The contribution of mangrove organic matter to fish assemblages and estuarine food-webs in the Southwestern Caribbean Sea (Colombia)

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Abstract

Mangroves provide several valuable ecosystem services, such as fish production, coastal protection, carbon storage, and sediment trapping. Literature on mangrove production highlights “outwelling" as a primary ecological function of mangroves in the coastal zone, described as the export of leaflitter and other components from the canopy that supports much of the secondary production of estuaries and nearshore waters. This dissertation provides a significant advance for understanding the contribution of mangrove primary productivity in the Caribbean, using as study models the Urabá Gulf and the Atrato River Delta (Southwestern Caribbean Sea), where mangroves are not directly connected to other highly productive coastal habitats, such as seagrasses and coral reefs.

The overall objectives were: 1) to examine the importance of mangroves for fishing in the Urabá Gulf and its vicinity through statistical correlations, 2) to determine the potential contribution of mangroves and other sources of organic matter for fish consumers at the Atrato River Delta estuary, using stable isotopic tracers and models, and 3) to determine the capacity of mangrove crabs to assimilate low-quality mangrove C through laboratory experiments. This dissertation is organized in six chapters: a general introduction, four chapters organized in the form of scientific manuscripts, and a last chapter accounting the general conclusions.

Chapter 1 shows the approaches and methods used to analyze links between mangroves and coastal food webs, likewise, the list of manuscripts and contributions of authors. Chapter 2 (*manuscript I - published*) is the first study of a mangrove-fishery relationship in the southern Caribbean and northern South America. The objective of Chapter 2 was to investigate the linkages between experimental fishing and several environmental variables. CPUE (catch per unit of effort), species richness, mangrove descriptors (area, perimeter, and above-ground carbon), water quality (salinity, total dissolved solids), and water column productivity parameters (chlorophyll a, seston, and zooplankton bio-volume) were analyzed. Mangrove area and zooplankton bio-volume were the main factors influencing the species richness of fish, while mangrove area was positively correlated with catches for three of the most common fish species in the local artisanal fishery.

In Chapter 3 (*manuscript II - published*), the trophic ecology of New Granada sea catfish, *Ariopsis canteri*, and their linkage to mangroves was investigated. Results suggested that mangroves are a nursery and feeding ground habitat for this species and this is mainly due to the substrate/habitat that supports sources in the food webs in which this species is imbedded.

In Chapter 4 (*manuscript III*), carbon and nitrogen isotopic composition (δ^{13}C and δ^{15}N) were used to identify the main food sources and describe the main trophic pathways in the Atrato River Delta estuary (ARD). The potential trophic pathways for phytoplankton, mangrove, microphytobenthos, macroalgae, and macrophytes sources were displayed. Mangroves partially supported finfish fisheries in the ARD. Mangroves could be a major food source for some consumers in areas not directly connected to other highly productive coastal habitats. Moreover, herbivorous crabs (sesarmids) and planktivorous fish (engraulids) were identified as key vectors of energy and nutrients from mangrove litter to higher trophic levels.

In Chapter 5 (*manuscript IV*), a series of experiments and isotopic mixing models were carried out to investigate the feeding habit of the tree-climbing crab *Aratus pisonii*. Fresh mangrove leaf litter of *Rhizophora mangle* dominated the diet of *A. pisonii* from ARD. Likewise, their capacity to assimilate the low-quality mangrove C would mediate the transfer of mangrove primary production to nearshore consumers.

The work in this thesis represents a significant input to the understanding of the contribution of mangrove productivity to food webs and fisheries in tropical estuarine systems of the Caribbean Sea. Through the different spatial scales of analysis, it is robustly demonstrated that mangroves support estuarine consumers, either because of their trophic contribution or the substrate/habitat they offer. Thus, the results highlight the usefulness of estuarine mangroves in the Caribbean as study models for the outwelling hypothesis. Finally, this thesis work may be useful for designing strategies that jointly address mangrove conservation and management of small-scale fisheries associated with mangroves. In this way, this dissertation evidenced that mangrove conservation strategies such as marine protected areas and co-management would benefit coastal communities through the fisheries provision service in the Urabá Gulf.

Resumen

Los manglares brindan valiosos servicios ecosistémicos, como producción de peces, protección costera, almacenamiento de carbono y captura de sedimentos. La literatura sobre la producción de manglares destaca el "*outwelling*" como una función ecológica primaria de los manglares en la zona costera, descrita como la exportación de hojarasca y otros componentes del dosel que sustenta gran parte de la producción secundaria de estuarios y aguas cercanas a la costa. Esta disertación proporciona un importante avance para comprender la contribución de la productividad primaria de los manglares en el Caribe, utilizando como modelos de estudio el Golfo de Urabá y el delta del río Atrato (Mar Caribe Suroccidental), donde los manglares no están conectados directamente a otros hábitats costeros altamente productivos, como pastos marinos y arrecifes de coral.

Los objetivos generales de esta tesis fueron: 1) examinar la importancia de los manglares para la pesca en el golfo de Urabá y sus alrededores a través de correlaciones estadísticas, 2) determinar la contribución potencial de los manglares y otras fuentes de materia orgánica para los consumidores en el estuario del delta del río Atrato, utilizando trazadores y modelos isotópicos, y 3) determinar la capacidad de los cangrejos de manglar para asimilar C de manglar de baja calidad mediante experimentos de laboratorio. Esta tesis está organizada en seis capítulos: una introducción general, cuatro capítulos organizados en forma de manuscritos científicos y un último capítulo con las conclusiones generales.

El Capítulo 1 muestra los enfoques y métodos utilizados para analizar los vínculos entre los manglares y las redes tróficas costeras, así como la lista de manuscritos y contribuciones de los autores. El Capítulo 2 (*manuscrito I - publicado*) es el primer estudio de una relación manglar-pesquería en el sur del Caribe y norte de Sudamérica. El objetivo del Capítulo 2 fue investigar los vínculos entre la pesca experimental y varias variables ambientales. CPUE (captura por unidad de esfuerzo), riqueza de especies, atributos del manglar (área, perímetro y carbono en el suelo), calidad del agua (salinidad, sólidos disueltos totales) y parámetros de productividad de la columna de agua (clorofila a, seston y biovolumen del zooplancton) fueron analizados. El área de los manglares y el biovolumen de zooplancton fueron los principales factores que influyeron en la riqueza de especies de peces. Mientras que el área de los

manglares se correlacionó positivamente con las capturas de tres de las especies de peces más comunes en la pesquería artesanal local.

En el Capítulo 3 (*manuscrito II - publicado*), se investigó la ecología trófica del bagre marino, *Ariopsis canteri*, y su vínculo con los manglares. Los resultados sugirieron que los manglares son un hábitat de cría y alimentación para esta especie. Ademas, que los manglares mantienen a esta especie debido principalmente al sustrato/hábitat que sustenta las fuentes en las redes tróficas en las que está inmersa.

En el capítulo 4 (*manuscrito III*), se utilizó la composición isotópica de carbono y nitrógeno (δ^{15}N y δ^{13}C) para identificar las principales fuentes y describir las principales vías tróficas en el estuario del delta del río Atrato (ARD). Se evidenciaron las vías potenciales para las fuentes de fitoplancton, manglares, microfitobentos, macroalgas y macrófitas. Se evidenció también que los manglares sustentan parcialmente las pesquerías de peces en el ARD. Los manglares podrían ser una importante fuente de alimento para algunos consumidores en áreas que no están conectadas directamente con otros hábitats costeros altamente productivos. Además, los cangrejos herbívoros (sesármidos) y los peces planctívoros (engraúlidos) fueron transferidores de carbono esenciales de la hojarasca de los manglares a niveles tróficos superiores.

En el Capítulo 5 (*manuscrito IV*), se llevaron a cabo una serie de experimentos y modelos de mezcla isotópica para investigar los hábitos alimenticios del cangrejo *Aratus pisonii*. La hojarasca fresca del mangle *Rhizophora mangle* dominó la dieta de *A. pisonii* del ARD. Asimismo, se evidenció que su capacidad para asimilar el C de manglar de baja calidad puede mediar en la transferencia de la producción primaria del manglar a los consumidores cercanos a la costa.

Los resultados de esta tesis representan un aporte significativo para comprender la contribución de la productividad de los manglares en las redes tróficas y la pesca en el Golfo de Urabá (sur del Mar Caribe). A través de las diferentes escalas espaciales de análisis, se demuestra de manera contundente que los manglares sustentan a consumidores estuarinos, ya sea por su contribución trófica o por el sustrato/hábitat que ofrecen. Se destaca así la utilidad de los manglares de estuarios en el Caribe como modelos de estudio para la hipótesis de “*outwelling*”. Finalmente, este trabajo de tesis puede ser útil para diseñar estrategias que aborden conjuntamente la conservación de manglares y el manejo de la pesca artesanal asociada. De esta manera, esta tesis evidencia que estrategias de conservación de manglares como áreas marinas protegidas y co-manejo beneficiarían a las comunidades costeras en el Golfo de Urabá a través del servicio de provisión de recursos pesqueros.

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Chapter 1. General introduction

Rionegro cove (J.F. Blanco)

Bocas del Atrato (L.A. Sandoval)

Bocas del Atrato (L.A. Sandoval)

Ariopsis canteri (L..A. Sandoval)

1.1. General context and outline of this thesis

Mangroves are the dominant habitats of tropical and subtropical shorelines of the World (Alongi 2014, Friess et al. 2020). They provide many valuable ecosystem services, such as fish production, coastal protection, carbon storage, and sediment trapping (Lee et al. 2014, Barbier 2016). The literature on mangrove production specially highlights "the organic matter outwelling" as a primary ecological function in the coastal zone, described as the export of leaflitter and other components from the canopy that supports much of the secondary production of estuaries and nearshore waters (Odum and Heald 1975).

The link between mangroves and coastal food webs have been analyzed using four main approaches (Twilley 1995, Mancera 2003): 1) flux studies and ecosystem mass balance, 2) surveys of habitat utilization and gut content analyses, 3) statistical correlations between mangrove area and fish or shrimp catches, and 4) abundance of natural isotopes on consumer tissues ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$). Stable-isotope analysis (SIA) in mangrove systems has increasingly been used to reconstruct consumer diets and organic matter cycling over the past two decades (Bouillon et al. 2008 Layman et al. 2012). It has clear advantages over more traditional dietary methods because it incorporates spatial and temporal aspects that stomach-content analysis (SCA) cannot realistically cover (Bouillon et al. 2011). Likewise, statistical correlations do not explain the causal relationship between mangroves and fisheries (Carrasquilla-Henao et al. 2013), and in flux studies and ecosystem mass balance remains a large degree of uncertainty about the overall fate of mangrove production (Bouillon et al. 2008). On the other hand, as another approach fatty acids as dietary biomarkers have been increasingly applied (Guo et al. 2020).

This dissertation provides a significant advance for understanding the contribution of mangrove primary productivity in the Caribbean, using as study models the Urabá Gulf and the Atrato River Delta (Southwestern Caribbean Sea), where mangroves are not directly connected to other highly productive coastal habitats, such as seagrasses and coral reefs. I used three of the above-mentioned approaches for assessing the linkage between mangrove primary productivity and fish assemblages and food webs, in the following way: 1) statistical correlations between mangrove area and fish catches, using various environmental variables (mangrove descriptors, water quality, and water column productivity parameters); 2 and 3) stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$) in combination with gut content analyses, to determine the potential contribution of food sources to the biomass of selected consumers. In addition, I used different methods to analyze databases, observations and experiments, thus developing further skills: Geographic Information System procedures to obtain and analyze mangrove descriptors, the latest mixing models (Bayesian) for stable isotopes analysis (SIA) to estimate sources contribution, and microcosmos set-up techniques aimed at determining assimilation of mangrove leaf elements by crabs in controlled feeding trials and further stable isotope analyses.

Using a correlational approach, various studies report positive linkages between mangrove extent and catch in nearby fisheries, suggesting that the former translates into the secondary production of fish and ultimately into commercial resource capture (Manson et al. 2005). However, most studies do not explain the causal (mechanistic) relationship between mangroves and fisheries (Blaber 2007, Lee et al. 2014, Carrasquilla-Henao and Juanes 2016). Moreover, most studies on the mangrove-fishery linkage have been performed in the Indo-West Pacific region and fewer in the Atlantic-Caribbean and Eastern Pacific regions (Carrasquilla-Henano and Juanes 2016). For the latter regions, most mangrove-fishery databases originate from Mexico (Yáñez-Arancibia et al. 1985, Aburto-Oropeza et al. 2008 Carrasquilla-Henao et al. 2013), while a majority of the field studies linking fishes with mangroves, seagrasses, and coral reefs have been conducted in the Caribbean islands (Nagelkerken and Van Der Velde 2004, Mumby et al. 2004, Serafy et al. 2015), thus biasing the conclusion to specific mangrove and coastline typologies. Despite having a wide range of mangrove settings along the Caribbean coast of Colombia, no such studies have been carried out there (Carrasquilla-Henao et al. 2013).

The use of stable isotopes in trophic ecology allows the evaluation of the origin and cycling of organic and inorganic matter, thus offering advantages for the study of estuarine food webs (Peterson and Fry 1987, Bouillon et al. 2011, Duarte et al. 2018). Stable-isotope analysis (SIA) has clear advantages over more traditional dietary methods because it incorporates spatial and temporal aspects that stomach content analysis (SCA) cannot realistically cover. However, the pitfalls of stable isotope techniques in complex systems, such as estuaries, are evident. With often a wide range of possible sources of carbon, nitrogen, or sulfur (the three main elements typically considered), overlapping signatures in the end members, and high spatial and temporal variability in source stable isotope signatures (Bouillon et al. 2011).

Each stable isotope analytical approach has distinct weaknesses. E.g., estimates of trophic position of individuals or species based on δ^{15}N lack of empirical estimates of discrimination in δ^{15}N with trophic transfers and it must have accurate isotopic baseline. To estimate sources contribution with Bayesian mixing models high data quality is required; models still remain sensitive to quality of input values, e.g. to trophic discrimination factors (TDFs) and to variability in source pool values (Layman et al 2012). TDFs are the difference in isotopic composition between an animal's tissue and its diet, which are a result of a plethora of physiological processes associated with consumption, excretion and assimilation (Caut et al. 2009).

Estuarine food webs are complex given the numerous potential inputs of matter, elements, and energy from upstream (riverine), downstream (oceanic), within estuary (e.g., seagrass and microalgae), and lateral (e.g., mangroves and salt marsh) sources (Bouillon et al. 2011). The hydrogeomorphologic variability and dynamic features of these systems reduce the ability to apply generalizations on structure and dynamics of food webs determined for well-studied coastal systems to lesser-studied ones (Hoeinghaus et al. 2011, Santos et al. 2020). Some studies on trophic networks in mangrove systems have found that mangrove carbon is essential for benthic and pelagic consumers (e.g., Giarrizzo et al. 2011, Lovelock et al. 2015, Abrantes et al. 2015, Medina-Contreras et al. 2020). Conversely, other studies have found that mangroves outwelling is exported offshore but its incorporation into coastal food webs is minimal (e.g., Lee 2000, Bouillon et al. 2002, Vaslet et al. 2015, Santos et al. 2020).

In the Caribbean, studies have focused on estuaries in the vicinity of seagrasses and/or coral reefs and, concluded that mangrove carbon is not an important resource (Nagelkerken and Van Der Velde 2004b, Vaslet et al. 2012, Igulu et al. 2013, Vaslet et al. 2015). However, Mancera (2003), through studies in the Ciénaga Grande de Santa Marta in the Colombian Caribbean, a system not directly connected with other highly productive coastal habitats, proposed that mangroves can be important sources in estuarine food webs depending on internal geomorphology, salinity and plankton productivity.

In addition, stable isotope analyses have been instrumental to understand that brachyuran crabs species from the Indo-West-Pacific region (families Grapsidae and Sesarmidae) may assimilate elements from mangrove leaves, their major food source (Steinke et al. 1993, Thongtham and Kristensen 2005, Kristensen et al. 2010, Bui and Lee 2014, Mackenzie et al. 2020), as they are responsible for removing more than 50% of annual litter production (Robertson 1986, Kristensen et al. 2010, Harada and Lee 2016). In this way, crabs play a significant role in detritus-based food chains and energy flow pathways in most mangrove environments, affecting nutrient retention, litter decomposition, and the offshore export of mangrove production (Robertson 1986, Lee 1995). Aside from their digestion and production of feces, crabs also can shred mangrove leaf litter into smaller particles (200 µm in size), that are later assimilated by zooplankton and incorporated into the pelagic trophic network (Werry and Lee 2005).

Aratus pisonii (Sesarmidae) is one of the most abundant crabs in Neotropical mangroves habitats (Chace and Hobbs 1969), where it characteristically forages on fresh leaf tissue in the canopy rather than on leaf litter on the forest floor. This species is the primary herbivore of the red mangrove *Rhizophora mangle*, accounting for over 40% of total leaf damage in monotypic red mangrove stands (Erickson et al. 2003, Feller et al. 2013). However, it is difficult to assess how much mangrove-derived C and N they assimilate as no trophic discrimination values have been estimated for $\delta^{13}C$ and $\delta^{15}N$ between mangrove leaves and *A. pisonii*. Likewise, there are still many unknown aspects of the trophic ecology of *A. pisonii* in the southern Caribbean, such their capacity to convert low-quality mangrove C into biomass and the possibility of mediating the transfer of mangrove primary production to nearshore consumers.

The Urabá Gulf is the largest estuary along the Southern Caribbean Sea: it is located in the Southwestern coast of Colombia, close to the border with Panama. The Atrato River discharges into the western coast of the Gulf, and it is the second-largest input of freshwater in the Colombian Caribbean, after the Magdalena River, in the Southern Caribbean (Garcia 2007). Extensive mangrove forests (totaling approximately 5700 ha) are found along the different deltas and river mouths. Mangroves are not directly connected with other highly productive coastal habitats, only small coral reef patches are found to the northwest of the

Urabá Gulf, in the vicinity of Panama (Díaz et al. 2000). The red mangrove *Rhizophora mangle* is the dominant tree species (> 80% by area), followed by the white mangrove *Laguncularia racemosa* and black mangrove *Avicennia germinans*. The largest mangrove areas are located on the Atrato River Delta, where most stands are monodominant (Blanco-Libreros 2016).

The estuary of the Atrato River Delta is considered as an essential aquatic habitat for biota and artisanal fisheries contributing to both local commerce and subsistence (Correa-Herrera et al. 2016). However, information concerning the contribution of these mangroves to local fisheries is limited and anecdotical. Moreover, information about estuarine fish and invertebrate community ecology is scarce (although species inventories are available), and there is not a fishery management plan for the Gulf. Finally, mangroves are threatened in some areas of the Gulf because *R. mangle* is predominantly exploited for poles (Blanco et al. 2012). In the Atrato River Delta, illegal logging is mostly restricted to the mangrove fringes. Therefore, given their potential importance, it is important to understand the importance of mangrove ecosystem function for ecosystem services such as growth habitat and nursery for commercially-important fish species in order to provide a scientific basis for marine conservation efforts and ecosystem-based fishery management.

The objectives of this thesis were: 1) to examine the importance of mangroves for fishing in the Urabá Gulf and its vicinity through statistical correlations, 2) to determine the potential contribution of mangroves and other sources of organic matter for fish consumers at the Atrato River Delta estuary, using stable isotopic tracers and models, and 3) to determine the capacity of mangrove crabs to assimilate low-quality mangrove C through of laboratory experiments. This dissertation is organized in six chapters as follows: a general introduction (this chapter), four chapters organized in the form of scientific manuscripts (Chapter 2 related to objective 1, Chapter 3 and 4 related to objective 2, and Chapter 5 related to objective 3), and a last chapter providing a synthesis and general conclusions.

Chapter 2 (*manuscript I – published: Sandoval et al. 2020a*) addressed the following research question: Do mangrove areas in the Urabá Gulf, and its vicinity have a direct relationship with the production of commercial fish assemblages? I hypothesized that mangrove descriptors (area, perimeter, and above-ground carbon) are positively correlated to the catch per unit of effort (CPUE: total and species-specific) and richness of fishes (total number of species) in the Colombian Southern Caribbean Sea. The objective of Chapter 2 was to investigate the linkages between experimental fishing and several environmental variables. In this way, CPUE (catch per unit of effort), species richness, mangrove descriptors (area, perimeter, and above-ground carbon), water quality (salinity, total dissolved solids), and water column productivity parameters (chlorophyll a, seston, and zooplankton bio-volume) were measured. The main result was that mangrove area and zooplankton bio-volume were the main factors influencing the species richness of fish assemblages. Mangrove area was positively correlated with catches for three of the most common fish species in the local artisanal fishery (*Ariopsis canteri*, *Mugil incilis*, and *Sciades proops*). Likewise, it suggested that the causal links between mangrove habitat and fishery production may be explained through the trophic contribution of mangroves in areas not directly connected to other highly productive coastal habitats (i.e., seagrasses and coral reefs).

Chapters 3 and 4 addressed the following research question: What is the importance of mangrove carbon as a primary source for fish from small-scale fisheries? I hypothesized that mangroves could be a major food source sustaining some estuarine consumers at the Atrato River Delta estuary. For this, Carbon and Nitrogen stable isotopes ($\delta^{15}N$ and $\delta^{13}C$), as well as Bayesian mixing models were used.

In Chapter 3 (*manuscript II – published: Sandoval et al. 2020b*), the trophic ecology of the New Granada sea catfish, *Ariopsis canteri*, and their linkage to mangroves was investigated. This fish is an endemic species of the Colombian Caribbean, and listed as endangered (national category EN A2d; B1b(iii)c(ii)) due to its degree of endemism and over-fishing pressure (Acero et al. 2017). It, however, is one of the most common species in artisanal fisheries in the region (LOPEGU 2017). The specific objectives of this Chapter were: a) to assess the ontogenic feeding shifts of *A. canteri*, and b) to assess the importance of various sources in supporting *A. canteri*. For this, carbon and nitrogen stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) were used, as well as Bayesian mixing models. The results confirming ontogenic feeding shifts allowing a decrease in intraspecific competition between small and large individuals. Likewise, results suggested that mangroves are a nursery and feeding ground habitat for this species, and mangroves supporting *A. canteri* are due mainly to the substrate/habitat that supports sources in the food webs in which this species is imbedded.

In Chapter 4 (*manuscript III*), nitrogen and carbon stable isotopes (δ^{15}N and δ^{13}C) were used to characterize the potential food sources and to identify the main trophic pathways within an estuarine embayment in the Atrato River Delta (ARD). The objectives of this chapter were: a) to estimate trophic position, and b) the potential contribution of food sources for epibenthic and fish consumers according to trophic guilds, using stable isotopic tracers and Bayesian mixing models, and c) to discuss the direct and indirect links between mangroves and artisanal fisheries. Results showed a food web with a maximum length of 4.6 trophic levels. Potential energy pathways were identified from mangrove, microphytobenthos, macroalgae, phytoplankton, and macrophytes. Mangroves contributed significantly to the diet of two of common fish species in the local artisanal fishery in ARD (*Centropomus pectinatus* and *Centropomus undicimalis*), and serve as substrate/habitat that supports sources as macroalgae and benthic algae supporting two other commercial fish species (*Ariopsis canteri* and *Mugil incilis*). Moreover, herbivorous crabs (sesarmids) and planktivorous fish (engraulids) are potential key carbon vectors from the mangrove resource base to higher trophic levels. It showed that fringing mangroves seem to be a major food source for consumers in areas not interlinked to other highly productive coastal habitats (i.e., seagrasses and coral reefs).

Chapter 5 (*manuscript IV*) addressed the following research question: Can predominant mangrove crabs, as mangrove leaf assimilators, be considered an essential link in the carbon flux into the pelagic environment? I hypothesized that the mangrove tree-climbing crab *Aratus pisonii* (Sesarmidae) has the ability to effectively digest and assimilate a low-quality mangrove leaf litter diet. There, a series of experiments and isotopic mixing models were carried out to investigate the feeding habits of *A. pisonii.* The specific objectives of this Chapter were: a) determine *R. mangle* leaf consumption rates and leaf preference (different stages of decay); b) empirically determine trophic discrimination values for δ^{13}C and δ^{15}N between *Rhizophora mangle* leaves and the crab, *A. pisonii*; and c) estimate and compare diet compositions through Bayesian stable isotope mixing models (MixSIAR) using commonly assumed values vs. empirically determined trophic discrimination factors (TDFs). The information in Chapter 5 identified that fresh mangrove leaf litter of *R. mangle* dominate the diet of *A. pisonii* from ARD. Mean (± SD) TDF estimates were 5.4 ± 0.9‰ for $\delta^{13}C$ and 3.9 ± 0.5‰ for $\delta^{15}N$, close to those suggested for other sesarmid crabs ($\delta^{13}C$: 4.9 ± 0.1‰ and $\delta^{15}N$: 3.5 ± 0.1‰). The results provided new insights into the importance of *A. pisonii* as a key herbivore converting low-quality mangrove tissues into nutritious secondary production (biomass), potentially linking primary producers with intermediate and top predators (both aquatic and terrestrial).

Finally, the main findings of the research are synthesized in Chapter 6 in the context of an understanding of the importance of mangrove production and function in the Urabá Gulf (southern Caribbean Sea) and the contribution of this study to the general understanding of mangrove habitats.

1.2. List of manuscripts and contribution of authors

Manuscript I (Published)

Sandoval L. A., Leal-Flórez J., and Blanco-Libreros J. F. 2020, Linking mangroves and fish catch: a correlational study in the southern Caribbean Sea (Colombia). *Bulletin of Marine Science*, 96(3): 415-430. https://doi.org/10.5343/bms.2019.0022

I developed the concept and designed the study with support from LFJ and BLJF. LFJ and BLJF obtained the funding. LFJ provided raw data from experimental fishing. I participated in experimental fishing campaigns. BLJF provided raw data from mangrove areas. I performed the analysis and wrote the manuscript. All authors discussed the results and commented on the various versions of the manuscript.

Manuscript II (Published)

Sandoval L. A., Leal-Flórez J., Blanco-Libreros J. F., Mancera-Pineda J. E., Delgado-Huertas A., and Polo-Silva C. J. 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*. *Journal of Fish Biology*. 97(2), 499-507. https://doi.org/10.1111/jfb.14404

I developed the concept and designed the study with support from LFJ, BLJF, and MPJE. LFJ, BLJF, and DHA obtained the funding. I carried out the field study, performed the analysis, and wrote the manuscript. I interpreted isotopic analysis results with support from DHA and MPJE. PSCJ aided in interpreting the results and worked on the manuscript. All authors discussed the results and commented on the various versions of the manuscript.

Manuscript III

Sandoval L. A., Mancera-Pineda J. E, Leal-Flórez J., Blanco-Libreros J. F., and Delgado-Huertas A. 2020 Potential food sources sustaining estuarine consumers in a significant mangrove area of the southern Caribbean Sea, using stable isotope analyses. To be submitted to *Marine Ecology Progress Series*.

I developed the concept and designed the study with support from LFJ, BLJF, and MPJE. LFJ, BLJF, and DHA obtained the funding. I carried out the field study, performed the analysis, and wrote the manuscript. I interpreted isotopic analysis results with support from MPJE and DHA. All authors discussed the results and commented on the various versions of the manuscript.

Manuscript IV

Sandoval L. A., Mancera-Pineda J. E, Leal-Flórez J., Blanco-Libreros J. F., Delgado-Huertas A. 2020. Experimental discrimination of stable isotopes between mangrove leaves and the tree-climbing crab (Brachyura: Sesarmidae: *Aratus pisonii*) and possible food sources in field diets. To be submitted to *Journal of Experimental Marine Biology and Ecology.*

MPJE and I developed the concept. I designed the study with support from LFJ, BLJF, and MPJE. JLF, JFBL, and ADH obtained the funding. I carried out the field and experimental study. I performed the analysis and wrote the manuscript. I interpreted isotopic analysis results with support from DHA and MPJE. All authors discussed the results and commented on the various versions of the manuscript.

Others Manuscript related to this thesis

It is worth mentioning that during this thesis, I participated as a co-author in the studies of the diets of some fish. These studies and my thesis were part of the project "Lineamientos Prioritarios para la Formulación de un Ordenamiento Pesquero del Golfo de Urabá" (hereafter LOPEGU project). As co-author, I supported stomach content analyses, discussed the results, and commented on the following manuscripts:

Arenas-Uribe, S., Leal-Flórez, J., **Sandoval, A.**, Villa, A. F. P., and Hernandez-Morales, A. F. 2019. Hábitos alimenticios del sable *Trichiurus lepturus* en el Golfo de Urabá, Caribe colombiano. *Biota Colombiana*, 20(2). DOI: 10.21068/c2019.v20n02a05

Hernández-Morales, A. F., Leal-Flórez, J., **Sandoval L. A.**, Arenas-Uribe, S., and Pérez-Villa, A. F. 2018. Feeding habits of the gafftopsail sea catfish *Bagre marinus* (Mitchill, 1815) (Siluriformes: Ariidae) in Urabá Gulf, Colombian Caribbean. *Actualidades Biológicas*, 40(109). http://dx.doi.org/10.17533/udea.acbi.v40n109a02

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Chapter 2. Linking mangroves and fish catch: a correlational study in the southern Caribbean Sea (Colombia)

Manuscript published in *Bulletin of Marine Science*

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Marirrio Bay, Atrato River Delta (J.F. Blanco)

2.1. Abstract

Mangroves provide habitat to a variety of fish species, potentially enhancing fish production in small-scale fisheries. Fish production ecosystem services have been correlated with mangrove area and perimeter in many tropical locations; however, nothing has been published linking small-scale fish catch and mangrove descriptors in the southern Caribbean Sea. We correlated environmental variables with experimentally derived catch per unit of effort (CPUE) and richness of fishes in the Colombian southern Caribbean Sea, an area not directly connected with other productive coastal habitats. We measured mangrove descriptors (area, perimeter, and above-ground carbon), water quality (salinity and total dissolved solids), and water column productivity parameters (chlorophyll *a*, seston, and zooplankton bio-volume). Mangrove area and zooplankton bio-volume were the main factors influencing the species richness of fish. Mangrove area was positively correlated with catches for three of the most common fish species in the local artisanal fishery: *Ariopsis canteri* Acero P., Betancur-R., and Marceniuk, 2017; *Mugil incilis* Hancock, 1830; and *Sciades proops* (Valenciennes, 1840), which represent *ca*. 22% of the total regional annual catch. Our results suggest the existence of causal links between mangrove habitat and fishery production through trophic contribution by mangrove derived organic matter. *A. canteri* appears to be a mangrove-dependent species and *M. incilis* a mangrove-associated species. Results support managing or preserving mangroves in the most extensive areas in the southern Caribbean to sustain small-scale fishery resources used mainly for community sustenance where alternative resources are limited.

Keywords: Estuarine fish catch, mangrove-dependence paradigm, blue carbon, regression analysis.

2.2. Introduction

Mangroves provide a number of valuable ecosystem services, such as fish production, coastal protection, carbon storage, and sediment trapping (Lee et al. 2014). Given the role of mangroves as nursery habitats for marine and estuarine species, linkages between mangroves and fisheries have been widely studied (Manson et al. 2005a; Blaber 2007; Carrasquilla-Henao and Juanes 2016). Various studies report positive correlations between the mangrove extent and catches in nearby fisheries, suggesting that the former translates into the secondary production of fish and ultimately into commercial resource capture (Manson et al. 2005a). According to government and non-government documents, "an estimated 75% of commercially caught fish and prawns depend directly on mangroves," but this is debatable (Sheaves 2017) because other factors influence catches, such as river discharge, connectivity with surrounding habitats, and the availability of diverse food source (Manson et al. 2005a, Blaber 2007, Carrasquilla-Henano and Juanes 2016).

Most studies on the mangrove-fishery linkage have been performed in the Indo-West Pacific region, with fewer studies conducted in the Atlantic-Caribbean and Eastern Pacific regions (Carrasquilla-Henano and Juanes 2016). Much of the evidence has been obtained from studies on penaeid prawns in the Gulf of Mexico (Turner 1977), Indonesia (Martosubroto and Naamin 1977), India (Kathiresan and Rajendran 2002), Australia (Staples et al. 1985), and the Philippines (Primavera 1998), with positive correlations between commercial offshore prawn catches and total area of adjacent mangroves. Additionally, positive correlations between commercial fin-fish catches and mangrove area have been reported in Australia (Manson et al. 2005b; Meynecke et al. 2008), the Gulf of Mexico (Yáñez-Arancibia et al. 1985), the Gulf of California (Aburto-Oropeza et al. 2008; Carrasquilla-Henao et al. 2013), and the Philippines (Paw and Chua 1991).

Recently, Carrasquilla-Henao and Juanes (2016) conducted a global meta-analysis providing strong evidence on the links between mangrove attributes and fisheries in a variety of mangrove settings. Their results agreed with other studies (Manson et al. 2005 a; Sheaves 2017) highlighting that future investigations should focus on the reasons behind the use of mangroves by different species at different life stages. This is necessary to understand the derived benefits and to identify mangrove attributes that contribute to greater fish abundance.

Furthermore, Manson et al. (2005a) recommended fine-scale mangrove-fishery analyses for predicting the effects of habitat loss. Hutchison et al. (2015) expanded on this idea by developing a preliminary global model of the spatial distribution of benefits to fisheries from mangroves. Although the model was based on expert knowledge of mangrove ecology and fisheries biology, it was not parameterized with field data and therefore qualitative.

For the Atlantic-Caribbean and Eastern Pacific regions, most mangrove-fishery databases originate from Mexico (Yáñez-Arancibia et al. 1985, Aburto-Oropeza et al. 2008 Carrasquilla-Henao et al. 2013), while the majority of field studies linking fishes with mangroves, seagrasses, and coral reefs have been conducted in the Caribbean islands (Nagelkerken and Van Der Velde 2004. Mumby et al. 2004, Serafy et al. 2015). Despite having a wide range of mangrove habitats along the Caribbean coast of Colombia, no such studies have been conducted there (Carrasquilla-Henao et al. 2013). The Colombian systems are mainly not directly connected with other highly productive coastal habitats, such as coral reefs and seagrasses (e.g., Ciénaga Grande de Santa Marta and Urabá Gulf), potentially easing studies examining putative links between mangroves and fisheries production.

Current knowledge on estuarine fisheries along the Caribbean coast of Colombia has been largely obtained from Ciénaga Grande de Santa Marta, a large coastal lagoon, located east of Barranquilla (Blaber and Barletta 2016). The Urabá Gulf, located near the western border between northern Colombia and Panama, is another major estuary with extensive mangrove areas and artisanal fisheries supplyning local commerce and subsistence. Information concerning these mangroves and local fisheries is limited; however, recent studies suggested that most of the commercial fish species use mangroves and mangrove lagoons at least during their early life cycle stages (Sandoval et al. 2014, LOPEGU 2017).

The aim of this study was to examine the importance of mangroves in terms of fishery production measured as catch per unit of effort (CPUE) in the Urabá Gulf and its vicinity, an area not directly connected with other highly productive coastal habitats. We investigated the linkages between CPUE and species richness using several environmental variables: mangrove descriptors (area, perimeter, and above-ground carbon), water quality (salinity, total dissolved solids), and water column productivity parameters (chlorophyll *a*, seston, and zooplankton bio-volume).

2.3. Methods

Study area

The Urabá Gulf is the largest estuary along the Caribbean coast of Columbia (7°50′−8º56′ N, 77°22′−76°25′ W). It is a semi-enclosed water body (length: 80 km, width: 6−45 km)

(Figure 1) and has a micro-tidal regime (<40 cm amplitude). The largest freshwater input on the southern Caribbean is the Magdalena River, followed by the Atrato River which discharges into the western coast of the Gulf (Garcia 2007). Additional freshwater is received from small rivers located along the southeastern coast. Extensive mangrove forests (approximately 6000 ha) can also be found along the different deltas and river mouths. The red mangrove *Rhizophora mangle* L. (1753) is the dominant species of mangroves (> 80% by area), followed by the white mangrove *Laguncularia racemosa* (L.) Gaertn (f.) and black mangrove *Avicennia germinans* (L.) L. The largest mangrove areas are located on the Atrato River delta, where most stands are monodominant (Blanco-Libreros 2016). The artisanal fishery is practiced only for local commerce and/or subsistence. It is the main income and food source for many low-income communities and is mostly associated with fringe mangroves (Sandoval et al. 2014, LOPEGU 2017). This situation is similar to other locations observed along the Colombian Caribbean and elsewhere in the tropics (Hutchison et al. 2014, Saavedra-Díaz et al. 2015). We examined the importance of mangroves to CPUE in the Urabá Gulf and its vicinity extending *ca.* 500 km, including protected-coast and mangrove-dominated sites (the Urabá Gulf) and open-coast and non-mangrove-dominated sites.

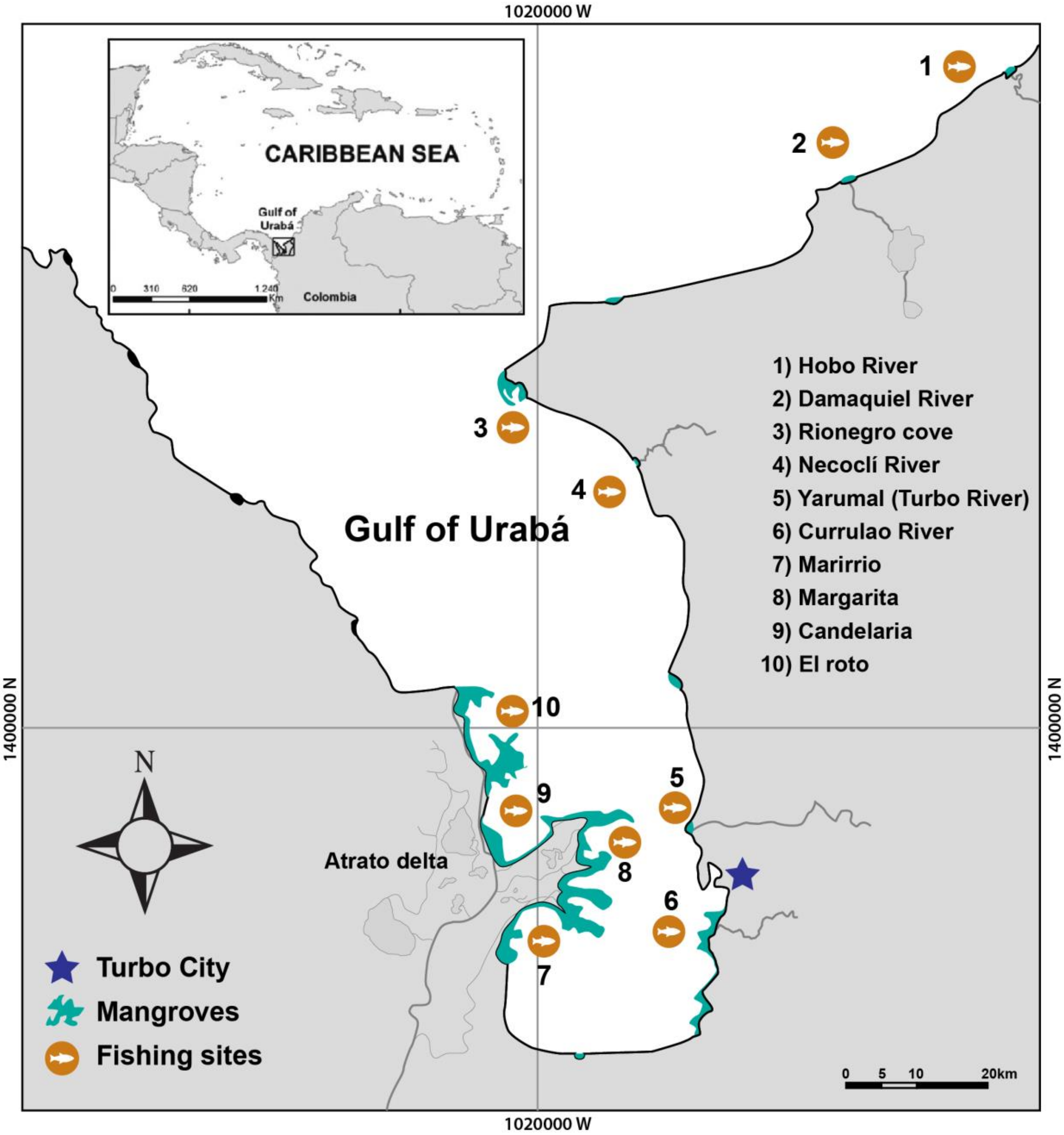

Figure 1. Map of the study area showing the 10 sites where experimental fishing was conducted, location of MAs, and a major human settlement (Turbo City).

Fishing data

Although the Urabá Gulf is a designated area for monitoring of fish landings by the National Aquaculture and Fisheries Authority (Autoridad Nacional de Acuicultura y Pesca, AUNAP), spatial and temporal coverage is limited. For this reason, data from experimental fishing campaigns conducted between 2015 and 2016 was used during a project aimed at providing guidelines for small-scale fisheries management in the area (hereafter LOPEGU project: “Lineamientos Prioritarios para la Formulación de un Ordenamiento Pesquero del Golfo de Urabá”). We used information from 10 sites, representing the most important Gulf fishing grounds (LOPEGU 2017). The focus of experimental fishing was to provide baseline information on fish catches from the most representative fishing grounds along the Gulf’s mangrove coastlines and the outer northeastern coastline where mangroves are less extensive and patchily distributed.

There were seven fishing campaigns included: four in 2015 (March, August, October, December) and three in 2016 (February, April, August). Operations were performed using two boats fishing in the southern sites and northern Gulf sites, respectively (Figure 1, Table 1). In each of the 10 sites, two gillnets, set side by side, were deployed during the day (07:00 to 11:00 hours) and the night (18:00 to 22:00 hours); day and night samples were treated as replicates for each campaign in subsequent analyses. Gillnets were similar to those used by local fishermen (800 m long and 7 m high, with mesh sizes of 7, 7.6, 10.2, and 12.7 cm). Gillnet hauls per site ranged from 14 to 29 (Table 1), depending on the weather. The gillnets were set between approximately 0.8 and 1.9 km away from mangroves (Table 1). The distance to the nearest sampling site ranged between 12 and 40 km (Table 1).

Fish were transported on ice, identified to species level and wighed at the Marine Ecology Laboratory of the Universidad de Antioquia (Marine Sciences Campus). A reference collection was sent to the National Museum of Marine Natural History (Museo de Historia Natural Marina de Colombia, MHNMC; collection code PEC9038). Species richness was estimated as the total number of species from 14 random hauls in each site, because fishing effort differed among sites. Fish catch was expressed as CPUE, estimated as mass (kg) per the number of hauls in each site.

Mangrove data

We examined mangrove forest descriptors within the coastal segments coinciding with fishing sites (bays and river deltas along the Urabá Gulf and the open coast; Figure 1). Mangrove area (MA, in ha) was obtained from a technical report based on high-resolution aerial imagery (Blanco et al. 2013). Mangrove perimeter (MP, in km) was computed from that mosaic using ArcGis 9.3. MP was estimated as the length of the mangrove fringe in contact with open water (interior perimeter in contact with terrestrial vegetation or wetlands was not considered).

Table 1. Fishery summary: zones and sites of fishing operations with two boats, fishing effort (number hauls) from seven campaigns, estimated distance between fishing set and mangroves (MA-Fishing), and estimated distance between fishing sites (Fishing-Fishing).

Fishing sites	Apr. 2015	Aug. 2015	Oct. 2015	Dec. 2015	Feb. 2016	Apr. 2016	Aug. 2016	Total Fishing effort	MA-Fishing	Fishing-Fishing
	Hauls								km	km
Northern sites										
Hobo River	0	4	4	4	0	2	0	14	1.9	-
Damaquiel River	0	0	4	4	2	4	2	16	1.5	15
Rionegro Cove	0	4	4	4	4	4	4	24	1	40
Necoclí River	0	4	4	4	4	4	4	24	1	17
Southern sites										
Yarumal	0	4	4	2	2	4	3	19	1.3	38
Currulao River	4	4	4	4	4	4	4	28	0.8	13
Marirrio	0	4	4	4	4	4	3	23	1.3	17
Margarita	4	4	4	4	3	4	4	27	0.7	13
Candelaria	4	4	4	4	4	4	4	28	1.5	12
El Roto	4	4	4	4	4	4	4	28	1	12

To estimate carbon accumulated in aerial biomass (CAB), we first estimated aerial biomass (AB) using the following equation for *R. mangle* reported by Fromard et al. (1998):

$$W = 0.178\ (DBH)^{2.47}$$

where W is tree weight (mass in kg) and DBH is diameter at breast height. This equation was selected as equations based on locally logged trees were not available. We used mean DBH and tree density per hectare in each area from Blanco et al. (2013). AB was calculated by multiplying mean tree weight and tree density for each site; tree densities were pre-obtained using sampling plots (10 x 10 m) (Blanco et al. 2013). Finally, CAB was estimated as 50% of the AB as suggested by Bouillon et al. (2008) and expressed in Tg after multiplying by the MA corresponding to each of the 10 fishing sites.

Quality and productivity of the water column

We characterized several physicochemical parameters from water column at each of the 10 sites where experimental fishing was conducted. Four sampling campaigns were included: one in 2015 (December) and three in 2016 (February to March, April to May, August). Water samples were more restricted than those from fishing sampling due to logistical difficulties. Nevertheless, all samples were obtained during the major fishing time, allowing for the establishment of different patterns of water variables among sites throughout the year. We determined salinity (SAL) and total dissolved solids (TDS) *in situ* using a multiparameter probe, while water samples were taken to determine seston and chlorophyll *a* in the laboratory. We measured seston (total suspended solids (TSS), g/l) according to USEPA (1999) and chlorophyll *a* (CHL, µgClha/l) according to Stricklan and Parson (1972). We obtained zooplankton samples from surface net tows (net mesh of 300 µm over 6 minutes at 2 knots), with a flow meter fixed to the plankton net to record the filtered volume. Subsequently, we estimated zooplankton bio-volume (ZB, ml/1000 m^3) using the displaced volume method (Escarria et al. 2005).

Data analysis

Given that water column sampling campaigns were fewer than fishing campaigns, we used site-specific mean values calculates for the entire study period for each of the 10 fishing sites as explanatory variables. Additionally, the absolute values of mangrove descriptors were used for each site. The dependent variables describing fish catches were CPUE (total and species-specific) and species richness (total number of species). We tested each variable distribution for normality (as a prerequisite for regression analyses), and all of them were rank-transformed to satisfy the normality assumption (Conover 2012). We performed Spearman rank correlation (SRC) analysis between explanatory variables to explore co-linearity, using XLSTAT software (Addinsoft 2019). Then, we then ran multiple linear regression (MLR) with backward elimination to determine the best environmental variables to predict CPUE and species richness, using the same software. In each step, we checked the model fit and significance of each covariate and manually eliminated non-significant terms. We examined the most common species collected where data was normally distributed. We considered $p < 0.1$ as significant correlation. We also used non-parametric Kruskal-Wallis (H) test in R Studio (version 3.5.3) to examine differences in water column variables, species richness, total fish CPUE, and species-specific CPUE among sites.

2.4. Results

Fishing data

We captured 77 species of fish, belonging to 30 families. Rionegro Cove and Marirrio Bay showed the highest species richness values: 32 and 30 species, respectively. Hobo River had the lowest species richness value with 13 species (Figure 2A). However, species richness among sites did not differ (Kruskal-Wallis test, $p = 0.28$, $df = 9$). The total catch from all 10 sites and 231 gillnet hauls in the Urabá Gulf was 870 kg. Nearly 40% of the biomass comprised three species: common snook, *Centropomus undecimalis* (Bloch, 1792) (Centropomidae), 0.44 kg/haul; New Granada sea catfish, *Ariopsis canteri* (Ariidae), 0.36 kg/haul; and serra Spanish mackerel, *Scomberomorus brasiliensis* Collette, Russo, and Zavala-Camin, 1978 (Scombridae), 0.31 kg/haul. The following species were secondarily abundant: tarpon, *Megalops atlanticus* Valenciennes, 1847 (Megalopidae), 0.27 kg/haul; castin leatherjacket, *Oligoplites saliens* (Bloch, 1793) (Carangidae), 0.22 kg/haul; gafftopsail sea catfish, *Bagre marinus* (Mitchill, 1815) (Ariidae), 0.21 kg/haul; coco sea catfish, *Bagre bagre* (Linnaeus, 1766) (Ariidae), 0.21 kg/haul; Atlantic bumper, *Chloroscombrus chrysurus* (Linnaeus, 1766) (Carangidae), 0.18 kg/haul; and largehead hairtail, *Trichiurus lepturus* (Trichuridae), 0.14 kg/haul (Figure 3A).

The mean total CPUE was 3.74 kg/haul. CPUE ranged from 6.68 to 1.64 kg/haul for Damaquiel River and Necoclí River, respectively (Figure 2B). *Scomberomorus brasiliensis* and *C. undecimalis* were the most important species in Damaquiel River. *Oligoplites saliens* and *S. brasiliensis* were the most important species in Yarumal. *Megalops atlanticus* was the most important species in Margarita. *Oligoplites saliens*, *T. lepturus*, and *A. canteri* were the most important species in Currulao River (Figure 3B). There was no significant difference in total CPUE among sites (Kruskal-Wallis test, $p = 0.47$, $df = 9$). There were significant differences in CPUE of *A. canteri* ($p = 0.03$, $df = 9$), *B. bagre* ($p < 0.01$, $df = 9$), and *O. saliens* ($p = 0.04$, $df = 9$) among sites. However, pairwise comparisons among sites using Wilcoxon rank sum test showed no significant differences due to reduced sample sizes (six for each site).

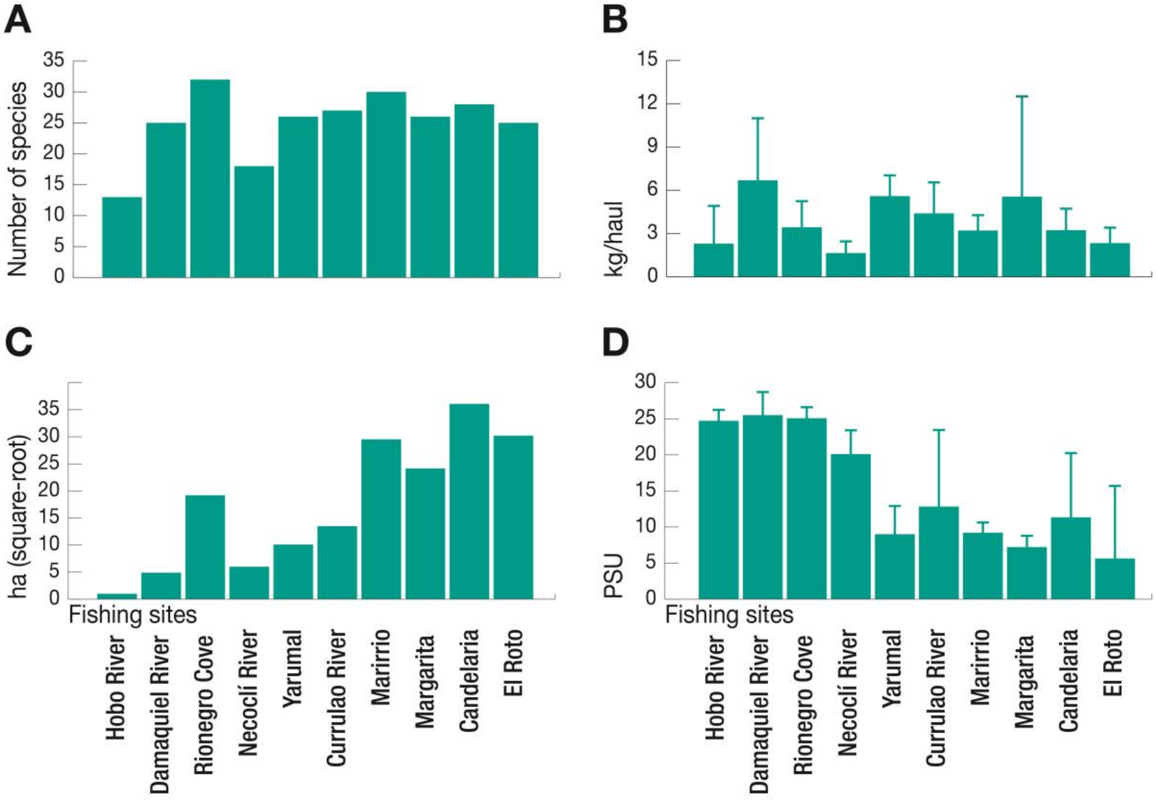

Figure 2. Main results of the total catch and environmental variables in each site of the southern Caribbean of Colombia. A) species richness (number), B) total CPUE (kg/haul), C) mangrove area (MA: ha square-root), and D) mean salinity (SAL: PSU). Error bars in B) and D) represent standard deviations.

Environmental data

The magnitude of mangrove variables (MA, MP, CAB) varied considerably among sites along the Urabá Gulf and the open coast. Values of all three variables were higher on the western coast of the Urabá Gulf (Marirrio, Margarita, Candelaria, and El Roto) where mangroves are more extensive (Table 2) (e.g., MA exceeded 20 ha) (Figure 2C). However, Rionegro Cove, a coastal lagoon located in the northeastern tip of the Urabá Gulf, exhibited higher MA, MP, and CAB values than the rest of the sites along the southeastern and northeastern coasts (Table 2, Figure 2C). The average of water column variables (TDS, CHL, SAL, TSS, ZB) also varied considerably among sites (Table 2). For instance, salinity exceeded 20 PSU in the northeastern sites (Hobo River, Damaquiel River, Rionegro Cove, Necoclí River), while it was persistently lower at sites in the interior of the Gulf (Table 2, Figure 2D). The Kruskal-Wallis test revealed significant differences in TDS ($p < 0.01$, df = 9), TSS (p =

0.02, df = 9), and SAL (p < 0.01, df = 9) among sites. However, pairwise comparisons among sites using Wilcoxon rank sum test showed no significant differences likely reflecting reduced sample sizes (four for each site).

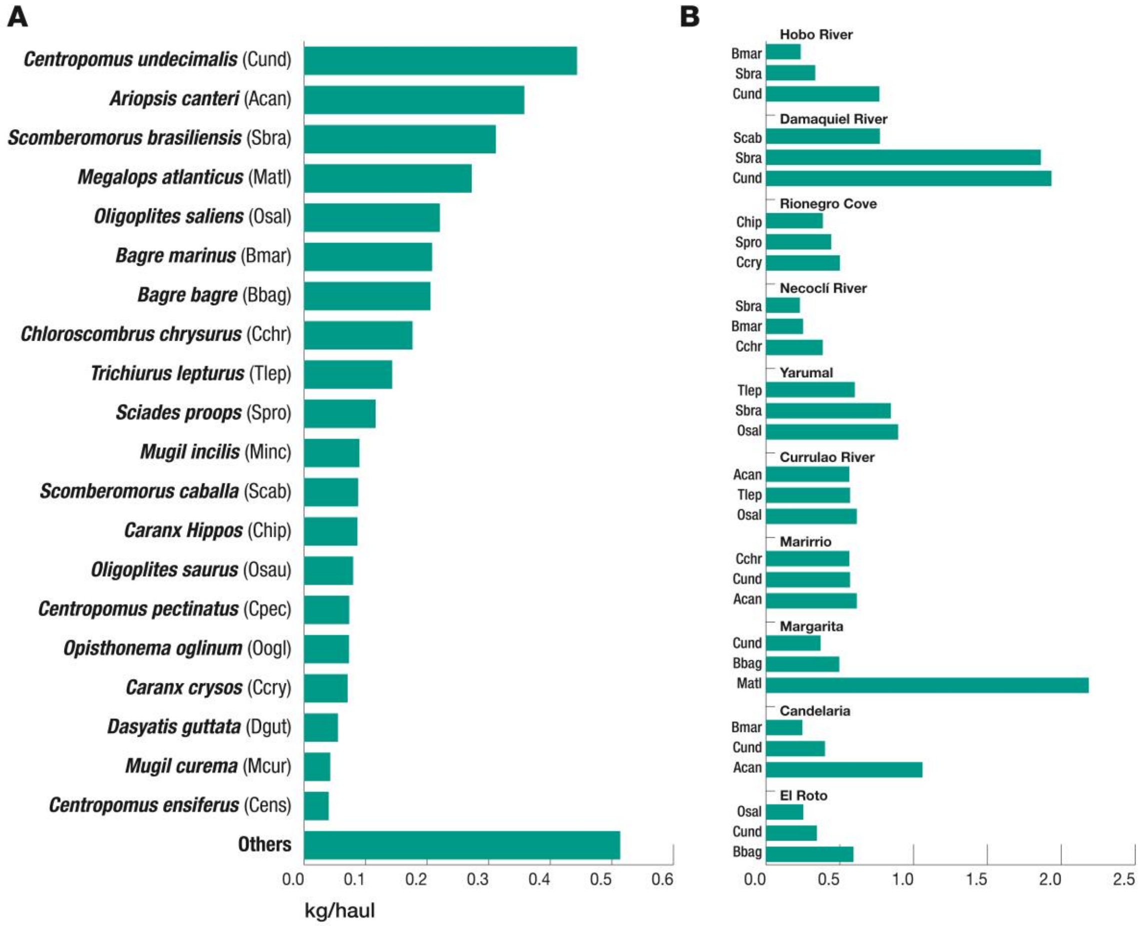

Figure 3. Fish total CPUE (kg/haul) for the most common species collected A) in the region and B) the three most important species in each site of the southern Caribbean of Colombia.

Table 2. Environmental variables (means ± standard deviations), including water quality, water column productivity, and mangrove descriptors estimated from 10 sites along the southern Caribbean of Colombia. Water quality-water column productivity means were computed from four (n=4) campaigns: December 2015, February 2016, April 2016, and August 2016, except for Hobo River where samples were obtained with three (n=3) campaigns. TDS: total dissolved solids, CHL: chlorophyll a, SAL: salinity, TSS: total suspended solids (seston), ZB: zooplankton bio-volume, MA: mangrove area, MP: mangrove perimeter, CAB: carbon accumulated in aerial biomass.

Site	TDS	TSS	SAL	CHL	ZB	MA	MP	CAB
	µg/L ± SD	g/L ± SD (n)	UPS ± SD (n)	µg/L ± SD (n)	ml/m3 ± SD (n)	ha	km	Tg

Northeastern Coast								
Hobo River	21.4±0.9	0.01 ±0	24.78 ± 1.0	1.46 ± 1.4	185.95 ± 112.3	1	0.38	0.19
Damaquiel River	21.6 ±2.2	0.01 ±0	25.5 ± 5.0	5.37 ± 2.9	192.86 ± 180.4	24	0.19	4.83
Southeastern Coast								
Rionegro Cove	21.2 ±1.0	0.01 ±0	25.07 ± 0.4	0.9 ± 1.5	126.53 ± 107	369	30.61	5.87
Necoclí River	17.6 ±2.2	0.01 ±0	20.11 ± 1.1	1.47 ± 3.0	35 ± 32.3	36	1.93	0.65
Yarumal	8.2 ±3.0	0.01 ±0	8.99 ± 3.4	4.46 ± 3.5	79.76 ± 70.1	102	20.72	0.8
Currulao River	11.4 ±7.6	0.03 ±0.01	12.82 ± 4.8	3.87 ± 9.3	48.54 ± 56.9	182	10.24	0.71
Western coast								
Marirrio	8.5 ±1.3	0.02 ±0	9.2 ± 1.6	2.53 ± 1.4	159.65 ± 212.2	873	60.23	82.86
Margarita	6.7 ±1.3	0.02 ±0.01	7.13 ± 1.7	2.81 ± 1.5	37.14 ± 29.9	584	32.45	31.85
Candelaria	10.1 ±6.6	0.02 ±0.01	11.33 ± 1.4	2.06 ± 7.8	40.37 ± 39.6	1303	102.1	93.01
El Roto	4.8 ±7.4	0.09 ±0.07	5.63 ± 8.6	7.17 ± 8.8	39.59 ± 46.0	913	89.31	40.73

Table 3. Spearman's rank correlation matrix between explanatory variables (n = 10, for all variables). *: $p < 0.05$, **: $p < 0.01$. TDS: total dissolved solids, TSS: total suspended solids (seston), SAL: salinity, CHL: chlorophyll a, ZB: zooplankton bio-volume, MA: mangrove area, MP: mangrove perimeter, CAB: carbon accumulated in aerial biomass.

	TDS μg/L	TSS g/L	SAL PSU	CHA ug/L	ZB ml/m^3	MA Ha	MP km	CAB Tg
TDS	**1**							
TSS	−0.82*	**1**						
SAL	0.99**	−0.79*	**1**					
CHA	−0.44	0.49	−0.46	**1**				
ZB	0.59	−0.57	0.56	0.01	**1**			
MA	−0.70*	0.76*	−0.64	0.13	−0.42	**1**		
MP	−0.75*	0.70	−0.70*	0.06	−0.42	0.98**	**1**	
CAB	−0.53	0.52	−0.47	0.19	−0.13	0.90**	0.87**	**1**

Relationships between mangrove, water column, and CPUE data

Based on SRC results, four environmental variables were retained for inclusion in regression analyses: MA, SAL, CHL, and ZB (Table 3). Regression analysis revealed that total CPUE was not correlated with any variable, but that species richness was positively correlated with MA and ZB ($R^2 = 0.56$). Two species were positively associated with MA (*Ariopsis canteri*, $R^2 = 0.50$ and *M. incilis*, $R^2 = 0.38$), while one species was negatively associated with MA (*S. brasiliensis*, $R^2 = 0.77$). A second group of species were consistently associated with

SAL (*Bagre bagre*, $R^2 = 0.45$; *O. saliens*, $R^2 = 0.52$ and *O. saurus*, $R^2 = 0.42$). A third group of species were associated with water column productivity variables (*Centropomus ensiferus* with CHL, $R^2 = 0.47$; *C. pectinatus* with SAL and CHL, R2 = 0.84 and *C. undecimalis* with ZB, $R^2 = 0.77$). *Sciades proops* CPUE was consistently associated with MA, CHL, and ZB ($R^2 = 0.83$) (Table 4).

2.5. Discussion

This is the first study of a mangrove-fishery relationship in the southern Caribbean and northern South America. By testing the relative contribution of environmental variables (water column quality and productivity, and mangrove metrics) for an area not directly connected with other highly productive coastal habitats, we demonstrated that MA predicted the catch for four of the most common fish species in local artisanal fisheries. This suggests mangrove shorelines are the prime fish habitat in this part of the Caribbean Sea.

Table 4. Environmental variables significantly explaining species richness and CPUE for 10 fish species, identified using Multiple Linear Regressions by backward elimination; *n* = 10 for all variables (R^2 and P-values are included). MA: mangrove area, CHL: chlorophyll *a*, SAL: salinity, ZB: zooplankton bio-volume. $p < 0.1$ was considered significant correlation.

	Value (slope)	Significance t	Significance F	R^2
Species richness				
Step 3 (MA + ZB)			0.06	0.56
ZB	0.60	0.06		
MA	0.76	0.03		
Ariopsis canteri				
Step 4 (MA)	0.70	0.02	0.02	0.50
Bagre bagre				
Step 4 (SAL)	−0.67	0.03	0.03	0.45
Centropomus ensiferus				
Step 4 (CHL)	0.66	0.03	0.03	0.47
Centropomus pectinatus				
Step 3 (SAL + CHL)			0.00	0.84
SAL	−0.48	0.03		
CHL	0.58	0.01		
Centropomus undecimalis				

Step 4 (ZB)	0.76	0.01	0.01	0.57
Oligoplites saliens				
Step 4 (SAL)	−0.72	0.02	0.02	0.52
Oligoplites saurus				
Step 4 (SAL)	−0.65	0.04	0.04	0.42
Mugil incilis				
Step 4 (MA)	0.61	0.06	0.06	0.38
Scomberomorus brasiliensis				
Step 4 (MA)	−0.88	0.00	0.00	0.77
Sciades proops				
Step 2 (MA + CHL + ZB)			0.01	0.83
CHL	−0.45	0.04		
ZB	0.90	0.00		
MA	0.54	0.03		

The partial contribution of MA and ZB to species richness variability suggests that mangrove coastlines play a role as habitat for a subset of the fish community in this area, while food availability in the water column plays a complementary role for mangrove-associated fish. Food and refuge are considered the key beneficial aspects of fishes’ mangrove use (Sheaves 2017). The lack of correlation between fish richness and salinity suggests a species turnover of the entire fish community along the geographic gradient observed between the Urabá Gulf and the open coast to the Caribbean Sea. Salinity may be one of the most important physical factors affecting estuarine fish (Blaber et al. 2013). For instance, in more constrained estuarine environments such as tropical coastal lagoons, higher species richness has been recorded under low salinity (Sosa-Lopez et al. 2007). However, CPUE of various species was correlated with salinity as discussed below.

Similar to previous studies, positive correlations between mangrove and fish catches have been obtained in a variety of mangrove settings globally, suggesting that mangroves have a strong effect on fisheries. However, most studies do not explain the causal relationship between mangroves and fisheries (Blaber 2007, Lee et al. 2014, Carrasquilla and Juanes 2016). Mangroves may serve as a nursery for fish (Nagelkerken 2009, Serafy et al. 2015) and make trophic contribution, i.e., litterfall detrital-based and/or attached algae-based food webs (Hyndes et al. 2014, Serafy et al. 2015), but these are primarily correlative.

MA partially predicted catches of *A. canteri* (50% variability) and *M. incilis* (38% variability) (Table 4). Such correlations may be a result of benthic feeding habits of both species, associated with mangrove fringes (see later), where other highly productive coastal habitats are absent. Only small coral reef patches are found to the northwest of the Urabá Gulf, in the vicinity of Panama, *ca.* 50 km from the study sites (Díaz et al. 2000). Moreover, soft bottoms in the Urabá Gulf are presumably un-productive. Contrary to our findings, most studies in the Caribbean have linked mangrove habitats to fish abundance, due to an enhancement by adjacent coral reefs, serving as habitat for juveniles (Mumby et al. 2004, Serafy et al. 2015). In our study area, in addition to mangrove extent, other environmental factors may influence fish catches, such as rainfall, water temperature, and extent of shallow waters, as reported elsewhere (Manson et al. 2005b). Future attempts to predict catches would benefit from more rigorous collection of climatic and oceanographic data. However, in this study, MA rather than water column variables best predicted catches of *A. canteri* and *M. incilis*, suggesting a greater relative contribution.

The New Granada sea catfish, *A. canteri*, is an endemic species from Colombia, which is listed as endangered (Colombian fish red list: national category EN A2d; B1b(iii)c(ii)) due to its degree of endemism and overfishing pressure (Acero et al. 2017). This species inhabits mangrove fringes in coastal lagoons and river deltas. Diet of juveniles and adults is mainly composed of crustaceans and mangrove-related fish. Males have also been observed incubating eggs for a period, and small individuals remain in mangrove lagoons and creeks possibly as a refuge against predators (Sandoval et al. 2014). Therefore, *A. canteri* appears to be a mangrove-dependent species (Manson et al. 2005a). Mangrove dependence has been associated with several marine-estuarine species having juveniles that are only found among mangroves (e.g., the banana prawn *P. merguiensis*; Staples et al. 1985, Manson et al. 2005a). *A. canteri* appear to use mangroves throughout their life cycle, because juveniles are found exclusively in mangroves, while adults use mangroves alternatively with open waters, but are trophically dependent on mangroves (Sandoval et al. 2014). However, adults have also been recorded entering upriver freshwaters (Acero et al. 2017). Therefore, a more detailed understanding of their life cycle and habitat use is required.

The Parassi mullet, *M. incilis*, is mainly found in brackish estuaries but also in marine and hyper-saline waters (Cervigon et al. 1992). In the Urabá Gulf, both juveniles and adults feed mainly on diatoms from the seabed near mangroves (Sandoval 2012). Therefore, *M. incilis* appears to be a mangrove-associated species. In the Gulf, the Crucifix sea catfish, *S. proops*, was also associated with mangroves; however, its ecology is poorly known, despite it having been documented inhabiting mainly brackish estuaries and lagoons and feeding mainly on fish (Cervigon et al. 1992).

The CPUE of the Spanish mackerel, *S. brasiliensis*, was negatively correlated with MA ($R^2 = -0.52$) (Table 4), consistent with mangrove-independent species or a marine straggler (Manson et al. 2005a). Additionally, seven species caught were better explained by water column variables than by MA. *Centropomus ensiferus* and *C. undecimalis* CPUE were best explained by CHL + ZB, suggesting a greater dependency on water column productivity. *Oligoplites saliens*, *O. sauros*, *B. bagre*, and *C. pectinatus* catches were best explained by SAL (Table 4), suggesting a distribution mediated by physiological constraints. Yet, we recommend further niche ecology studies to better understand how the biology and life cycle of each species affects their dependence on mangroves and other environmental variables.

Although we did not analyze temporal variability, our results may be useful for predicting the effects of habitat loss on fisheries, as suggested by Manson et al. (2005a), and for generating preliminary local models regarding spatial (geographical) distribution of benefits that mangroves provide to local small-scale fisheries. Specifically, we highlight the importance of the largest MAs (i.e., Atrato River delta) as the major habitats for selected commercially valuable fish species, and we urge for their conservation within ecosystem-based fishery management or spatial planning frameworks (Pikitch et al. 2004). Ineffective management and planning of small-scale fisheries has resulted in the decline of mangrove-associated fish (Reis-Filho et al. 2018). Currently, the National Aquaculture and Fisheries Authority is drafting a fishery management plan for the Urabá Gulf based on the spatially explicit mangrove-fishery linkages reported in the present study.

Our results suggest that the most extensive MA, the Atrato River delta, supports the fish production for some of the most common fish species captured in local artisanal fisheries. For instance, *A. canteri*, *M. incilis*, and *S. proops* CPUE was positively correlated with MA, which jointly represent *ca*. 22% of the total regional annual catch, being some of the most important in local trade among *ca*. 100 registered species of crustaceans and fish (LOPEGU 2017). Moreover, mangroves settled in the Atrato River delta may be important in sustaining fishing livelihoods in the extensive Urabá region, inhabited by more than 47 villages, and 1500 families engaged in fishing for local commerce and/or subsistence (LOPEGU 2017). Thus, our results suggest that mangrove conservation strategies such as marine-protected areas and co-management would benefit coastal communities through the fisheries provision service.

In summary, MA and food availability in the water column were the main factors explaining fish species richness distribution in the Urabá Gulf. MA significantly explained catches of three of the most common species in artisanal fisheries. MA, rather than water column variables, was the best predictor of the catches of the benthivore species, *A. canteri* and *M. incilis*. The former appears to be a mangrove-dependent species, the latter a mangrove-associated species. It suggests that the causal links between mangrove habitat and fishery production may be explained through the trophic contribution of mangroves in areas not directly connected to other highly productive coastal habitats (i.e., seagrasses and coral reefs). These results may be useful for designing strategies that jointly address mangrove conservation and management of small-scale fisheries associated with mangroves.

2.6. Acknowledgments

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Chapter 3. Stable isotope analysis reveals sources of organic matter and ontogenic feeding shifts of a mangrove-dependent predator species, New Granada Sea Catfish, *Ariopsis canteri*.

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Artisanal fishery, Atrato River Delta (L.A. Sandoval).

4.1. Abstract

We used nitrogen and carbon stable isotopes ($\delta^{15}N$, $\delta^{13}C$) and Bayesian mixing models to gain a better understanding on the trophic ecology of New Granada sea catfish, *Ariopsis canteri,* and their linkage to mangroves. We explored trophic dynamics and potential ontogenetic feeding shifts across three different size classes: class I (8–20 cm), class II (21–32 cm), and class III (> 32 cm). The study area was the estuary of the Atrato River Delta, Colombia where information about fish ecology is limited. Fish from size class I had lower $\delta^{13}C$ values (mean ± SD = -25.0 ± 0.7 ‰) than that of conspecifics in size classes II (-22.2 ± 0.9 ‰) and III (-22.0 ± 2.0 ‰). The $\delta^{15}N$ of fish in size class I was lower (8.5 ± 0.7‰) than individuals from both size classes II (9.8 ± 0.6 ‰) and III (10.0 ± 0.7 ‰). Body size was positively and significantly correlated to $\delta^{15}N$ and $\delta^{13}C$. Individuals with $L_T > 32$ cm presented the highest estimated trophic position (3.8). Five-source mixing models indicated that for class I, the macroalgae made the largest estimated contribution to assimilated diet (34% median: 95% credibility intervals 6 to 57% CI), while for classes II and III, the macrophytes made the highest contribution to assimilated diet (27%: 3 to 53% CI, and 30%: 4 to 53% CI, respectively). Ontogenic feeding shifts of *A. canteri* were confirmed, reflecting decreasing intraspecific competition between small and large individuals. Results suggest that mangroves are a nursery and feeding ground habitat for this species but that the association between mangroves and *A. canteri* is indirect, and mainly reflects substrate/habitats that supports other primary producers rather than direct use of mangrove-derived organic materials. These results can be used in ecosystem-based fishery management focused on the protection of extensive mangroves areas in the southern Caribbean Sea.

Key words: Bayesian mixing models, Southern Caribbean Sea, Urabá Gulf, Mangroves, size structure.

4.2. Introduction

Catfishes of the family Ariidae are benthivorous fishes well adapted to live in different habitats of estuaries of the tropical and subtropical world, and are considered as an essential group in terms of density and biomass in tropical estuaries, (Lowe-McConnell 1987, Barletta and Blaber 2007, Dantas et al. 2010). They make important contribution to both artisanal and subsistence fisheries (Barletta and Costa, 2009, Dantas et al. 2012). In South America, information about catfishes is more extensive for the South Western Atlantic (SWA) than for the Caribbean coast. (Blaber and Barletta 2016). For example, ontogenetic and seasonal shifts in the diets of catfishes species from SWA have been reported (Giarrizzo and Saint-Paul 2008, Dantas et al. 2013). Likewise, movement patterns (Dantas et al. 2010), and nursery habitat shifts for several species have been shown (Dantas et al. 2012). However, little is known regarding their ecology in the Southern Caribbean Sea (Colombia).

The New Granada sea catfish, *Ariopsis canteri* Acero P., Betancur-R. and Marceniuk, 2017 is endemic to the Colombian Caribbean, and endangered (national category EN A2d; B1b(iii)c(ii)) due to its degree of endemism and fishing pressure (Acero et al. 2017). This species was previously recognized but misidentified in literature as *A. bonillai* (non Miles). Nevertheless, Marceniuk et al. (2017), based on morphological and molecular evidence, revised the taxonomy of the New World genus *Ariopsis* describing *A. canteri*. This species is found in coastal marine and brackish waters; sometimes entering freshwaters (e.g., Atrato, Sinú, Magdalena, and Ranchería rivers) (Marceniuk et al. 2017), it is abundant in coastal lagoons, river deltas, estuaries and mangrove areas (Acero et al. 2017). *A. canteri* has recently been classified as a mangrove-dependent species (Sandoval et. al, 2020). Mangrove dependence has been associated with several marine-estuarine species having juveniles that are only found among mangroves (e.g., the banana prawn; Manson et al. 2005).

The diet of juveniles and adults of *A. canteri* is mainly composed of fish and crustaceans living in proximity to mangroves. Larger individuals (>19.2 cm LT) feed mainly on other fish, anomuran crustaceans and shrimps, while smaller fish largely consume copepods (Sandoval et al. 2014). Although stomach-content analyses (SCA) have provided useful information on its feeding habits, ontogenic feeding shifts have not been fully confirmed. Male *A. canteri* have been observed to incubate eggs for some time, and once hatched, the small fry remains in mangrove fringes, possibly seeking shelter from predators. It has been shown that this species may present patterns of distribution and habitat use in coastal lagoons in a sequential form in time and space, or seasonal programming, which would imply a feeding on different types of prey during its ontogeny (Yáñez-Arancibia et al. 1994, Sandoval et al. 2014).

Stomach content analysis can allow diets to be characterized to high levels of taxonomic resolution if entire individuals or diagnostic body structures are found. However, SCA can be biased due to the difficulty of determining the origin of partially digested food items and the impossibility of evaluating the real assimilation of nutrients derived from ingested food. Stable-isotope analysis (SIA) has increasingly been used to reconstruct consumer diets and food assimilation patterns over the past two decades (Layman et al. 2012). It has clear advantages over more traditional dietary methods because it incorporates spatial and temporal aspects that SCA cannot realistically cover (Bouillon et al. 2011).

In order to quantify the relative contribution of different prey sources to predator diets, stable-isotope studies increasing utilize mixing models that incorporate stable-isotope values from potential food sources, consumers, and the change in stable-isotope values between predator and prey due to biochemical processes such as assimilation and excretion (trophic discrimination factor; TDF). By taking, the error associated with these isotopic parameters into account, Bayesian mixing models can estimate proportional contributions of source pools (Jackson et al. 2009, Moore and Semmens, 2008, Parnell et al. 2010). Likewise, isotopic niche metrics have been proposed as useful proxies to evaluate the breadth and overlap of trophic niches (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2011).

Mangrove-associated fisheries in the Urabá Gulf provide a critical source of food and income for many people who have few economic alternatives (Sandoval et al. 2020). *A. canteri* is one of the most common species in artisanal fisheries in the region. Nevertheless, there is little management or planning for fisheries in the region (LOPEGU, 2017, Sandoval et al. 2020). Knowledge of ecosystem processes is necessary for understanding the likely consequences of human actions, and as such understanding consumer diet and the essential sources of organic matter fueling dominant species is a crucial input for ecosystem-based fishery management (EBFM) (Pikitch et al. 2004). Accordingly, the specific objectives of this study are: (a) assess ontogenic feeding shifts of *A. canteri*, and (b) assess the importance of various production sources in supporting *A. canteri*; following two hypotheses: (a) stable isotopic values ($\delta^{15}N$ and $\delta^{13}C$) and isotopic niche metrics are different between size classes, and (b) mangrove is the source of significant importance in the *A. canteri* diet using five-source mixing models.

4.3. Materials and methods

Study location

The Urabá Gulf is the southernmost area of the Caribbean, located at the southern end of the northern coast of Colombia (Figure 9). The Atrato River discharges into the western coast of the Gulf and is the second-largest freshwater input for the Southern Caribbean after the Magdalena River, for the Southern Caribbean (Garcia-Valencia 2007). The estuary of the Atrato River Delta is considered essential aquatic habitat for biota and artisanal fisheries; however, information about fish is limited (Correa-Herrera et al. 2016, Correa-Herrera et al. 2017, Sandoval et al. 2020). The system has a micro-tidal regime with a tidal range < 40 cm. Salinity varies throughout the year (0.8 to 35.5), with the lowest values during the dry period in response to trade winds retaining freshwater in the Gulf (García-Valencia 2007). About 78% of the total mangrove extent in the Urabá Gulf is located in the Atrato River Delta (ARD) (approximately 4500 ha), the fringe forest is the dominant physiographic type of mangroves. Red mangrove, *Rhizophora mangle*, is the dominant species in more than 80% of the area, followed by white mangrove, *Laguncularia racemossa*, and black mangrove *Avicennia germinans* (Blanco-Libreros 2016). Likewise, the cattail, *Typha* sp. (Typhaceae), occurs in small extensions (Correa-Herrera et al. 2016).

Sample collection

Sampling of consumers and basal resources was undertaken between September and October 2016 in La Paila Bay, located at the center of the ARD (Figure 4). Ethical research protocols and sampling guidelines were authorized by National Aquaculture and Fisheries Authority (Autoridad Nacional de Acuicultura y Pesca) and the National Authority of Environmental Licensing (Autoridad Nacional de Licencias Ambientales) under the permits for fish catches 0524 (May 27th, 2014) and 00001827 (October 15th, 2015), respectively. Fish were collected using two gillnets, set side by side (200 m long and 2 m high, with mesh sizes of 7, 7.6, 10.2, and 12.7 cm), which were deployed during the day (06:00 to 12:00 hours) and the night (18:00 to 24:00 hours), and set near the mangrove fringe. Fish capture data was expressed as the total number of individuals and biomass (kg) for each of the species; also, it was expressed as catch per unit of effort (CPUE), estimated as mass (kg) per the number of hauls. We collected muscle tissue from 21 individual. *A. canteri* sized (total length) between 8.5 cm (minimum size captured) to 43.2 cm (maximum size captured). Muscle tissue was taken immediately below the anterior end of the dorsal fin. The sample size was due mainly to guarantee a similar number of samples per class since the smallest and largest fish were difficult to capture. Potentially important primary producers were collected in mangroves and the nearshore. Samples of fresh leaves (green) and senescent (yellow) mangrove leaves were collected from the dominant species (*Rhizophora mangle*). Samples of fresh live (green) macrophyte leaves, cattail blades (Typha sp.) were also collected. Epiphytic macroalgae (Chlorophytes; *Rhizoclonium* sp.) were sampled by scraping the roots of *R. mangle* using forceps. Suspended particulate organic matter (SPOM) as a proxy for phytoplankton, was sampled using a phytoplankton net (mouth diameter 35 cm; mesh size 25 µm). Unfortunately, sampling of benthic algae without sediment contamination was not possible, the benthic algae stable isotope values applied were instead global averages (δ^{13}C= -20.2 ± 2.1‰ and δ^{15}N= 2.4 ± 1.2‰) as described by Kristensen et al. (2017).

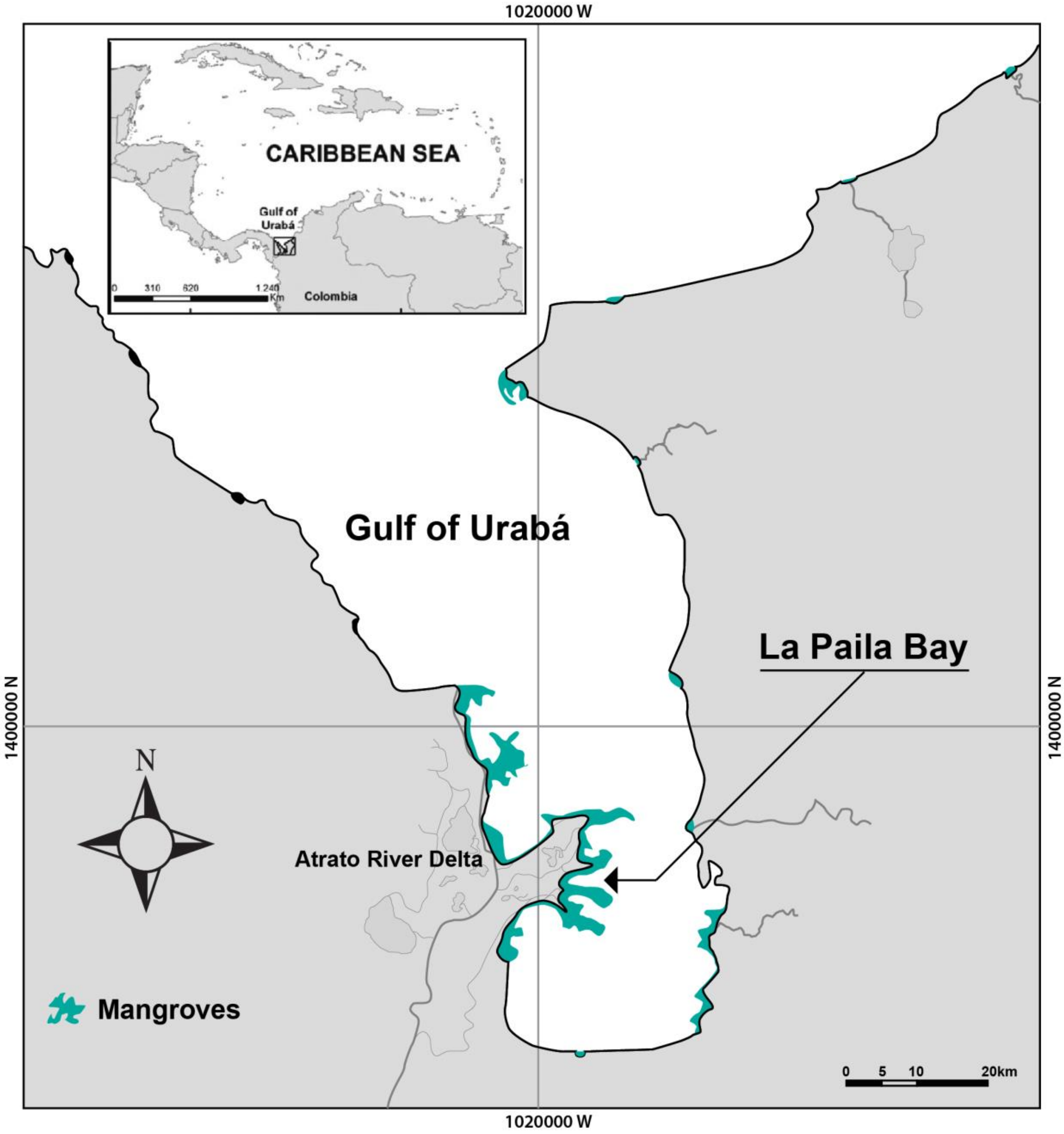

Figure 4. Map showing the study site in the Atrato River Delta of the Gulf Urabá, Caribbean Sea.

Sample processing

SPOM samples were passed through a 63 µm screen to remove large particles and zooplankton and then filtered on pre-combusted Whatman GF/F glass fiber filter. All samples were dried at 60 °C for at least 48 h in Petri dishes. 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 on a micro-scale and deposited in a tin capsule for isotopic analysis. Analyses were carried out 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 (Milan, Italy) coupled online via ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest, Bremen, Germany). Internal standards of - 30.6‰ and - 11.7‰ (V-PDB) were used for $\delta^{13}C$ analysis and internal standards of - 1.0‰ and + 16.0‰ (AIR) for $\delta^{15}N$. Precision calculated, after correction of the mass spectrometer daily drift, from standards systematically interspersed in analytical batches was better than ± 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$. Reference gases and in-house standards (with different C/N ratios and isotopic composition) 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 were expressed in delta notation in ppm (‰) based on the following equation: $\delta^{13}C$ or $\delta^{15}N$ = [(Rsample/Rstandard)-1], where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Data analysis

Because the variation of lipid content in tissues affects $\delta^{13}C$ 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: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3{:}32 + 0.99 \times C{:}N$, where $\delta^{13}C_{untreated}$ corresponds to the original $\delta^{13}C$ measurement of the sample. For primary producer samples, normalization was done when C% was >40%, following the equation: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 5.83 + 0.14 \times \%C$.

Ariopsis canteri individuals were grouped into three size classes using total length through the Sturges' rule (Daniel, 1997): k = 1 + 3,322 (log10 n) and w = R / k; where n is the number of individuals, k the number of intervals, R the path or range (major length – minor length) and W the amplitude. Eight (8) intervals were estimated. For class I (8-20 cm), the first three intervals were combined, the following two intervals for class II (21–32 cm), and the last three intervals for class III (> 32 cm). Kruskal–Wallis method was used to test for significant differences in $\delta^{13}C$ and $\delta^{15}N$ values relative to body size classes, followed by a Wilcoxon-paired test for differences in $\delta^{13}C$ and $\delta^{15}N$ values between size classes. Linear regressions were used to relate either $\delta^{15}N$ or $\delta^{13}C$ values to body size. Trophic levels (TL) of *A. canteri* classes were calculated following the mathematical formula proposed by Post (2002): $TL = \lambda + (\delta^{15}N_{consu} - \delta^{15}N_{base})/\Delta N$, where λ corresponds to the trophic level of the taxon producer representing the base of the trophic web, in this case, $\lambda = 1$ (primary producer). $\delta^{15}N_{base}$ corresponds to the average $\delta^{15}N$ value (mean for all primary producer) of the species used as the base of the trophic web.

The small sample size corrected SIBER ellipse areas (SEAc) (Jackson *et al.* 2011), and isotopic niche overlaps among classes were generated and calculated via Bayesian modeling with the SIBER package in R (R Core Team 2019). Likewise, Bayesian stable isotope (Five-source: SPOM (phytoplankton), mangrove, benthic algae, macrophytes, macroalgae) mixing models (MixSIAR) were used to determine the proportional contribution of different primary producers (Stock and Semmens, 2018). MixSIAR graphical user interface and model used were written in open source languages R (R Development Core Team, 2013) and Just Another Gibbs Sampler. The models were run with “fixed effects” and 3 chains until they “converged” using long or very long Markov Chain Monte Carlo (MCMC) length. The enrichment factors in MixSIAR models were used according to McCutchan et al. (2003): $\delta^{13}C$ (1.3 ± 0.3‰) and $\delta^{15}N$ (2.9 ± 0.32‰) per TL calculated for each size class. To present and interpret the mixing model outputs, we considered the conservative ranges (95% credible Bayesian intervals), as suggested by Fry (2013).

4.4. Results

Sampling fish and isotopic composition

In total, we collected fish from 72 sperate gillnet hauls. The total catch of individuals was 951 (CPUE: 13.2 ind./haul) and for biomass was 87.6 kg (CPUE: 1.2 kg/haul). Of this, *A. canteri* was the highest fish catch, representing 16.2% of individuals and 38.2% of total biomass (Figure 5). The variation of the isotopic composition of primary producers showed a range of 14.4‰ for $\delta^{13}C$ and 5.5‰ for $\delta^{15}N$ (Figure 6). $\delta^{13}C$ and $\delta^{15}N$ mean values for *R. mangle* leaves were -31.0 ±1.5‰ and 0.5 ± 0.7‰, respectively; for macroalgae $\delta^{13}C$ -30.8 ±0.0‰ and $\delta^{15}N$ 2.9 ± 0.3‰ (Table 5). SPOM (phytoplankton) exhibited the most enriched

^{13}C values (-24.7 ±1.6‰), not including the global average value for benthic algae (20.2 ±2.1‰). The macrophyte (*Typha* sp.) was the most ^{15}N-depleted (-0.6 ±0.1‰) (Table 5).

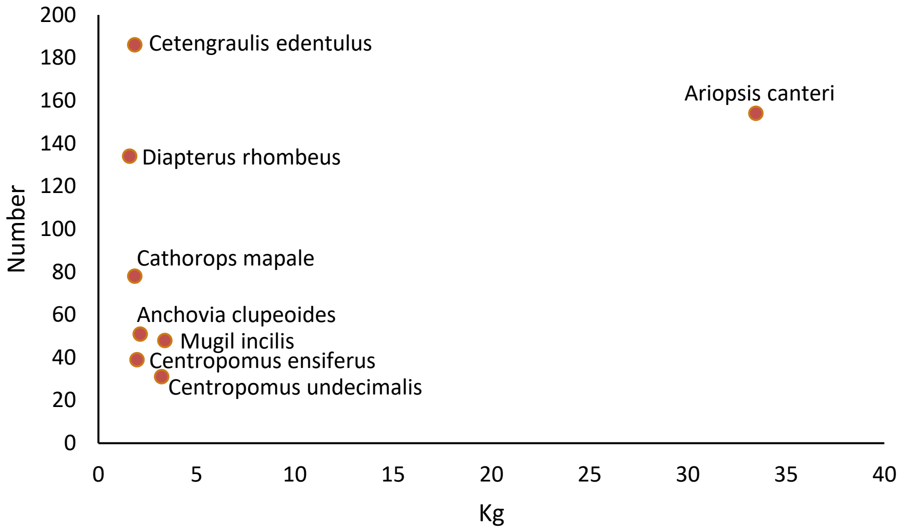

Figure 5. Biomass (Kg) and individuals (number) of fish species from total catch in La Paila Bay, Atrato River Delta.

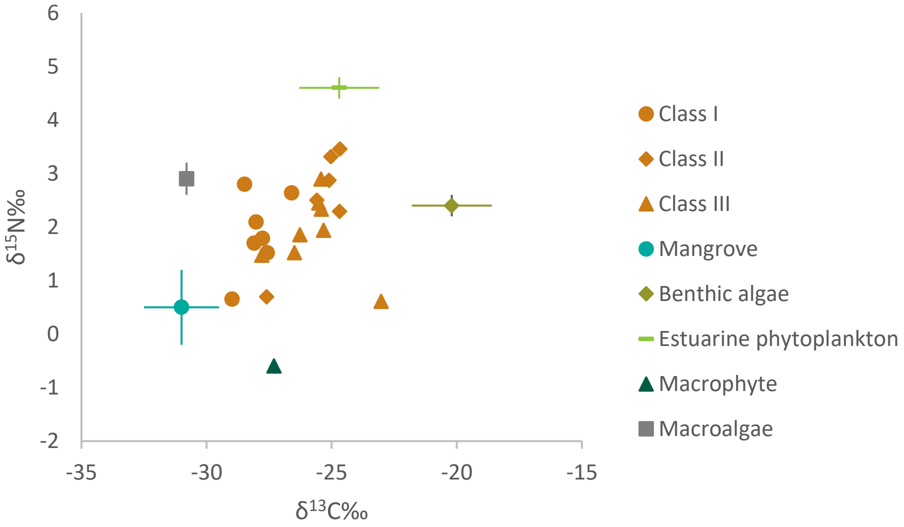

Figure 6. Plot of mean δ^{13}C vs δ^{15}N values (± SD) of basal resources and size classes of *Ariopsis canteri* in La Paila Bay, Atrato River Delta. Values have been adjusted for fractionation.

Variation in isotopic composition among the size of *A. canteri* classes showed a range of 6.6‰ for δ^{13}C and 3.5‰ for δ^{15}N (Figure 6). Ontogenetic changes were exhibited through significant differences in δ^{15}N among size classes (Kruskal–Wallis, $p<0.01$). The δ^{15}N of size class I was significantly lower (mean ± SD = 8.5 ± 0.7‰) than that of size classes II (9.8 ± 0.6 ‰; $p<0.05$) and III (10.0 ± 0.7 ‰; $p<0.01$) (Table 6). Likewise, significant differences in δ^{13}C were detected among size classes (Kruskal–Wallis, $p<0.01$). The δ^{13}C of size class I was significantly lower (mean ± SD = -25.0 ± 0.7 ‰) than that of size classes II (-22.2 ± 0.9 ‰; $p<0.01$) and III (-22.0 ± 2.0 ‰; $p<0.01$) (Table 6). The body size of *A. canteri* was positively and significantly correlated with δ^{15}N and δ^{13}C values ($P < 0.05$; Figure 7).

Table 5. Carbon and nitrogen stable isotope values from primary producers collected in the Urabá Gulf, and benthic algae values from global averages by Kristensen et al. (2017).

Species/Taxon	**N**	**δ^{13}C (‰) Mean ± SD**	**δ^{15}N (‰) Mean ± SD**
Mangrove			
Rizhophora mangle	10	-31.0 ± 1.5	0.5 ± 0.7
Macroalgae			
Chlorophytes (*Rhizoclonium* sp.)	3	-30.8 ± 0.0	2.9 ± 0.3
Microalgae			
SPOM (Phytoplankton)	2	-24.7 ± 1.6	4.6 ± 0.2
Benthic algae		-20.2 ± 2.1	2.4 ± 1.2
Macrophyte			
Typha sp.	3	-27.3 ± 0.1	-0.6 ± 0.1

Table 6. Values of δ^{15}N and δ^{13}C in different size classes of *Ariopsis canteri*.

Samples	**n**	**L_T**	**δ^{15}N(‰)**				**δ^{13}C(‰)**			
			Mean	**SD**	**Minimum**	**Maximum**	**Mean**	**SD**	**Minimum**	**Maximum**
Class I	7	8 – 20	8.5	0.7	7.3	9.4	-25.0	0.7	-26.0	-23.6
Class II	6	21 – 32	9.8	0.6	8.56	10.4	-22.2	0.9	-24.1	-21.2
Class III	8	> 32	10.0	0.7	8.8	11.0	-22.0	1.3	-24.1	-19.4

Stable-isotope mixing models

Isotopic niche overlap measures showed that class III SIBER ellipse overlapped 31% with that of class II, though only 10% of the class I ellipse overlapped with that of class III. Class I SIBER ellipse overlapped 13% with that of class II (Table 7). Class III presented the highest total occupied isotopic niche area (Table 7), as well as the highest SEAc values (Table 8).

Class III *A. canteri* showed the highest estimated trophic level (TL: 3.8), followed by class II (TL: 3.7) and class I (TL: 3.3) (Table 9). For class I, the median estimated contribution of macroalgae was the highest (34%: 6% to 57% CI), followed by macrophytes (26%: 7% to 50% CI). For class II, the median estimated contribution of macrophytes was the highest (17%: 7% to 53% CI), followed by benthic algae (26%: 3% to 50% CI). For class III, the estimated contribution of macrophytes was the highest (30%: 4% to 53% CI), followed by SPOM (phytoplankton) (26%: 1% to 42% CI) (Table 9).

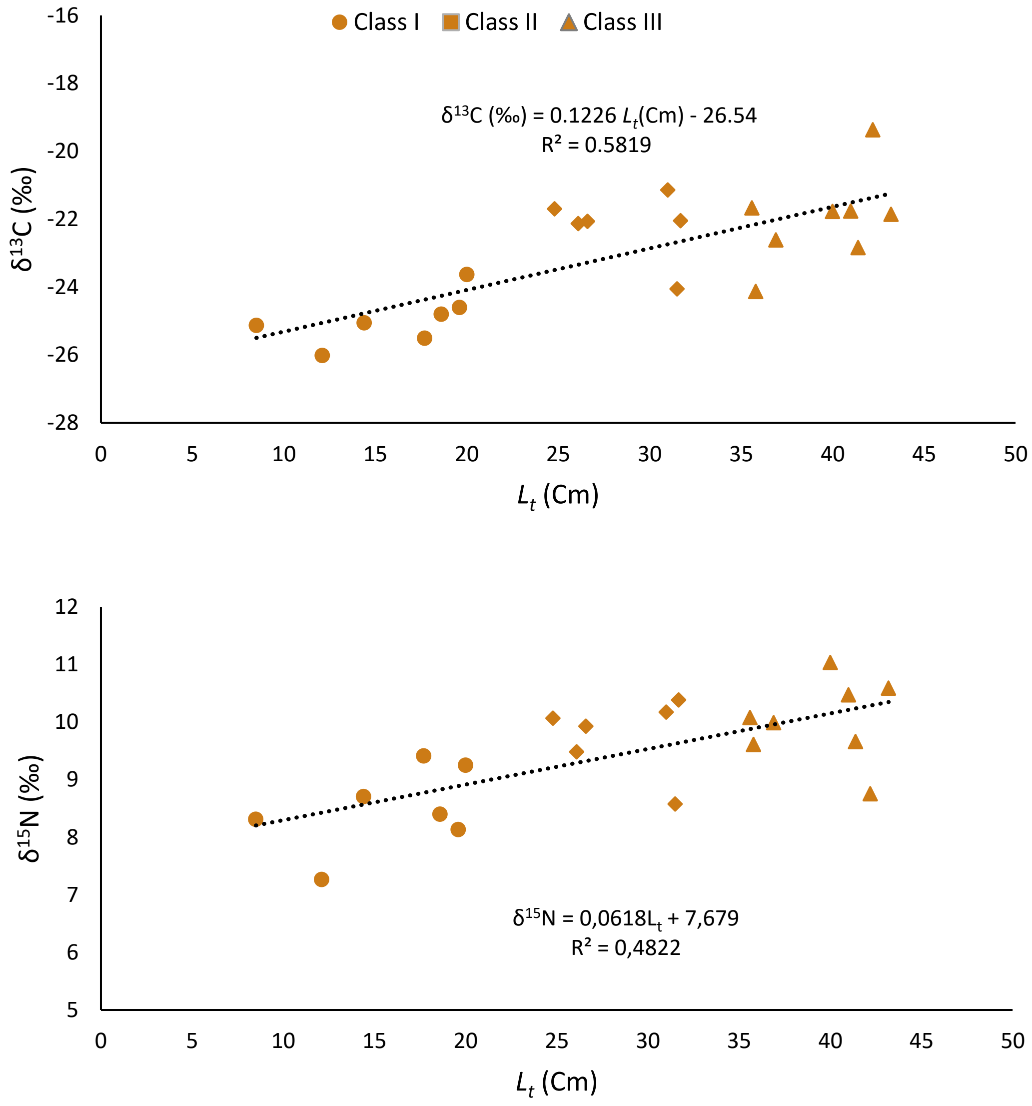

Figure 7. Relationships of (higer) δ^{13}C and (lower) δ^{15}N values with total length (Lt) of *Ariopsis canteri* (n = 21).

4.5. Discussion

Previous stomach content analysis evidenced an ontogenic change in the diet of *A. canteri*, the largest sized fish fed mainly on other fish, anomuran crustaceans and shrimp, tending to a generalist diet (Levins index = 0.76), while the smaller fish fed mainly on copepods, being specialist feeders (Levins index = 0.075) (Sandoval et al. 2014). The present findings using stable isotopes values are consistent with those based on diets, where isotopic niche breadth was highest in the largest body-size class. Likewise, we showed that as this species increased in size, nitrogen isotopic value increased, indicating that larger individuals were feeding at a higher trophic level, supporting our first hypothesis.

Table 7. Proportion of observed overlapped Bayesian ellipses, mean % overlap area of ellipses and standard deviation in different size classes of *Ariopsis canteri*.

Classes	**Proportion of the overlaps**	**Mean % overlaps**	**Standard Deviation**
I-II	0.98	12.99	9.25
I-III	1.00	9.83	7.82
II-III	1.00	30.64	11.61

Many fish species have displayed similar patterns of increasing trophic position and niche breadths with size (e.g., pacific blue marlin and yellowfin tuna), with larger individuals exhibiting higher $\delta^{15}N$ values presumably due to larger fish consuming larger prey that feed at higher trophic levels (Davenport and Bax, 2002, Graham et al. 2007, Chang et al. 2019). Likewise, ontogenetic variation in the diet has been common for estuarine fish, including catfishes (Gning et al. 2008, Pessanha and Araujo, 2012, Ramos et al. 2014, Giarrizzo and Saint-Paul 2008, Dantas et al. 2013). This may be related to changes in abundance, diversity, and prey availability (Gerking 1994, Pessanha and Araujo 2012), but may also be due to changes in the type of prey according to season and estuarine habitat used (Ramos et al. 2014, Vaslet et al. 2012), and to the size of the mouth, since adults can successfully capture larger preys or larger quantities of particular items (Dantas et al. 2013). Ontogenetic variation in *A. canteri* diet may be better related to changes in the type of prey according to the estuarine habitat used and the size of the mouth, as described below.

Table 8. Calculated total occupied niche area generated based on specific convex hull estimates generated via Bayesian modeling with SIAR package in R for different size classes of *Ariopsis canteri*.

Class	**TA (‰^{2})**	**SEA (‰^{2})**	**SEAc (‰^{2})**
I	2.42	1.46	1.76
II	1.25	0.93	1.16
III	4.41	2.89	3.37

The highest catches for *A. canteri* show their importance in artisanal fisheries in the region, and support the idea that mangroves are an essential habitat for them since fishing was taken near the mangrove fringe. Catches of different size classes of *A. canteri* suggest that mangroves likely act simultaneously as nursery and feeding ground habitats for this species. Likewise, ontogenetic variation in its diet may be related to changes in the type of prey according to estuarine habitat used, and the mouth size; regarding that the largest fish fed mainly on other fish, anomuran crustaceans and shrimp near the mangrove fringe, while smaller fish fed mainly on harpacticoid copepods near mangrove roots (Sandoval et al. 2014). The above decreasing intraspecific competition between small and large individuals, as evidenced for catfishes (Dantas et al. 2013), and other estuarine fish (Brito et al. 2019).

Table 9. Primary producer contributions (50% quantiles = median estimates, range = 95% Bayesian credible intervals) for size classes of *Ariopsis canteri* using MixSIAR.

Class	**TL**	**SPOM (Phytoplakton)**		**Mangrove**		**Benthic algae**		**Macrophytes**		**Macroalgae**	
		50%	**Range**	**50 %**	**Range**	**50%**	**Range**	**50%**	**Range**	**50%**	**Range**
I	3.3	14	01-35	12	1-45	9	0-26	26	7-50	34	6-57
II	3.7	14	1-43	10	0-37	26	3-50	27	3-53	17	0-40
III	3.8	26	1-42	11	0-40	16	1-42	30	4-53	12	1-39

The overlap in food niches between classes is also consistent with ontogenic feeding shifts of *A. canteri*, also supporting our first hypothesis. Whereas much of class II total occupied niche area fell within that class III, the latter displayed a wider isotopic niche area that barely overlapped with class I. Conversely, our isotopic results for the trophic levels were similar to those observed from stomach content analyses for other catfish species with zoo-benthivores habits in the Colombian Caribbean, i.e., *Bagre marinus* (3.6) and *Cathorops spixii* (3.5)

(García and Contreras 2016). Thus, the New Granada Sea Catfish may be classified as a second-level consumer in ARD estuary.

This study considered the most abundant primary sources in the ARD, whose values were relatively ^{13}C depleted relative, to the ranges values from the literature indicated by Bouillon et al. (2008): for mangrove leaves (-29.4 to -27.0 ‰), microalgae (-23.0 to -18.0‰) and macroalgae (-23.1 to -16.4‰). In this way, for benthic algae from ARD is expected to be slightly depleted from global averages values used, having implications on the interpretation of the result (see later). Further, δ^{13}C values for macrophytes (Typha sp.) were similar to values previously reported from the Gulf (-27.3 ±0.1‰) (Rua et al. 2017). The highest estimated contribution of primary producers for each class was different. For class I, the highest estimated contribution was macroalgae, which are usually abundant on the roots of *R. mangle* from ARD (Hurtado-Santamaria and Quan-Young 2016). It is suggesting that the smallest *A. canteri* fish use the roots of *R. mangle* as nurseries and feeding habitats, where fish could feed mainly on small preys as harpacticoid copepods (Sandoval et al. 2014). For class II, the highest estimated contributions were macrophytes and benthic algae, suggesting that medium-sized fish feed beyond the mangrove roots, where fish could feed mainly on larger preys than copepods as shrimps and anomurans (Sandoval et al. 2014). For class III, the highest estimated contributors were macrophytes and SPOM (phytoplankton), suggesting that the biggest fish feed also beyond the mangrove roots, where fish could feed mainly on larger preys such as shrimps and anomurans, but also fish as centropomids (Sandoval et al. 2014). Since benthic algae from ARD is expected to be slightly depleted from global averages values used, benthic algae contribution may be being slightly underestimated, and mangrove contribution slightly overestimated.

Based on the above, our second hypothesis that mangrove is the main source fueling *A. canteri* was rejected. However, mangrove contribution was slightly greater for the smallest fish. Giarrizzo et al. (2011) for the ariid fish, *Cathorops* sp., from northern Brazilian mangrove ecosystem estimated mangrove contribution *ca.* 20% to 40% CI, although their model includes only two sources, which may inflate the estimated contribution of mangrove swamp higher (Phillips et al. 2014). The authors described that mangrove carbon could be assimilated as POM by calanoid copepods and transferred to higher trophic levels by ingestion of these invertebrates by chaetognaths small and zooplanktivorous pelagic fish. Furthermore, mangrove carbon can also be transferred through the crab, *Aratus pisonii*, which consumes mangrove leaves (Giddins et al. 1986) and has been found in the gut content of *A. canteri* (Sandoval et al. 2014). However, a detailed understanding of the primary contributors and possible pathways in ARD estuary food webs are required.

In conclusion, results support our first hypothesis confirming ontogenic feeding shifts of *A. canteri*. Results suggest that mangroves serve as nurseries and feeding habitats for this species and that ontogenic feeding shifts allow a decrease in intraspecific competition between small and large individuals. Our second hypothesis was rejected; the estimated contribution of macroalgae and macrophytes were the highest. However, the importance of mangroves supporting *A. canteri* seems unquestionable, either because of their relative trophic contribution or mainly because of the substrate/habitat that supports sources as macroalgae and benthic algae in the food webs.

The New Granada sea catfish is one of the most common species in mangrove-associate fisheries in the Urabá Gulf, where there are more than 47 villages and 1500 families engaged in local commerce and/or subsistence fishing, with few economic alternatives. (LOPEGU 2017). Therefore, this has important conservation implications. These results can be used in EBFM focused on the protection of extensive mangroves areas in the Southern Caribbean, since the general objective of this approach is to maintain healthy marine ecosystems and the fisheries they support (Pikitch et al. 2004).

4.6. Acknowledgements

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Chapter 4. Diversity in food sources sustaining estuarine consumers in a major mangrove area of the southern Caribbean Sea: a stable isotope analysis.

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Rhizophora mangle, Atrato River Delta (L.A. Sandoval).

3.1. Abstract

Much research on marine food webs is aimed at understanding the pathways of energy and elements from the resource base to top consumers. In the Caribbean, studies on trophic networks in mangrove systems, using isotopic analysis, have typically focused on settings where mangroves are found in the proximity of seagrasses, coral reefs or both. Here stable isotopes of carbon and nitrogen were used to describe the main resource base to the food-web and to determine the main trophic pathways in an estuarine embayment of the Atrato River Delta, Colombia, where fringing mangroves dominate the coastline and are not directly connected with other productive coastal habitats such as seagrass or coral reefs. Results showed a food web with a maximum length of 4.6 trophic levels. Bayesian mixing models with previous knowledge on feeding habits of consumers suggests that most consumers use a mixture of sources and therefore the food wed includes materials moving along a mix of intertwined energertic pathways. However, the potential pathways for five different basal sources of organic matter were shown: (1) Estuarine phytoplankton contributes directly to mesozooplaknton and is transferred to the zooplanktivorous food chains. (2) Mangrove contributes directly to herbivorous crabs (sesarmids) and indirectly to planktivorouss fish (engraulids) and the zooplanktivorous food chains. (3) Microphytobenthos contributes directly and indirectly to phytobenthivorous fish (mugilds) and carnivorous epibenthic shrimp (peneids), respectively. (4) Macroalgae contributes directly to epibenthic omnivorous epibenthos (gastropods: neritids) and omnibenthivorous fishes (ariids and gerrids), and indirectly to different epibenthic carnivores and zoobenthivorous fish. (5) Macrophytes contributes directly and indirectly to herbivorous (ocypodids) and carnivorous (panopeids) crabs, respectively. Mangroves contributed significantly to the diet of two of the most common fish species in the local artisanal fishery: *Centropomus undecimalis* (45.7% median estimate: 1.3% to 80.3% CI) and *Centropomus pectinatus* (33.1% median estimate: 1.0% to 78.5% CI), and serve as substrate/habitat that supports sources as macroalgae and benthic algae supporting two other commercial fish species (*A. canteri* and *M. incilis*). These results can potentially be used in ecosystem-based fishery management.

Key words: Colombia, Gulf of Urabá, Atrato River Delta, Pathway, MixSIAR, Carbon, Nitrogen.

3.2. Introduction

Much research conducted 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 webs 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 trophic flows, as proxies of ecosystem functioning, is important for predicting the resilience of coastal ecosystems to human disturbances (Gascuel et al. 2008). The loss or disturbance of key primary producers, density or composition of predators or preys, or food web connectivity can lead to populations collapses (Link 2002, Abrantes et al. 2015a). Food web studies in estuarine communities tracing energy sources are scarce. Yet, such studies are important for the informed management and mitigation of human impacts, and the conservation and restoration of coastal ecosystems (e.g. Abrantes et al. 2015a, Qu et al. 2019).

Food webs and pathways of organic matter in estuaries are complex due to existence of the potential inputs from upstream (riverine), downstream (oceanic), within estuary (e.g., seagrass and microalgae), and lateral (e.g., mangroves and salt marsh) sources of matter, elements and energy (Bouillon et al. 2011). The use of stable isotopes in such a setting potentially allows the characterization of the origins and movements of organic and inorganic matter, offering advantages for the study of estuarine food webs (Peterson and Fry 1987, Bouillon et al. 2011, Duarte et al. 2018). For invertebrate consumers, stable isotope studies have also been instrumental in pointing out the surprising diversity in food sources and specialization in mangrove ecosystems (Bouillon et al. 2011). Moreover, the potential of isotopic analysis to identify the primary sources that support fish production and to understand habitat use by diverse fish species has benn highlighted (Fry and Ewel 2003, Layman 2007, Layman et al. 2012).

Some studies have found that mangrove carbon is important for benthic and pelagic consumers (e.g. Giarrizzo et al. 2011, Lovelock et al. 2015, Abrantes et al. 2015b, Medina-Contreras et al. 2020). Conversely, other studies have found that mangrove detritus is only exported and incorporated into coastal food webs to a very limited extent (e.g. Lee 2000, Bouillon et al. 2002, Vaslet et al. 2015, Santos et al. 2020). Previous studies have identified varous primary sources for consumers in mangrove ecosystems including algae (Nyunja et al.

2009), microphytobenthos (Lee 2000), particulate organic matter (Chanton and Lewis 2002), phytoplakton (Rodelli et al. 1984), and sea grasses (Loneragan et al. 1997, Nyunja et al. 2009). Other authors have shown the importance of mangrove carbon for juvenile shrimp species (Loneragan et al. 1997, Chong et al. 2001, Abrantes et al. 2015b), reef fish (Nagelkerken and Van Der Velde 2004a), estuarine fish (Giarrizzo et al. 2011, Zagars et al. 2013, Abrantes et al. 2015b), crabs (Harada and Lee 2016), and sessile coral invertebrates (Granek et al. 2009).

In the Caribbean, studies of trophic networks in mangrove systems, using isotopic analysis, have focused on settings in the vicinity of seagrasses, coral reefs or both, in which, mangrove carbon has not been found to be an important source (Nagelkerken and Van Der Velde 2004b, Vaslet et al. 2012, Igulu et al. 2013, Vaslet et al. 2015). However, Mancera (2003), through studies in the Ciénaga Grande de Santa Marta in the Colombian Caribbean, a system not directly connected with other highly productive coastal habitats, such as seagrasses and coral reefs, proposed that mangroves can be important sources in estuarine food webs depending on the coastal geomorphology, salinity and plankton productivity.

The Atrato River Delta (ARD) is an estuary with extensive fringing mangrove areas (ca. 4450 ha) in the southern Caribbean Sea (Colombia), lacking other highly productive coastal habitats (Sandoval et al. 2020). Leaf litter mean mass in ARD mangroves is the highest reported for *R. mangle* dominated forests world-wide (Riascos and Blanco-Libreros 2019). ARD has been recently highlighted as an important habitat sustaining artisanal fisheries (Correa-Herrera et al. 2016, LOPEGU 2017, Arango-Sánchez et al. 2019). Recently, Sandoval et al. (2020) positively correlated mangrove area with catches for three of the most common fish species in the local artisanal fishery in the southern Caribbean Sea (*Ariopsis canteri*, *Mugil incilis*, and *Sciades proops*). However, mangroves are threatened by illegal logging (Blanco et al. 2012), ecological information about estuarine nekton and benthos is limited (but see Hernandez-Morales et al. 2018, Arenas-Uribe et al. 2019, Sandoval et al. 2020), and a fishery management plan for the region does not exist. Accordingly, to provide evidence on the function of fringing mangroves along the ARD, the aims of this study were: a) to determine the number of trophic levels, b) to determine the potential contribution of food sources for epibenthic and fish consumers according to trophic guilds, using stable isotopic tracers and models, and c) to discuss the direct and indirect links between mangroves and artisanal fisheries. We hypothesized that mangroves could be a major food source sustaining some estuarine consumers in the ecosystem.

3.3. Material and methods

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 (Figure 8). 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 to 100mm in the dry season (December to April) and 200 to 300mm in the rainy season (May to 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 to 35.5), with a counter-intuitive pattern, with lowest salinity values being recorded during the dry period in response to trade winds increasing residence times of fresh water in the Gulf (García-Valencia 2007). The Atrato River Delta (ARD) includes an extensive mangrove habitats (approximately 3700 ha), where fringe forest is the dominant physiographic type of mangroves, 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 mangroves is practiced only for local commerce and/or subsistence (Sandoval et al. 2020, LOPEGU 2017). The study was undertaken between September and October 2016 (rainy season) in La Paila Bay, an embayment in the ARD (Figure 4). The bay is shallow (< 5m) with waters that are poorly win-mixed as the Atrato River plume has a strong stratification around 2 m (LOPEGU 2017, Montoya et al. 2017).

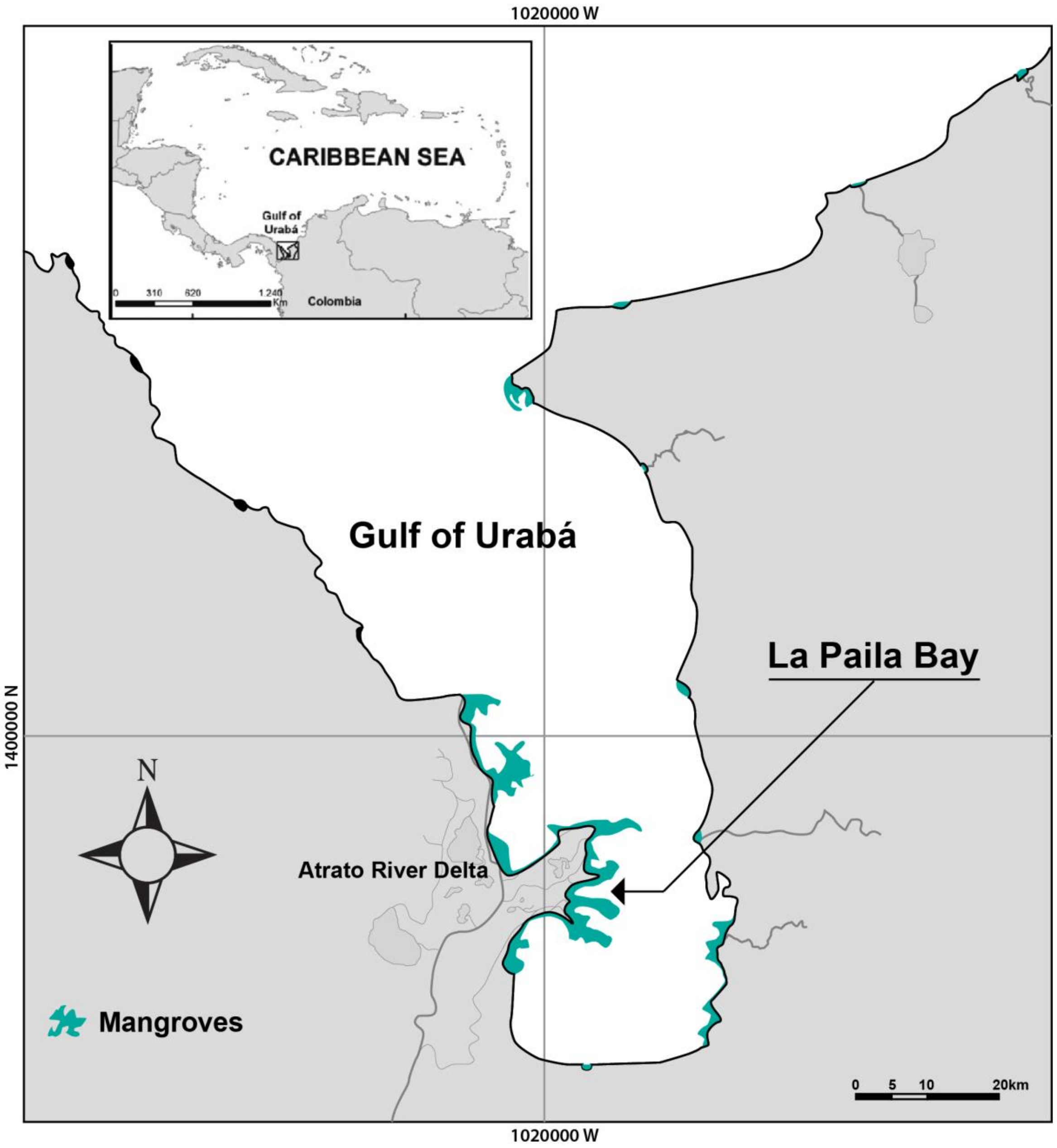

Figure 8. Map showing the study site in the Atrato River Delta of the Gulf Urabá, Caribbean Sea.

Sample collection

Potential food sources and consumers were collected in mangroves and the nearshore of La Paila Bay. Each biological sample consisted of a pool of several specimens of the same species of about the same length. At least three samples of each basal resource (Table 10) and consumer (Table 11 and 12) were collected when possible. Samples of fresh live (green) and senescent (yellow) mangrove leaves were collected from the dominant species (*R. mangle*).

Samples of fresh live (green) macrophyte leaves, cattail blades (*Typha* sp.), were also collected. Epiphytic macroalgae (Chlorophytes; *Rhizoclonium* sp.) were sampled by scraping the roots of *R. mangle* using forceps. Unfortunately, sampling of benthic algae without sediment contamination was not possible, the benthic algae stable isotope values applied were instead global averages (δ^{13}C= -20.2 ± 2.1‰ and δ^{15}N= 2.4 ± 1.2‰) as described by Kristensen et al. (2010). Phytoplankton samples were taken using a phytoplankton net (mouth diameter 35 cm; mesh size 25 µm), which were included in the analysis as estuarine phytoplankton due to their relatively lower δ^{13}C value. Likewise, another possible source for marine phytoplankton stable isotope values (with higher δ^{13}C) were included from global averages (δ^{13}C= -21.3 ± 1.1‰ and δ^{15}N= 8.6 ± 1.0‰) following Peterson et al. (1985). Meso-zooplankton samples were taken using a plankton net (mouth diameter 35 cm; mesh size 300 µm). Additionally, epibenthos was collected manually from inside the mangroves (three herbivorous crabs, one omnivorous gastropod, and three carnivorous crabs).

Table 10. Carbon and nitrogen stable isotope values from primary producers collected in the Gulf of Urabá, Colombian Caribbean. ACR: acronym; n: number of samples. SD: standard deviation. Marine phytoplankton: global averages from Peterson et al. (1985). Benthic algae: global averages from Kristensen et al. (2017).

Species/Taxon	**ACR**	**n**	**δ^{13}C (‰) Mean ± SD**	**δ^{15}N (‰) Mean ± SD**	**C/N Mean ± SD**
Mangrove					
Rizhophora mangle	Rhiz	10	-31 ± 1.5	0.5 ± 1	155.1 ± 23
Macrophyte					
Typha sp.	Typh	3	-27.3 ± 0.1	-0.6 ± 0	24.3 ± 1
Macroalgae					
Chlorophytes (*Rhizoclonium* sp.)	Chlo	3	-30.8 ± 0.0	2.9 ± 0	20.5 ± 1
Phytoplankton					
Estuarine phytoplankton	Ephy	2	-24.7 ± 1.6	4.6 ± 0	8.3 ± 2
Marine phytoplankton	Mphy		-21.3 ± 1.1	8.6 ± 1.0	ND
Microphytobenthos					
Benthic algae	Balg		-20.0 ± 2.1	2.4 ± 1.2	ND

Table 11. Mean and standard deviation of carbon and nitrogen stable isotope values of invertebrate consumers collected in the Gulf of Urabá, Colombian Caribbean. ACR: acronym; n: number of samples; N: number of pooled individuals in each sample; TL: trophic levels; L: body length.

Species/Taxon	**ACR**	**n(N)**	**L(cm)**	**δ^{13}C(‰)**	**δ^{15}N(‰)**

Meso-zooplankton											
Zooplankton	Zoop	3				-24.3	±	3.1	6.0	±	1.2
Luciferids	Luci	3(300)				-19.5	±	0.0	5.7	±	0.0
Brachyuran zoeae	Zoea	1(50)				-19.9			4.4		
Panaeoidean mysis	Mysi	1(500)				-29.9			4.3		
Calanoid copepods	Cope	3(600)				-20.7	±	0.9	6.1	±	1.1
Epibenthos											
Gastropoda											
Thaisella coronata trinitatensis	Tcor	3	2.3	±	0.1	-24.5	±	0.2	8.0	±	0.1
Neritina virgínea	Neri	9(6)	1.5	±	0.2	-25.7	±	1.1	5.8	±	0.7
Grapsidea											
Aratus pisonii	Apis	9(5)	2.1	±	0.2	-25.6	±	0.8	3.9	±	0.7
Pachygrapsus transversus	Pach	3(3)	1.4	±	0.1	-25.4	±	0.3	4.8	±	0.1
Ocypodidae											
Uca spp.	Uca	9(3)	2.0	±	0.3	-27.8	±	0.8	3.6	±	0.9
Panopeidae											
Panopeus rugosus	Prug	3	3.6	±	0.0	-25.6	±	0.8	7.7	±	0.8
Eurytium limosum	Elim	3	3.4	±	0.1	-25.3	±	0.3	6.8	±	0.3
Shrimp and swimming crab											
Penaeidae											
Litopenaesu schmitii	Lsch	3(2)	12.6	±	0.7	-23.7	±	0.2	7.3	±	0.1
Portunidae											
Callinectes bocourti	Cboc	3	4.7	±	0.3	-26.0	±	0.3	7.1	±	0.3

Four plankthivorous fishes, one phytobenthivorous fish, three omnibenthivorouss fishes, five zoobenthivorous fishes, five piscivorous fishes, one shrimp and one swimming crab species were collected using a gillnet (100 m long and 2 m high, with mesh sizes of 7, 7.6, 10.2, and 12.7 cm). 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, muscle was taken from chelae.

Table 12. Mean and standard deviation for carbon and nitrogen stable isotope values of fish collected in the Gulf of Urabá, Colombian Caribbean. N: number of samples. L: total length.

Species/Taxon	**ACR**	**N**	**L(cm)**			**δ^{13}C (‰)**			**δ^{15}N (‰)**		
Ariidae											
Ariopsis canteri	Acan	3	19.4	±	0.6	-24.3	±	0.5	8.6	±	0.5
Cathorops mapale	Cmap	3	19.4	±	1.0	-26.4	±	0.6	8.6	±	0.2
Carangidae											
Caranx crysus	Ccry	2	14.5	±	0.6	-21.6	±	0.1	10.1	±	0.6
Caranx hipos	Chip	3	24.0	±	0.2	-20.0	±	1.2	11.0	±	0.2

Oligoplites saliens	Osal	3	26.3 ± 0.2	-20.8 ± 0.4	11.3 ± 0.2
Centropomidae					
Centropomus ensiferus	Cens	4	21.6 ± 0.5	-24.4 ± 0.8	10.9 ± 0.5
Centropomus pectinatus	Cpec	3	20.8 ± 0.8	-25.0 ± 1.8	9.7 ± 0.5
Centropomus undecimalis	Cund	3	26.7 ± 1.0	-24.3 ± 1.5	11.0 ± 0.8
Clupeidae					
Opisthonema oglinum	Oogl	2	21.8 ± 0.0	-20.0 ± 0.6	9.3 ± 0.0
Engraulidae					
Anchovia clupeoides	Aclu	3	21.3 ± 0.2	-25.2 ± 0.2	9.9 ± 0.1
Centengraulis edentulous	Cede	3	11.1 ± 0.0	-21.4 ± 0.4	8.5 ± 0.3
Ephippidae					
Chaetodipterus faber	Cfab	3	21.6 ± 4.2	-26.1 ± 0.8	9.8 ± 0.4
Gerridae					
Diapterus rhombeus	Drho	2	16.5 ± 0.0	-25.5 ± 0.8	9.2 ± 0.4
Eugerres plumieri	Eplu	3	17.2 ± 0.2	-26.5 ± 0.3	8.9 ± 0.1
Lutjanidae					
Lutjanus jocu	Ljoc	3	16.8 ± 0.3	-24.9 ± 1.1	9.8 ± 0.1
Mugilidae					
Mugil incilis	Minc	3	25.3 ± 0.6	-17.7 ± 0.9	5.8 ± 0.4
Scianidae					
Bardiella ronchus	Bron	3	18.5 ± 0.4	-23.4 ± 0.7	10.6 ± 0.4
Trichuiridae					
Trichurus lepturus	Tlep	3	71.7 ± 0.9	-21.1 ± 0.2	12.2 ± 0.3

Sample processing

Water samples for phytoplankton were filtered onto pre-combusted (450 °C, 24 h) glass fiber filters (GF/C filters) with a nominal pore-size of 1.2 µm. Mangrove leaves, cattail blades and macroalgae were cut into small pieces and rinsed with distilled water. Zooplankton samples were examined microscopically, identifying representative taxa, then isolated and consolidated onto pre-combusted filters using forceps. For crabs and molluscs, the chelae and foot muscle, respectively, were removed to form individual or composite samples according to the size of the specimens. For macro-consumers, all muscle tissue samples were thoroughly rinsed with distilled water.

All samples were dried at 60 °C for at least 48 h in Petri dishes. 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 capsule for isotopic analysis. Analysis 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 (Milan, Italy) coupled online via ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest, Bremen, Germany). Internal standards of - 30.63‰ and - 11.65‰ (V-PDB) have been used for $\delta^{13}C$ analysis and internal standards of - 1.0‰ and + 16.0‰ (AIR) for $\delta^{15}N$. Precision calculated, after correction of the mass spectrometer daily drift, from standards systematically interspersed in analytical batches was better than ± 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$. Reference gases and in-house standards (with different C/N ratios and isotopic composition) 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 were expressed in delta notation in ppm (‰) based on the following equation: $\delta^{13}C$ or $\delta^{15}N = [(Rsample/Rstandard)-1]$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Data analysis

Because variation in tissue lipid content can affect $\delta^{13}C$ values and ecological interpretations, a mathematical normalization method was used to standardize lipid content for samples (Post et al. 2002). Animal samples were normalized if C:N was >3.5, following the equation: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3:32 + 0.99 \text{ x } C : N$, where $\delta^{13}C_{untreated}$ corresponds to the original $\delta^{13}C_{measurement}$ of the sample. For primary producer samples, normalization was done when C% was >40%, following the equation: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 5.83 + 0.14 \text{ x } \%C$.

Trophic levels (TL) of consumers were calculated following the mathematical formula proposed by Post (2002): $TL = \lambda + (\delta^{15}N_{consu} - \delta_{15}N_{base})/\Delta_N$, where λ corresponds to the trophic level of the primary producer representing the base of the trophic web, in this case $\lambda = 1$. $\delta^{15}N_{base}$ corresponding to an overlla mean $\delta^{15}N$ value (1.8‰) calculated for primary producers but excluding marine phytoplankton and benthic algae since both not were estimated from ARD (Table 1). Δ_N corresponds to the average trophic enrichment value for $\delta^{15}N$, in the present case with value of 2.9‰ for nitrogen according to McCutchan et al. (2003).

Epibenthos were classified into three trophic categories: herbivores, omnivores and carnivores, while fish were classified into five trophic categories: planktivores, phytobenthivores, omnibenthivores, zoobenthivores, and piscivores. Feeding guilds were assigned according to information found in local literature (Sandoval 2012) and Fishbase

(Froese and Pauly 2007). Bayesian stable isotope mixing models based on the open source language R (R Development Core Team 2013) were used to estimate the proportional contribution of different primary producers to consumers using MixSIAR (Stock and Semmens 2015). The models were run with “fixed effects” and 3 chains until they “converged” using long or very long Markov Chain Monte Carlo (MCMC) length. Primary sources included were mangrove (*R. mangle*), macrophyte (*Typha sp.*), macroalgae (Chlorophytes: *Rhizoclonium* sp.), benthic algae, estuarine and marine phytoplankton. To select the most accurate sources for testing, excluding food sources was based on the knowledge of their local availability and feeding behavior of species (Phillips at al. 2014). To illustrate the difference in the selection of sources in mixing models, the results with all endmembers for some fishes are showed.

The trophic enrichment factors in MixSIAR models were used according to McCutchan et al. (2003). For mesozooplankton 0.5 ± 0.3‰ for δ^{13}C and 2.3 ± 0.18‰ for δ^{15} N. For fish and epibenthos 1.3 ± 0.3‰ for δ^{13}C and 2.9 ± 0.32‰ for δ^{15} N, per TL 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 tipically used (e.g. Harada and Lee 2016). Accordingly, for herbivorous crabs we used meand ± SD values based on our experiments examinning trophic discrimination between the crab *Aratus pisonii* and its diet of mangrove leaves: δ^{13}C: 5.4 ± 0.9 ‰ and δ^{15} N: 3.9 ± 0.5 ‰ (Sandoval et al. submitted: *Chapter five of this thesis*).

3.4. Results

Isotopic composition of carbon sources

The variation of the isotopic composition of analyzed primary producers showed a range of 6.3‰ for δ^{13}C and 5.6‰ for δ^{15}N (Fig. 2). Mean ±SD δ^{13}C and δ^{15}N values for *R. mangle* leaves were -31.0 ±1.5‰ and 0.5 ± 0.7‰, respectively (Table 1). Macrophyte (*Rhizoclonium* sp.) has similar δ^{13}C -30.8 ± 0.0‰ but slightly higher δ^{15}N 2.9 ± 0.3‰ values (Table 10). Estuarine phytoplankton exhibited ^{13}C enriched values (-24.7 ± 1.6‰) relative to otrher putative source (Table 10), while the macrophyte (*Typha* sp.) was the most ^{15}N-depleted (-0.6 ± 0.1‰) (Table 10).

Isotopic composition of consumers

A total of five meso-zooplankton categories were analyzed: luciferids, brachyuran zoeae, paneoidean mysis, calanoid copepods, and zooplankton, the latter consisting of a mixture of the other four categories (Table 11). Mean δ^{13}C values ranged between -29.9‰ (panaeoidean mysis) and -19.5‰ (luciferids). Mean δ^{15}N values ranged between 4.3‰ (panaeoidean mysis) and 6.1 ± 1.1‰ (calanoid copepods) (Table 11). A total of nine epibenthic species were analyzed (Table 11). Mean δ^{13}C values ranged between -27.8 ± 0.8‰ (*Uca* spp.) and -23.7 ± 0.2‰ (*Litopenaesu schmitii*). Mean δ^{15}N values oscillated between 3.6 ±0.9‰ (*Uca* spp.) and 8 ± 0.1‰ (*Thaisella trinitatensis*) (Table 11).

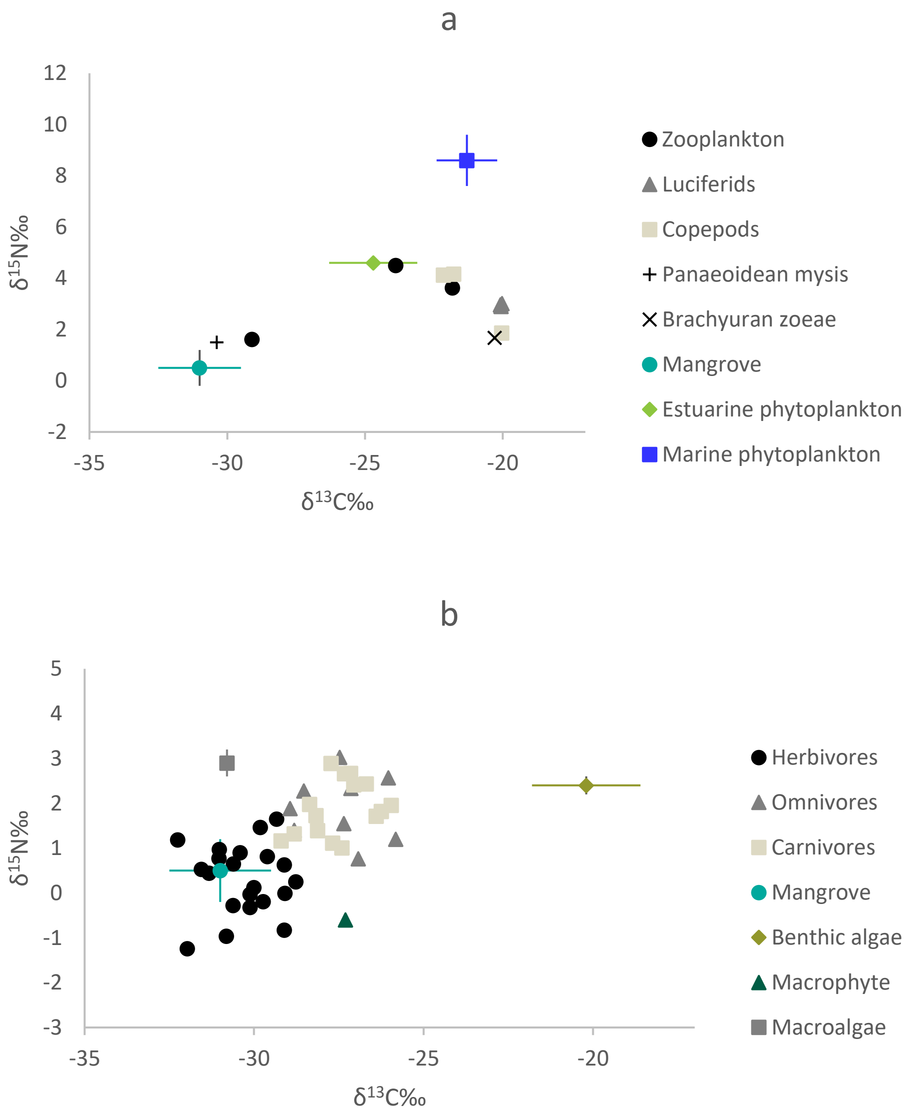

Figure 9. The plot of mean δ^{13}C vs δ^{15}N values (± SD) of basal resources and δ^{13}C vs δ^{15}N values (multiplied by the trophic level) of a) mesozooplankton and b) benthic invertebrate consumers in the Gulf of Urabá, Colombian Caribbean. Values have been adjusted for fractionation and some food sources was excluded based on the knowledge of their local availability and feeding behavior of species.

A total of 18 fish species were analyzed. Mean δ^{13}C values ranged between -26.5 ±0.3‰ (*Eugerres plumieri*) and -17.7±0.9‰ ‰ (*mugil incilis*). Mean δ^{15}N values ranged between 5.8±0.4‰ (*Mugil incilis*) and 12.2±0.3‰ (*Trichurus lepturus*) (Table 12). Zoobenthivores and piscivores were the most ^{13}C-depleted fish, while phytobenthivores were the most ^{13}C-enriched fish. Zoobenthivores were most ^{15}N-depleted fish, while plankthivores were most ^{15}N-enriched fish (Figure 10).

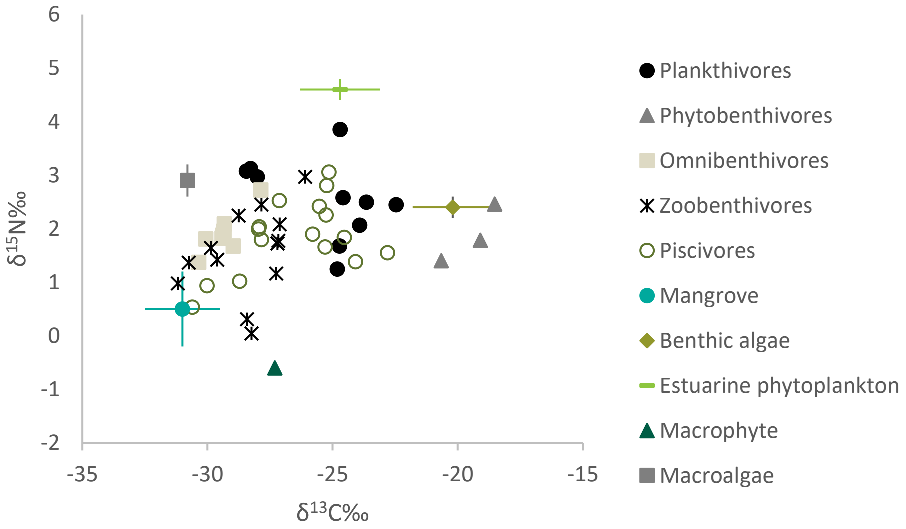

Figure 10. The plot of mean δ^{13}C vs δ^{15}N values (± SD) of basal resources and δ^{13}C vs δ^{15}N values (multiplied by the trophic level) of fish consumers in the Gulf of Urabá, Colombian Caribbean. Values have been adjusted for fractionation and some food sources was excluded based on the knowledge of their local availability and feeding behavior of species.

Mixing models results (MixSIAR)

We included global average marine phytoplankton in the mixing model for mesozooplaknton, as consumer values fell outside the source polygon when using estuarine phytoplankton (Figure 9a), which suggested marine phytoplankton as other possible source. We also excluded benthic algae, macrophyte and macroalgae as sources as the ARD is not a well-mixed estuary, and because phytoplankton and mangroves are the main primary sources for consumers in the pelagic environment (see discussion section). For mesozooplakton consumers, the mixing model indicated that estuarine phytoplankton made the largest contribution contributer the highest δ^{13}C source, followed by mangrove (Figure 11a), which ranged from 14% (1% to 68% CI) to 73% (10% to 97% CI) and 18% (1% to 55% CI) to 75% (11% to 93% CI), respectively (Table 13).

Table 13. Percent of primary producer's contributions (50% quantiles, range = 95% Bayesian credibility intervals) for Meso-zooplankton using MixSIAR. TP = estimated trophic position.

Species/Taxon		**Marine phytoplankton Median**		**Estuarine phytoplankton Median**		**Mangrove Median**	
	TP	**%**	**95 % CI**	**%**	**95 % CI**	**%**	**95 % CI**
Zooplankton	2.3	11	0-55	**50**	**6-92**	35	2-68.
Luciferids	2.1	5	0-62	**73**	**10-97**	18	1-55
Brachyuran zoeae	1.6	8	0-87	40	0.8-90.1	**41**	**3-70**
Panaeoidean mysis	1.6	7	0-45	14	1.1-67.9	**75**	**11-93**
Calanoid copepods	2.2	10	0-57	**62**	**51-98**	24	3.3-56.0

For omnivorous and carnivorous epibenthos, phytoplankton was excluded from the models based on the knowledge of availability for this consumers and since mixture data are well in - side the source polygon without phytoplankton values (Figure 9b). The estimated contribution of macroalgae was the highest (Figure 9b), ranging from 31% (9% to 49% CI) to 54% (9% to 71% CI) (Table 14). Mangrove was estimated to be the most important contribution for the herbivore crabs *Aratus pisonii* (75%; 23% to 93% CI) and *Pachygrapsus transversus* (60%; 25% to 95% CI) (Table 14). Macrophyte was the most important estimated source for the fiddler crab, *Uca* sp. (38%; 10% to 55% CI) (Table 14).

Table 14. Percent of primary producer's contributions (50% quantiles, range = 95% Bayesian credibility intervals) for Epibhentos using MixSIAR. TP = estimated trophic position.

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

For planktivorous fishes, marine phytoplankton stable isotopes values were included from global averages but three sources (benthic algae, macrophyte and macroalgae) were excluded from the models since ARD is not a well-mixed estuary. Estuarine phytoplankton and mangrove were the most important estimated sources for consumers (Figure 12), which ranged from 34% (5% to 77% CI) to 54% (4% to 90% CI) and 35% (5% to 70% CI) to 55% (24% to 80% CI), respectively (Table 15). To illustrate the difference in the selection of sources in mixing models the results with all end-members for *Anchovia clupeoides* are showed.

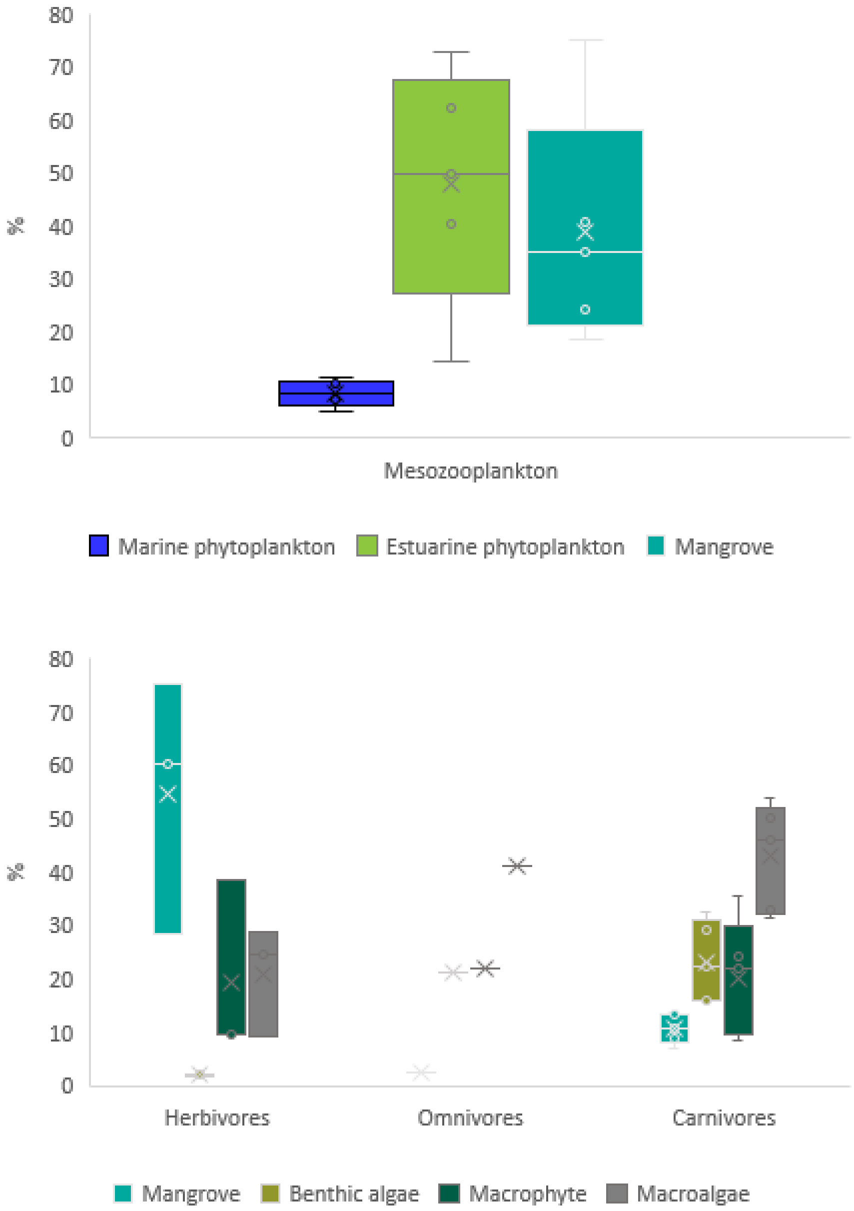

Figure 11. Comparision of estimated contribution made by different primary producer's (50% quantiles, range = 95% Bayesian credibility intervals) for a) mesozooplankton, b) trophic guilds of epibenthivores.

For phytobenthivorous fish (*M. incilis*), the marine and estuarine phytoplankton sources were excluded from the model since ARD is not a well-mixed estuary and they are not part of their diet, based on previous stomach contents analysis (Sandoval 2012). For this fish, the estimated contribution of benthic algae was the highest (48%; 13% to 85% CI) (Table 15; Figure 12). To illustrate the difference in the selection of sources in mixing models, the results with all end-members are showed, where contribution of benthic algae decreased (21%; 1% to 63 CI) (Table 15), which is not in accordance with previous information on their diet since the main prey for *M. incilis* are benthic algae (87% IRI) (Sandoval 2012).

For omnibenthivorous, zoobenthivorous and piscivorous fish, marine phytoplankton was excluded from the models since consumers' values fell inside the source polygon without that source (Figure 6), also because estuarine phytoplankton and mangrove were the major sources for primary consumers in the pelagic environment. For omnibenthivores and zoobenthivores fish, macroalgae was the most important estimated source (Figure 12) ranging from 23% (1% to 66. CI) to 63% (24% to 82% CI) (Table 15). For piscivores fish, mangrove and benthic algae were the most important estimated sources (Figure 12), which ranged from 14% (1% to 40% CI) to 46% (1% to 80% CI) and 12% (1% to 41% CI) to 38% (8% to 45% CI), respectively (Table 15). To illustrate the difference in the selection of sources in mixing models, the results with all end-members for *Diapterus rhombeus* are showed.

Table 15. Percent of primary producer's contributions (50% quantiles, range = 95% Bayesian credibility intervals) for trophic guilds and fish species. ACR: acronym. CI: credibility intervals *Models whit all end-members.

Guilds/Species	**T L**	**Marine phytoplankton Media n %**	**95 % CI**	**Estuarine phytoplankton Media n %**	**95 % CI**	**Mangrove Media n %**	**95 % CI**	**Benthic algae Media n %**	**95 % CI**	**Macrophytes Media n %**	**95 % CI**	**Macroalgae Media n %**	**95 % CI**
Plankthivores													
Anchovia clupeoides	3.8	8	0-36	34	5-67	**55**	**24-80**	NC		NC		NC	
**A. clupeoides*		*3*	*0-14*	*4*	*0-19*	*17*	*0-65*	*7*	*0-26*	***56***	***4-80***	*6*	*0-33*
Centengraulis edentulus	3.3	5	0-57	40	3-76	**49**	**16-82**	NC		NC		NC	
Caranx crysus	3.8	11	0-59	**51**	**4-88**	36	6-65	NC		NC		NC	
Opisthonema oglinum	3.6	6	0-66	**54**	**4-90**	35	5-70	NC		NC		NC	
Phytobenthivores													
Mugil incilis	2.3	NC		NC		12	0-50	**48**	**13-85**	20	0-56	10	0-47
**M. incilis*		*1*	*0-34*	*14*	*1-48*	*12*	*0-48*	***21***	***1-63***	*20*	*1-54*	*9*	*0-40*
Omnibenthivores													
Cathorops mapale	3.3	NC		3	0-21	15	0-60	5	0-19	17	1-40	**53**	**11-78**
Diapterus rhombeus	3.5	NC		6	0-38	9	0-50	11	0-30	11	1-36	**55**	**10-78**
**D. rhombeus*		*2*	*0-20*	*2*	*0-26*	***51***	***1-89***	*6*	*0-34*	*11*	*0-50*	*9*	*0-82*
Eugerres plumieri	3.4	NC		3	0-19	9	0-48	4	0-16	17	0-36	**63**	**24-82**
Zoobenthivores													
Ariopsis canteri	3.3	NC		7	0-27	13	1-43	14	1-34	24	2-47	**37**	**15-58**
Centropomus pectinatus	3.7	NC		9	0-34	**33**	**1-78**	8	0-45	11	0-51	23	1-66
Lutjanus jocu	3.7	NC		12	0-38	23	1-69	7	0-37	16	0-49	**30**	**2-69**
Chaetodipterus faber	3.7	NC		7	0-31	23	0-70	5	0-26	12	0-41	**44**	**2-80**
Bardiella ronchus	4.0	NC		17	0-46	19	2-47	11	0-33	13	1-36	**34**	**4-63**
Piscivores													
Centropomus ensiferus	4.1	NC		12	1-31	**34**	**2-64**	16	2-35	15	1-41	20	1-52
Caranx hipos	4.2	NC		10	0-46	17	1-50	**38**	**8-45**	18	0-52	7	0-30
Centropomus undecimalis	4.2	NC		8	0-33	**46**	**1-80**	12	1-41	8	0-39	17	0-60
Oligoplites saliens	4.3	NC		15	0-47	16	1-48	**30**	**1-60**	19	0-48	12	1-38
Trichurus lepturus	4.6	NC		**29**	**0-62**	14	1-40	23	1-52	9	0-32	19	0-52

Trophic levels

Consumers with the lowest trophic levels were mesozooplankton larvae (Table 8) and herbivore crabs (Table 9). While piscivore fish, *T. lepturus*, exhibited the highest trophic position (Table 10). Overall, Mesozooplankton, herbivore epibenthos and phytobenthivore fish correspond to the first consumers (Table 8, 9 and 10). Intermediate trophic level consumers included carnivore epibhentos and two fish trophic guilds; planktivore and omnibenthivores (Table 8 and 9). While high trophic level consumers included zoobenthivores and piscivore fishes (Table 10).

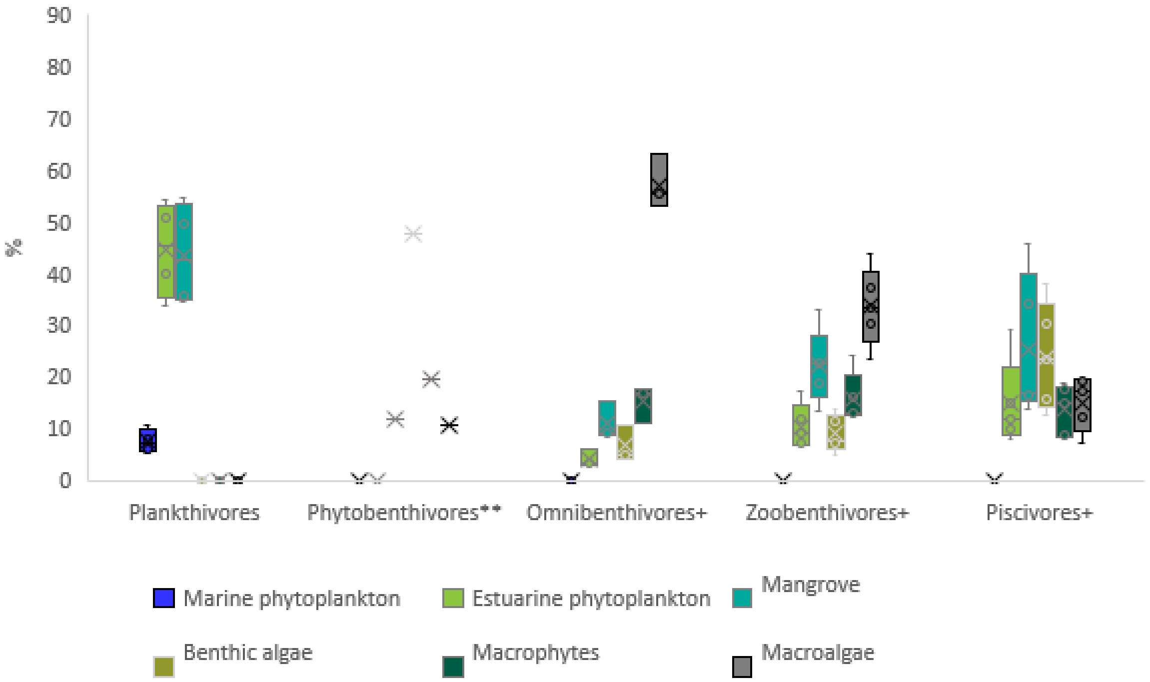

Figure 12. Comparision of estimated contribution made by different primary producer (50% quantiles, range = 95% Bayesian credibility intervals for trophic guilds of fish.

3.5. Discussion

Isotope values sources and consumers

The wide range of δ^{13}C values for sources (-31.0‰ for mangrove to -22.2‰ for benthic algae) helped to run the mixing models fittingly and evidence sources segregation into distinct food webs (Layman et al. 2012). There is however, an effect of mangrove-derived POC-$\delta^{13}C$ on the $\delta^{13}C$ of primary producers from ARD. ^{13}C depleted sources in estuarine systems has been attributed to incorporation of ^{13}C depleted carbon of mangrove origin (Bouillon et al. 2000, Sepúlveda-Lozada et al. 2017). This is explained because in sites with significant mangrove coverage the initial pool of carbon available for aquatic producers includes not only bicarbonate and dissolved CO_2, but also respiratory ^{13}C depleted CO_2 from mangrove origin (Abrantes and Sheaves 2008).

Mesozooplankton consumers showed a relative wide (7.9‰) range of $\delta^{13}C$ values, varying from -27.4‰ (zooplankton) to -19.5% (Luciferids), indicating the use of different carbon sources raning from mangrove carbon (^{13}C depleted values) and marine phytoplankton carbon (^{13}C-enriched values). Epibenthos showed a slightly more restricted range in their $\delta^{13}C$ values (5.7‰), varying between-28.6% (*Uca* sp.) and -22.9‰ (*L. schmittii*), indicating also the use of different carbon sources, however, more depleted values indicate incrase assimilation of mangrove carbon, mainly for herbivores crabs, as have been indicated by Bouillon et al. (2008). Fish showed a wide range of $\delta^{13}C$values (9.4‰); -25.2‰ (*E. plumiere*) to -16.8‰ (*M. incilis*), indicating varied use of carbon sources, but also the effect of the fractionation by each trophic level. Overall, results suggest a wide variety of carbon sources are important for consumers in the ARD estuary.

Consumer trophic position

Four trophic levels were estimated in the ARD, which is very similar to several mangrove systems (e.g., Abrantes and Sheaves 2009, Giarrizo et al. 2011, Sepúlveda-Lozada et al. 2017, Stuthmann and Castellanos-Galindo 2020). Mean $\delta^{15}N$ values for aquatic primary consumer (meso-zooplankton and phytobenthivores fish) were 3‰ enriched relative to the mean $\delta^{15}N$ values for sources (5.4‰ and 2.4‰, respectively), evidencing that the factor discrimination of 2.9 used by the formula was fitting for trophic level estimation (McCutchan et al. 2003). An overlla mean $\delta^{15}N$ value was calculated for primary producers to estimate baseline $\delta^{15}N$ and finally to estimate trophic position. Nevertheless, previous food web studies in mangrove systems have successfully used mangrove as a ^{15}N reference (Medina et al. 2017), as well as sediments (Mancera 2003). Mancera (2003) recommends the use of the mean between mangrove and sediments. However, we believe that the average of $\delta\ ^{15}N$ value for primary sources was fitting for trophic level estimation due to similar values for fish using stomach content analyses at the Colombian Caribbean, as showed below.

Trophics position estimates for fish were similar to those found by Garcia and Contreras (2011) at the Colombian Caribbean; e.g., *M incilis* (2.3 this study; 2.2 literature data), *E. plumieri* (3.4; 3.1, respectively) *C. ensiferus* (4.1; 4.3, respectively), *C. undecimalis* (4.2: 4.1, respectively), and *T. lepturus* (4.6; 4.5, respectively). Further, TPs of fish community were similar to those found on the Pacific coast of Colombia by Medina-Contreras et al. (2017): mean community TL of 3.7 and 3.6, respectively. In contrast, calculated TPs of fish community were lower on the Caribbean coast of Panama (Stuthmann and Castellanos-Galindo 2020), with a mean community TL of 3.2. Nevertheless, in this latest study a different TP calculation techniques was used (tRophicPosition), which could explain the differences.

The highest trophic levels (4.6) in ARD could be an indicator of the high complexity of their food webs since food chains are typically short, reaching a maximum of four or five trophic levels (Pimm and Lawton 1977). The trophic level measures could be essential for ecosystem-based fishery management (EBFM). The strength of TL 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 TL of the catch for a series of years, it is useful to identify the ‘fishing down the marine food webs’ process (Pauly et al. 1998), and to estimate other indicators such as the primary production required to support fisheries (Pauly and Christensen 1995) and the ‘Fishery in Balance’ index (Pauly et al. 2000).

Contribution of food sources for consumers

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 (Abrante and Sheaves 2009). It is worth highlighting is that we first ran the mixing models with all end-members since estuaries are complex systems offering different primary sources for consumers (Bouillon et al. 2011). Yet, the interpretation of results was difficult since they gave rise to conflicting with some fish previous diets information. Then, we excluded some food sources for trophic guilds, based on 1) the knowledge of some sources being not important in their diet (Phillips at al. 2014), 2) the ARD being a not well-mixed estuary, and

3) that it is possible to exclude sources which practically do not contribute to diets to get a reliable interpretation of results (Phillips at al. 2014). When interpreting our findings and the knowledge about feeding habits for some fish species, most consumers use a mixture of sources and therefore a combination of different pathways. This was mainly shown for higher trophic level consumers as zoobenthivorous and piscivorous fishes. This reflects the complexity of the ARD estuary and the diversity in food sources for consumers. However, we suggest at least five potential trophic pathways in ARD ecosystem food webs, as described below (Figure 13).

1. *Phytoplankton pathway*. Phytoplankton contributes directly to mesozooplankton (TL≈2) and is transferred to higher TLs, first to planktivorous fish (TL ≈3), and subsequently to piscivorous fishes (TL≈4); e.g., *Trichurus lepturus*.

2. *Mangrove trophic pathway*. Mangrove is incorporated by herbivorous epibenthic crabs; *A. pisonii* and *P. transversus*. It can also be transferred to the adjacent TL through the crab, *A. pisonii,* who has been found in the diet of the zoobenthivore fish, *Ariopsis canteri* in a mangrove lagoon in the Urabá Gulf (Sandoval et al. 2014). On the importance of the mangrove as a source of food for grapsid crabs it has been recently accepted that the values of discrimination are higher than average values traditionally used following Post et al. (2002) and MacCuthchan et al. (2003) (Harada and Lee 2016). For this 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* crab (Sandoval et al. in preparation: see chapter 5), which are close to those suggested for sesarmid crabs (δ13C: 4.88 ± 0.1‰ and δ15 N: 3.5 ± 0.1‰) by Harada and Lee (2016). This finding points to the importance of mangrove leaves for herbivore crabs from the ARD.

Furthermore, the results suggest that herbivorous crabs in ARD indirectly could be exporting mangrove organic production either as preys or carcasses thus supplying the near-shore pelagic food webs (Werrry and Lee 2005, Lee 2008). Thus mangrove also contributes directly to mesozooplankton, as shrimp larvae (TL≈2) and is transferred to higher TLs, first to plankthivore fish (TL ≈3), mainly engraulids (*A. clupeoides* and *C. edentulus*), and subsequently to piscivore fish (TL≈4), as centropomids (*Centropomus undecimalis* and *C. ensiferus*). In Brazil, Giarrizo et al. (2011) described the same mangrove trophic pathway.

That study was also conducted in an area where mangroves are interlinked to other productive coastal habitats such as seagrass beds. Likewise, engraulid fish, were also key carbon transfer from mangrove to higher trophic levels. These results have important implications on the trophic role of mangroves in tropical estuarine and marine ecosystems since engraulids are abundant in these systems and are prey for important commercial piscivore fish species (Giarrizo et al. 2011). In the Gulf of Urabá, the importance of the engraulids for piscivores fish has been evidenced in the diet of the Atlantic cutlassfish, *Trichiurus lepturus* (RII=56%) (Arenas-Uribe et al. 2019), and the Gafftopsail Sea Catfish *Bagre marinus* (RII=15%) (Hernandez-Morales et al. 2018).

3. *Microphytobenthos (benthic microalgae) pathway*. Microphytobhentos contributes directly to phytobenthivore fish, *Mugil incilis* (TL=2), consistent with a previous study in the Gulf of Urabá, where both juveniles and adults feed mainly on diatoms from the seabed near mangroves (Sandoval 2012). Which can also corroborate the proper use of the isotopic benthic algae values from global averages in our models. *M. incilis* can also transfer energy to higher TLs (TL≈4), as it has been found in the diet of species such as *Trichiurus lepturus* (Arenas-Uribe et al. 2019) and *C. ensiferus* (Sandoval 2012). Likewise, microphytobhentos also significantly contributes indirectly to the white shrimp *Litopenaesu schmitii* (TL≈3).

4. *Macroalgae pathway.* The macroalgae are usually abundant on the roots of *R. mangle* in the ARD (Hurtado-Santamaria and Quan-Young, 2016), and apparently contribute to omnivore and carnivore epibenthos, and omnibenthivorous fish (TL≈3). It coincides with a previous study, where the importance of algae was evident in the diet of omnibenthivorous fish; *Diapterus rhombeus* and *Eugerres plumieri* (Sandoval 2012). In this way, macroalgae can be also transferred to piscivore fish (TL≈4), as centropomids.

5. Macrophytes pathway. Macrophytes contribute directly to herbivore crab *Uca*. sp. (TL≈2) and apparently is transferred to the carnivore crab, *Eurytium limosum* (TL ≈3) since the first species is prey to the second (Kneib and Weeks 1990). Nevertheless, a more detailed study of the sources sustaining *Uca* sp. is required since they incorporated mainly microphytobentos in different mangorves (Bouillon et al. 2004, Medina-Contreras et al. 2020).

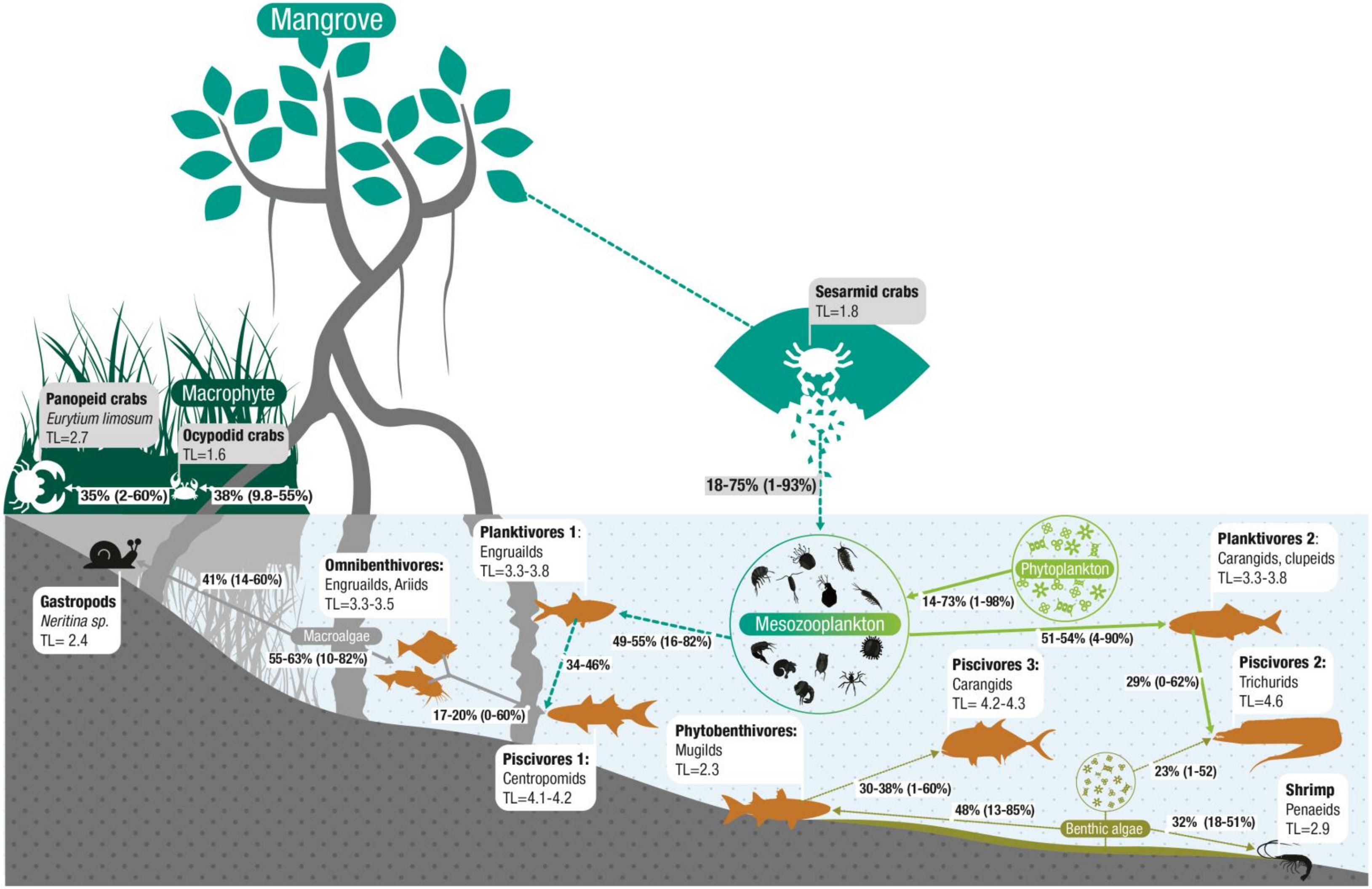

Figure 13. Diagram of the main consumers and sources showing the relative contribution of the main energetic sources in the Atrato River Delta estuary.

Based on the above, mangrove was the main assimilated basal food source for herbivore epibenthic crabs and piscivore fish in the ARD, 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 to November), during which samples were collected. However, during the dry season more estuarine and river-influenced carbon sources will likely dominate, since the lowest salinity values are encountered during the dry period (December to April) in response to trade winds maintaining fresh water in the Gulf (García-Valencia 2007). Likewise, our mixing models results for fish based on a carbon TEF of δ^{13}C: 1.3 ± 0.3 ‰, can be considered conservative regarding the contribution of mangroves, as higher TEF values lead to lower corrected δ^{13}C which in turn leads to higher contributions of mangrove, 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 two of the most common fish species in the local artisanal fishery (LOPEGU 2017): the piscivore *C. undicimalis* and the zoobenthivore *C. pectinatus*. Furthermore, results suggest that mangroves serve as substrate/habitat that supports sources as macroalgae and benthic algae supporting the zoobenthivores *A. canteri* and the phytobenthivores *M. incilis*, both also commercial fish species (LOPEGU 2017).

Nevertheless, regarding that Bayesian mixing models are sensitive to quality of input values, e.g. TDFs and variability in source pool values (Layman et al 2012), we recommend a more detailed study of possible pathways, due to we could not used local phytoplankton and benthic algae values, and in some cases, we used small sample size (e.g. estuarine phytoplankton, n=2), which could lead to more uncertain outputs. Likewise, it is important to study the possible differences of mangrove contribution to food webs both across the rainfall regime and spatially in the ARD. For which, δ^{34}S as a tracer would be useful since it varies substantially among primary producers, but changes relatively little with progression through a food web (Layman et al. 2012).

Based on other studies, mangroves can be important 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 to other highly productive coastal habitats (i.e., seagrasses and coral reefs), as reported only a few studies, e.g. in a northern Brazilian mangrove ecosystem (Giarrizo 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 mangroves areas in the Southern Caribbean.

Conclusions

Results showed a food web with a maximum length of 4.6 in the Atrato River Delta estuary. Diversity in food sources support the food webs, most consumers assimilated a mixture of carbon sources as a product of intertwined pathways. However, the potential pathways for mangrove, microphytobenthos, macroalgae, phytoplankton, and macrophyte carbon sources were suggested through the isotopic analysis and the gained knowledge about feeding habits for some fish species. Fringing mangroves seem to be a major food source for consumers in areas not interlinked to other highly productive coastal habitats (i.e., seagrasses and coral reefs). Herbivorous crabs (sesarmids) and planktivorouss fish (engraulids) are potential key carbon vectors from the mangrove resource base to higher trophic levels. Mixing model results indicated that mangrove-derived materials contributed significantly to the production of two fish species common in the local artisanal fishery in the ARD (*C. pectinatus* and *C. undicimalis*). Mangroves, also serve as substrate/habitat that supports sources as macroalgae and benthic algae supporting production in two others commercial fish species (*A. canteri* and *M. incilis*).

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Chapter 5. Experimental discrimination of C and N stable isotopes between mangrove leaves and the tree-climbing crab (Brachyura: Sesarmidae: *Aratus pisonii*) and possible estimation of food sources in field diets.

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Aratus pisonii, in a microcosmos for experiments (L.A. Sandoval).

Abstract

The mangrove tree-climbing crab *Aratus pisonii* (Sesarmidae) is one of the most abundant and iconic arboreal brachyurans in the Neotropics. Despite being traditionally regarded as an herbivorous consumer leaving visible rasping marks on *Rhizophora mangle* leaves, gut content analyses, field observations and experimental feeding trials also suggest facultative omnivory. In addition, there are still questions regarding the nutritional challenge of leaf consumption, particularly if the relatively nutrient-poor mangrove leaf litter is assimilated when offered as the sole component of the diet. This study aimed to: 1) experimentally compare consumption rates of fresh (green) and senescent (yellow) *Rhizophora mangle* leaves during 26 d; 2) estimating stable isotope trophic discrimination of carbon and nitrogeno between leaves and muscle tissue after 58 d in a controlled feeding experiment; and 3) identifying potential food sources in the diet of *A. pisonii* in a major monospecific mangrove area in the Southwestern Caribbean Sea (Atrato River Delta, Colombia) using stable isotope mixing models. *A. pisonii* consumed a total of 17.11 ± 20.75 mg leaf g^{-1} crab wet wt d^{-1} of *R. mangle* leaves during the experimental trial. However, total consumption was greater for green leaves (12.05 ± 13.07 mg) than for yellow leaves (5.06 ± 13.85 mg). Our experimental estimates of mean ± SD TDF were $\Delta^{13}C$ 5.4 ± 0.9‰ and $\Delta^{15}N$ 3.9 ± 0.5‰, close to those suggested for other sesarmid crabs ($\Delta^{13}C$: 4.9 ± 0.1‰ and Δ^{15} N: 3.5 ± 0.1‰). We concluded that this species met its N demand for at least 50 d on a strict diet of mangrove leaf. Mixing models using discrimination values for sesarmid crabs elsewhere and for our study, suggested that mangrove leaves made the largest estimated contribution to assimilated diet. Nitrogen requirements for growth in the field can be met by a mangrove-leaf diet and may be supplemented with the intake of macroalgae. These results provide new insights into the importance of *A. pisonii* as a key herbivore converting low-quality mangrove tissues into nutritious secondary production (biomass), potentially linking primary producers with intermediate and top predators (both aquatic and terrestrial). Future research is needed to understand the transfer of mangrove primary production to nearshore consumers mediated by *A. pisonii*.

Key words: Caribbean Sea, Atrato River Delta, mangrove outwelling hypothesis, carbon cycling, feeding experiment, stable isotopes, Bayesian stable isotope mixing models

5.1. Introduction

The literature on mangrove production highlights “organic matter outwelling” as a critical function of this ecosystem in coastal zones supporting mangrove habitats, stating that the export of primary production from trees supports much of the secondary production of estuaries and nearshore waters (Odum and Heald 1975). However, a significant direct assimilation of the exported mangrove litter into nearshore food webs appears to be questionable (Lee 1995, Harada and Lee 2016), since mangrove leaves have high tannin contents and C/N ratios greater than 17, normally taken as the maximum for sustainable animal nutrition (Skov and Hartnoll 2002). Indeed, direct consumption of mangrove litter by crabs in mangrove forests is well documented, and the benthic foodweb in mangrove environments is to a large extent dominated by semi-terrestrial leaf-eating crabs (Giddins et al. 1986, Kristensen et al. 2017). However, there are still questions regarding the potencial nutritional challenge of eating leaves for some crabs, particularly if diet may is based on the consumption of relatively nutrient-poor mangrove leaf litter (Bui and Lee 2014, Kristensen et al. 2017).

Studies in the Indo-West-Pacific region have showed that brachyuran crab species belonging mainly to the families Grapsidae and Sesarmidae can consume mangrove leaves as their major food source (Steinke et al. 1993, Thongtham and Kristensen 2005, Kristensen et al. 2010, Bui and Lee 2014, Mackenzie et al. 2020), and can, remove more than 50% of annual litter production (Robertson 1986, Kristensen et al. 2010, Harada and Lee 2016). As such, crabs play a significant role in the detritus-based food chain and energy flow in most mangrove environments, affecting nutrient retention, litter decomposition, and the offshore export of mangrove production (Robertson 1986, Lee 1995). Aside from their digestion and subsequent fecal production, crabs also have the ability to shred mangrove matter into particles smaller than 200 µm in size that are later incorporated by zooplankton into the pelagic trophic network (Werry and Lee 2005). All of the above is, however, dependent on the crabs’ ability to effectively digest and assimilate low-quality mangrove leaf litter (Bui and Lee 2014).

Although a number of studies have examined the food composition and food choice of brachyuran crabs using stable isotope analyses and mixing models (e.g., Thongtham and Kristensen 2005, Nerot et al. 2009, Kristensen et al. 2010, Nordhaus et al. 2011), only few studies have provided estimates of trophic discrimination for $\Delta^{13}C$ and $\Delta^{15}N$ in sesarmid crabs

(Herbon and Nordahus 2013, Kristensen et al. 2017). Trophic discrimination values are the difference in isotopic composition between an animal's tissue and its diet, which are a result of a plethora of physiological processes associated with consumption, excretion and assimilation (Caut et al. 2009). The most commonly used trophic discrimination factor (TDF) per trophic level in aquatic food web studies have been +0.4 ‰ for δ^{13}C and +2.3‰ for $\delta\,^{15}$N, which are global means for a large range of aquatic animals foraging on different food sources (McCutchan et al. 2003). However, the use of an incorrect TDFs can have strong impacts on the interpretation of stable isotope data, and thus our understanding of the importance of different trophic links, especially for detritivorous crabs such as sesarmid species which can have unusual TDFs (Herbon and Nordahus 2013, Bui and Lee 2014, Kristensen et al. 2017, MacKenzie 2020).

Aratus pisonii (Sesarmidae) is one of the most abundant tree-climbing crabs found in Neotropical mangrove habitats (Chace and Hobbs 1969). Unudually, it directly consumes fresh leaf tissue in the canopy rather than feeding on fallen leaf litter on the forest floor (Yeager et al. 2016). This species is the primary herbivore of the red mangrove *Rhizophora mangle*, accounting for over 40% of total leaf damage in monotypic red mangrove stands (Erickson et al. 2003, Feller et al. 2013). Fresh red mangrove leaves compose an estimated 84% of the diet of adult *A. pisonii* under natural settings, but they commonly supplement their plant diet with opportunistic scavenging and predation on insects, benthic infauna, and juvenile conspecifics (Díaz and Conde 1988, Erickson et al. 2003, Riley et al. 2014). In addition, recent experiments have demonstrated that *A. pisonii* is able to discriminate between leaf species and condition, as well as the chemical composition of food offered to them experimentally (Erickson et al. 2008, Miranda et al. 2017). However, there are no experimentally-derived TDFs for carbon and nitrogeno stable isotopes ratios between mangrove leaves and *A. pisonii* that are required to fully use this approach to undertand the importance of mangroves in the crab´s diet. Furthermore, data for this species consumption of mangroves are not-existent from the southern Caribbean Sea.

In the present study we report on a series of experiments and field stidies using isotopic mixing models carried out to investigate the feeding habit of *A. pisonii* inhabiting monotypical mangrove forests in the southwestern Caribbean Sea (Colombia). These studies were conducted to improve our undersatanding of their ability to provide a link to mangrove-derived carbon pool for marine predators (mangrove outwelling hypothesis). We conducted experiments to 1) determine *R. mangle* leaf consumption rates and leaf condition preference (different stages of decay); 2) empirically determine trophic discrimination factors for carbon and nitrogeno stable isotopes between *R. mangle* leaves and *A. pisonii;* and 3) estimate and to compare estimated dietary contributions through Bayesian stable isotope mixing models (MixSIAR) using commonly assumed vs. empirically determined trophic discrimination values.

5.2. Materials and methods

Sampling and handling of crabs and leaf materials Samples

Samples were collected in the Atrato River Delta (ARD), Urabá Gulf. The Gulf is the southernmost area of the Caribbean Sea, located at the southwestern end of the coast of Colombia (Figure 14). The Atrato River discharges into the western coast of the Gulf, and it is the second largest freshwater input, after the Magdalena River, for the Southern Caribbean (Garcia-Valencia 2007). The Atrato River Delta (ARD) has extensive mangrove areas (approximately 5700 ha) with exclusive ecological characteristics. Red mangrove (*Rhizophora mangle*), is the dominant species in more than 80% of the area, followed by white mangrove (*Laguncularia racemossa*), and black mangrove (*Avicennia germinans*) (Blanco-Libreros 2016). The benthic fauna consists mostly of fiddler crabs, *Uca* spp. (family Ocypodidae) and the mangrove tree crab, *Aratus pisonni* (family Grapsidae).

Mangrove leaf and specimens of *A. pisonii* were collected from La Paila Bay, located at the center of the ARD, from October 2016 and May 2017 (Figure 14). Experiments were conducted in the laboratory of Marine Ecology at Universidad de Antioquia (Sede Ciencias del Mar). Leaf preference and consumption rate experiments were conducted from May to June 2017 (over 26 days), while studies examining changes in muscle $\delta^{15}N$ and $\delta^{13}C$ values of *A. pisonii* fed on a *R. mangle* diet, were conducted from October to December 2016 and replicated from May to July 2017 (over 58 days). Individuals from both sexes were taken into account, but only intact crabs with hard carapaces were selected. Thirty-one individuals (carapace width of 21.0 ± 1.8 mm) were selected for 2016 and twenty-eight for 2017 (carapace width of 20.7 ± 1.5 mm). The crabs were acclimated to laboratory conditions for 5 days.

For leaf preference and consumption rate experiments, *R. mangle* leaves from two stages of decay, namely fresh (green) and senescent (yellow), were picked from trees. After selecting leaves of each category with similar color and morphology, each leaf was divided into two halves along the midrib and labelled; one half was used for determination of dry/fresh-weight (D/F) correlation and the other half was used for the feeding experiments. For conversion of fresh mass (F) to dry weight (D), leaves were dried at 60 °C for 48 h. This study was endorsed by the ethics committee for animal experimentation at the Universidad de Antioquia (Record 109, April 2017).

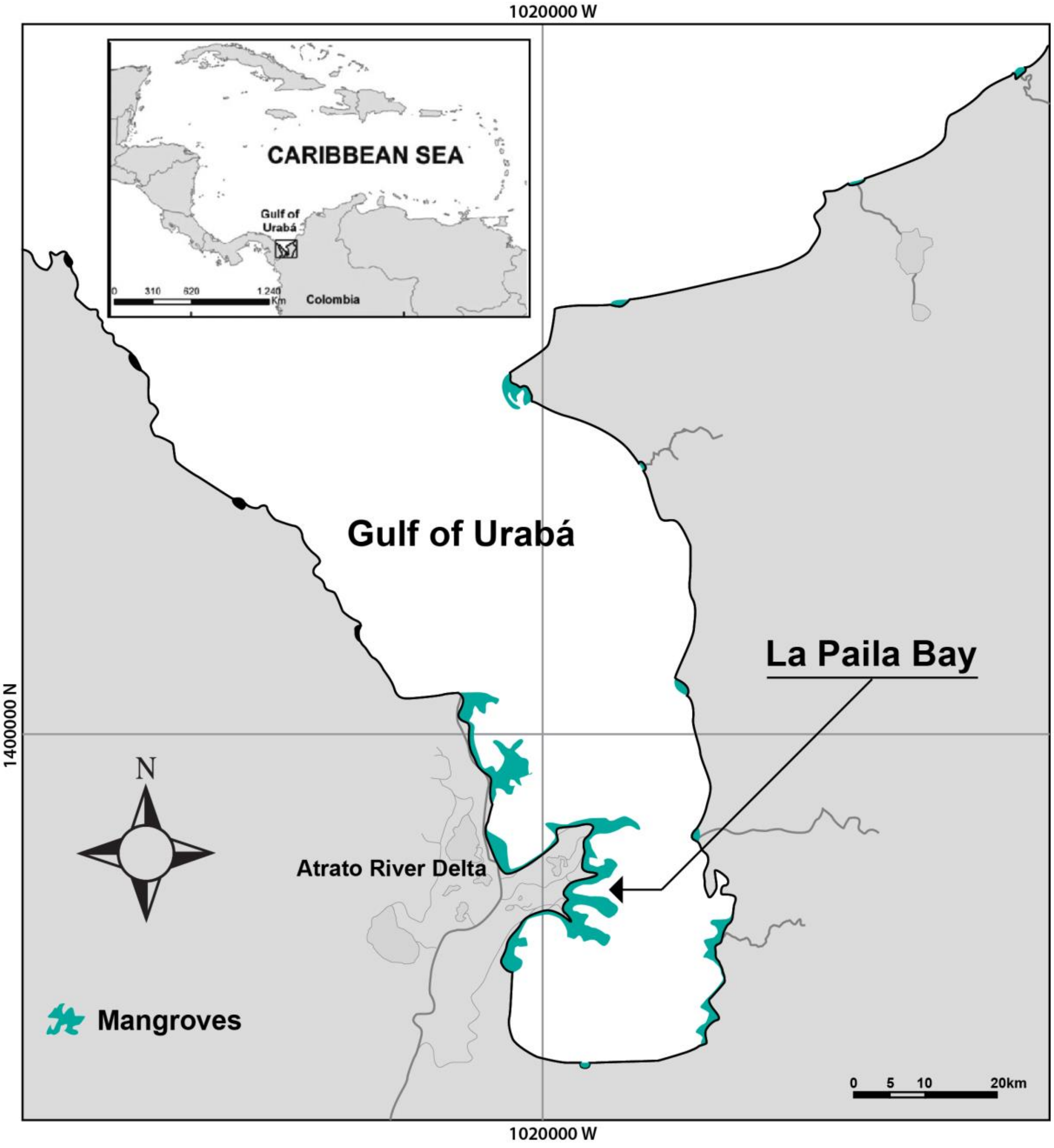

Figure 14. Map showing the study site in the Atrato River Delta of the Gulf Urabá, Caribbean Sea.

Leaf preference and consumption rate experiment

Leaf preferences and consumption rates were assessed for a total of 24 crabs (12 males and 12 females) was ran twice. Each crab was placed in an individual plastic tank measuring 40 x 30 x 25 cm long, wide and deep respectively, supplied with seawater from the Gulf. The tanks were filled to a depth of 2 cm with natural brackish water, and slightly tilted by elevating one side about 3 cm to provide a dry refuge for the crabs. Crabs were allowed to empty their gut contents for 24 h before starting the experiments. A choice was given to crab by placing a piece of leaf of known mass (c. 1 g) of each leaf type into the tanks. Leaves were placed next to each other, to ensure that the chance of being selected was the same between both leaf types. Prior to being placed in the tanks, leaves were washed with distilled water and placed on dry section of each tank to avoid leaching. After 48 h, all uneaten leaf remains were collected, rinsed briefly with tap water, dried and weighed. The consumption rate was calculated as the difference between the estimated initial dry mass calculated from D/F ratios and the measured final dry mass of uneaten leaves expressed as g dry weight and were correlated to crab wet mass.

Isotopic discrimination experiment

The change in δ^{15}N and δ^{13}C in the muscle tissue of *A. pisonii* fed on a *R. mangle* diet was investigated over 58 d during two separated trials in 2016 and 2017 which were treated as replicates in subsequent analyses since no significant differences were found between 2016 and 2017 isotopic values of δ^{13}C and δ^{15}N (Mann-Whitney U-test: $p = 0.606$ and 0.681, respectively). Previous studies on similar animals suggests that eight weeks is usually sufficient for tissue turnover to result in isotopic equilibrium with the diet (Bui and Lee 2014). Long-term experiments were assessed by a total of 58 crabs kept in pairs in tanks and acclimated to experimental conditions for 5 days. Tanks were cleaned every second day, and water was replaced with natural brackish water. Sufficient fresh (green) *R. mangle* leaves were placed on the dry section of each tank. New leaves were placed every second day when tanks were cleaned. Leaves and feces were collected regularly to obtain stable isotope values.

Over the 58-day period, 3 to 5 individuals were sampled 5 times (T-0, T-8, T-22, T-36, T-50, T-58). Crabs were killed by freezing and kept frozen for about 24 h to be dissected and remove muscle tissue from the chelae. Samples were dried at 60 °C for at least 48 h in Petri dishes. Dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials. Between 0.7 and 1.0 mg of the sample was weighed in a micro scale and deposited in a tin capsule for isotopic analysis.

Stable isotope Mixing models

For determination of proportional contribution of different primary producers to the diet of wild-living *A. pisonii*, potential food sources were collected from the same location. Samples of fresh leaves (green) mangrove leaves were collected from the dominant species (*Rhizophora mangle*). Epiphytic macroalgae (Chlorophytes; *Rhizoclonium* sp.) were sampled by scraping the roots of *R. mangle* using forceps. Microphytobenthos was sampled by gently scraping the visible, green and brown mats of benthic diatoms on the sediment surface (Giarrizzo et al. 2011). Samples were dried at 60 °C for at least 48 h in Petri dishes and were prepared for isotopic analysis as described in the previous section.

Stable isotope analysis

Analyses were carried out in Laboratorio de Biogeoquímica de Isotopos Estables at Instituto Andaluz de Ciencias de la Tierra (Granada, Spain), in a Carlo Erba NA 1500 NC elemental analyzer (Milan, Italy) coupled on-line via a ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest, Bremen, Germany). Commercial CO_2 and N_2 were used as the internal standard for the carbon and nitrogen isotopic analyses. For $\delta^{13}C$ analysis an internal standard of -30.6 ‰ and -11.7 ‰ (V-PDB) were used, and for $\delta^{15}N$ an internal standard of -1.0 ‰ and +16.0 ‰ (air). Analytical precision calculated following correction of mass spectrometer daily drift, from standards systematically interspersed in analytical batches was better than ± 0.1 ‰ for both $\delta^{15}N$ and $\delta^{13}C$. Reference gases and in-house standards (with different C/N ratios and isotopic composition) 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 were expressed in delta notation in ppm (‰) based on the following equation: $\delta^{13}C$ or $\delta^{15}N$ = [(Rsample/Rstandard)-1], where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Data analysis

To test for significant differences between consumption rates for the two leaf decay stages and between males and females, a non-parametric Mann–Whitney U test was used ($\alpha = 0.05$). The same statistical method was applied to analyze the difference between leaf stages, isotopic values, and C/N between leaves and crab feces.

For stable isotopic data, since the variation of lipid content in tissues affects $\delta^{13}C$ values and ecological interpretations, a mathematical normalization method was used to standardize lipid content for animal samples (Post et al. 2007). When carbon-nitrogen ratio (C/N) was greater than 3.5%, the following equation was used: $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3{:}32 + 0.99 \times C/N$, where $\delta^{13}C_{untreated}$ corresponds to the original $\delta^{13}C$ measurement of the sample. For carbon sources, normalization was done when the carbon-to-nitrogen ratio (C/N) was higher than 40% using the following formula proposed by Post et al. (2007): $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 5.83 + 0.14 \times \%C$.

To axamine changes in crab muscle isotope values between the start and all five times of observation over 58 days we used non-parametric Mann–Whitney U test ($\alpha = 0.05$). The same statistical analyses were applied to analyze the difference between leaves and feces isotopic values and C/N. Food specific trophic discrimination factors ($\Delta^{13}C$ or $\Delta^{15}N$) were calculated as the difference between the mean isotopic values of the end of the experiments (day 58) and the mean isotopic value of the food (*R. mangle*), as in similar experiments (Bui and Lee 2014).

Trophic level (TL) of *A. pisonii* from mangroves was calculated following the mathematical formula proposed by Post (2002): $TL = \lambda + (\delta^{15}N_{consu} - \delta^{15}N_{base})/\Delta N$, where λ corresponds to the trophic level of the primary producer representing the base of the trophic web, in this case $\lambda = 1$, and $\delta^{15}N_{base}$ corresponding to an overlla mean $\delta^{15}N$ value (1.8‰) calculated for primary producers.

Bayesian stable isotope mixing models (MixSIAR) were used to determine proportional contribution of different primary producers in *A. pisonii* from mangroves (Stock and Semmens 2018). MixSIAR graphical user interface and model were used written in the open source language R (R Development Core Team 2013) and Just Another Gibbs Sampler. Primary sources included were mangrove (*R. mangle*), macrophyte (*Typha sp.*), macroalgae (Chlorophytes: *Rhizoclonium* sp.) and benthic algae. The models were run with “fixed effects” and 3 chains until they “converged” using long or very long Markov Chain Monte Carlo (MCMC) length. For comparing the effect of variation on trophic discrimination factors on food assimilation, three different factors in MixSIAR models were used: a) frequently used in studies of mangrove food webs according to McCutchan et al. (2003) ($\delta^{13}C$: 1.3 ± 0.3‰ and $\delta^{15}N$: 2.9 ± 0.3‰), b) suggested for sesarmid crabs by Harada and Lee (2016) ($\delta^{13}C$: 4.9 ±

0.1‰ and δ^{15} N: 3.5 ± 0.1‰), and c) estimated with the 58-d experiments in this study (δ^{13}C: 5.4 ± 0.9‰ and δ^{15} N: 3.9 ± 0.5‰).

5.3. Results

Leaf preference and consumption rate experiment

Aratus pisonii total consumption rate of *R. mangle* was 17.11 ± 20.75 mg leaf g^{-1} crab wet wt d^{-1}. They consumed more green leaves (mean ± SD: 12.05 ± 13.07 mg) than yellow leaves (5.06 ± 13.85 mg) (Figure 15b) (Mann-Whitney U tests p = 1.255e-06). Consumption rates were greater in females than in male (19.53 ± 25.53 mg and 14.69 ± 14.05 mg, respectively), but theses values were statistically indistinguishable (Mann-Whitney U tests p = 0.967, Figure 15a). There were no significant differences in either δ^{13}C or δ^{15}N between leaves stages (Mann- Whitney U-test: p = 0.206 in both comparisons; Table 16), but C/N ratios were greater in yellow leaves (Mann- Whitney U-test: p = 0.000).

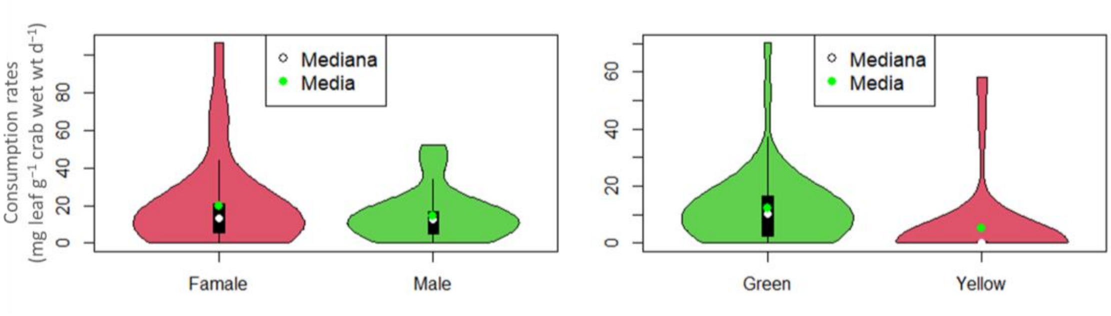

Figure 15. Consumption rates of (left) females and males of *A. pisonni*, and (rigth) green and yellow leaves of *R. mangle* (n=28: 14 females and 14 males).

Isotopic discrimination experiments

The mean isotopic values of food (*R. mangle* green leaves) were δ^{13}C: -31.9 ± 1.5‰ and δ^{15} N: 0.8 ± 1.0‰ (Table 16). The variation of isotopic composition of muscle tissue in the experiments showed a range of 0.97‰ for δ^{13}C and 1.35‰ for δ^{15}N (Table 17). A significant increase in δ^{15}N was recorded between T-0 and T-58 (Mann- Whitney U-test: p = 0.007) (Table 18). There was no significant increase in δ^{13}C between T-0 and T-58 (Figure 16, Table

18). Enrichment factors estimated during the experiments (isotopic values of food - isotopic values of T_{50}) were δ^{13}C: 5.38 ± 0.90‰ and δ^{15} N: 3.94 ± 0.51‰. Feces values were δ^{13}C -33.2 ±1.2‰ and δ^{15}N 2.2 ± 0.6‰ (Table 17). No significant differences were found between δ^{13}C values of green leaves and feces (Mann- Whitney U-test: $p = 0.112$). However, there were significant differences in δ^{15}N values and C/N between green leaves and feces (Mann-Whitney U-test: $p = 0.004$).

Table 16. Carbon and nitrogen stable isotope values from primary producers collected in the Urabá Gulf, Colombian Caribbean. SD: Standard deviation.

Species/Taxon	**N**	**δ^{13}C (‰) Mean ± SD**	**δ^{15}N (‰) Mean ± SD**	**C/N Mean ± SD**
Mangrove				
Rizhophora mangle (green leaves)	9	-31.9 ± 1.5	0.8 ± 1.0	51.3 ± 18.0
Rizhophora mangle (yellow leaves)	10	-31.0 ± 1.1	0.0 ± 1.6	155.1 ± 23.4
Macroalgae				
Chlorophytes (*Rhizoclonium* sp.)	3	-30.8 ± 0.0	2.9 ± 0.3	20.5 ± 1.0
Microalgae				
Microphytobenthos	3	-26.6 ± 0.6	4.8 ± 0.6	14.3 ± 1.0
Macrophyte				
Typha sp.	3	-27.3 ± 0.1	-0.6 ± 0.1	24.3 ± 0.8

Table 17. Crab mean and standard deviation of carbon and nitrogen stable isotope values and C/N for durations (d) in experiments, n: number of samples; N: number of pooled individuals in each sample. SD: Standard deviation.

Time (d) and Feces	**n(N)**	**δ^{13}C (‰) Mean ± SD**	**δ^{15}N (‰) Mean ± SD**	**C/N Mean ± SD**
A. pisonii* fed on *R. mangle				
T-0	9(5)	-25.6 ± 0.8	3.9 ± 0.7	3.9 ± 0.1
T-8	3(3-5)	-26.2 ± 0.6	4.4 ± 0.7	3.7 ± 0.1
T-22	2(3-5)	-25.3 ± 0.2	4.7 ± 0.2	3.7 ± 0.1
T-36	2(3-5)	-25.4 ± 0.0	4.4 ± 0.4	3.5 ± 0.0
T-50	2(3-5)	-25.6 ± 0.3	4.3 ± 0.5	3.6 ± 0.0
T-58	5(3-4)	-25.4 ± 0.5	5.2 ± 0.4	3.6 ± 0.1
Feces	6	-33.2 ± 1.2	2.2 ± 0.6	31.5 ± 3.9

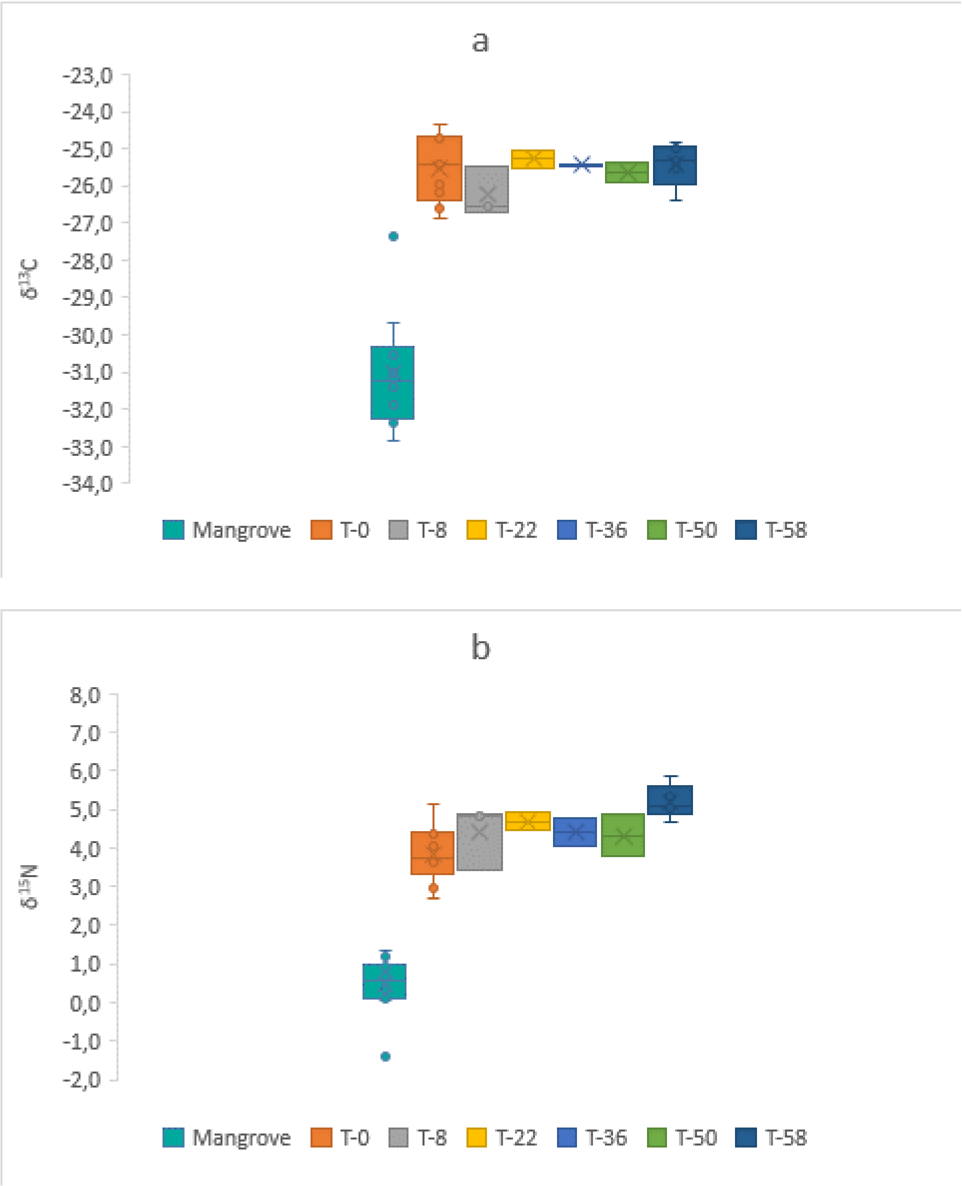

Figure 16. Change in nitrogen (a) and carbon (b) isotopic composition of muscle tissue over time (T-days) in *Aratus pisonii* fed on *Rhizophora mangle* leaves. n = 2 to 9 samples each.

Table 18. Mann- Whitney U-test (p-values) between the start and all five times of observation (T-days) over 58 days of the isotopic discrimination experiment. *: $p < 0.05$.

	T-0 / T-8	**T-0 / T-22**	**T-0 / T-36**	**T-0 / T-50**	**T-0 / T-58**
$\delta^{13}C$	0.282	0.909	0.909	0.909	1.000
$\delta^{15}N$	0.484	0.218	0.436	0.436	0.007*

Stable-isotope Mixing models

Aratus pisonii exhibited a typical herbivore trophic level of 1.8. The different potential primary producers collected in the field showed a range of 5.3‰ for $\delta^{13}C$ and 4.8‰ for $\delta^{15}N$ (Table 16). $\delta^{13}C$ and $\delta^{15}N$ mean values for green leaves were used in mixing models (Table 16), because crabs preferred green leaves and there were no significant differences between isotopic values of leaf types. Macroalgae values were $\delta^{13}C$ -30.8 ±0.0‰ and $\delta^{15}N$ 2.9 ± 0.3‰ (Table 16). Microphytobenthos presented the most ^{13}C-enriched values (-26.6 ±0.6‰) of the different primary producers sampled (Table 16).

The mixing model method that considered TDF according to McCutchan et al. (2003), indicated that a macrophyte was the most important source (median estimate: 64%, 95% credibility interval: 44 – 78), followed by MFB (25, 12 – 84 %) (Table 19). For the TDF previously estimated for a sesarmid crab by Harada and Lee (2016), mangrove was the most important source (56, 22 – 84 %), followed by a macrophyte (24, 3 – 50 %) (Table 19). The species-specifec TDF for *A. pisonii* from this study indicated that mangrove was the most important source (73, 29 – 94 %), followed by macroalgae (11, 1 – 42 %) (Table 19).

Table 19. Primary producer contributions (50% quantiles, range = 95% Bayesian credible intervals) with three TDFs using MixSIAR for *Aratus pisonii* from mangrove environments.

TDF	**Mangrove**		**MFB**		**Macroalgae**		**Macrophyte**	
Source	**50%**	**Range**	**50%**	**Range**	**50%**	**Range**	**50%**	**Range**
McCutchan et al. (2003)	4	0-21	25	12-40	4	0-17	64	44-78
Harada and Lee (2016)	56	22-84	3	0-15	14	1-50	24	3-50
This estudy	73	29-94	3	0-14	11	1-42	9	0-46

5.4. Discussion

Leaf preference and consumption rate

Our experimental trials respectedly demonstrated that *Aratus pisonii* preferred to feed on fresh over senescent leaves of *R. mangle*. Leaf consumption in all subjects was confirmed by observation of feeding-related removal and defecation. Previous studies on the diet of the crab

A. pisonii based on stomach content analyses, have reported important amounts of mangrove leaf tissues among its food items (Beever et al. 1979, Erickson et al. 2003, López and Conde 2013). The classic study by Beever et al. (1979) in Florida, recorded *A. pisonii* feeding upon fresh *R. mangle* leaves both in the field and in the laboratory. Based on gut contents of individuals from the northwest coast of Venezuela, López and Conde (2013) found that mangrove fragments varied between 58% and 96% (Index of relative importance: IRI), however, other items supplemented the diet: seagrass, algae, insects and crustaceans.

Erickson et al. (2003) also examined gut contents and leaf damage to determine herbivory in Florida, finding that mangrove leaves composed about 84% of the identifiable gut contents, and that *A. pisonii* preferred *R. mangle* leaves over two other mangroves species (*Avicennia germinans* and *Laguncularia racemosa*), as well as fresh (green) over senescent (yellow) leaves.

Several studies have stated that crabs feeding intensity on mangrove leaves depends on the concentration of nitrogen and tannins present. These compounds influence the choice of food, with crabs preferring food items with low levels of tannins and high levels of nitrogen (Ashton 2002, Erickson et al. 2004, Nordhaus et al. 2011, Christofoletti et al. 2011). In this study a relationship was found between ingestion rate and bulk chemical composition of leaves: while the nitrogen-poor yellow leaves (bulk C:N=155.13±23.35, N%=0.4±0.1) were consumed at the lowest rate, the nitrogen-rich green leaves (bulk C:N=51.27±17.97, N%=1.3±0.4) were preferred. Recently fallen yellow leaves are poor in nitrogen and rich in tannins (Poovachiranon and Tantichodok 1991). In contrast, Miranda et al. (2017) carried out an experiment regarding feeding rates on fresh and senescent leaves of three mangrove species (*Rhizophora mangle, Laguncularia racemosa* and *Avicennia germinans*) from southeastern Mexico, finding that this species mostly consumed senescent leaves of *Laguncularia racemosa*. To explain this, studies have shown that the food quality of these leaves increases after they lose part of the chemical components that render them unpalatable to crabs, such as tannins and polyphenols, while their C:N ratio decreases to equal or <17:1 in order to become palatable (Russell-Hunter 1970, Miranda et al. 2017). In this way, Erikson et al. (2008) showed for *A. pisonii* feeding preferences according chemical composition of food resources, where crabs preferred nitrogen-rich food resources, displaying opportunistic feeding.

In this study, we reported feeding rates on fresh and senescent leaves of *R. mangle* of 12.05 ± 14 and 5.06 ± 14 in mg leaf g^{-1} crab wet wt d^{-1}, respectively. Miranda et al. (2017) reported markedly higher (but also more variable) feeding rates (20 ± 30 and 30 ± 30 mg leaf g^{-1} crab wet wt d^{-1}, respectively), probably related to differences in experimental conditions and chemical composition of leaves as discussed above. Likewise, in the present experiment, crabs were allowed to feed on *R. mangrove* leaves only, while Miranda et al. (2017) provided access to other two mangrove species as well. Crabs in this study consumed an amount (dry weight) equivalent to 1.7±2.1 % of their body weight per day, similar to that reported for other sesarmid crabs (≈2%) from the Indo-West-Pacific region (Machiwa and Hallberg 2002, Thongtham and Kristensen 2005). We did not find significant differences in consumption rates between female and male crabs: however, the mean female consumption rate was qualitatively slightly higher than that of male individuals (Figure 15). It has been suggested that female crabs feed more than males due to the higher energy requirements of oogenesis (Cannicci et al. 1996).

Our results provide insight into the ecological implications of *A. pisonii* in mangrove ecosystems in the south Caribbean Sea, highligthting its importance as a consumer, contributing to nutrient cycling and availability through a more rapid decomposition of leaf fragments and feces (Lee 1997, Linton and Greenaway 2007). In this way, the capacity of *A. pisonii* to convert low-quality mangrove C into consumer biomass would mediate the transfer of mangrove primary production to nearshore consumers (Bui and Lee 2015, Yeager et al. 2016). Recent studies indicate that leaf litter fall mean annual rate in ARD mangroves is the highest reported for *R. mangle* dominated forests world-wide (Riascos and Blanco-Libreros 2019), and that mangrove area supports fish catch for some of the most common fish species in the local artisanal fisheries (Sandoval et al. 2020, chapter 1). Thus *A. pisonii* likely facilitate transfer of mangrove carbon and other nutrients into the nearshore food webs, ultimately sustaining small-scale fishing activities in the ARD, being consistent with the predictions of recent updates of the outwelling hypothesis. Therefore, further studies are required for a more detailed understanding of the mechanistic linkage between mangrove leaf litter carbon and support for fisheries ecosystem services.

Isotopic discrimination experiments

This study is the first to empirically estimate a trophic discrimination factor for Δ^{13}C and Δ^{15}N between *R. mangrove* leaves and *A. pisonii*. The physiological capacity for *A. pisonii* to assimilate low-quality mangrove C in tropical estuaries of the Caribbean was demonstrated by the survival of all individuals during *ca.* 2 months in forced feeding trials and the incorporation of mangrove leaf C into the tissues. C and N discrimination values in this species were similar to those discovered for sesarmid crabs from the Indo-West-Pacific region also eating mangrove leaf litter (Δ^{13}C = 4–6 ‰ and Δ^{15}N = 0-5‰) (Herbon and Nordahus 2013, Bui and Lee 2015, MacKenzie et al. 2020). These vales are notable higher than most commonly used general TDFs, e.g. as reported by McCutchan et al. (2003) (+0.4 ‰ for δ^{13}C and +2.3‰ for δ^{15}N).

Despite of the conceptual simplicity of the discrimination factor, the difference in isotopic composition between an animal's tissue and its diet is the result from a plethora of possible processes. Variation in trophic discrimination values may be attributed to food quality (e.g. lipid and protein contents), tissue type analyzed, feeding mode (e.g. fluid-feeding vs. others), and habitat of consumers (Caut et al. 2009, Bui and Lee 2015, Kristensen et al. 2017, Mackenzie et al. 2020).

Higher discrimination values among mangrove leaf eating crabs are probably coupled to the balance between isotopic fractionation and isotopic routing (Martínez del Rio et al. 2009, Kristensen et al. 2017). The term isotopic fractionation refers strictly to the kinetic effect of the difference in mass during metabolic processes that lead to excretion of isotopically light C and N compounds (Florin et al. 2011, Martínez del Rio and Wolf 2005), whereas isotopic routing refers to organisms selectively routing macronutrients and associated macronutrient isotopes from diet into the same macronutrient types in their tissues, because synthesis of a given macronutrient from another can be difficult and is always energetically expensive (Martínez del Rio and Wolf 2005). According to Kristensen et al. (2017), a high discrimination between *R. mangrove* leaves and *A. pisonii* muscle tissue is likely mainly due to routing and to a lesser degree due to fractionation. Proteins in crab muscle tissue are not synthetized as a homogenous subsample of C and N atoms from mangrove leaves, but are rather composed of few types of specific amino acids, while carbohydrates are poorly transferred to muscle tissue.

The stable isotopic values of *A. pisonni* diet stayed more or less constant during the feeding experiments, except for the final nitrogen isotopic composition (Figure 16). Stabilization of isotopic values in our case may be due to the similarities between the experimental and natural diet of the animal (Bui and Lee 2015), given that in *A. pisonii* mangrove fragments in gut contents can reach up to 96% (IRI). Similar results have been shown for sesarmid crabs *Episesarma singaporense* and *E. versicolor* over a 12 week long feeding experiment, with *Rhizophora apiculata* senescent leaves as the sole dietary item (Herbon and Nordahus 2013), and for grapsid *Parasesarma erythodactyla* over a 8 week feeding experiment, with freshly senescent *Avicennia marina* as the dietary item (Bui and Lee 2015).

The difference in δ^{15}N values between leaf and crab muscle tissue (= Δ^{15}N) was similar at the beginning and at week 7 (T-50) of the experiment. However, past week 8, there was a difference between δT-58^{15}N (+5.2%) and the beginning δT-0^{15}N (+4.7%) (Figure 15), which corroborates that crabs assimilated nutrients from mangrove leaves despite low protein content. Nevertheless, past week 8, the assimilated nitrogen possibility does not meet the crabs' requirements, forcing animals to metabolized their own proteins, continuously excreting ^{14}N without replenishment from the diet, and thus progressively becoming enriched in ^{15}N (McCutchan et al. 2003; Bui and Lee 2014). Long-term N starvation has also been evidenced for sesarmids *E. singaporense* and *E. versicolor* past 50 d. (Herbon and Nordahus 2013). It should be highlighted, that in our study, some crabs molted during the experiment. Crabs molt only if they have a sufficient food supply (Micheli 1993, Herbon and Nordahus 2013), providing evidence that *A. pisonni* can meet its nutrient demand during nearly 2 mo on a strict *R. mangle*leaf diet. However, in the field, the diet is complemented wiht other items to meet nitrogen demand and therefore the low quality of fresh leaves and leaf litter becomes less restrictive.

The differences in δ^{15}N and C/N between leaves and crab feces, corroborate that more heavy nitrogen (^{15}N) was taken up by the crabs through a selective assimilation of amino acids and others, as reported by Herbon and Nordahus (2013) in feces of the sesarmid crabs *E. singaporense* and *E. versicolor* fed on *Aegiceras cornicula* mangrove leaves. Thus, our work provides additional evidence that *A. pisonii* contributes to improve the quality of mangrove derived production from the system, acting as a vector easing the transfer of mangrove-derived materials to other ecosystem compartments and trophic levels, as part of the outwelling process.

Stable-isotope mixing models

This study considered the most abundant primary producers found in ARD mangrove fringe habitats. Mean δ^{13}C values for sources from ARD were relatively ^{13}C-depleted compared to values in the literature summarized by Bouillon et al. (2008): for mangrove leaves (-29.4 to -27.0 ‰), microalgae (-23.0 to -18.0‰) and macroalgae (-23.1 to -16.4‰). Estimates from mixing models using commonly used TDFs (McCutchan et al. 2003), indicated that macrophyte was the most important source in field diets followed by MFB (Table 5), as showed by Mazumder and Saintilan (2010) for sesarmid crabs, using nonspecific TDF for these species. Nevertheless, discrimination values used for sesarmids crabs by Harada and Lee (2016) and the results of our study, suggest a significantly higher contribution of mangrove leaf to the crab’s diet in the field. In this way, mangrove leafs were the primary contributor to the diet of *A. pisonii* (> 50%), which corroborates their significance in directly processing mangrove leaf organic matter from the canopy. However, the discrepancies between our results and others elsewhere highlight the risk of applying ‘global’ trophic discrimination values to analyzing stable isotope food web data, which underestimates the importance of mangrove C in the diet of crabs, as evidenced for specific regions and species (Bui and Lee 2014).

Mangrove leaf has also benn reported as the most important C source in the diet of others sesarmid crabs from the Indo-West-Pacific region (Harada and Lee 2016, Kristensen et al. 2017). Crab foraging on fresh leaves may be a behavior due to an adaptation to the limited availability of high-quality food in the intertidal mangrove environment compounded by high predation risk (Harada and Lee 2016). These conditions may give rise to a larger range of discrimination thresholds as similarly observed in this study (Kristensen et al. 2017).

Our result also suggests that *A. pisonii* assimilated macroalgae and macrophyte respectively, as a supplement of their diet in the field. Epiphytic macroalgae (Chlorophytes; *Rhizoclonium* sp.) are usually abundant on the roots of *R. mangle* from ARD (Hurtado-Santamaria and Quan-Young 2016). Therefore, crabs foraging on macroalgae are not forced to use excessive amounts of energy to access this food resource. Likewise, macroalgae can provide requirements for growth in terms of N (C/N < 20) (Russell-Hunter 1970, Kristensen et al. 2017). However, a more detailed understanding of the primary contributor in terms of N and foraging behavior in the field for this species and estimates of TDF for the others souerces are required.

Conclusions

The results show that fresh mangrove leaf litter of *R. mangle* dominate the diet of *A. pisonii* from ARD. The fractionation values of $\delta^{13}C$ and $\delta^{15}N$ experimentally examined between mangrove leaves and *A. pisonii* muscle tissue was 5.38 ± 0.90‰ and 3.94 ± 0.51‰, respectively. Such high isotopic shifts between diet and consumer´s tissuesare likely mainly due to routing and to a lesser extent, to fractionation. Our results indicate that *A. pisonii* can meet their nitrogen demand over an almost 2 months period on a strict mangrove leaf diet. Mangrove leaf diet in the field for *A. pisonii* and its requirements for growth in terms of N is likely supplemented mainly with the intake of macroalgae, however, N requirements and dietary N utilization needs further investigations. These results provide a view to the ecological implications of *A. pisonii* in mangrove ecosystems in the southern Caribbean Sea, their capacity to convert the low-quality mangrove C into biomass which mediate the transfer of mangrove primary production to nearshore consumers, even supporting fishery production as part of the mangrove outwelling process.

5.5. Acknowledgements

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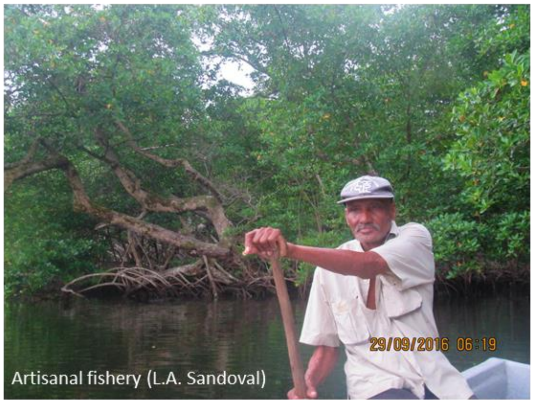
Chapter 6. General conclusions

Atrato River Delta (J.F. Blanco)

20/10/2016 14:55

Rhizophora mangle (L.A. Sandoval)



29/09/2016 06:19

Artisanal fishery (L.A. Sandoval)

Aratus pisonii (L.A. Sandoval)

The work in this thesis represents a significant contribution to our understanding of the contribution of mangrove productivity to food webs and fisheries in the Urabá Gulf (southern Caribbean Sea) and further afield. Through the different spatial scales of analysis, it is robustly demonstrated that mangroves support estuarine consumers, either because of their trophic contribution or the substrate/habitat they offer. These findings expand current understanding of mangrove-fisheries linkage given that the Urabá Gulf is an area not directly connected to other highly productive coastal habitats, while most of the studies in the Caribbean have been conducted in islands, near seagrasses, and coral reefs. This work therefore highlights the usefulness of estuarine mangroves in the Caribbean as simplified study models for the mangrove outwelling hypothesis. Likewise, the research presented in this thesis filled various knowledge gaps regarding food web structure and elemental pathways in an estuarine mangrove system.

The three origanal hypotheses of this thesis were partially accepted: 1) “mangrove descriptors (area, perimeter, and above-ground carbon) are positively correlated to the catch per unit of effort (CPUE: total and species-specific) and richness of fishes (total number of species) in the Colombian Southern Caribbean Sea”, 2) “mangroves could be a major food source sustaining some estuarine consumers at the Atrato River Delta estuary (ARD)”, and 3) “the mangrove tree-climbing crab *Aratus pisonii* (Sesarmidae) has the ability to effectively digest and assimilate a low-quality mangrove leaf litter diet”.

Chapter 2 demonstrated how mangrove areas in the Urabá Gulf and its vicinity have a direct relationship (based on ranked values) with the captures per effort unit (CPUE) of some commercial fish, and that mangrove areas and food availability in the water column were the main factors explaining fish species richness distribution in the Gulf. The above supporting partially the hypothesis that mangrove descriptors are positively correlated to CPUE and richness of fishes in the Colombian Southern Caribbean Sea since total CPUE was not correlated to any variable. In this way, mangrove area rather than variables reflecting the water column was the best predictor of the catches of benthivore species, *Ariopsis canteri* and *Mugil incilis* (Figure 17). The former appears to be a mangrove-dependent species, the latter a mangrove-associated species. It is suggested that causal links between mangrove habitat and fishery production may be explained through the trophic contribution of mangrove fringes in areas not directly connected to other highly productive coastal habitats (i.e., seagrasses and coral reefs).

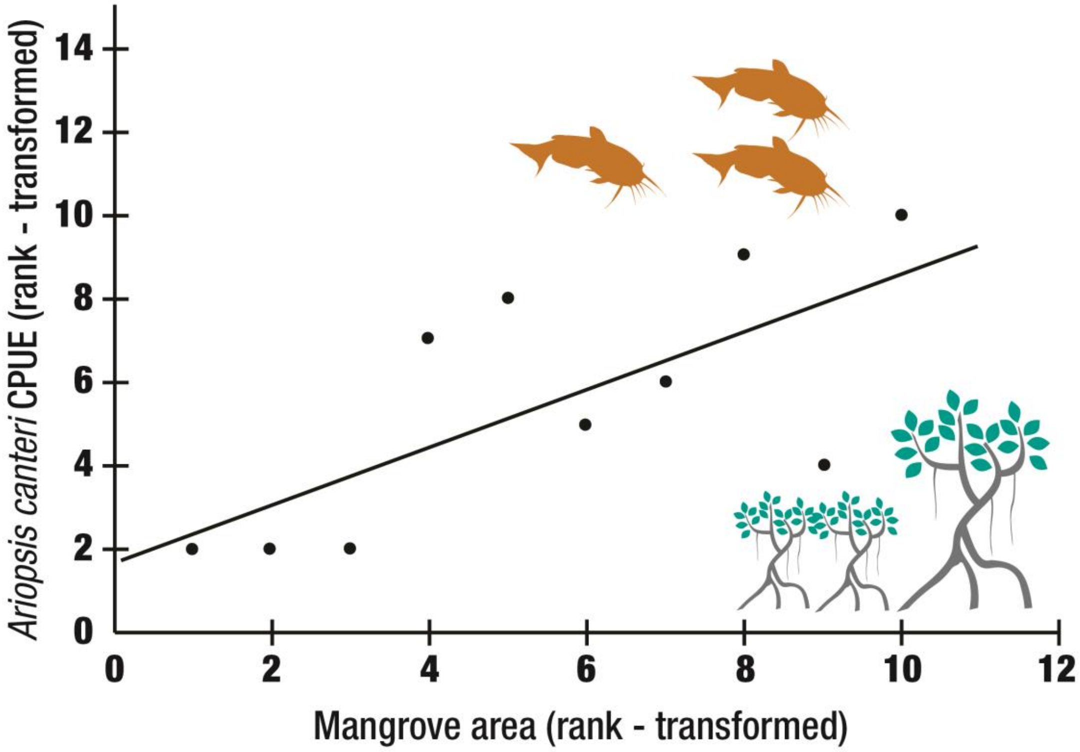


Figure 17. Ariopsis canteri CPUE vs mangrove area (R^2 = 0.50).

Chapter 3 demonstrated the ontogenic feeding shifts of sea catfish, *A. canteri* (an endemic species of the Colombian Caribbean, and endangered due to its degree of endemism and fishing pressure), which allows a decrease in intraspecific competition between small and large individuals (Figure 18). Furthermore, this chapter expanded on the finding of Chapter 2 regarding this fish being a mangrove-dependent species since evidence suggests that mangroves serve as nurseries and feeding habitats for this species, although, the hypothesis that mangrove is the source of major importance in their diet was rejected. But, it’s important to note that mangroves represent habitat rather than a major source of energy and nutrients to *A. canteri*.

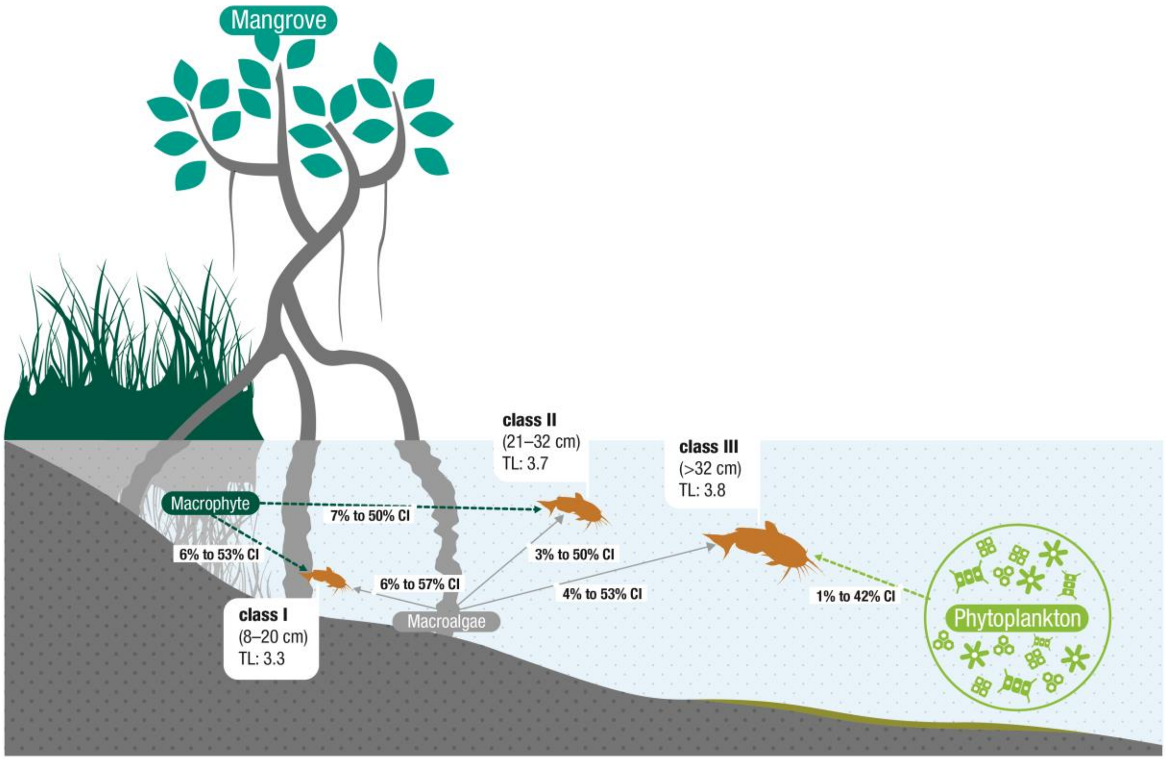


Figure 18. Diagram of the sources supporting A. canteri, showing their ontogenic feeding shifts at the Atrato River Delta estuary

In Chapter 4, the contribution of mangrove organic matter as a primary source of carbon was shown for selected fish species from small-scale fisheries and other consumers in the Atrato River Delta estuary (ARD), supporting the hypothesis that mangroves could be a major food source sustaining some estuarine consumers at ARD. Likewise, the potential pathways for phytoplankton, mangrove, microphytobenthos, macroalgae, and macrophytes sources were demostrated via isotopic analysis and previous knowledge regarding feeding habits for some fish species (see later). As such, the importance of baseline knowledge of diets in different species to better understand stable isotope data in tropical estuarine systems is higghlighted.

Chapter 4 specifically established that different carbon sources play an essential role in the food webs in the Atrato River Delta estuary, because most consumers used a mixture of sources, resulting from intertwined pathways. However, the potential pathways for five main sources were evidenced as follows. (1) *Estuarine phytoplankton* contributes directly to mesozooplankton and it is later transferred to the zooplanktivorous food chains. (2) *Mangrove* contributes directly to herbivores crabs (sesarmids) and indirectly to planktivores fish (engraulids) and the zooplanktivorous food chains. (3) *Microphytobhentos* contributes directly and indirectly to phytobenthivore fish (mugilds) and carnivores epibenthic shrimp (peneids), respectively. (4) *Macroalgae* contribute directly to omnivores epibenthos (gastropods: neritids) and omnibenthivores fish (ariids and gerrids), and indirectly to different carnivores epibenthos and zoobenthivores fish. (5) *Macrophytes* contribute directly and indirectly to herbivores crab (ocypodids) and carnivores (panopeids), respectively (Figure 19).

Mangroves could be a major food source for consumers, as brachyuran zoeae, panaeoidean mysis, sesarmid crabs as well as, engraulid, and centropomid fishes, in those areas not directly connected to other highly productive coastal habitats. Likewise, herbivorous crabs (sesarmids) and planktivorous fish (engraulids) are likely to represent key links between mangrove-derived organic matter and higher trophic levels.

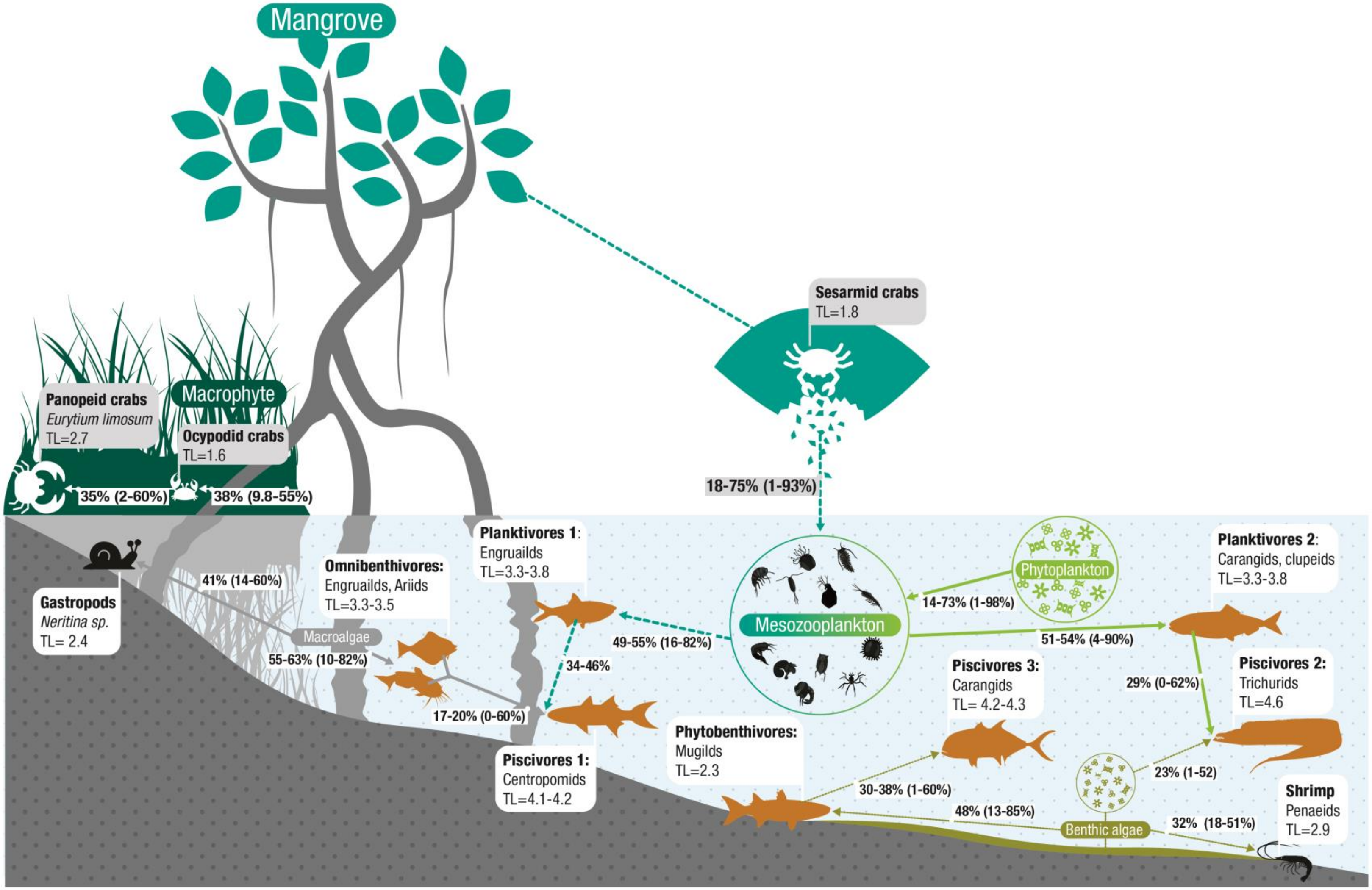


Figure 19. Diagram of the main consumers and sources showing estimated contributions of yhe main energetic pathways found in the Atrato River Delta estuary (from Chapter 4).

Chapter 5 demostred that *A. pisonii*, one of the most abundant herbivorous crabs found in neotropical mangrove systems, exhibits the physiological capacity for processing low-quality mangrove C in tropical estuaries of the Caribbean, supporting the initial hypothesis. Furthermore, in this chapter, it was shown that the fresh mangrove leaf litter of *Rhizophora mangle* dominate their diet in the ARD. Empirically-derived fractionation values for muscle tissue of *A. pisonii* fed on mangrove leaves (mean ± SD Δ^{13}C: 5.4 ± 0.9‰; Δ^{15}N: 3.9 ± 0.5‰) were similar to those reported from sesarmid crabs eating mangrove leaf litter in the Indo-West-Pacific. These values were higher than general TDFs commonly used in the isotope ecology literature thus highlighting the need for local studies representing particular ecosystem settings and species composition. Finally, the results provide insights into organic matter and carbon cycling of mangrove forests from the Neotropic, where *A. pisonii* mediate the transfer of mangrove primary production to the pelagic environment (expanding on the findings of Chapter 4), even supporting fishery production as part of the mangrove outwelling process.

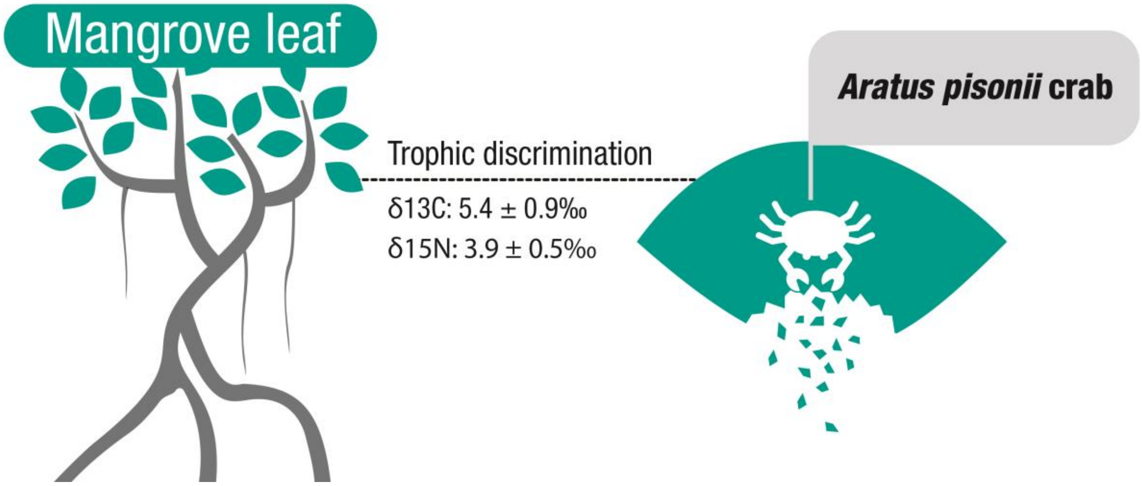


Figure 19. Diagram of trophic discrimination between mangrove leaves and *A. pisonii* muscle tissue.

In general, this dissertation provides some important insights how mangroves support some of the most common species in artisanal fisheries in the Urabá Gulf (southern Caribbean Sea). For *A. canteri*, this is demonstrated through positive correlations between mangrove and fish catch (Chapter 2) and indications of a direct relationship supported by the relative contribution mede by mangroves to their assimilated diet, and an indirect role where mangroves act as substrate/habitat that supports sources as macroalgae and benthic algae in the food webs in which this species lives (Chapter 3). In similar way, *M. incilis* showed positive correlations between mangrove area and fish catch (Chapter 2), with a causal relationship indicated by mangroves supporting benthic algae production in the food webs where this species is imbedded (Chapter 4). *Sciades proops* showed positive correlations between mangrove are and fish catch (Chapter 2). Finally, both *Centropomus pectinatus* and *Centropomus undicimalis* showed direct trophic contribution from mangrove-derived organic matter (Chapter 4).

Based on other studies, mangroves can be important sources in estuarine food webs depending on system conditions. We showed that fringing mangroves seem to be a major food source for some consumers in areas not interlinked to other highly productive coastal habitats (i.e., seagrasses and coral reefs), as reported only a few recent studies. This work therefore highlights the usefulness of estuarine mangroves in the southern Caribbean Sea as simplified study models for the mangrove outwelling hypothesis.

Nevertheless, a detailed understanding of the primary contributors and possible pathways in the ARD estuary food webs are required since Bayesian mixing models are sensitive to quality of input values (e.g. to TDFs and to variability in source pool values). We could not used local phytoplankton and benthic algae values, and in some cases, we used small sample size (e.g. estuarine phytoplankton, n=2), which could lead to more uncertain outputs. Furthemore, $\delta^{34}S$ as a tracer would be useful since it varies substantially among primary producers, but changes relatively little with progression through a food web. Even other methodological approaches can be useful such as fatty acid analysis and DNA-Based Diet Analysis.

With regard to developing a more detailed understanding of the contribution of mangrove productivity to food webs and fisheries in the Urabá Gulf (southern Caribbean Sea), this thesis leads to some questions: How does the importance of mangrove organic matter change over time and space? How is mangrove organic matter transferred into the mesozooplanktonic black box? What is the role of other crab species into organic matter processing and carbon cycling in estuarine mangrove forests? What is the TDFs values for crabs feeding on other non-mangrove sources? What is the microbial contribution in terms of conditioning of leaf litter and potentially in the gut of crabs and other detritivores? What is the community-wide food web structure and the isotopic niche of the communities and/or species? How do fishes such as *Centropomus* spp. and *S. proops*, use mangrove habitats, what is the contribution of the mangrove for possible ontogenetic changes in their diet?

The results presented in this thesis may aid the designing of strategies that jointly address mangrove conservation and management of small-scale fisheries associated with mangroves. This largely extend to ecosystem-based fishery management (EBFM) focused on the protection of extensive mangroves areas in the southern Caribbean Sea, since the general objective of this approach is to maintain healthy marine ecosystems and the fisheries they support.

This dissertation provided evidence that mangrove conservation strategies such as marine protected areas and co-management will likely benefit coastal communities through the provisions of fisheries services in the Urabá Gulf. This would directly benefit the more than 47 villages, and 1500 families who are engaged in fishing for local commerce and subsistence. Conservation strategies (protected areas and co-management) should focus on the Atrato River Delta estuary where the most extensive mangrove areas are found.