (e.g. Abrantes et al. 2015b, Lovelock et al. 2015, Medina-Contreras et al. 2020). This includes shrimp species (Loneragan et al. 1997, Chong et al. 2001, Abrantes et al. 2015b), reef fish (Nagelkerken & van der Velde 2004a), estuarine fish (Giarrizzo et al. 2011, Zagars et al. 2013, Abrantes et al. 2015b), crabs (Harada & Lee 2016), and sessile coral invertebrates (Granek et al. 2009). In contrast, other studies have found that mangrove detritus makes little contribution to coastal and mangrove food webs (e.g. Bouillon et al. 2002, Vaslet et al. 2015, Santos et al. 2020), with consumers relying instead on algae (Nyunja et al. 2009), microphytobenthos (Lee 2000), particulate organic matter (Chanton & Lewis 2002), phytoplankton (Rodelli et

al. 1984), and sea grasses (Loneragan et al. 1997, Nyunja et al. 2009).

In the Caribbean, isotopic studies have found that mangrove carbon makes little contribution to the food web (e.g. Nagelkerken & van der Velde 2004b, Igulu et al. 2013, Vaslet et al. 2015). However, this research was undertaken in areas close to other productive habitats, such as seagrass beds or coral reefs. There is evidence that mangroves are likely to play a much greater trophic role in areas that are remote from other productive ecosystems, such as the Ciénaga Grande de Santa Marta, a large swamp area on the outer delta of the Magdalena River, Colombia (Mancera 2003). In other parts of the world, a few studies also have evidence supporting the trophic importance of mangroves, e.g. northern Brazil (Giarrizzo et al. 2011) and northern Australia (Abrantes et al. 2015b), where high sedimentation excludes other systems like seagrass beds and coral reefs.

The Atrato River Delta (ARD) is an estuary in the southern Caribbean Sea (Colombia) that encompasses extensive fringing mangrove areas (ca. 100 km) (Riascos & Blanco-Libreros 2019) and lacks other highly productive coastal habitats, such as coral reefs and seagrasses (Sandoval Londoño et al. 2020). Leaf litter mean mass in ARD mangroves is the highest reported for *Rhizophora mangle*-dominated forests worldwide (Riascos & Blanco-Libreros 2019). The ARD has been highlighted as an important habitat for sustaining artisanal fisheries (Correa-Herrera et al. 2016, LOPEGU 2017, Arango-Sánchez et al. 2019). This assertion is supported by recent research in the southern Caribbean Sea which has found a positive correlation between mangrove area and the catch of 3 common artisanal fish species (*Ariopsis canteri*, *Mugil incilis*, and *Sciades proops*) (Sandoval Londoño et al. 2020). Unfortunately, mangroves are threatened by illegal logging (Blanco et al. 2012), ecological information about estuarine nekton and benthos is limited (but see Hernández-Morales et al. 2018, Arenas-Uribe et al. 2019, Sandoval Londoño et al. 2020), and a fishery management plan for the region does not exist. Accordingly, this study investigated the importance of mangrove carbon as an energy source for estuarine consumers. We used stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to (1) describe the food web and the number of trophic positions (TPs) of the mangrove and nearshore ecosystem and (2) determine the contribution of different food sources to the epibenthic invertebrates and fish communities. We hypothesized that mangroves are an important food source sustaining estuarine consumers, including artisanal fish, in the study area. Our findings provide insight into the food web of

the coastal ecosystem and can assist in the protection of mangrove habitat in the ARD and other similar systems.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The Atrato River delivers the second largest input of freshwater to the southern Caribbean, specifically into the western coast of the Urabá Gulf (Fig. 1). The Gulf is a semi-enclosed body of water (length: 80 km; width: 6–45 km). Mean air temperature is 27°C, relative humidity 84.5%, and monthly precipitation varies between 40 and 100 mm in the dry season (December–April), and 200–300 mm in the rainy season (May–November) (García-Valencia 2007). There is a micro-tidal regime with a tidal range of <40 cm amplitude. Salinity varies throughout the year (0.8–35.5) with a counter-intuitive pattern; the lowest salinity values are recorded during the dry period in response to trade winds in-

creasing residence times of fresh water in the Gulf (García-Valencia 2007). The ARD includes an extensive mangrove habitat (approximately 3700 ha), where fringe forest is the dominant physiographic type of mangrove, and the red mangrove *Rhizophora mangle* (Rhizophoraceae) is the dominant species in more than 80% of the area, followed by the white mangrove *Laguncularia racemosa* (Combretaceae) (Blanco-Libreros 2016). Likewise, the cattail *Typha* sp. (Typhaceae) occurs in small patches along the fluvial environment in the distributaries of the delta (Correa-Herrera et al. 2016). An artisanal fishery near the mangroves is practiced only for local commerce and/or subsistence (LOPEGU 2017, Sandoval Londoño et al. 2020). The study was undertaken in La Paila Bay (Fig. 1) as a model of embayments in the ARD since all of them mainly comprise monospecific stands of *R. mangle*, and mangrove isotopic values did not vary among the embayments (authors' unpubl. data). The bay is shallow (<5 m) with waters that are poorly wind-mixed, as the Atrato River plume has a strong stratification around 2 m (LOPEGU 2017, Montoya et al. 2017).

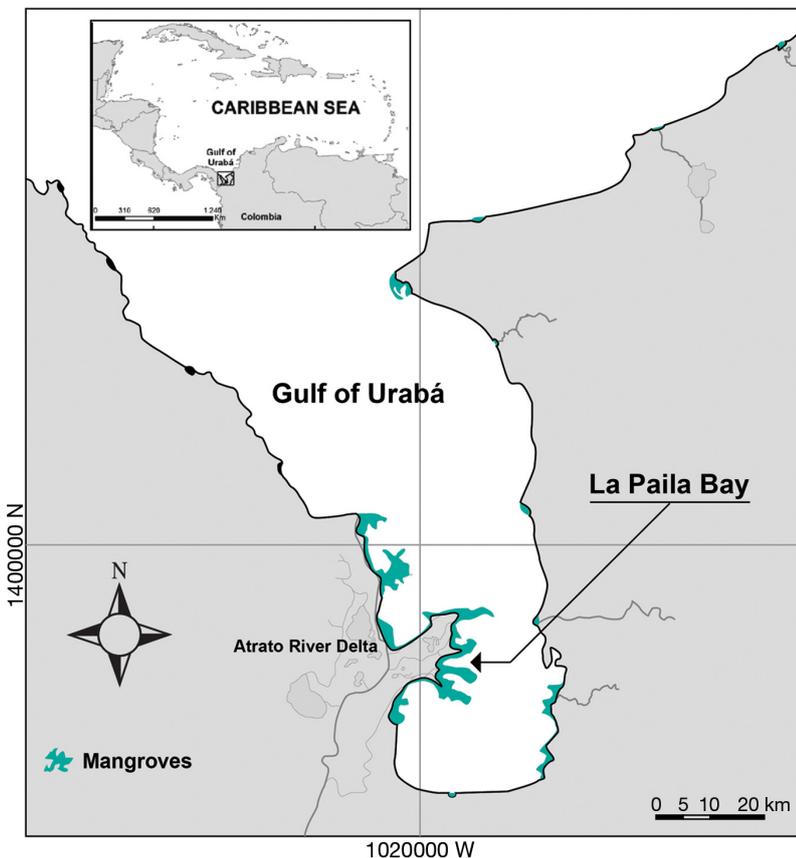


Fig. 1. Study area at La Paila Bay in the Atrato River Delta of the Gulf Urabá, Caribbean Sea. The projected coordinate system is MAGNA-SIR-GAS Colombia Oeste

### 2.2. Sample collection

We aimed to include as many species as possible and to have representatives from the main trophic groups in order to allow better identification of possible trophic pathways within the food webs. Basal resources and consumers were collected from mangrove and nearshore habitats at La Paila Bay during the rainy season (September–October) of 2016. Each biological sample consisted of a pool of several specimens of the same species of about the same length. At least 3 samples of each basal resource (see Table 1) and consumer (see Tables 2 & 3) were collected when possible. Samples of fresh live (green) mangrove leaves were collected from the dominant species (*R. mangle*; tall trees with diameter at breast height of 15–35 cm) along an approximately 2 km long section. Epiphytic macroalgae (chlorophytes; *Rhizoclonium* sp.) were sampled by scraping the roots of *R. mangle* using forceps. Samples of fresh live (green) macrophyte leaves and cattail *Typha* sp. blades were col-

lected near mangroves along a ca. 0.1 km section. Unfortunately, as sampling benthic microalgae without sediment and other organic matter contamination was not possible, the benthic microalgae stable isotope values applied were instead global averages (see below). Suspended particulate organic matter (SPOM), a proxy for estuarine phytoplankton, was sampled using a phytoplankton net (mouth diameter: 35 cm; mesh size: 25  $\mu\text{m}$ ) approximately 0.1 km away from mangroves. Meso-zooplankton samples were taken using a plankton net (mouth diameter: 35 cm; mesh size: 300  $\mu\text{m}$ ) approximately 0.1 km away from the mangroves. Additionally, epibenthos was collected manually from inside the mangroves (3 herbivorous crabs, 1 omnivorous gastropod, and 3 carnivorous crabs).

Four planktivorous fish, 1 phytobenthivorous fish, 3 omnibenthivorous fish, 5 zoobenthivorous fish, 5 piscivorous fish, 1 carnivorous shrimp, and 1 carnivorous swimming crab species were collected using a gillnet (100 m long; 2 m high; with mesh sizes of 7, 7.6, 10.2, and 12.7 cm), approximately 0.1 km away from the mangroves.

### 2.3. Sample processing and isotopic analysis

Water samples of SPOM (phytoplankton) were passed through a 300  $\mu\text{m}$  mesh to remove zooplankton and visually inspected to remove large particulate contaminants and zooplankton, then filtered onto pre-combusted (450°C, 24 h) glass-fiber filters (GF/C filters) with a nominal pore size of 1.2  $\mu\text{m}$ . Mangrove leaves, cattail blades, and macroalgae were cut into small pieces and rinsed with distilled water. Zooplankton samples were examined microscopically for identification of representative taxa, then isolated and consolidated onto pre-combusted filters using forceps. For fish samples, white muscle tissue was taken from immediately below the anterior end of the dorsal fin. For shrimp, a sample of abdomen muscle tissue was taken after exoskeleton and digestive tract removal. For crabs and mollusks, the chelae and foot muscle, respectively, were removed to form individual or composite samples according to the size of the specimens. For macroconsumers, all muscle tissue samples were thoroughly rinsed with distilled water.

All samples were dried in Petri dishes at 60°C for at least 48 h. The dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials. Between 0.7 and 1 mg of the sample was weighed in a micro scale and deposited in a tin cap-

sule for isotopic analysis. Analyses were done in the Laboratorio de Biogeoquímica de Isotopos Estables at Instituto Andaluz de Ciencias de la Tierra (Granada, Spain). The carbon and nitrogen isotopic compositions of organic matter were determined using an online Carlo Erba NA 1500 NC elemental analyzer coupled online via a ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest). Internal standards of  $-30.63\%$  and  $-11.65\%$  (V-PDB) were used for  $\delta^{13}\text{C}$  analysis, and internal standards of  $-1.0\%$  and  $+16.0\%$  (AIR) were used for  $\delta^{15}\text{N}$ . Precision was calculated, after correction of the mass spectrometer daily drift, from standards systematically interspersed in analytical batches and was better than  $\pm 0.1\%$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Reference gases and in-house standards (with different C:N ratios and isotopic compositions) were calibrated against International Reference Materials (IAEA-N1, IAEA-N2, and IAEA-N3 for nitrogen; NBS-21, USGS-24, and IAEA-C6 for carbon). Results are expressed in delta notation in ppm (‰) based on the following equation:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = (R_{\text{sample}} / R_{\text{standard}}) - 1$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ .

As variation in tissue lipid content can affect  $\delta^{13}\text{C}$  values and ecological interpretations, a mathematical normalization method was used to standardize lipid content for samples (Post et al. 2007). Animal samples were normalized if C:N was  $> 3.5$ , following the equation:  $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$ , where  $\delta^{13}\text{C}_{\text{untreated}}$  corresponds to the original  $\delta^{13}\text{C}$  of the sample (Post et al. 2007). For basal source samples, normalization was done when the percent of carbon was  $> 40\%$ , following the equation:  $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 5.83 + 0.14 \times \% \text{C}$  (Post et al. 2007).

The TP of consumers was calculated following the mathematical formula proposed by Post (2002):  $\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_{\text{N}}$ , where  $\lambda$  corresponds to the TP of the basal resource representing the base of the trophic web (in this case,  $\lambda = 1$ );  $\delta^{15}\text{N}_{\text{base}}$  corresponds to an overall mean  $\delta^{15}\text{N}$  value (1.8‰) calculated for basal resources but excluding marine phytoplankton and benthic microalgae since neither were estimated from ARD (Table 1); and  $\Delta_{\text{N}}$  corresponds to the average trophic enrichment factors (TEFs) for  $\delta^{15}\text{N}$ , in the present case with value of 2.9‰ for nitrogen according to McCutchan et al. (2003).

### 2.4. Data analysis

Bayesian stable isotope mixing models (MixSIAR; Stock & Semmens 2016) were used to estimate the

proportional contribution of different basal resources to consumers. Prior to running the models, epibenthos were classified into 3 trophic categories: herbivorous, omnivorous, and carnivorous, while fish were classified into 5 trophic categories: planktivorous, phytobenthivorous, omnibenthivorous, zoobenthivorous, and piscivorous. Feeding guilds were assigned according to information found in local literature (Sandoval Londoño 2012) and FishBase (Froese & Pauly 2007). MixSIAR models were run separately for each consumer trophic category, and fish species within each category were coded as 'fixed effects' inside each model.

Basal resources included in the MixSIAR models were selected according to knowledge of their local availability and the feeding behavior of species consumers (Phillips et al. 2014). However, as the discriminatory power of mixing models generally decreases as the number of sources increases, the number of sources should be kept as low as possible without missing relevant and isotopically distinct sources (Phillips et al. 2014, Medina-Contreras et al. 2020). Potential primary sources included in MixSIAR models included mangrove (*R. mangle*), macrophyte (*Typha* sp.), macroalgae (Chlorophytes: *Rhizoclonium* sp.), benthic microalgae, and estuarine and marine phytoplankton (see Table 1). Benthic microalgae stable isotope values applied were global averages ( $\delta^{13}\text{C} = -20.2 \pm 2.1\text{‰}$  and  $\delta^{15}\text{N} = 2.4 \pm 1.2\text{‰}$ ) suggested by Kristensen et al. (2017), compiled from various sources (e.g. Dittel et al. 1997, France 1998, Lee 2000, Bouillon et al. 2002, Hsieh et al. 2002, Guest & Connolly 2004, Guest et al. 2004, Demopoulos et al. 2007). Marine phytoplankton stable isotope values (with higher  $\delta^{13}\text{C}$ ) were included from global averages ( $\delta^{13}\text{C} = -20.1 \pm 2.0\text{‰}$  and  $\delta^{15}\text{N} = 7.1 \pm 1.7\text{‰}$ ) compiled from various sources (Peterson et al. 1985, Cifuentes et al. 1996, Vizzini & Mazzola 2003, Garcia et al. 2018, Muro-Torres et al. 2019, Qu et al. 2019) (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m681p021\\_supp.pdf](http://www.int-res.com/articles/suppl/m681p021_supp.pdf)).

The MixSIAR evaluation of mesozooplankton and planktivorous fish included marine and estuarine phytoplankton and mangroves, as the ARD is not a well-mixed estuary and the narrow feeding behavior of these species make all other sources irrelevant. For omnivorous and carnivorous epibenthic invertebrates and phytobenthivorous fish, all basal resources were included except marine and estuarine phytoplankton, as these species do not feed directly off this food source. For omnibenthivorous, zoobenthivorous, and piscivorous fish, marine phytoplankton was excluded from the models because this food

source was irrelevant for mesozooplankton and planktivorous fish, at the bottom of their trophic chains. Detailed justification about the inclusion or exclusion of basal resources for each trophic guild category is presented in Table S2. To illustrate the difference in the selection of sources in mixing models, the results with all endmembers (basal sources of organic matter) for some fish are shown.

The TEFs in MixSIAR models were used according to McCutchan et al. (2003). For mesozooplankton, these values were  $0.5 \pm 0.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.3 \pm 0.18\text{‰}$  for  $\delta^{15}\text{N}$ . For fish and epibenthos, the values were  $1.3 \pm 0.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.9 \pm 0.32\text{‰}$  for  $\delta^{15}\text{N}$ , per TP previously calculated for trophic guilds (Phillips et al. 2014). Currently, several studies for leaf-eating mangrove crabs have shown that C and N discrimination values are higher than those that are typically used (e.g. Harada & Lee 2016). Accordingly, for herbivorous crabs, we used mean ( $\pm$ SD) values based on our experiments examining trophic discrimination between the crab *Aratus pisonii* and its diet of mangrove leaves ( $\delta^{13}\text{C}$ :  $5.4 \pm 0.9\text{‰}$ ,  $\delta^{15}\text{N}$ :  $3.9 \pm 0.5\text{‰}$ ; L. A. Sandoval et al. unpubl. data).

MixSIAR was run in R v.3.5.1 (R Core Team 2018). Models were fitted using 3 chains until they 'converged' using long or very long Markov chain Monte Carlo lengths.

### 3. RESULTS

#### 3.1. Isotopic composition

The variation of the isotopic composition of basal resources collected in the Gulf of Urabá, excluding global averages for marine phytoplankton and benthic microalgae, showed a width of 6.3‰ for  $\delta^{13}\text{C}$  and 5.6‰ for  $\delta^{15}\text{N}$  (Fig. 2). Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for mangrove *Rhizophora mangle* leaves were  $-31.0\text{‰}$  (the most  $^{13}\text{C}$ -depleted value) and 0.5‰, respectively (Table 1, Fig. 2). Macroalgae (*Rhizoclonium* sp.) had similar  $\delta^{13}\text{C}$  values ( $-30.8\text{‰}$ ) but a higher  $\delta^{15}\text{N}$  value (2.9‰) (Table 1). Estuarine phytoplankton was relatively enriched in  $^{13}\text{C}$  (excluding global averages for marine phytoplankton and benthic microalgae;  $-24.7\text{‰}$ ) relative to other sources and had the most  $^{15}\text{N}$ -enriched values (4.6‰) (Table 1), while the macrophyte *Typha* sp. was the most  $^{15}\text{N}$ -depleted ( $-0.6\text{‰}$ ) (Table 1).

A total of 5 mesozooplankton taxa were analyzed: Luciferidae, Brachyura zoeae, Penaeidae mysis, calanoid copepods, and zooplankton—the latter consisting of a mixture of the other 4 categories (Table 2).

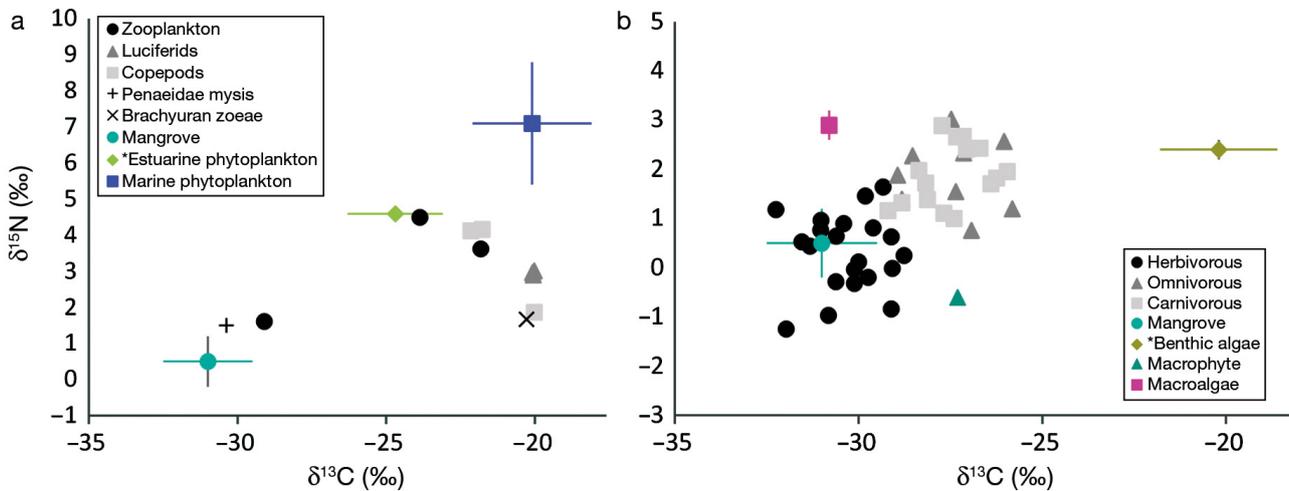


Fig. 2. Carbon and nitrogen stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) biplots of (a) mesozooplankton and (b) benthic invertebrates in the Gulf of Urabá. Consumer values are shown using grey symbols and represent individual samples. To illustrate their alignment with potential basal resources, isotopic values of sources (mean  $\pm$  SD) are shown with colored symbols. Consumer values have been adjusted by their trophic level to ease visual interpretation. The proximity of consumer values to source values broadly reflects its reliance on a basal source. (\*) Source based on global values

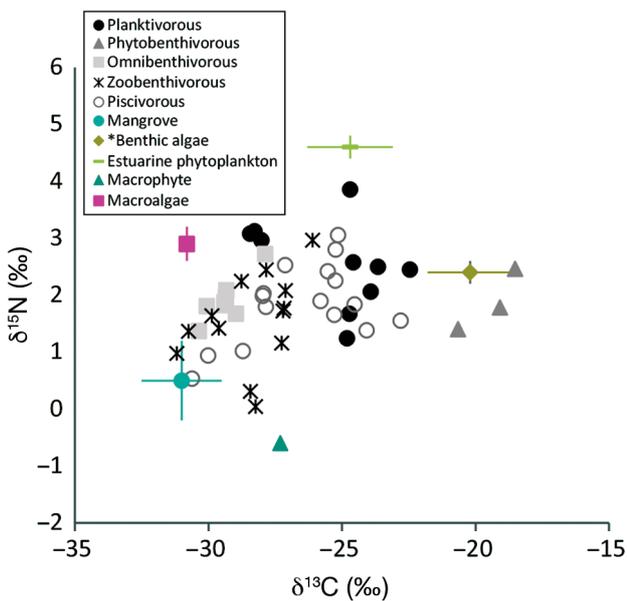


Fig. 3. Same as Fig. 2, but for fish consumers

Mean  $\delta^{13}\text{C}$  values ranged between  $-29.9\text{‰}$  (Penaeidae mysis) and  $-19.5\text{‰}$  (Luciferidae). Mean  $\delta^{15}\text{N}$  values ranged between  $4.3\text{‰}$  (Penaeidae mysis) and  $6.1\text{‰}$  (calanoid copepods) (Table 2). A total of 9 epibenthic species were analyzed (Table 2). Mean  $\delta^{13}\text{C}$  values ranged between  $-27.8\text{‰}$  (*Uca* spp.) and  $-23.7\text{‰}$  (*Litopenaeus schmitii*). Mean  $\delta^{15}\text{N}$  values oscillated between  $3.6\text{‰}$  (*Uca* spp.) and  $8\text{‰}$  (*Thaisella trinitatensis*) (Table 2).

A total of 18 fish species were analyzed. Mean  $\delta^{13}\text{C}$  values ranged between  $-26.5\text{‰}$  (*Eugerres plumieri*) and  $-17.7\text{‰}$  (*Mugil incilis*) (Table 3). Mean  $\delta^{15}\text{N}$  values ranged between  $5.8\text{‰}$  (*M. incilis*) and  $12.2\text{‰}$  (*Trichurus lepturus*) (Table 3). When  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were adjusted for consumer fractionation, zoobenthivorous and piscivorous fish were the most  $^{13}\text{C}$ -depleted, while phytobenthivorous fish were the most  $^{13}\text{C}$ -enriched (Fig. 3). Zoobenthivorous fish were the most  $^{15}\text{N}$ -depleted, while planktivorous were most  $^{15}\text{N}$ -enriched (Fig. 3).

### 3.2. Mixing model results (MixSIAR)

For mesozooplankton consumers, the mixing model indicated that estuarine phytoplankton made the largest contribution to diet, ranging from 22% (credibility interval [CI]: 1–78%) to 63% (CI: 3–96%) (Table 4, Fig. 4a), followed by mangroves, which ranged from 18% (CI: 1–55%) to 61% (CI: 15–86%) (Table 4, Fig. 4a).

For omnivorous and carnivorous epibenthos, the estimated contribution of macroalgae was the highest (Fig. 4b), ranging from 31% (CI: 9–49%) to 55% (CI: 9–71%) (Table 5). Mangroves were the most important contribution for the herbivorous crabs *Aratus pisonii* (75%; CI: 23–93%) and *Pachygrapsus transversus* (60%; CI: 26–95%) (Table 5). Macrophytes were the most important estimated source for the fiddler crab *Uca* spp. (38%; CI: 10–55%) (Table 5).

Table 1. Mean  $\pm$  SD carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values and C:N ratios of primary producers collected in the Gulf of Urabá, Colombian Caribbean. n: number of samples; NA: not applicable

Species/taxon	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N
<b>Mangrove</b>				
<i>Rizophora mangle</i>	10	$-31 \pm 1.5$	$0.5 \pm 1.0$	$155.1 \pm 23$
<b>Macrophyte</b>				
<i>Typha</i> sp.	3	$-27.3 \pm 0.1$	$-0.6 \pm 0.1$	$24.3 \pm 1$
<b>Macroalgae</b>				
Chlorophytes ( <i>Rhizoclonium</i> sp.)	3	$-30.8 \pm 0.0$	$2.9 \pm 0.3$	$20.5 \pm 1$
<b>Phytoplankton</b>				
Estuarine phytoplankton	2	$-24.7 \pm 1.6$	$4.6 \pm 0.2$	$8.3 \pm 2$
Marine phytoplankton <sup>a</sup>		$-21.3 \pm 1.1$	$8.6 \pm 1.0$	NA
<b>Microphytobenthos</b>				
Benthic microalgae <sup>a</sup>		$-20.0 \pm 2.1$	$2.4 \pm 1.2$	NA

<sup>a</sup>Global average used; from Peterson et al. (1985) for marine phytoplankton and Kristensen et al. (2017) for benthic microalgae

Table 2. Mean  $\pm$  SD carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values of invertebrate consumers collected in the Gulf of Urabá, Colombian Caribbean. n: number of samples; N: number of pooled individuals in each sample; L: body length; NA: not applicable

Species/taxon	n (N)	L (cm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<b>Mesozooplankton</b>				
Zooplankton	3	NA	$-24.3 \pm 3.1$	$6.0 \pm 1.2$
Luciferidae	3 (300)	NA	$-19.5 \pm 0.0$	$5.7 \pm 0.0$
Brachyura zoeae	1 (50)	NA	$-19.9$	4.4
Panaeidae mysis	1 (500)	NA	$-29.9$	4.3
Calanoid copepods	3 (600)	NA	$-20.7 \pm 0.9$	$6.1 \pm 1.1$
<b>Epibenthos</b>				
<b>Gastropoda</b>				
<i>Thaisella coronata</i> <i>trinitatis</i>	3	$2.3 \pm 0.1$	$-24.5 \pm 0.2$	$8.0 \pm 0.1$
<i>Neritina virginea</i>	9 (6)	$1.5 \pm 0.2$	$-25.7 \pm 1.1$	$5.8 \pm 0.7$
<b>Grapsidea</b>				
<i>Aratus pisonii</i>	9 (5)	$2.1 \pm 0.2$	$-25.6 \pm 0.8$	$3.9 \pm 0.7$
<i>Pachygrapsus</i> <i>transversus</i>	3 (3)	$1.4 \pm 0.1$	$-25.4 \pm 0.3$	$4.8 \pm 0.1$
<b>Ocypodidae</b>				
<i>Uca</i> spp.	9 (3)	$2.0 \pm 0.3$	$-27.8 \pm 0.8$	$3.6 \pm 0.9$
<b>Panopeidae</b>				
<i>Panopeus rugosus</i>	3	$3.6 \pm 0.0$	$-25.6 \pm 0.8$	$7.7 \pm 0.8$
<i>Eurytium limosum</i>	3	$3.4 \pm 0.1$	$-25.3 \pm 0.3$	$6.8 \pm 0.3$
<b>Shrimp and swimming crab</b>				
<b>Panaeidae</b>				
<i>Litopenaesu schmitii</i>	3 (2)	$12.6 \pm 0.7$	$-23.7 \pm 0.2$	$7.3 \pm 0.1$
<b>Portunidae</b>				
<i>Callinectes bocourti</i>	3	$4.7 \pm 0.3$	$-26.0 \pm 0.3$	$7.1 \pm 0.3$

For planktivorous fish (excluding the model with all end-members for *Anchovia clupeioides*), estuarine phytoplankton and mangroves were the most important estimated sources for consumers (Fig. 5), which ranged from 31 % (CI: 3–72 %) to 46 % (CI: 2–93 %) and 31 % (CI: 4–57 %) to 54 % (CI: 19–77 %), respectively (Table 6). To illustrate the difference in the selection of sources in mixing models, the results with all end-members for *A. clupeioides* are shown (Table 6).

For phytobenthivorous fish (excluding the model with all end-members), the estimated contribution of benthic microalgae was the highest (48 %; CI: 13–85 %) (Table 6, Fig. 5). To illustrate the difference in the selection of sources in mixing models, the results with all end-members are shown in Table 6. This shows that the contribution of benthic microalgae decreased considerably (25 %; CI: 1–67 %) (Table 6).

For omnibenthivorous and zoobenthivorous fish (excluding the model with all end-members), macroalgae was the most important estimated source (Fig. 5), ranging from 23 % (CI: 1–66 %) to 63 % (CI: 24–82 %) (Table 6). For piscivorous fish, mangroves and benthic microalgae were the most important estimated sources (Fig. 5), which ranged from 14 % (CI: 1–40 %) to 46 % (CI: 1–80 %) and 12 % (CI: 1–41 %) to 38 % (CI: 8–45 %), respectively (Table 6). To illustrate the difference in the selection of sources in mixing models, the results with all end-members for *Diapterus rhombeus* are shown (Table 6).

Overall, mixing model results showed that mangrove carbon was an important source of energy for Sesarimididae crabs (herbivorous) and Engraulidae (planktivorous) and Centropomidae (piscivorous) fish (Fig. 6). Estuarine phytoplankton was an important source of energy for Carangidae, Clupeidae (planktivorous), and Trichuridae (piscivorous) fish (Fig. 6). Benthic algae was an important source of energy for Mugilidae (phytobenthivorous) and Carangidae (piscivorous) fish, and Panaeidae (carnivorous) shrimp (Fig. 6). Macroalgae was an important source of energy for Gerridae and Ariidae (omnibenthivorous) fish, and Gastropoda (omnivorous) (Fig. 6). Macrophyte was an important source of energy for Ocypodidae (herbivorous) and Panopeidae (carnivorous) crabs (Fig. 6).

### 3.3. TPs

Results showed a food web with a maximum TP of 4.6 in the ARD estuary. Consumers with the lowest TPs were mesozooplankton larvae (Table 4) and her-

bivorous crabs (Table 5), while the piscivorous fish *T. lepturus* exhibited the highest TP (Table 6). Overall, mesozooplankton, herbivorous epibenthos, and phytobenthivorous fish corresponded to the first

consumers (Tables 4–6); intermediate TP consumers included carnivorous epibenthos and 2 trophic guilds: planktivorous and omnibenthivorous fish (Tables 5 & 6); and high TP consumers included zoobenthivorous and piscivorous fish (Table 6).

Table 3. Mean  $\pm$  SD carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values of fish collected in the Gulf of Urabá, Colombian Caribbean. n: number of samples; L: fish total length (mean  $\pm$  SD)

Species/taxon	n	L (cm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<b>Ariidae</b>				
<i>Ariopsis canteri</i>	3	19.4 $\pm$ 0.6	-24.3 $\pm$ 0.5	8.6 $\pm$ 0.5
<i>Cathorops mapale</i>	3	19.4 $\pm$ 1.0	-26.4 $\pm$ 0.6	8.6 $\pm$ 0.2
<b>Carangidae</b>				
<i>Caranx crysus</i>	2	14.5 $\pm$ 0.6	-21.6 $\pm$ 0.1	10.1 $\pm$ 0.6
<i>Caranx hipos</i>	3	24.0 $\pm$ 0.2	-20.0 $\pm$ 1.2	11.0 $\pm$ 0.2
<i>Oligoplites saliens</i>	3	26.3 $\pm$ 0.2	-20.8 $\pm$ 0.4	11.3 $\pm$ 0.2
<b>Centropomidae</b>				
<i>Centropomus ensiferus</i>	4	21.6 $\pm$ 0.5	-24.4 $\pm$ 0.8	10.9 $\pm$ 0.5
<i>Centropomus pectinatus</i>	3	20.8 $\pm$ 0.8	-25.0 $\pm$ 1.8	9.7 $\pm$ 0.5
<i>Centropomus undecimalis</i>	3	26.7 $\pm$ 1.0	-24.3 $\pm$ 1.5	11.0 $\pm$ 0.8
<b>Clupeidae</b>				
<i>Opisthonema oglinum</i>	2	21.8 $\pm$ 0.0	-20.0 $\pm$ 0.6	9.3 $\pm$ 0.0
<b>Engraulidae</b>				
<i>Anchovia clupeioides</i>	3	21.3 $\pm$ 0.2	-25.2 $\pm$ 0.2	9.9 $\pm$ 0.1
<i>Centengraulis edentulous</i>	3	11.1 $\pm$ 0.0	-21.4 $\pm$ 0.4	8.5 $\pm$ 0.3
<b>Ephippidae</b>				
<i>Chaetodipterus faber</i>	3	21.6 $\pm$ 4.2	-26.1 $\pm$ 0.8	9.8 $\pm$ 0.4
<b>Gerridae</b>				
<i>Diapterus rhombeus</i>	2	16.5 $\pm$ 0.0	-25.5 $\pm$ 0.8	9.2 $\pm$ 0.4
<i>Eugerres plumieri</i>	3	17.2 $\pm$ 0.2	-26.5 $\pm$ 0.3	8.9 $\pm$ 0.1
<b>Lutjanidae</b>				
<i>Lutjanus jocu</i>	3	16.8 $\pm$ 0.3	-24.9 $\pm$ 1.1	9.8 $\pm$ 0.1
<b>Mugilidae</b>				
<i>Mugil incilis</i>	3	25.3 $\pm$ 0.6	-17.7 $\pm$ 0.9	5.8 $\pm$ 0.4
<b>Scianidae</b>				
<i>Bardiella ronchus</i>	3	18.5 $\pm$ 0.4	-23.4 $\pm$ 0.7	10.6 $\pm$ 0.4
<b>Trichuridae</b>				
<i>Trichurus lepturus</i>	3	71.7 $\pm$ 0.9	-21.1 $\pm$ 0.2	12.2 $\pm$ 0.3

#### 4. DISCUSSION

A maximum TP of 4.6 was estimated in the ARD. The number of different TPs was similar to that found in other mangrove systems (e.g. Abrantes & Sheaves 2009, Giarrizzo et al. 2011, Sepúlveda-Lozada et al. 2017). Mean  $\delta^{15}\text{N}$  values for aquatic primary consumers (meso-zooplankton and phytobenthivorous fish) were enriched by 3‰ relative to the mean  $\delta^{15}\text{N}$  values for sources (5.4 and 2.4‰, respectively), suggesting that the TEF of 2.9 used by the formula fit adequately for estimation of TPs (McCutchan et al. 2003). An overall mean  $\delta^{15}\text{N}$  value was calculated for basal resources to estimate baseline  $\delta^{15}\text{N}$  and finally to estimate TP. Nevertheless, previous food web studies in mangrove systems have successfully used mangroves as a  $^{15}\text{N}$  reference (Medina-Contreras et al. 2018) as well as sediments (Mancera 2003). Mancera (2003) recommended the use of the mean value between mangroves and sediments. However, we believe that the average  $\delta^{15}\text{N}$  value for primary sources was appropriate for TP estimation due to the similar values obtained for fish using stomach content analyses in the Colombian Caribbean, as shown below.

TP estimates for fish were similar to those found by García & Contreras (2011) in the Colombian Caribbean, e.g. *Mugil incilis* (this study: 2.3; literature data: 2.2), *Eugerres plumieri* (3.4 and 3.1, respectively), *Centropomus ensiferus* (4.1 and 4.3, respectively), *C. undecimalis* (4.2 and 4.1, respectively), and *Trichurus lepturus* (4.6 and 4.5, respectively). Further, the TPs of the fish community were similar to those found on the Pacific coast of Colombia by Medina-Contreras et al. (2018) (mean community

Table 4. Percent of primary producer's contributions (50% quantiles; range: 95% Bayesian credibility intervals) to the diet of mesozooplankton estimated using MixSIAR. TP: estimated trophic position

Species/taxon	TP	Marine phytoplankton		Estuarine phytoplankton		Mangrove	
		Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI
Zooplankton	2.3	19	0–60	34	2–90	42	2–70.
Luciferidae	2.1	12	0–79	63	3–96	18	1–55
Brachyura zoeae	1.6	16	0–82	33	0–90	36	4–86
Penaeidae mysis	1.6	13	1–45	22	1–78	61	15–86
Calanoid copepods	2.2	21	1–68	50	6–89	26	3–55

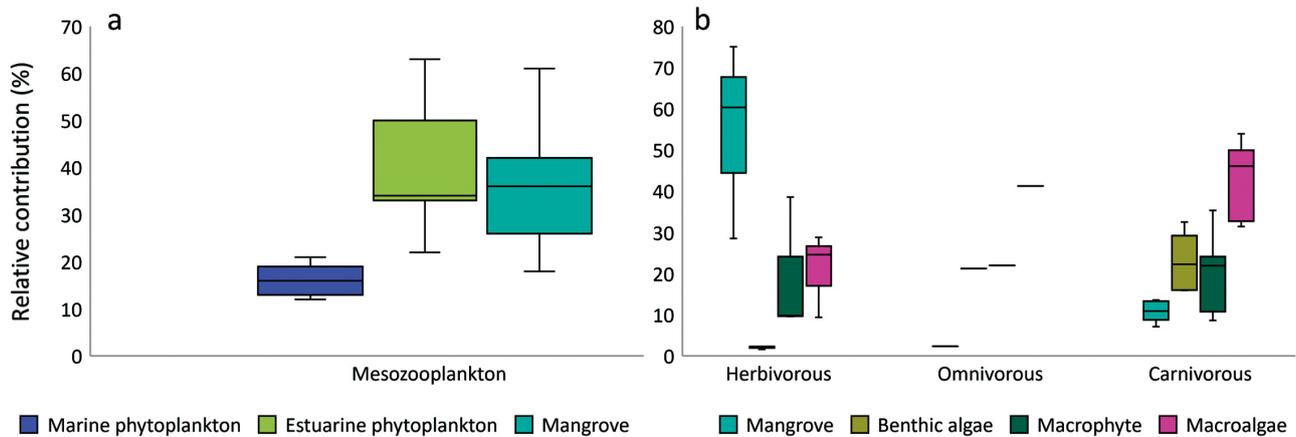


Fig. 4. Isotope mixing model (MixSIAR) estimates of percent contributions from different basal resources to the diet (tissue) of (a) mesozooplankton and (b) trophic guilds for epibenthivorous species. Horizontal lines in boxplots: means; filled colored boxes: 25th–75th percentiles; whiskers: maximums and minimums. Basal resources excluded from models are shown with 0%. Omnivorous values are for only one species (*Neritina virginea*)

Table 5. Percent of primary producer's contributions (50% quantiles; range: 95% Bayesian credibility intervals) to different epibenthic species using MixSIAR. TP: estimated trophic position

Species/taxon	TP	Mangrove		Benthic microalgae		Macrophyte		Macroalgae	
		Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI
<b>Herbivorous</b>									
<i>Aratus pisonii</i>	1.8	75	23–93	2	0–23	10	1–40	9	1–41
<i>Uca</i> sp.	1.6	28	0–68	2	0–13	38	10–55	29	4–58
<i>Pachygrapsus transversus</i>	2.0	60	26–95	2	0–13	10	0–35	25	0–61
<b>Omnivorous</b>									
<i>Neritina virginea</i>	2.4	13	0–46	21	8–37	22	1–49	41	14–60
<b>Carnivorous</b>									
<i>Tahisella coronata</i>	3.1	7	0–36	29	17–42	11	1–33	50	20–64
<i>Panopeus rugosus</i>	3.0	11	0–61	22	11–34	9	1–29	55	9–71
<i>Eurytium limosum</i>	2.7	13	0.3–60	16	6–33	35	2–60	33	7–50
<i>Litopenaesu schmitii</i>	2.9	9	0–40	32	18–51	24	1–52	31	9–49
<i>Callinectes bocourti</i>	2.8	14	1–50	16	8–29	22	3–42	46	19–63

TGs of 3.7 and 3.6, respectively). In contrast, the calculated TP of the fish community was lower on the Caribbean coast of Panama (Stuthmann & Castellanos-Galindo 2020), with a mean community TP of 3.2. However, in that study a different TP calculation technique was used (R package 'tRophicPosition'), which could explain the differences. Likewise, ontogenetic changes in fish feeding behavior are common (e.g. Ariidae; Sandoval et al. 2020). This can also explain the lower fish TPs from the Caribbean coast of Panama since based on the size of the captured fish there, the communities consisted mostly of juveniles (Stuthmann & Castellanos-Galindo 2020).

The highest TP (4.6) in ARD is evidence of the high complexity of estuarine food webs since food chains are typically short, reaching a maximum of 4 or 5 TPs

(Pimm & Lawton 1977). TP measures can be essential for ecosystem-based fishery management (EBFM). The strength of a TP as an ecological indicator lies in its efficiency in capturing and revealing ecosystem effects of fishing (Stergiou et al. 2007). For instance, the mean weighted TP of a catch over a series of years is useful to identify the 'fishing down the marine food web' process (Pauly et al. 1998) as well as to estimate other indicators such as the primary production required to support fisheries (Pauly & Christensen 1995) and the 'Fishery in Balance' index (Pauly et al. 2000). In this way, studying TPs using isotopic signatures can be used in EBFM in ARD, Urabá Gulf, where there are more than 1500 Columbian families engaged in local commerce and/or subsistence fishing, with few economic alternatives (LOPEGU 2017).

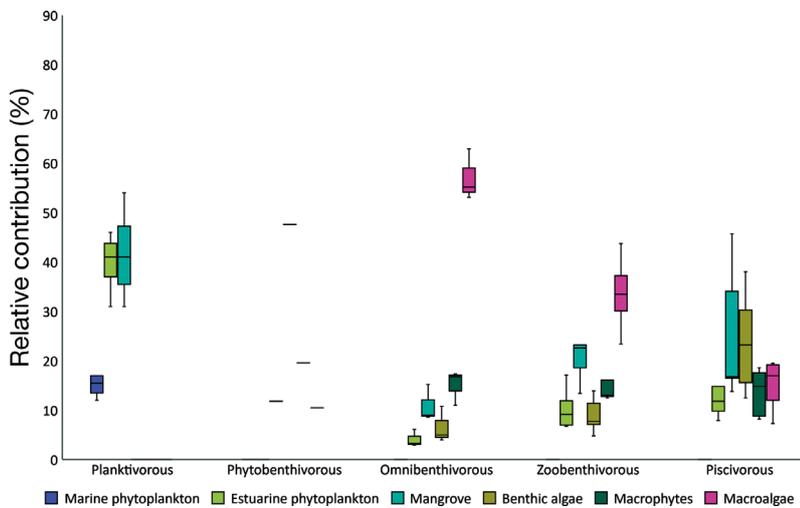


Fig. 5. Isotope mixing model (MixSIAR) estimated percentages of the percent contribution from different basal resources to the diet (tissue) of trophic guilds of fish. Boxplot parameters as in Fig. 4. Basal resources excluded from models are shown with 0%. Phytobenthivorous values are for only one species (*Mugil incilis*)

This study observed species from a wide range of potential trophic groups in order to allow better identification of possible trophic pathways within the food webs (Abrantes & Sheaves 2009). We suggest a diversity of food sources exists for consumers in ARD's ecosystem food webs, with at least 5 potential trophic pathways.

(1) Phytoplankton pathway. Phytoplankton contributes directly to mesozooplankton (TP  $\approx$  2) and is transferred to higher TPs; first to planktivorous fish (TP  $\approx$  3) and subsequently to piscivorous fish (TP  $\approx$  4) (e.g. *T. lepturus*).

(2) Mangrove pathway. Mangroves are incorporated by herbivorous epibenthic crabs (*Aratus pisonii* and *Pachygrapsus transversus*) and can also be transferred to the adjacent TP through *A. pisonii*, which has been found in the diet of the zoobenthivorous fish *Ariopsis canteri* in a mangrove lagoon in the Urabá Gulf (Sandoval-Londoño et al. 2015). On the importance of the mangrove as a source of food for grapsid crabs, it has recently been accepted that the values of discrimination are higher than average values traditionally used following Post (2002) and McCutchan et al. (2003) (Harada & Lee 2016). For our study, discrimination values for this group of crabs were obtained from our own experiment of trophic discrimination of stable isotopes between mangrove leaves and *A. pisonii* (L. A. Sandoval et al. unpubl. data), which are close to those suggested for sesarimid crabs ( $\delta^{13}\text{C}$ :  $4.88 \pm 0.1\text{‰}$ ;  $\delta^{15}\text{N}$ :  $3.5 \pm 0.1\text{‰}$ ) by Harada & Lee (2016). This finding points to the

importance of mangrove leaves for herbivorous crabs from the ARD.

Furthermore, our results suggest that herbivorous crabs in the ARD could be exporting mangrove organic production indirectly, either as prey or carcasses, thus supplying the near-shore pelagic food webs (Werry & Lee 2005, Lee 2008). Mangroves also contribute directly to mesozooplankton as shrimp larvae (TP  $\approx$  2) and are transferred to higher TPs, first to planktivorous fish (TP  $\approx$  3; mainly engraulids *Anchovia clupeioides* and *Centengraulis edentulus*), and subsequently to piscivorous fish (TP  $\approx$  4) such as centropomids (*C. ensiferus* and *Centropomus undecimalis*). In Brazil, Giarrizzo et al. (2011) described the same mangrove trophic pathway. That study, as the present one, was also conducted in an area where mangroves are interlinked to

other productive coastal habitats such as seagrass beds. Likewise, engraulid fish were also a key source of carbon transfer from the mangroves to higher TPs. These results have important implications for the trophic role of mangroves in tropical estuarine and marine ecosystems since engraulids are abundant in these systems and are prey for important commercial piscivorous fish species (Giarrizzo et al. 2011). In the Gulf of Urabá, the importance of the engraulids for piscivorous fish has been shown in the diet of the Atlantic cutlassfish *T. lepturus* (index of relative importance [IRI] = 56%) (Arenas-Urbe et al. 2019), and the Gafftopsail Sea catfish *Bagre marinus* (IRI = 15%) (Hernández-Morales et al. 2018).

(3) Microphytobenthos (benthic microalgae) pathway. Microphytobenthos contribute directly to the phytobenthivorous fish *M. incilis* (TP = 2). This finding is consistent with a previous study in the Gulf of Urabá, where both juveniles and adults were found to feed mainly on diatoms (87% IRI) from the seabed near mangroves (Sandoval Londoño 2012) and can also corroborate the proper use of the isotopic benthic microalgae values from global averages in our models. *M. incilis* can also transfer energy to higher TPs (TP  $\approx$  4), as it has been found in the diet of species such as *T. lepturus* (Arenas-Urbe et al. 2019) and *C. ensiferus* (Sandoval Londoño 2012). Likewise, the microphytobenthos also contributes significantly, although indirectly, to the white shrimp *Litopenaesu schmitii* (TP  $\approx$  3).

(4) Macroalgae pathway. Macroalgae are usually abundant on the roots of *Rhizophora mangle* in the

Table 6. Percent of primary producer's contributions (50% quantiles; range: 95% Bayesian credibility intervals) for trophic guilds and fish species. TP: estimated trophic position; CI: credibility intervals; NA: not applicable

Guild/species	TP	Marine phytoplankton		Estuarine phytoplankton		Mangrove		Benthic microalgae		Macrophytes		Macroalgae	
		Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI	Median (%)	95% CI
<b>Planktivorous</b>													
<i>Anchovia clupeioides</i>	3.8	14	1–39	31	3–72	54	19–77	NA	NA	NA	NA	NA	NA
<i>A. clupeioides</i> <sup>a</sup>	4	4	0–16	6	0–31	19	1–63	12	0–44	37	2–77	9	0–44
<i>Centegraulis edentulus</i>	3.3	12	0–49	39	1–87	45	8–74	NA	NA	NA	NA	NA	NA
<i>Caranx crysus</i>	3.8	17	0–58	43	2–91	37	5–67	NA	NA	NA	NA	NA	NA
<i>Opisthonema oglinum</i>	3.6	17	0–64	46	2–93	31	4–67	NA	NA	NA	NA	NA	NA
<b>Phytoenthivorous</b>													
<i>Mugil incilis</i>	2.3	NA	0–46	NA	0–50	12	0–50	48	13–85	20	0–56	10	0–47
<i>M. incilis</i> <sup>a</sup>	12	12	0–46	13	0–50	10	0–43	25	1–67	14	1–48	9	0–40
<b>Omnibenthivorous</b>													
<i>Cathorops mapale</i>	3.3	NA	0–15	3	0–21	15	0–60	5	0–19	17	1–40	53	11–78
<i>Diapterus rhombeus</i>	3.5	NA	0–15	6	0–38	9	0–50	11	0–30	11	1–36	55	10–78
<i>D. rhombeus</i> <sup>a</sup>	2	2	0–15	3	0–38	42	1–91	6	0–63	14	0–70	7	0–71
<i>Eugerres plumieri</i>	3.4	NA	0–15	3	0–19	9	0–48	4	0–16	17	0–36	63	24–82
<b>Zoobenthivorous</b>													
<i>Ariopsis canteri</i>	3.3	NA	0–27	7	0–27	13	1–43	14	1–34	24	2–47	37	15–58
<i>Centropomus pectinatus</i>	3.7	NA	0–38	9	0–34	33	1–78	8	0–45	11	0–51	23	1–66
<i>Luftjanus jocu</i>	3.7	NA	0–38	12	0–38	23	1–69	7	0–37	16	0–49	30	2–69
<i>Chaetodipterus faber</i>	3.7	NA	0–31	7	0–31	23	0–70	5	0–26	12	0–41	44	2–80
<i>Bardiella ronchus</i>	4.0	NA	0–46	17	0–46	19	2–47	11	0–33	13	1–36	34	4–63
<b>Piscivorous</b>													
<i>Centropomus ensiferus</i>	4.1	NA	1–31	12	1–31	34	2–64	16	2–35	15	1–41	20	1–52
<i>Caranx hipos</i>	4.2	NA	0–46	10	0–46	17	1–50	38	8–45	18	0–52	7	0–30
<i>Centropomus undecimalis</i>	4.2	NA	0–33	8	0–33	46	1–80	12	1–41	8	0–39	17	0–60
<i>Oligoplites saliens</i>	4.3	NA	0–47	15	0–47	16	1–48	30	1–60	19	0–48	12	1–38
<i>Trichurus lepturus</i>	4.6	NA	0–62	29	0–62	14	1–40	23	1–52	9	0–32	19	0–52

<sup>a</sup>Models with all primary producers (end members) included

ARD (Hurtado-Santamaria & Quan-Young 2016) and apparently contribute to omnivorous and carnivorous epibenthos as well as omnibenthivorous fish (TP  $\approx$  3). This finding agrees with Medina-Contreras et al. (2020), who also found a significant relative contribution of macroalgae for the same trophic guilds of epibenthos from the Colombian Pacific. Furthermore, the importance of algae was evident in the diet of the omnibenthivorous fish *Diapterus rhombeus* and *E. plumieri* from Urabá Gulf (Sandoval Londoño 2012). In this way, macroalgae can be also transferred to piscivorous fish (TP  $\approx$  4) such as centropomids.

(5) Macrophyte pathway. Macrophytes contribute directly to the herbivorous crab *Uca* sp. (TP  $\approx$  2). This energy is apparently transferred to the carnivorous crab *Eurytium limosum* (TP  $\approx$  3) since the first species is prey to the second (Kneib & Weeks 1990). Nevertheless, a more detailed study of the sources sustaining *Uca* spp. is required since they incorporated mainly microphytobenthos in mangroves elsewhere in the world (Bouillon et al. 2004, Medina-Contreras et al. 2020).

Based on the above results, mangroves are the main basal food source assimilated by herbivorous epibenthic crabs and piscivorous fish in the ARD, including artisanal fish, supporting our hypothesis. The relative importance of mangroves for pelagic consumers may differ seasonally as has been reported in other systems (Abrantes et al. 2015b). The ARD has a long rainy season (May–November), during which the samples for this study were collected. However, during the dry season (December–April), more estuarine and river-influenced carbon sources will likely dominate since the lowest salinity values occur during the dry period in response to trade winds maintaining fresh water in the Gulf (García-Valencia 2007). Likewise, our mixing

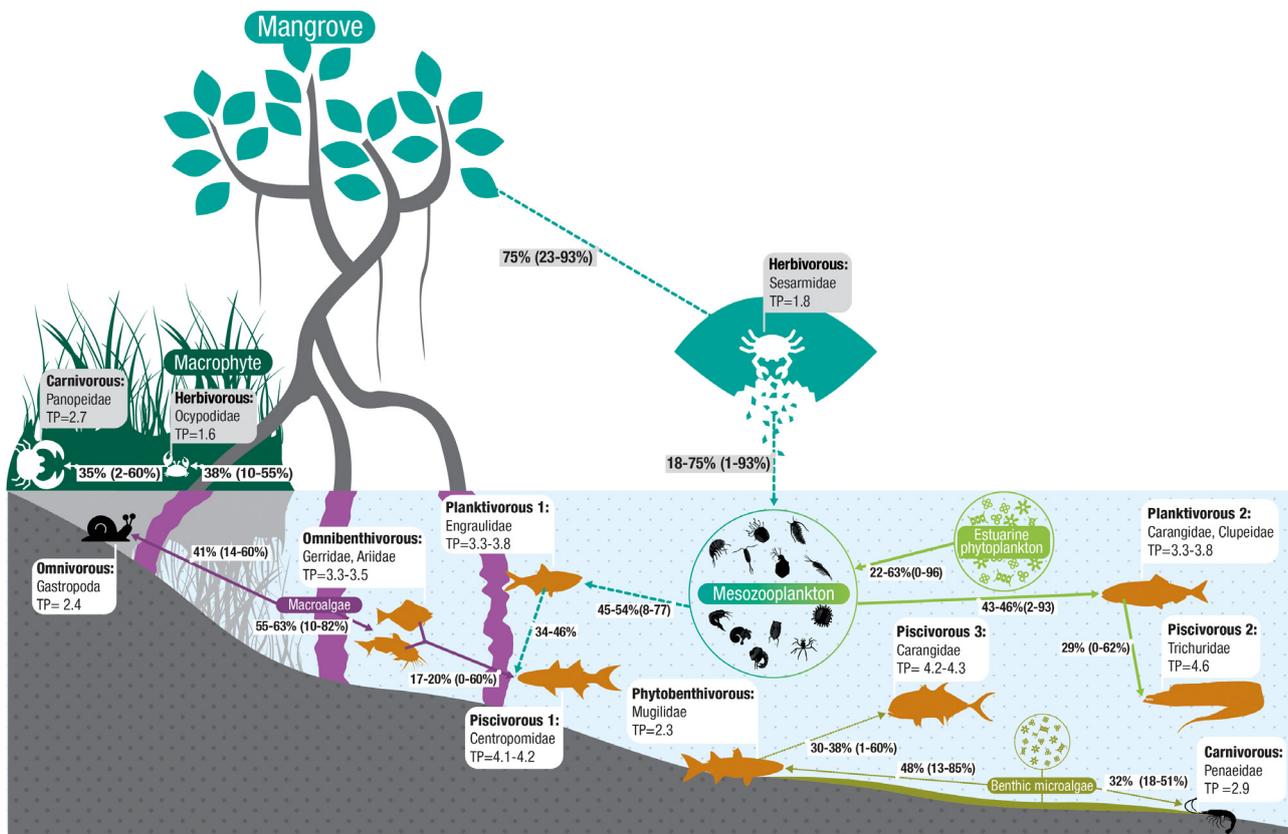


Fig. 6. Main consumers and sources showing the relative contribution of the main energetic sources in the Atrato River Delta estuary. Different trophic pathways are shown with different colors

model results for fish based on a carbon TEF of  $\delta^{13}\text{C}$ :  $1.3 \pm 0.3\%$  can be considered conservative regarding the contribution of mangroves, as higher TEF values lead to lower corrected  $\delta^{13}\text{C}$  that in turn leads to a higher contribution of mangroves, which for these systems can use values of up to 2% (Abrantes et al. 2015b).

The results showed that mangroves contributed significantly to the diet of 2 of the most common fish species in the local artisanal fishery (LOPEGU 2017): the piscivore *C. undecimalis* and the zoobenthivore *C. pectinatus*. Furthermore, results suggest that mangroves serve as substrate/habitat that supports sources such as macroalgae and benthic microalgae, which in turn support the zoobenthivorous *A. canteri* and the phytobenthivorous *M. incilis*—both also commercial fish species (LOPEGU 2017).

Other studies have suggested that mangroves can be important food sources in estuarine food webs, depending on system conditions (Mancera 2003, Abrantes et al. 2015b). We showed that fringing mangroves seem to be a major food source for some consumers in areas not interlinked with other highly

productive coastal habitats (i.e. seagrasses and coral reefs), which has been reported in only a few studies: e.g. in a northern Brazilian mangrove ecosystem (Giarrizzo et al. 2011) and northern Australian estuaries (Abrantes et al. 2015b). These results can potentially be used in EBFM focused on the protection of extensive mangrove areas in the southern Caribbean. However, since differences in the mangrove contribution to food webs are possible in the ARD, both across the rainfall regime and spatially, and because there were data limitations for local marine phytoplankton and benthic algae stable isotope values, we recommend a more detailed study of food webs in this area.

## 5. CONCLUSIONS

The results of this study showed a food web with a maximum TP of 4.6 in the ARD estuary. Diversity in food sources supports the food web, and most consumers assimilated a mixture of carbon sources as a result of intertwined trophic pathways. However, iso-

topic analysis identified 5 potential energy pathways that sustain fish. These included the mangrove, microphytobenthos, macroalgae, phytoplankton, and macrophyte pathways. Our study indicates that fringing mangroves can be an important food source for consumers in areas not interlinked to other highly productive coastal habitats (i.e. seagrasses and coral reefs), supporting the mangrove outwelling hypothesis. Herbivorous crabs (sesarmids) and planktivorous fish (engraulids) appear to be important vectors moving mangrove energy to higher TPs. Mixing model results indicated that mangrove-derived materials contributed significantly to the production of 2 fish species common in the local artisanal fishery in the ARD (*Centropomus pectinatus* and *Centropomus undecimalis*). Mangroves also served as a substrate/habitat for other sources of energy (carbon) such as macroalgae and benthic microalgae. These results can potentially be used in EBFM focused on ecosystem effects of fishing and protection of extensive mangrove areas in the southern Caribbean.

**Acknowledgements.** We thank the project LOPEGU funded by Sistema General de Regalías, Gobernación de Antioquia, and Universidad de Antioquia (agreement no. 4600000983). We also express our gratitude to the National Aquaculture and Fisheries Authority (Autoridad Nacional de Acuicultura y Pesca) and National Authority of Environmental Licensing (Autoridad Nacional de Licencias Ambientales) for fish catch permits 0524 (27 May 2014) and 00001827 (15 October 2015), respectively. We thank the Consejo Comunitario Mayor de Bocas del Atrato y Leoncito for their hospitality, for granting us access to their territory, supporting fieldwork, and sharing traditional and local ecological knowledge. We thank A. Sepúlveda-Lozada for helpful comments on isotope fractionation and mixing models. L.A.S.L. acknowledges financial support from the Doctoral Fellowship Program of the Administrative Department for Science, Technology, and Innovation (Departamento Administrativo de Ciencia, Tecnología e Innovación)—COLCIENCIAS.

#### LITERATURE CITED

- Atlantic cutlass fish *Trichiurus lepturus* in the Urabá Gulf, Colombian Caribbean. *Biota Colomb* 20:59–75
- ✦ Blaber SJM (2013) Fishes and fisheries in tropical estuaries: the last 10 years. *Estuar Coast Shelf Sci* 135:57–65
- ✦ Blanco JF, Estrada EA, Ortiz LF, Urrego LE (2012) Ecosystem-wide impacts of deforestation in mangroves: the Urabá Gulf (Colombian Caribbean) case study. *ISRN Ecol* 2012:958709
- ✦ Blanco-Libreros JF (2016) Cambios globales en los manglares del golfo de Urabá (Colombia): entre la cambiante línea costera y la frontera agropecuaria en expansión. *Actual Biol* 38:53–70
- ✦ Bouillon S, Koedam N, Raman AV, Dehairs F (2002) Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* 130:441–448
- ✦ Bouillon S, Moens T, Overmeer I, Koedam N, Dehairs F (2004) Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. *Mar Ecol Prog Ser* 278:77–88
- ✦ Bouillon S, Connolly RM, Gillikin DP (2011) Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. In: Wolanski E, McLusky DS (eds) *Treatise on estuarine and coastal science*, Vol 7. Academic Press, Waltham, MA, p 143–173
- ✦ Bukovinszky T, van Veen FF, Jongema Y, Dicke M (2008) Direct and indirect effects of resource quality on food web structure. *Science* 319:804–807
- ✦ Chanton J, Lewis FG (2002) Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, USA. *Limnol Oceanogr* 47:683–697
- ✦ Chong VC, Low CB, Ichikawa T (2001) Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Mar Biol* 138:77–86
- ✦ Cifuentes LA, Coffin RB, Solorzano L, Cardenas W, Espinoza J, Twilley RR (1996) Isotopic and elemental variations of carbon and nitrogen in a mangrove estuary. *Estuar Coast Shelf Sci* 43:781–800
- ✦ Correa-Herrera T, Jiménez-Segura LF, Barletta M (2016) Fish species from a micro-tidal delta in the Caribbean Sea. *J Fish Biol* 89:863–875
- ✦ Demopoulos AWJ, Fry B, Smith CR (2007) Food web structure in exotic and native mangroves: a Hawaii–Puerto Rico comparison. *Oecologia* 153:675–686
- ✦ Dittel AI, Epifanio CE, Cifuentes LA, Kirchman DL (1997) Carbon and nitrogen sources for shrimp postlarvae fed natural diets from a tropical mangrove system. *Estuar Coast Shelf Sci* 45:629–637
- ✦ Duarte CM, Delgado-Huertas A, Anton A, Carrillo-de-Albornoz P and others (2018) Stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{18}\text{O}$ ,  $\delta\text{D}$ ) composition and nutrient concentration of Red Sea primary producers. *Front Mar Sci* 5:298
- ✦ France R (1998) Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna Joyuda, Puerto Rico, using dual stable isotopes. *J Trop Ecol* 14:413–425
- ✦ Froese R, Pauly D (eds) (2007) *FishBase*. [www.fishbase.org](http://www.fishbase.org) (accessed 27 Jan 2018)
- ✦ Fry B, Ewel KC (2003) Using stable isotopes in mangrove fisheries research—a review and outlook. *Isotopes Environ Health Stud* 39:191–196
- ✦ Garcia AF, Santos ML, Garcia AM, Vieira JP (2018) Changes in food web structure of fish assemblages along a river-to-ocean transect of a coastal subtropical system. *Mar Freshw Res* 70:402–416
- ✦ Abrantes KG, Sheaves M (2009) Food web structure in a near-pristine mangrove area of the Australian wet tropics. *Estuar Coast Shelf Sci* 82:597–607
- ✦ Abrantes KG, Barnett A, Baker R, Sheaves M (2015a) Habitat-specific food webs and trophic interactions supporting coastal-dependent fishery species: an Australian case study. *Rev Fish Biol Fish* 25:337–363
- ✦ Abrantes KG, Johnston R, Connolly RM, Sheaves M (2015b) Importance of mangrove carbon for aquatic food webs in wet–dry tropical estuaries. *Estuaries Coasts* 38:383–399
- Arango-Sánchez LB, Correa-Herrera T, Correa-Rendón JD (2019) Diversidad de peces en hábitats estuarinos delta del río Atrato, golfo de Urabá. *Bol Cient Mus His Nat* 23: 191–207
- Arenas-Urbe S, Leal-Flórez J, Sandoval A, Pérez-Villa AF, Hernández-Morales AF (2019) Feeding habits of the

- García CB, Contreras CC (2011) Trophic levels of fish species of commercial importance in the Colombian Caribbean. *Rev Biol Trop* 59:1195–1203
- García-Valencia C (2007) Atlas del golfo de Urabá: una mirada al Caribe de Antioquia y Chocó. Serie de Publicaciones Especiales de INVEMAR N°12. Instituto de Investigaciones Marinas y Costeras -Invemar- y Gobernación de Antioquia, Santa Marta
- Gascuel D, Morissette L, Palmomares MLD, Christensen V (2008) Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. *Ecol Modell* 217:33–47
- Giarrizzo T, Schwamborn R, Saint-Paul U (2011) Utilization of carbon sources in a northern Brazilian mangrove ecosystem. *Estuar Coast Shelf Sci* 95:447–457
- Granek EF, Compton JE, Phillips DL (2009) Mangrove-exported nutrient incorporation by sessile coral reef invertebrates. *Ecosystems* 12:462–472
- Guest MA, Connolly RM (2004) Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals. *Aquat Ecol* 38:599–609
- Guest MA, Connolly RM, Loneragan NR (2004) Carbon movement and assimilation by invertebrates in estuarine habitat at a scale of metres. *Mar Ecol Prog Ser* 278:27–34
- Harada Y, Lee SY (2016) Foraging behavior of the mangrove sesamid crab *Neosarmatium trispinosum* enhances food intake and nutrient retention in a low-quality food environment. *Estuar Coast Shelf Sci* 174:41–48
- Hernández-Morales AF, Leal-Flórez J, Sandoval-Londoño LA, Arenas-Urbe S, Pérez-Villa AF (2018) Hábitos alimenticios del barbudo de pluma *Bagre marinus* (Mitchill, 1815) (Siluriformes: Ariidae) en el golfo de Urabá, Caribe colombiano. *Actual Biol* 40:123–138
- Hsieh HL, Chen CP, Chen YG, Yang HH (2002) Diversity of benthic organic matter flows through polychaetes and crabs in a mangrove estuary:  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  signals. *Mar Ecol Prog Ser* 227:145–155
- Hurtado-Santamaria K, Quan-Young L (2016) Algas y cianobacterias asociadas a las raíces de *Rhizophora mangle* en el Golfo de Urabá. In: Blanco-Libreros JF, Londoño-Mesa M (eds) Expedición Caribe sur: Antioquia y Chocó costeros. Secretaría Ejecutiva de la Comisión Colombiana del Océano, Bogotá
- Igulu M, Nagelkerken I, van der Velde G, Mgaya Y (2013) Mangrove fish production is largely fueled by external food sources: a stable isotope analysis of fishes at the individual, species, and community levels from across the globe. *Ecosystems* 16:1336–1352
- Kneib RT, Weeks CA (1990) Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. *Estuaries* 13:462–468
- Kristensen E, Lee SY, Mangion P, Quintana CO, Valdemarsen T (2017) Trophic discrimination of stable isotopes and potential food source partitioning by leaf-eating crabs in mangrove environments. *Limnol Oceanogr* 62:2097–2112
- Layman CA (2007) What can stable isotope ratios reveal about mangroves as fish habitat? *Bull Mar Sci* 80:513–527
- Layman CA, Araújo MS, Boucek R, Hammerschlag-Peyer CM and others (2012) Applying stable isotopes to examine food web structure: an overview of analytical tools. *Biol Rev Camb Philos Soc* 87:545–562
- Lee SY (2000) Carbon dynamics of Deep Bay, eastern Pearl River estuary, China. II: trophic relationship based on carbon- and nitrogen-stable isotopes. *Mar Ecol Prog Ser* 205:1–10
- Lee SY (2008) Mangrove macrobenthos: assemblages, services, and linkages. *J Sea Res* 59:16–29
- Link JS (2002) Ecological considerations in fisheries management: When does it matter? *Fisheries* (Bethesda, Md) 27:10–17
- Loneragan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Mar Biol* 130:289–300
- LOPEGU (Lineamientos prioritarios para la formulación de un ordenamiento pesquero del golfo de Urabá) (2017) Technical report by Gobernación de Antioquia y Universidad de Antioquia, Medellín
- Lovelock CE, Simpson LT, Duckett LJ, Feller IC (2015) Carbon budgets for Caribbean mangrove forests of varying structure and with phosphorus enrichment. *Forests* 6:3528–3546
- Mancera JE (2003) The contribution of mangrove outwelling to coastal food webs as a function of environmental settings. PhD dissertation, University of Louisiana, Lafayette, LA
- McCutchan JH Jr, Lewis WM Jr, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. *Oikos* 102:378–390
- Medina-Contreras D, Kintz JC, González AS, Mancera E (2018) Food web structure and trophic relations in a riverine mangrove system of the Tropical Eastern Pacific, central coast of Colombia. *Estuaries Coasts* 41:1511–1521
- Medina-Contreras D, Arenas-Gonzalez F, Cantera-Kintz J, Sánchez-González A, Giraldo A (2020) Food web structure and isotopic niche in a fringe macro-tidal mangrove system, Tropical Eastern Pacific. *Hydrobiologia* 847:3185–3199
- Montoya LJ, Toro-Botero FM, Gomez-Giraldo A (2017) Study of Atrato river plume in a tropical estuary: effects of the wind and tidal regime on the Gulf of Urabá, Colombia. *Dyna* (Bilbao) 84:367–375
- Muro-Torres VM, Soto-Jiménez MF, Green L, Quintero J and Amezcua F (2019) Food web structure of a subtropical coastal lagoon. *Aquat Ecol* 53:407–430
- Nagelkerken I, van der Velde G (2004a) Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Mar Ecol Prog Ser* 274:153–159
- Nagelkerken I, van der Velde G (2004b) Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Mar Ecol Prog Ser* 274:143–151
- Nyunja J, Ntiba M, Onyari J, Mavuti K, Soetaert K, Bouillon S (2009) Carbon sources supporting a diverse fish community in a tropical coastal ecosystem (Gazi Bay, Kenya). *Estuar Coast Shelf Sci* 83:333–341
- Odum WE, Heald E (1975) The detritus-based food web of an estuarine mangrove community. In: Cronin LE (ed) *Estuarine research*. Academic Press, New York, NY, p 265–286
- Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374:255–257
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. *Science* 279:860–863
- Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impacts on marine ecosystems. *ICES J Mar Sci* 57:697–706

- ✦ Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- ✦ Peterson BJ, Howarth RW, Garritt RH (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361–1363
- ✦ Phillips DL, Inger R, Bearhop S, Jackson AL and others (2014) Best practices for use of stable isotope mixing models in food-web studies. *Can J Zool* 92:823–835
- ✦ Pimm SL, Lawton JH (1977) Number of trophic levels in ecological communities. *Nature* 268:329–331
- ✦ Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- ✦ Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- ✦ Qu P, Zhang Z, Pang M, Li Z and others (2019) Stable isotope analysis of food sources sustaining the subtidal food web of the Yellow River Estuary. *Ecol Indic* 101:303–312
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Riascos JM, Blanco-Libreros JF (2019) Pervasively high mangrove productivity in a major tropical delta throughout an ENSO cycle (Southern Caribbean, Colombia). *Estuar Coast Shelf Sci* 227:106301
- ✦ Rodelli MR, Gearing JN, Gearing PJ, Marshall N, Sasekumar A (1984) Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia* 61:326–333
- Sandoval LA, Leal-Flórez J, Blanco-Libreros JF, Mancera-Pineda JE, Delgado-Huertas A, Polo-Silva CJ (2020) Stable-isotope analysis reveals sources of organic matter and ontogenic feeding shifts of a mangrove-dependent predator species, New Granada sea catfish, *Ariopsis canteri*. *J Fish Biol* 97:499–507
- Sandoval Londoño LA (2012) Efecto de la sedimentación sobre la ictiofauna en el delta del río Turbo (Golfo de Urabá, Caribe colombiano). MSc dissertation, Universidad de Antioquia, Medellín
- Sandoval-Londoño LA, Leal-Flórez J, Blanco-Libreros JF, Taborda-Marín A (2015) Hábitos alimenticios y aspectos del uso del hábitat por el chivo cabezón *Ariopsis* sp. (aff. *assimilis*) (Siluriformes: Ariidae), en una laguna costera neotropical (Ecorregión Darién, Colombia). *Actual Biol* 37:295–306
- Sandoval Londoño LA, Leal-Flórez J, Blanco-Libreros JF (2020) Linking mangroves and fish catch: a correlational study in the southern Caribbean Sea (Colombia). *Bull Mar Sci* 96:415–430
- ✦ Santos EP, Condini MV, Santos ACA, Alvarez HM, de Moraes LE, Garcia AFS, Garcia AM (2020) Spatio-temporal changes in basal food source assimilation by fish assemblages in a large tropical bay in the SW Atlantic Ocean. *Estuaries Coasts* 43:894–908
- ✦ Sepúlveda-Lozada A, Saint-Paul U, Mendoza-Carranza M, Wolff M, Yáñez-Arancibia A (2017) Flood pulse induced changes in isotopic niche and resource utilization of consumers in a Mexican floodplain system. *Aquat Sci* 79:597–616
- ✦ Stergiou KI, Moutopoulos DK, Casal HJ, Erzini K (2007) Trophic signatures of small-scale fishing gears: implications for conservation and management. *Mar Ecol Prog Ser* 333:117–128
- Stock BC, Semmens BX (2016) MixSIAR GUI user manual, version 3.1. Scripps Institution of Oceanography, UC San Diego, CA
- ✦ Stuthmann LE, Castellanos-Galindo GA (2020) Trophic position and isotopic niche of mangrove fish assemblages at both sides of the Isthmus of Panama. *Bull Mar Sci* 96:449–468
- ✦ Vaslet A, Phillips DL, France C, Feller IC, Baldwin CC (2015) Trophic behavior of juvenile reef fishes inhabiting interlinked mangrove–seagrass habitats in offshore mangrove islets. *J Fish Biol* 87:256–273
- ✦ Vizzini S, Mazzola A (2003) Seasonal variations in the stable carbon and nitrogen isotope ratios ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) of primary producers and consumers in a western Mediterranean coastal lagoon. *Mar Biol* 142:1009–1018
- ✦ Werry J, Lee SY (2005) Grapsid crabs mediate link between mangrove litter production and estuarine planktonic food chains. *Mar Ecol Prog Ser* 293:165–176
- ✦ Zagars M, Ikejima K, Kasai A, Arai N, Tongnunui P (2013) Trophic characteristics of a mangrove fish community in Southwest Thailand: important mangrove contribution and intraspecies feeding variability. *Estuar Coast Shelf Sci* 119:145–152

Editorial responsibility: John Griffin,  
Swansea, UK

Reviewed by: L. Pelage, L. Beesley and 1 anonymous referee

Submitted: April 12, 2021

Accepted: September 20, 2021

Proofs received from author(s): November 26, 2021