

Food web dynamics in coastal vegetated habitats of the Southern Gulf of Mexico

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Alejandra Sepúlveda Lozada

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8. Attending student: Ms. Lara Stuthmann
MSc student in International Studies in Aquatic Tropical Ecology (ISATEC) – University of Bremen

A mi papá

Abstract

Food web studies in coastal vegetated ecosystems, such as marshes and mangroves, have gained special interest not only in Ecology but also in the field of resource management and conservation. This is because food webs are recognized as a central organizing theme in ecology, and also because of the interconnected relationship of these ecosystems with fisheries production.

A central question dealing with the role of marshes and mangroves in sustaining aquatic food webs relates to their specific importance as basal resources for the aquatic faunal communities. The variability in results among studies addressing this aspect still emphasizes the need for further research across coastal settings differing in geomorphology, availability of resources, and the degree of connectivity with other ecosystems (e.g., seagrasses). In addition, the forces or pulsing events influencing the shifts in energy fluxes and habitat connectivity via animal movements still need to be understood in many coastal regions.

This dissertation aims to study the food web dynamics and fish assemblage connectivity in different coastal settings in the microtidal tropical portion of the Southern Gulf of Mexico comprised by the Centla Wetlands Biosphere Reserve and the Terminos Lagoon Protected Area. This region represents a prime location to conduct food web studies at different spatio-temporal scales due to the variability in geomorphic settings, habitats from deltaic floodplain ecosystems to the large Terminos Lagoon, and plant communities, in addition to the marked dry season and rainy season, the latter influenced by strong northerly winds (*nortes*). Moreover, Centla Wetlands and Terminos Lagoon have been so far studied separately despite being interconnected by the Grijalva-Usumacinta river system. Thus, studies focusing on energy fluxes and food webs encompassing the two areas are still necessary.

The study was conducted during both a dry and a rainy season in four sites located 26, 25, 13 and < 1 km from the coast, respectively, in the two protected areas. The former three sites comprised river-influenced deltaic lagoons (fluvio-lagoons) mainly characterized by: 1) marsh vegetation interconnected with the submerged macrophyte *Vallisneria americana*, 2) marsh and riverine mangrove forest, and 3) basin mangrove forest. The fourth site was a marine fringe mangrove creek interconnected with seagrasses (*Thalassia testudinum*, *Halodule wrightii*). The degree of openness and connectivity of the study sites to the open sea varied from 'more enclosed' (fluvio-lagoons) to 'more open' systems (fringe mangrove).

Based on stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of riparian and aquatic basal resources (marginal vegetation, detrital mangrove leaves, seston, seagrass leaves, *V. americana* leaves, epiphytic algae, macroalgae, fine particulate organic matter, sediments), and representative consumer taxa (fishes, crustaceans and mollusks), the overall hypothesis is that the importance of riparian-derived carbon for aquatic consumers is highly variable across spatial scales, and that the periodic dry and wet conditions in the area drive the major changes in resource availability and the connectivity of aquatic food webs. The individual hypotheses are: 1) the importance of riparian-derived carbon for aquatic consumers highly depends on habitat geomorphology (predicted to be higher in 'more enclosed' vs 'more open' habitats) and on availability of basal resources, 2) larger consumers' isotopic niches in the rainy season are induced by energetic pulsing events like the riverine pulse (flood pulse concept), and 3) the connectivity between fish assemblages of

marine and low-salinity habitats increases in the rainy season, under the influence of *nortes*, as higher food availability enhances fish migration towards productive river-influenced habitats.

Stable Isotope Analysis in R (SIAR) and Stable Isotope Bayesian Ellipses in R (SIBER) were used to estimate the distribution of possible contributions of basal resources to the diet of consumers as well as the isotopic niches of consumers and their seasonal variation per site, respectively. Moreover, estimations of isotopic niche areas and their overlap based on standard ellipses and the Layman's convex hull metric were used to assess the seasonal connectivity of fish assemblages from the marine and one of the fluvio-lagoon sites.

The results confirmed the prediction that higher dietary contributions of riparian-derived carbon are found in the 'more enclosed' fluvio-lagoons compared to the 'more open' fringe mangrove site, and the availability of basal resources in the studied habitats plays an important role in the energy flow patterns detected. In the dry season, few basal resources were dominant in terms of their dietary contributions to consumers in all sites (e.g., riparian-derived carbon in the fluvio-lagoon habitats and seston and macroalgae in the fringe mangrove site), whereas in the rainy season basal resources showed more even dietary contributions to consumers. This, together with the larger isotopic niche width observed for the majority of consumers in the rainy season corresponds with an increase in resource use diversification by consumers and helped to corroborate the flood pulse concept for the river-influenced sites.

In the latter habitats (fluvio-lagoons), the relevance of lateral linkages as stated by the flood pulse concept was specifically manifested with the high contribution of riparian-derived carbon for most or some groups of consumers (e.g., omnivore and zoobenthivore species) during the dry season when the receding water (after the previous rainy-flood season) could potentially drag the organic matter into the water bodies. However, other basal resources presumably transported from upstream areas (longitudinal connectivity), like sediments and fine particulate organic matter, were observed to be important in the floodplain ecosystems during the time of highest freshwater discharge during the rainy season.

On the other hand, the different factors influencing the fate and utilization of basal resources in the fringe mangrove site stress the importance of considering additional or complementary conceptual frameworks to the flood pulse concept for a better understanding of the main factors driving the energy fluxes in marine-influenced habitats in the study area. For instance, the 'coastal flooding' influenced by the *nortes* via the intrusion of saline water into the system seems to be an important driver of ecosystem changes in the fringe mangrove site.

The results of this work also confirmed that connectivity of fish assemblages between marine and low-salinity habitats (fringe mangrove/fluvio-lagoon) increases at times of higher river discharge, under the influence of *nortes*, whereas connectivity decreases in the dry season. Nevertheless, it is still necessary to understand the effect that winds exert on this connectivity.

The twofold increase in the number of marine species in the low-salinity habitat during the rainy season can be attributed to the increased primary productivity and food supply in this river-influenced area during the

rainy season, thus becoming an attractive zone for marine species that can temporally exploit abundant resources. In this season, the considerable increase in isotopic niche area of the fish species sampled in the low-salinity habitat also highlighted the significant intrusion of marine species with extreme enriched positions along the $\delta^{13}\text{C}$ axis (recent migrants). It is noteworthy that while half of the marine species in this habitat were recognized as recent migrants, the other half were isotopically on par with the $\delta^{13}\text{C}$ values of the freshwater consumers and basal resources therein, indicating the potential role of the low-salinity habitat as a feeding area for these species. The connectivity of the marine and freshwater fish assemblages was also illustrated with the overlap of the isotopic niches of these groups in the rainy season, whereas no isotopic overlap was observed in the dry season.

This work contributes to the body of research addressing the different basal resources to aquatic consumers and food web connectivity in tropical coastal regions, as well as the specific importance of riparian-derived carbon in different ecosystems and under contrasting seasonal influences. Moreover, this study comprises the first effort in addressing these issues simultaneously in the two interconnected and important coastal ecosystems of Centla Wetlands and Terminos Lagoon in the Southern Gulf of Mexico. Knowledge about energy fluxes and the food web dynamics in these spatially and temporally complex ecosystems can be useful for management and conservation, particularly in face of the vulnerability and degradation of these ecosystems.

Zusammenfassung

Nahrungsnetzstudien in mit Bewuchs bedeckten Küstenökosystemen, wie Sümpfen und Mangroven, haben nicht nur in der Ökologie, sondern auch im Bereich des Ressourcenmanagements und des Umweltschutzes besondere Aufmerksamkeit erlangt. Diese beruht darauf, dass Nahrungsnetze in der Ökologie als ein zentrales organisierendes Thema anerkannt sind, sowie auf den wechselseitigen Beziehungen zwischen diesen Ökosystemen und der Fischereiproduktion.

Eine zentrale Frage, die sich mit der Rolle von Sümpfen und Mangroven im Erhalt aquatischer Nahrungsnetze befasst, bezieht sich auf ihre spezifische Bedeutung als basale Ressource für die aquatischen Faungemeinschaften. Die Variabilität unter Ergebnissen von Studien, die diesen Aspekt behandeln, unterstreicht zusätzlich die Notwendigkeit weiterer Forschung an Küstenregionen, die sich in der Geomorphologie, der Verfügbarkeit der Ressourcen und dem Grad der Konnektivität mit anderen Ökosystemen (z. B. Seegräser) unterscheiden. Zudem müssen die Kräfte oder pulsierenden Ereignisse, die durch Tierbewegungen die Verschiebungen der Energieflüsse und der Lebensraumkonnektivität beeinflussen, in vielen Küstengebieten noch verstanden werden.

Diese Dissertation hat zum Ziel, die Nahrungsnetzynamiken und Konnektivität der Fischansammlungen in verschiedenen Küstenhabitaten des mikrotidalen tropischen Bereiches des südlichen Golfes von Mexiko, bestehend aus dem Biosphärenreservat des Centla-Feuchtgebietes und dem Schutzgebiet der Terminos Lagune, zu untersuchen. Dank der Variabilität der geomorphen Umgebung, die Habitate von deltaischen Überschwemmungsgebiet-Ökosystemen bis hin zur großen Terminos-Lagune und Pflanzengemeinschaften aufweist, und der ausgeprägten Trocken- und Regenzeit, letztere beeinflusst durch die starken nördlichen Winde (*Nortes*), repräsentiert diese Region einen hervorragenden Standort, um Nahrungsnetzstudien in verschiedenen räumlich-zeitlichen Skalen durchzuführen. Darüber hinaus wurden das Centla-Feuchtgebiet und die Terminos-Lagune bisher separat untersucht, obwohl sie durch das Grijalva-Usumacinta-Flusssystem miteinander vernetzt sind. Somit sind Studien zu Energieflüssen und Nahrungsnetzen, die beide Gebiete umfassen, noch erforderlich.

Die Studie wurde sowohl während einer Trocken- als auch während einer Regenzeit in den beiden Schutzgebieten jeweils an vier Standorten durchgeführt, die 26, 25, 13 und <1 km von der Küste entfernt liegen. Die erstgenannten drei Standorte umfassten flussbeeinflusste deltaische Lagunen (Fluvio-Lagunen), die vor allem gekennzeichnet sind durch: 1) Sumpf-Vegetation in Verbindung mit dem untergetauchten Makrophyten *Vallisneria americana*, 2) Sumpf- und Flussmündungsmangrove und 3) Basinmangrove. Der vierte Standort war ein mariner mangrovengesäumter Bach, vernetzt mit Seegräsern (*Thalassia testudinum*, *Halodule wrightii*). Der Grad der Offenheit und Konnektivität der Studienstandorte zum offenen Meer variierte von "geschlosseneren" (Fluvio-Lagunen) zu "offeneren" Systemen (Küstenmangrove).

Basierend auf stabiler Isotopen-Analyse ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) von basalen Ressourcen des Ufers und Wassers (Randvegetation, detritische Mangrovenblätter, Seston, Seegrasblätter, *V. americana*-Blätter, epiphytische Algen, Makroalgen, feines partikuläres organische Material, Sedimente) und in repräsentativen Konsumenten-Taxa (Fische, Krustentiere und Mollusken), ist die Gesamthypothese, dass die Bedeutung

vom Ufer stammenden Kohlenstoffes für aquatische Konsumenten über räumliche Skalen sehr variabel ist, und dass die periodischen trockenen und feuchten Verhältnisse in diesem Gebiet die wesentlichen Änderungen in der Ressourcenverfügbarkeit und der Konnektivität der aquatischen Nahrungsnetze antreiben. Die einzelnen Hypothesen sind: 1) die Bedeutung des vom Ufer stammenden Kohlenstoffes für aquatische Konsumenten hängt in hohem Maße von der Geomorphologie des Habitats ab (unter der Annahme, dass sie in ‚geschlosseneren‘ Habitaten höher ist als in ‚offeneren‘) sowie von der Verfügbarkeit basaler Ressourcen, 2) die isotopischen Nischen größerer Konsumenten während der Regenperiode werden durch energetische pulsierende Ereignisse wie den Fluss-Puls verursacht (Flutpuls-konzept), und 3) die Konnektivität zwischen Fischansammlungen in marinen und niedrig-salinen Habitaten nimmt in der Regenzeit unter dem Einfluss der *Nortes* zu, wenn höhere Nahrungsverfügbarkeit die Fischwanderung in Richtung der produktiven fluss-geprägten Habitate verstärkt.

Um die Verteilung möglicher Beiträge basaler Ressourcen zur Nahrung von Konsumenten, sowie die isotopischen Nischen der Konsumenten und ihre saisonale Variation am jeweiligen Standort einzuschätzen, wurden Stabile Isotopen-Analyse in R (SIAR) and Stabile Isotopen-Bayes'sche Ellipsen in R (SIBER) verwendet. Zusätzlich wurden Abschätzungen von isotopischen Nischengebieten und ihrer Überlappung, die auf Standard-Ellipsen und der Laymanschen Konvexe-Hülle-Metrik basierten, verwendet, um die saisonale Konnektivität von Fischansammlungen des marinen und eines der Fluvio-Lagunen Standorte abzuschätzen.

Die Ergebnisse bestätigten die Annahme, dass höhere Beiträge an vom Ufer stammenden Kohlenstoffes zur Nahrung in den ‚geschlosseneren‘ Fluvio-Lagunen gefunden werden im Vergleich zu den ‚offeneren‘ Standorten mit Küstenmangroven, und die Verfügbarkeit der basalen Ressourcen in den untersuchten Habitaten eine wichtige Rolle in den ermittelten Energieflussmustern spielt. In der Trockenperiode dominierten an allen Standorten wenige basale Ressourcen hinsichtlich ihres Beitrages zur Nahrung der Konsumenten (z.B. vom Ufer stammender Kohlenstoff in den Fluvio-Lagunen-Habitaten, und Seston und Makroalgen am Küstenmangroven-Standort), wohingegen während der Regenzeit basale Ressourcen gleichmäßigere Anteile in der Nahrung der Konsumenten aufwiesen. Zusammen mit der größeren isotopischen Nischenweite, die in der Regenperiode für den Großteil der Konsumenten beobachtet wurde, spricht diese Feststellung für einem Anstieg der Ressourcennutzungsdiversifikation durch Konsumenten und half, das Flutpuls-konzept für die flussbeeinflussten Standorte zu bekräftigen.

In den letztgenannten Habitaten (Fluvio-Lagunen) machte sich die Relevanz der Lateralverknüpfungen, wie durch das Flutpuls-konzept erklärt, besonders bemerkbar in dem hohen Anteil des vom Ufer stammenden Kohlenstoffes in den meisten oder einigen Gruppen von Konsumenten (z.B. omnivore and zoobenthivore Arten) während der Trockenperiode, wenn das zurückweichende Wasser (nach der vorhergehenden regnerischen Überschwemmungs-Periode) möglicherweise die organische Substanz in die Gewässer tragen konnte. Jedoch haben sich andere basale Ressourcen, wie Sedimente und feines partikuläres organisches Material, die vermutlich von flussaufwärts gelegenen Gegenden transportiert wurden (longitudinale Konnektivität), in den Überschwemmungsgebiet-Ökosystemen als wichtig erwiesen in der Zeit des höchsten Süßwassereintrages während der Regenperiode.

Die unterschiedlichen Faktoren, die das Schicksal und die Nutzung der basalen Ressourcen am Küstenmangroven-Standort beeinflussen, betonen hingegen die Wichtigkeit, zusätzliche oder komplementäre Rahmenkonzepte zum Flutpuls-konzept zu erwägen, um die Hauptfaktoren, die die Energieflüsse in den marin-beeinflussten Habitaten im Untersuchungsgebiet steuern, besser zu verstehen. Beispielsweise scheint die "Küstenüberschwemmung", die von den *Nortes* über die Intrusion von salzreichem Wasser in das System beeinflusst wird, ein wichtiger Treiber von Veränderungen des Ökosystems am Küstenmangroven-Standort zu sein.

Die Ergebnisse dieser Arbeit bestätigen auch, dass die Konnektivität von Fischansammlungen zwischen marinen und niedrig-salinen Habitaten (Küstenmangroven/Fluvio-Lagunen) während Zeiten höheren Flusseintrages unter dem Einfluss der *Nortes* zunimmt, wohingegen die Konnektivität in der Trockenperiode abnimmt. Jedoch ist es noch erforderlich, die Wirkung zu verstehen, die Winde auf diese Konnektivität ausüben.

Die Verdopplung der Zahl der marinen Arten im niedrig-salinen Habitat während der Regenperiode kann auf die gesteigerte Primärproduktion und Nahrungsverfügbarkeit in diesem fluss-beeinflussten Gebiet zurückgeführt werden, das somit eine attraktive Zone für marine Arten wird, die temporär reichhaltige Ressourcen nutzen können. In dieser Periode unterstreicht auch die beträchtliche Vergrößerung des isotopischen Nischenbereiches der im niedrig-salinen Habitat untersuchten Fischarten die signifikante Intrusion mariner Arten mit extrem angereicherten Positionen entlang der $\delta^{13}\text{C}$ -Achse (Neueinwanderer). Bemerkenswert ist, dass während die eine Hälfte der marinen Arten in diesem Habitat als Neueinwanderer erfasst wurden, die andere Hälfte isotopisch gleichwertig mit den $\delta^{13}\text{C}$ -Werten der Konsumenten und basalen Ressourcen im Süßwasser war, was auf die mögliche Rolle des niedrig-salinen Habitats als Nahrungsgebiet für diese Arten hinweist. Die Konnektivität der Meeres- und Süßwasser-Fischansammlungen wurde auch aufgezeigt in der Überlappung der isotopischen Nischen dieser Gruppen während der Regenperiode, wohingegen keine isotopische Überlappung in der Trockenperiode beobachtet wurde.

Diese Arbeit trägt sowohl zur Forschung über die unterschiedlichen basalen Ressourcen in Bezug auf aquatische Konsumenten und Nahrungsnetz-konnektivität in tropischen Küstenökosystemen bei, als auch über die besonderen Bedeutung von vom Ufer stammenden Kohlenstoffes in verschiedenen Ökosystemen und unter gegensätzlichen saisonalen Einflüssen. Darüber hinaus umfasst diese Studie den ersten Aufwand, diese beiden Aspekte gleichzeitig in den beiden miteinander vernetzten und wichtigen Küstenökosystemen des Centla-Feuchtgebietes und der Terminos-Lagune im südlichen Golf von Mexiko zu behandeln. Kenntnisse über Energieflüsse und über die Dynamik von Nahrungsnetzen in diesen räumlich und zeitlich komplexen Ökosystemen kann nützlich für das Management und für den Umweltschutz sein, vor allem in Anbetracht der Verletzlichkeit und der Zerstörung dieser Ökosysteme.

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¡Para mi maravillosa madre y para mi hermana Diana!

Chapter I

General Introduction

General Introduction

1.1 Coastal vegetated habitats: distribution, ecological processes and functions

The coastal environment is comprised of a complex “mosaic of interconnected habitats” (Sheaves 2009) including prominent and iconic vegetated ecosystems like mangroves, salt marshes, and seagrasses (Roundtree and Able 2007; Davis et al. 2012; Gaiser et al. 2015).

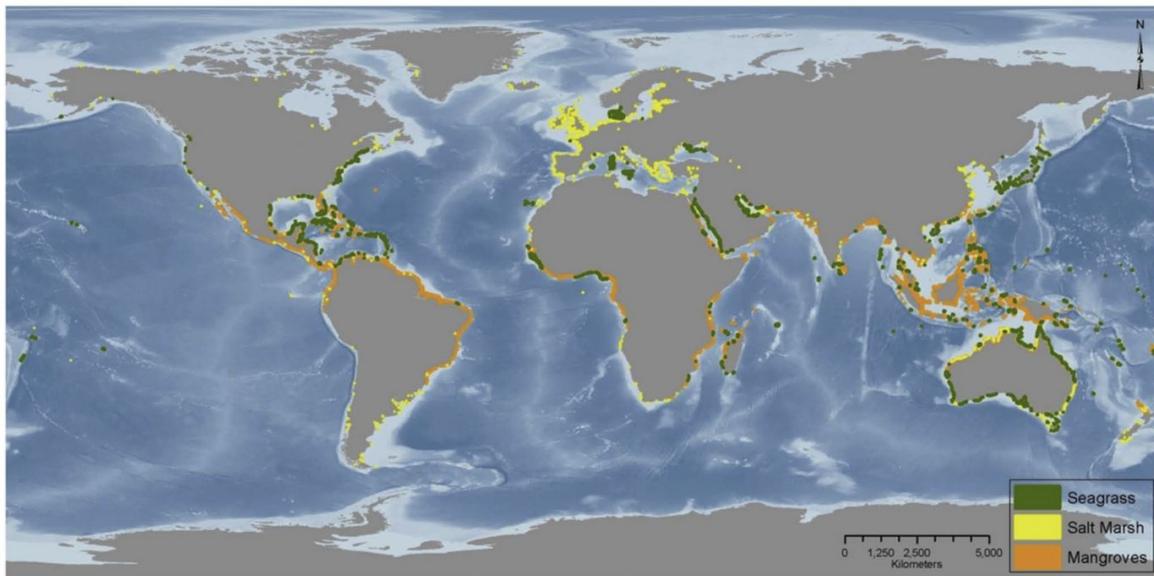


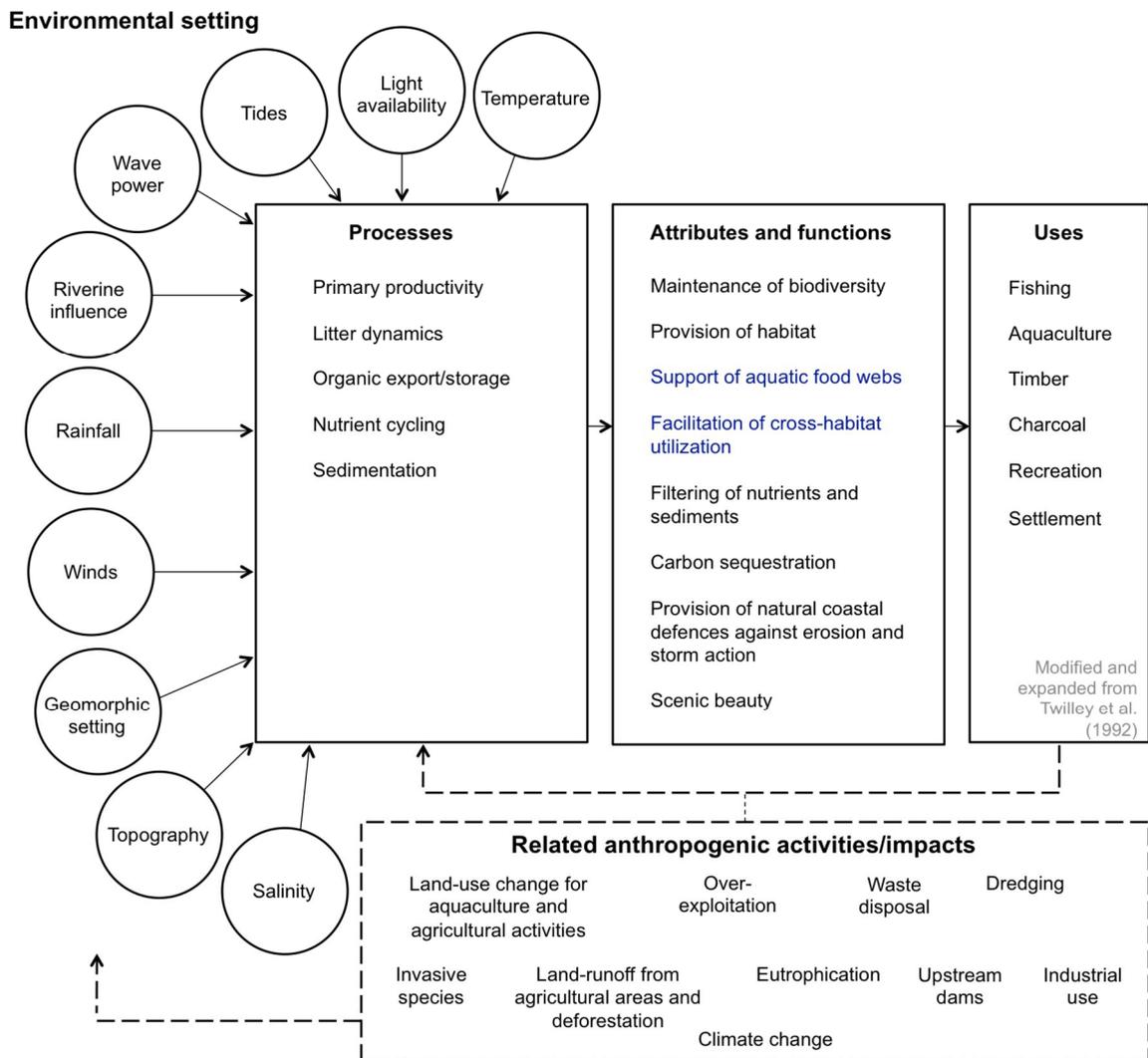
Fig. 1.1 Global distribution of mangroves, salt marshes, and seagrasses (taken from Pendleton et al. 2012)

Mangroves are distributed in the upper half of the intertidal zone along the tropical and subtropical regions of the world (Fig. 1.1), between approximately 30°N and 30°S latitude (Duke 1992; Giri et al. 2011). The distributional limits generally coincide with the 20 °C winter isotherm of seawater (Goudie and Viles 2016). Mangroves are constrained by sensitivity to freezing, but with increasing temperatures and fewer coastal freezes, these forests may expand their latitudinal range (Goudie and Viles 2016, and references therein). Mangroves mainly grow on soft substrates along sheltered coastlines, shallow lagoons, estuaries, rivers or deltas (FAO 2007), and cover an approximated global area of 15.3 million hectares (Hutchison et al. 2014).

Salt marshes comprise the dominant intertidal vegetation on shorelines at a global scale, from arctic to tropical areas, dominating in temperate zones (Fig. 1.1) (Adam 1990; Kangas and Lugo 1990; McKee et al. 2012a). Although it is often reported that mangroves replace salt marsh vegetation on tropical coasts, salt marshes may exist above the higher elevation of tropical swamps (Chmura 2009). They occur in protected, low-energy estuaries, lagoons, bays and river

mouths, and grade into brackish and freshwater marshes under significant river inflow, where the presence of freshwater submerged aquatic vegetation (SAV) can also be important (Broome and Craft 2000; Rozas and Minello 2006; Chmura 2009). Their global aerial extent is not well documented (Chmura 2009), but it is estimated to be up to 40 million hectares (Pendleton et al. 2012).

Seagrasses are widely distributed along temperate and tropical coastlines (Fig. 1.1) (Short et al. 2007), and are generally thought of as plants which grow submerged in seawater; although several species, both in temperate and tropical regions, grow in intertidal habitats where they are exposed to air for part of the day, and where they cope with high irradiance and desiccation (Jupp et al. 1996; Björk et al. 1999; Shafer et al. 2007). A conservative estimate of the total area covered by seagrasses is 17.7 million hectares with many areas yet to be documented (Spalding et al. 2003).



◀ **Fig. 1.2** Diagram of the linkages among the environmental setting, ecological processes, functions and uses of mangroves, marshes, and seagrass ecosystems. Modified from Twilley et al. (1992), and expanded based on the following references: for mangroves, Bouillon et al. (2009), Manna et al. (2012), Lee et al. (2014); for marshes, Chmura (2009); for seagrasses, Hemminga and Duarte (2000), Orth et al. (2006), Kennedy and Björk (2009), Short et al. (2011), Fourqurean et al. (2012), Hejnowicz et al. (2015); for the three ecosystems, Laffolley and Grimsditch (2009). The approached functions are highlighted in blue

Mangroves, salt marshes and seagrasses comprise some of the world's most productive ecosystems, and play a significant role in human livelihoods (Short et al. 2011; Sheaves et al. 2015). The interplay between the environmental setting and the ecological processes, functions and benefits to humans of these ecosystems, as well as the feedback effects of anthropogenic activities, is complex and region-specific (see Fig. 1.2, based on a diagram of Twilley et al. 1992 for mangrove ecosystems, and adapted to include salt marshes and seagrasses).

The processes and specific ecological functions of these ecosystems are related to the environmental setting and forcing functions of the coastal zone (Twilley et al. 1992). Mangroves' coverage is limited globally by temperature, but variations in rainfall, tides, waves, winds, river flow and salinity greatly determine their productivity, expanse and biomass at the regional and local scale (Wafar et al. 1997; Ball 2002; Alongi 2009). Salt marsh processes are also determined by a variety of climatic, hydrologic and physical factors including temperature and rainfall, tidal inundation, wave energy, elevation, slope, sediment, soil composition and salinity (U.S. Fish and Wildlife Service 1999). As for seagrasses, some of the most important environmental factors influencing their distribution and productivity are light, temperature, salinity, wave action and nutrient availability (Hemminga and Duarte 2000; Björk et al. 2008).

The balance of organic matter export/storage from and within coastal vegetated areas is determined by the geomorphological setting in combination with tidal regime and river flows (Lee et al. 2014). Nutrient cycling is highly influenced by production, decomposition and export of leaf litter in concert with intrasystem processes such as regeneration, accumulation and denitrification (Twilley et al. 1992). Submerged and emerged hydrophytes are also efficient at removing nutrients (e.g., nitrogen and phosphorus) and therefore play an important role in the cycling of these nutrients (Erftemeijer and Middelburg 1995; Sousa et al. 2010). Sedimentation depends strongly on local geomorphology and rainfall/tidal/wind/storm regimes (Lee et al. 2014), and results from the reduction in current velocity and attenuation of wave action by the dense vegetation (Augustinus 1995; Vassallo et al. 2013). Salt marshes and mangroves, for example, directly influence accretion and vertical land development by enhancing sedimentation and/or through direct organic contributions to soil volume (i.e., peat formation) (Chmura 2011; Drexler 2011; Lee et al. 2014).

Ecological processes, as those mentioned above, support varied and important functions and services provided by mangroves, marshes and seagrasses (Twilley et al. 1992; Beck et al. 2001). For instance, in addition to their extremely high primary productivity, structurally these ecosystems provide substantial and complex habitats, and therefore support a great abundance and diversity of fish and invertebrates (Beck et al. 2001; Laffoley and Grimsditch 2009; Whitfield 2017). These often dominant primary producers, together with their epiphytes and associated benthic algae, provide an important energy source to support local, transient and distant food webs (Heck et al. 2008; Hejnowicz et al. 2015). Moreover, the proximity of these ecosystems with each other in some settings facilitates trophic transfers and cross-habitat utilization by fishes and invertebrates (Beck et al. 2001; Orth et al. 2006). Other important functions include the enhancement of water quality, and the amelioration of erosion and natural hazards in the coastal zone, as well as climate change mitigation through carbon storage and sequestration (Twilley et al. 1992; Laffoley and Grimsditch 2009; Hejnowicz et al. 2015).

The human use of these ecosystems in any coastal region (Fig. 1.2) depends on the nature of their functions together with the cultural and economic conditions of the area (Twilley et al. 1992). The local uses of these ecosystems (e.g., fishing, aquaculture, timber, charcoal, recreation, settlement) can have a feedback effect on the ecological processes carried out in these ecosystems, and thus influence their capacity to provide certain functions (Twilley et al. 1992). The impact to these ecosystems can also be intensified by diverse anthropogenic activities at the regional and global scale including aquaculture and agricultural activities, over-exploitation of resources, waste disposal, dredging, introduction of invasive species, land-runoff from agricultural areas and deforestation, eutrophication, industrial activities, construction of upstream dams, and climate change (Lee et al. 2014; Hejnowicz et al. 2015) (Fig. 1.2).

Taking these interactions into consideration, and based on stable isotope analysis of basal resources and representative consumer taxa, this dissertation investigates the food web dynamics and fish assemblage connectivity in coastal ecosystems of the Southern Gulf of Mexico where marshes, mangroves and seagrasses are conspicuous and interconnected in some instances.

Accounting for the spatio-temporal variability of these ecosystems is indispensable in order to get a better understanding of their role in sustaining aquatic food webs, and facilitating cross-habitat utilization by fishes. Food web research in this direction can address important questions and fill knowledge gaps regarding how these ecosystems function (e.g., as feeding areas). For example, there is still a lack of knowledge about the specific importance of riparian vegetation for food webs across different settings (Mancera-Pineda 2003; Bouillon et al. 2004; Vaslet et al. 2012; Claudino et al. 2015; Whitfield 2017), and the balance of contributions from different basal

resources to aquatic consumers (Abrantes et al. 2015). Moreover, seasonal influences on coastal food webs are rarely considered (Abrantes et al. 2015; Garcia et al. 2017), and a systematic understanding of how different sources of variability influence the niche space is lacking (Yeakel et al. 2016).

The following section outlines the current understanding, including knowledge gaps, of the role coastal vegetated habitats play in sustaining aquatic food webs, and facilitating cross-habitat utilization by fishes. The ecosystem-level concepts ‘outwelling’ and ‘flood pulse’ are used as a theoretical background to approach these topics as they provide an important baseline for the understanding of energy fluxes and food web dynamics across spatial and temporal scales.

1.2 Knowledge gaps

1.2.1 Sustenance of food webs

The impetus for estuarine food-web studies is often the desire to understand sources of nutrition supporting fisheries’ production (Bouillon et al. 2011). The link between mangroves, marshes and seagrasses with fisheries production is based on the fact that they serve as nursery grounds, provide shelter and supply a rich food source (Kathiresan 2014), all of which have been attributed to their physical structure, high primary production rates and the provision of abundant food resources.

Also, the ‘outwelling’ of nutrients and detritus from productive tidal wetlands to coastal and offshore waters has been a core aspect highlighting the importance of these wetlands for fisheries (Nagelkerken et al. 2008).

The outwelling hypothesis of Odum (1968, 1980) has been one of the dominating ecosystem-level hypotheses in estuaries for the past four decades (Lee et al. 2014). It originally described salt marshes as net exporters of carbon thus contributing significantly to the productivity of off-shore waters, and their secondary production via the export of detritus (Odum 1968, 1980). For tropical systems, this translates as a potential dependency on mangrove-derived organic matter for secondary production in adjacent systems (Bouillon and Connolly 2009).

But the apparent variability in results among studies of movement of carbon from inshore to offshore waters led to a refinement of theories about outwelling of energy (Connolly et al. 2005). Recent investigations suggest that the variation in carbon store and accumulation rate on coastal wetland settings is driven primarily by the hydro-geomorphic setting (Bouillon et al. 2004; Vaslet et al. 2012; Saintilan et al. 2013). Indeed, since the late 70’s and early 80’s, Odum et al. (1979) and Odum (1980) suggest that geomorphometry of the coastal bays and estuaries, tidal amplitude

and magnitude of freshwater inputs are the three key factors which determine whether there is outwelling. For example, where channels between offshore and inshore waters are narrow, or where tidal action is weak, one would not expect to find extensive outwelling; and where there is a more open estuary with extensive exchanges between estuarine and continental shelf waters, then one would expect outwelling (Odum 1980) (Fig. 1.3). Moreover, outwelling is periodic or seasonal and associated especially with high spring tides and storms (Odum 1980).

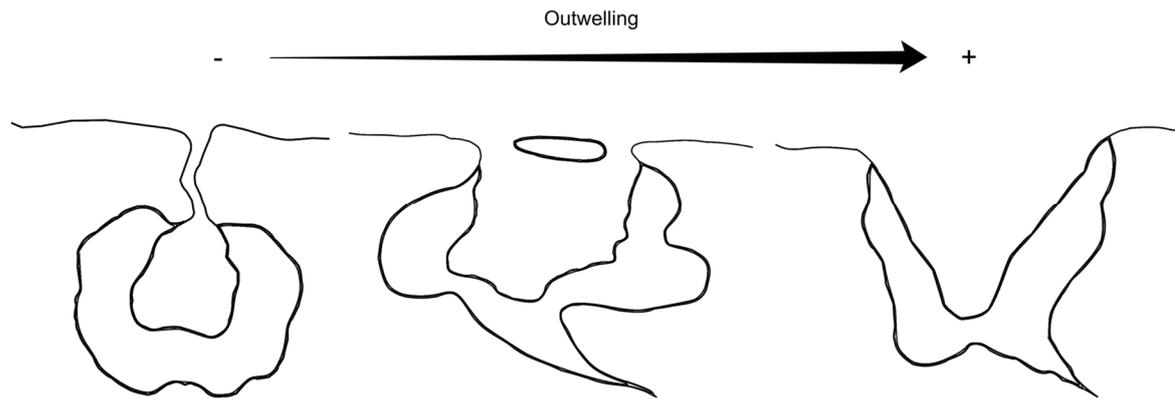


Fig. 1.3 Geomorphometric patterns of estuaries which are thought to influence the degree of outwelling according to Odum (1980). Figures were redrawn and adapted from Odum (1980)

Given these considerations, which were outlined over four decades ago, there is still considerable uncertainty as to the exact importance of coastal vegetated habitats in providing carbon to the aquatic faunal communities in diverse coastlines (Abrantes et al. 2015; Whitfield 2017). General conclusions regarding food assimilation patterns by estuarine consumers along environmental gradients require further study and analysis (Claudino et al. 2015).

Only recently, some studies have motivated a renewed interest in carbon dynamics related to the direct opposite of the outwelling paradigm (Lee et al. 2014). For example, Bouillon et al. (2004) and Vaslet et al. (2012) addressed the importance of mangrove production in different geomorphic settings including the Kakinada Bay in India, the Gazi Bay in Kenya, the Chilaw Lagoon in Sri Lanka, the Florida Keys and Indian River Lagoon in the US, and the Twin Cays in Belize. Their results suggest, in line with the predictions of Odum (1980), that mangrove-derived carbon is more important for consumers in more ‘enclosed’ systems compared to more ‘open’ ones, where sources like phytoplankton, macroalgae, seagrasses and epiphytes are more important.

Thus, the availability of autotrophic food sources plays an important role in the food web structure among and within estuaries (Abrantes et al. 2015; Claudino et al. 2015). In addition to the production within estuaries (e.g., seagrass and microalgae) and lateral sources (e.g.,

mangroves and salt marsh), the complexity of food webs is driven by potential inputs longitudinally transported from upstream (riverine) and downstream (oceanic) (Bouillon et al. 2011; Alongi et al. 2014) (Fig. 1.4).

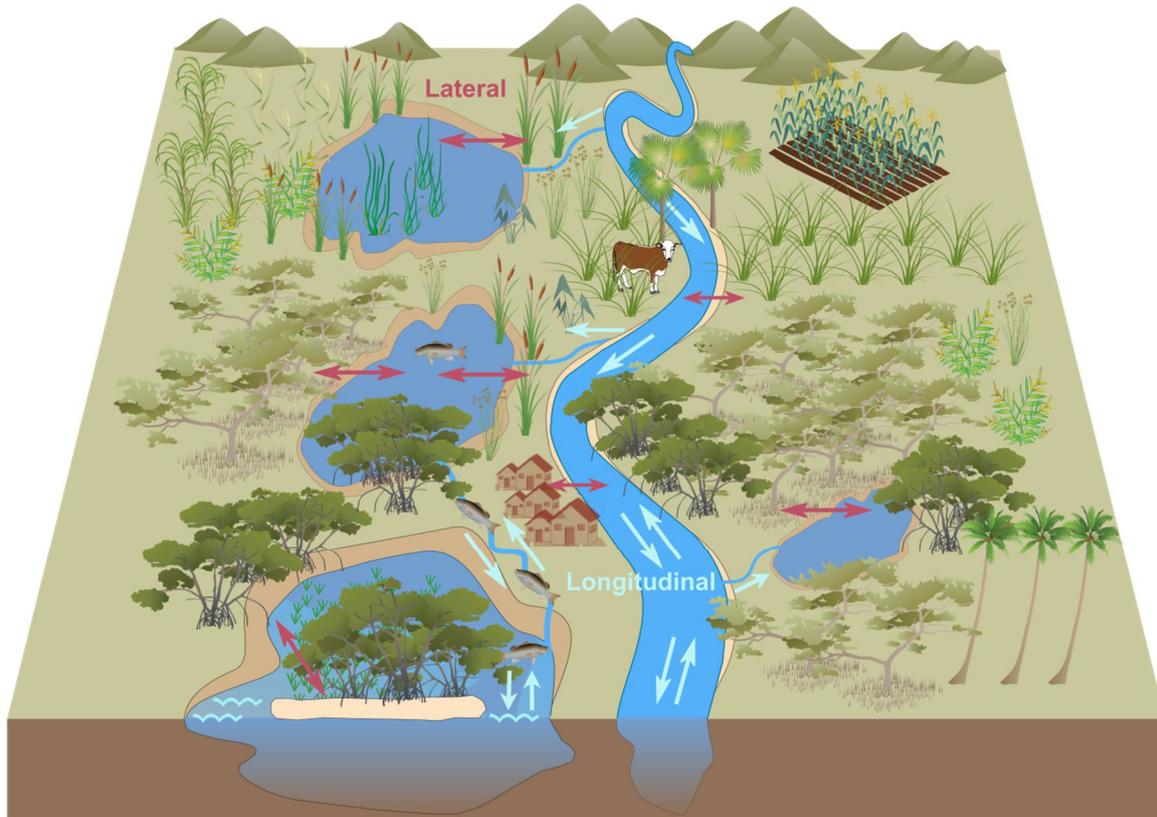


Fig. 1.4 Lateral and longitudinal fluxes of organic matter sources and energy in an estuary. The scheme depicts a simplified configuration of the study area in the Southern Gulf of Mexico based on image templates authored by T. Saxby, D. Kleine, J. Hawkey, J. Thomas, K. Kraeer and L. Van Essen-Fishman, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

On the other hand, the hierarchical series of overlapping energetic forces or pulsing events that sustain and give structure to coastal systems vary on spatial and temporal scales (Yáñez-Arancibia et al. 2013a). Therefore, energetic pulsing (e.g., in terms of precipitation, freshwater discharge and flooding) can be linked to primary productivity pulses, seasonal changes in the contribution of different basal resources, and connectivity.

Most river-dominated wetlands in North America and elsewhere exhibit considerable water-level fluctuations between dry and rainy seasons, and function as floodplains where flood pulses control their ecology (reviewed in Moreno-Casasola et al. 2012).

The flood-pulse concept (FPC) of Junk et al. (1989) and its updated version (Junk and Wantzen 2004) highlight the importance of the lateral-mediated transfer of energy, materials and organisms

in large river floodplains, where the annual flood pulse, characterized by periodic inundation and drought events, is the most important hydrological feature and driving force. Contrary to the river-continuum concept (RCC) of Vannote et al. (1980), the FPC predicts organic matter from upstream origins is insignificant for floodplain production relative to organic material produced and consumed locally. Therefore, most secondary production is attributed to the high in situ aquatic and riparian production. This concept also states that food supply during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic organisms (Junk et al. 1989; Junk and Wantzen 2004).

The seasonal shifts in resource availability, and the reliance upon a wider variety of resources by aquatic consumers during the flood phase can thus be strongly associated with habitat changes due to the flood pulse (Wantzen et al. 2002).

According to Ou and Winemiller (2016), many studies of tropical food webs in river-dominated systems have shown spatial rather than temporal variation, which reflects the need for more detailed studies of seasonal variation in food web structure and function in these systems, especially in regions where seasonal flooding is pronounced and prolonged. This knowledge is essential for elucidating the adaptive nature of complex ecological systems (Yeakel et al. 2016).

1.2.2 Facilitation of cross-habitat utilization

Knowledge about food-web interactions across boundaries is important to understand the ecological connectivity within the seascape (Berkström et al. 2013). The meaning of connectivity is complex and is more than just the proximity of different habitats and the movement of individuals among them; it is a facilitator that allows the spatio-temporal matching between the functional requirement to use the particular habitat (e.g., refuge), the occurrence of appropriate resources (e.g., flood marsh surface), and physical conditions in the habitat (e.g., oxygen levels) (Berkström et al. 2012; Sheaves et al. 2015).

Population dynamics (including ontogenetic/feeding migrations and movements to refugia), together with ecophysiological factors, food/predation trade-offs, environmental factors, and resource availability, all contribute to connectivity and the nursery ground value of coastal ecosystems (Sheaves et al. 2015, and references therein).

For the Western Atlantic, coastal lagoons have been considered to play an important role in the life cycle of many coastal fishes, and are viewed as major elements of small-scale migrations, which by involving lagoon/estuarine habitats allow a high standing stock to be maintained (Pauly and Yáñez-Arancibia 2012).

The high carrying capacities of these ecosystems in terms of seasonal food availability to fishes play a crucial role in these migrations, and evolutionary mechanisms have emerged that have stabilized and refined such seasonal programming, making fish populations gradually more dependent on the estuarine system for the maintenance of high biomass (Pauly and Yáñez-Arancibia 2012).

Studies carried out by Yáñez-Arancibia et al. (1980, 1988) in the Terminos Lagoon system showed that fishes come in, leave and disperse throughout the estuary during seasons in response to changes in environmental conditions, but particularly with respect to primary productivity and food availability pulses.

Freshwater inflow is one of the most influential pulses affecting community structure and function in estuaries because under predictable flood pulse regimes it delivers resources to large expanses of estuarine habitat, and also makes high-quality habitats available for exploitation by resident consumers and marine higher-order consumers able to tolerate sub-optimal conditions to exploit resources (Odum et al. 1995; Piazza and La Peyre 2012).

The interactions between the highly available resources (e.g., resident preys) and migratory marine predators are critical in the transfer and outwelling of energy across habitat boundaries and to near-shore systems through a process known as trophic relay (Kneib 1997; Rehage and Loftus 2007; Piazza and La Peyre 2012). Identifying these interactions, and the habitats and physical connectivities that need to be preserved to maintain recruitment and survival of the different life stages of fish species is crucial in determining habitat value, and bears important management and conservation implications (França 2011; López-Duarte et al. 2012; Abrantes et al. 2015).

1.3 Motivation and study setting

As mentioned in the previous section, the role of coastal vegetated ecosystems in sustaining food webs and facilitating cross-habitat utilization is still poorly understood across multiple spatial and temporal scales. Thus, research focusing on carbon fluxes needs to provide a better spatial resolution by considering contrasting hydrogeomorphic settings (Kristensen et al. 2008; Marchio et al. 2016), as well as to identify the main regulating factors and mechanisms controlling changes in availability of food resources and habitat connectivities (Able 2005; França 2011; López-Duarte et al. 2012; Abrantes et al. 2015).

Centla Wetlands and the adjacent Terminos Lagoon in the southern tropical portion of the Gulf of Mexico afford a prime location to conduct food web studies at different spatio-temporal scales due to the variability in geomorphic settings, habitats and plant communities, in addition to the strong seasonality in environmental conditions, particularly in terms of freshwater discharge and

winds (Kjerfve et al. 1988; Gómez-Pompa and Dirzo 1995; Carranza-Edwards 2011; Yáñez-Arancibia and Day 2013b). The area occupies major portions of the Grijalva-Usumacinta delta, the second largest in the Gulf of Mexico after the Mississippi (Yáñez-Arancibia et al. 2009; 2013b), with mangroves, marshes and seagrass ecosystems well represented there. Figure 1.5 and Table 1.1 illustrate and define some of these coastal and landscape features in the area, as well as for the selected study sites (more information is found in chapters III, IV and V).

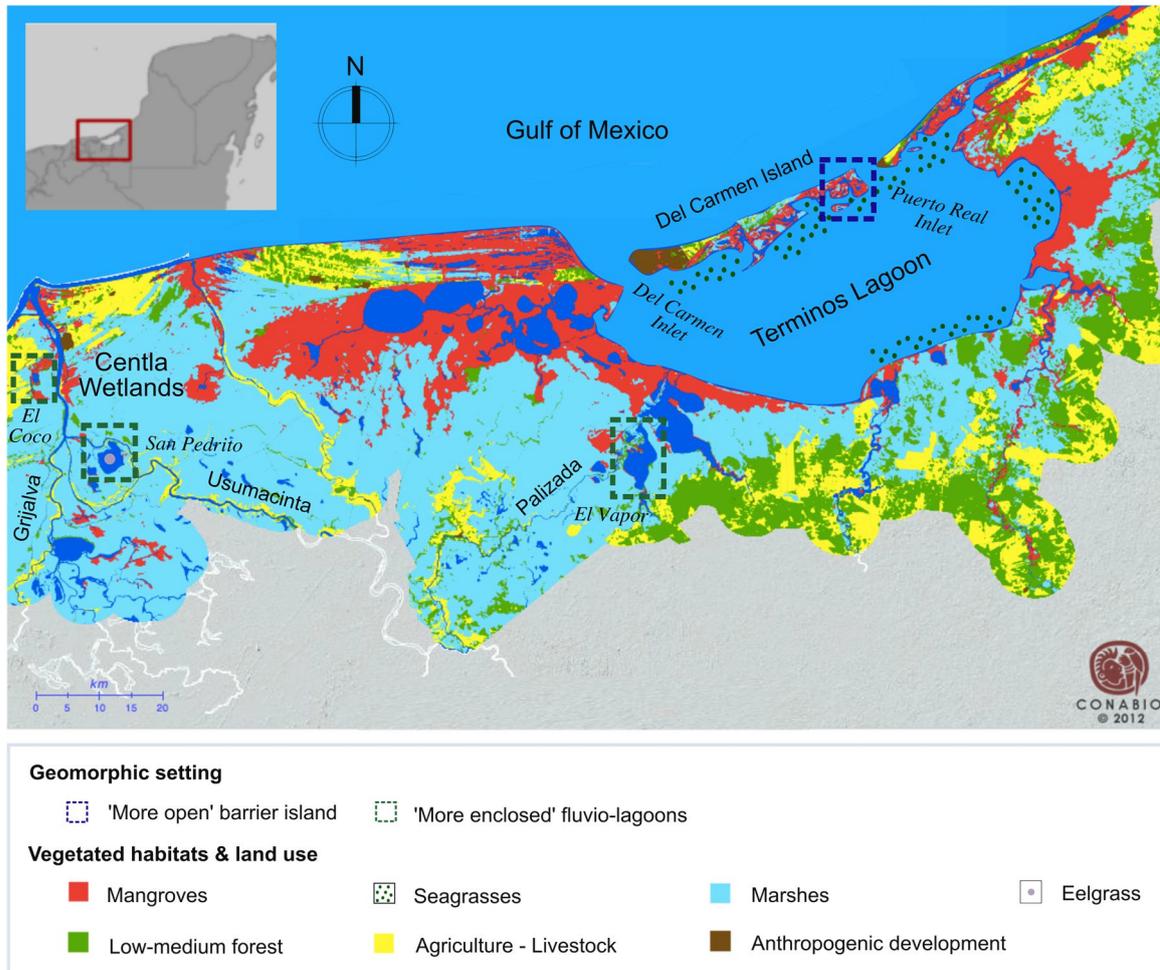


Fig. 1.5 Centla Wetlands and Terminos Lagoon, and the geomorphological and vegetational settings in the area. The four study sites of this work are framed with dash-lines. Adapted from: <http://www.conabio.gob.mx/informacion/gis/>, based on land-use and vegetation maps of 2010 from the coastal zone associated with mangroves in the Gulf of Mexico and Yucatan Peninsula (CONABIO 2013a,b). The use of this material and its adaptation is allowed based on the creative commons license 2.5 Mexico (CC BY-NC 2.5 MX)

These coastal ecosystems in the Southern Gulf of Mexico are known to host a high diversity of aquatic species, some of which sustain the multispecies fishery of the adjacent continental platform (Yáñez-Arancibia and Sánchez-Gil 1986; Gracia 1989; Yáñez-Arancibia et al. 2013b). Nevertheless, little is known in terms of energy fluxes and the structure of aquatic food webs in the habitat continuum from the more inland freshwater-dominated marsh habitats where the

presence of the American eelgrass *Vallisneria americana* is important to the fringing mangrove-seagrass areas neighboring to the sea.

Most of the studies already conducted in the area have shown that detritus is the base of the food webs (Manickhand-Heileman et al. 1998a,b; Vega-Cendejas and Arreguín-Sánchez 2001; Rivera-Arriaga et al. 2003), but these studies only consider the adjacent continental platform and Terminos Lagoon, and do not account for small-scale habitat variability across and within these systems. For example, there has been a lack of attention to the freshwater-dominated habitats of the area.

Table 1.1 Representative features of the study sites in terms of geomorphology, vegetational characteristics and connectivity in Centla Wetlands and Terminos Lagoon, Southern Gulf of Mexico

Degree of openness & geomorphic setting / distance to the sea	Tidal regime *	Characteristic riparian vegetation and coverage (border) / mangrove forest type **	Submerged aquatic grasses	Name of the site and location
'More enclosed' Fluvial-deltaic lagoon (26 km)	Microtidal (< 0.5 m)	Marshes (95 %)	<i>Vallisneria americana</i>	San Pedrito, Centla Wetlands
'More enclosed' Fluvial-deltaic lagoon (25 km)	Microtidal (< 0.5 m)	Marshes (40 %) Riverine mangrove (20 %)	–	El Vapor, Terminos Lagoon
'More enclosed' Fluvial-deltaic lagoon (13 km)	Microtidal (< 0.5 m)	Basin mangrove (98 %)	–	El Coco, Centla Wetlands
'More open' Barrier island (< 1 km)	Microtidal (< 0.5 m)	Fringe mangrove (98-100 %)	<i>Thalassia testudinum</i> <i>Halodule wrightii</i>	Isla del Carmen (east), Terminos Lagoon

* Kemp et al. (2016)

** Jardel et al. (1987) and Domínguez-Domínguez et al. (2011), based on the classification of Lugo and Snedaker (1974)

Note based on Jardel et al. (1987) and Smardon (2006): The riparian vegetation assemblages consist of diverse communities in the area, particularly in the freshwater-influenced zone. Mixed mangrove forests predominantly composed by *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* are found from the fringe marine areas to the transition zone with freshwater swamps. In the latter zones, mangroves form gallery forests that interconnect with flooded forest trees, shrub-scrub wetlands and marshes dominated by *Thalia geniculata* and *Typha domingensis* ("popal-tular" vegetation). In addition to this habitat heterogeneity, the area contains an important reservoir of aquatic hydrophytes (submerged and floating), particularly in Centla Wetlands.

Second, research on the energy fluxes sustaining secondary production in the area, including the studies mentioned above, and others based on stable isotope analysis (e.g., Raz-Guzmán and de la

Lanza 1991; Mendoza-Carranza et al. 2010), have not considered the strong seasonality in the area.

Third, the dynamic conditions in the area, the high diversity of fish species and the variety of habitats they utilize – from the adjacent continental shelf to high-salinity mangrove-seagrass areas and low-salinity fluvial lagoons with bordering mangroves and/or freshwater marshes (Yáñez-Arancibia et al. 1988; Sirot et al. 2015) – make the study area a compelling ecological setting for addressing the topic of fish assemblage connectivity.

1.4 Research objectives and hypotheses

The present thesis, based on stable isotope analysis, aims to analyze the food web dynamics and fish assemblage connectivity in different coastal vegetated ecosystems in the southern Gulf of Mexico (Centla Wetlands and Terminos Lagoon) during a dry and a rainy season, the latter influenced by northerly winds (*nortes*).

The study particularly seeks to assess:

- 1) The food web structure and contribution of different basal resources for aquatic consumers in sites differing in geomorphology, distance to the sea and vegetational characteristics (Table 1.1). – *Manuscripts I & II*
- 2) The seasonal shifts in food web structure, dietary contribution of resources and consumers' isotopic niche width. – *Manuscript II*
- 3) The connectivity of fish assemblages in spatially separated habitats under contrasting seasonal conditions. – *Manuscript III*

The hypotheses related to these topics are:

- 1) The importance of riparian-derived carbon for aquatic consumers highly depends on habitat geomorphology (predicted to be higher in 'more enclosed' vs 'more open' habitats) and on availability of basal resources. – *Manuscripts I & II*
- 2) Larger consumers' isotopic niches in the rainy season are induced by energetic pulsing events like the riverine pulse (flood pulse concept). – *Manuscript II*
- 3) The connectivity between fish assemblages of marine and low-salinity habitats increases in the rainy-*nortes* season as higher food availability enhances fish migration towards productive river-influenced habitats. – *Manuscript III*

The overall hypothesis of this work is that the importance of riparian-derived carbon for aquatic consumers in coastal marshes and mangrove ecosystems in the Southern Gulf of Mexico is highly

variable across spatial scales, and that the periodic dry and wet conditions in the area drive the major changes in resource availability and the connectivity of aquatic food webs.

1.5 Thesis outline

After the introductory chapter (I), this dissertation contains six additional chapters. Chapter II consists of a general overview about the use of stable isotope analysis in food web ecology, the definition of ‘isotopic niche’ and its approximation to the ecological niche concept, and an overview of isotopic models for the estimation of dietary proportions to consumers and their isotopic niche, with special emphasis on the methods used in this work. Chapters III to V are organized in the form of scientific publications covering the spatio-temporal assessment of aquatic food webs in the study area, as well as the connectivity of fish assemblages. These chapters address the specific objectives and hypotheses outlined above. Chapter VI addresses the general discussion, highlighting the main findings and their relationship with outcomes from other studies. Chapter VII integrates the conclusions of this study and an outlook for further research.

1.6 List of manuscripts and authors’ contributions

Manuscript I

Sepúlveda-Lozada, A., Mendoza-Carranza, M., Wolff, M., Saint-Paul, U., Ponce-Mendoza, A. 2015. Differences in food web structure of mangroves and freshwater marshes: evidence from stable isotope studies in the Southern Gulf of Mexico. *Wetlands Ecology and Management* 23:293-314

Contribution of the PhD candidate in % of the total work load (100% for each of the following categories):

- | | |
|---------------------------------------|----------|
| a) Concept and design: | ca. 70 % |
| b) Aquisition of data: | ca. 80 % |
| c) Data analysis and interpretation: | ca. 95 % |
| d) Preparation of figures and tables: | ca. 95 % |
| e) Drafting of the manuscript: | ca. 85 % |

Manuscript II

Sepúlveda-Lozada, A., Saint-Paul, U., Mendoza-Carranza, M., Wolff, M., Yáñez-Arancibia, A. 2017. Flood pulse induced changes in isotopic niche and resource utilization of consumers in a Mexican floodplain system. *Aquatic Sciences*, doi 10.1007/s00027-017-0520-9

Contribution of the PhD candidate in % of the total work load (100% for each of the following categories):

- | | |
|---------------------------------------|-----------|
| a) Concept and design: | ca. 90 % |
| b) Aquisition of data: | ca. 80 % |
| c) Data analysis and interpretation: | ca. 100 % |
| d) Preparation of figures and tables: | ca. 80 % |
| e) Drafting of the manuscript: | ca. 85 % |

Manuscript III

Sepúlveda-Lozada, A., Saint-Paul, U., Wolff, M., Mendoza-Carranza, M. Fish assemblage connectivity between marine and low salinity mangrove habitats in the southern Gulf of Mexico: insights from stable isotope analysis

Contribution of the PhD candidate in % of the total work load (100% for each of the following categories):

- | | |
|---------------------------------------|-----------|
| a) Concept and design: | ca. 100 % |
| b) Aquisition of data: | ca. 80 % |
| c) Data analysis and interpretation: | ca. 100 % |
| d) Preparation of figures and tables: | ca. 100 % |
| e) Drafting of the manuscript: | ca. 95 % |

Chapter II

Application of Stable Isotope Analysis in Food Web Ecology

Application of Stable Isotope Analysis in Food Web Ecology

2.1 Generalities

The research focused on food webs and cross-habitat interactions, necessitates a range of approaches. Some of them include gut contents analysis, fecal analysis, direct observation both in the field and laboratory, radiotracer and fatty acid applications, and stable isotope analysis (Michener and Kaufman 2007 and references therein).

Analysis of stable isotope ratios has offered an effective natural tracer approach for following energy and element cycling in ecosystems, as well as a means of characterizing trophic structure (Michener and Kaufman 2007; Fry 2008). Elements of particular interest in Ecology are those that cycle tightly with organic matter like the widely used C and N, but also H, O and S (Fry 2008; Newton 2016).

Stable isotope ratios of heavy to light isotopes (e.g., $^{13}\text{C}:^{12}\text{C}$, $^{15}\text{N}:^{14}\text{N}$) from a sample are measured using stable isotope mass spectrometry (Newton 2016). The mass spectrometer measures the mass of gaseous inorganic compounds such as CO_2 and N_2 , so the 1st step in measuring the isotopic ratios in organic compounds requires their transformation to gases (Ben-David and Flaherty 2012). Once in gaseous form, the now-inorganic molecules are injected into the source of the mass spectrometer, where they are ionized and accelerated into an evacuated flight tube where a strong magnet deflects and separates them based on mass (Ben-David and Flaherty 2012). The resulting beams of ionized, gaseous molecules are collected at the end of the flight tube in Faraday cups; their collection creating a weak electrical current that is measured by the controlling computer (Ben-David and Flaherty 2012).

The measured ratios are reported with the δ notation that signifies difference relative to an internationally set standard so that the data collected in different studies are comparable (Fry 2008; Ben-David and Flaherty 2012). The δ values or signatures derive from the formula:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1000$$

where X is the element in its heavy form (e.g., ^{13}C , or ^{15}N) and R is the ratio of heavy to light isotopes (e.g., $^{13}\text{C}:^{12}\text{C}$). The δ value calculation involves a final multiplication by 1000 to amplify very small differences measured between samples and standards, and therefore the units of measurements are reported in parts per mil (‰) (Fry 2008; Ben-David and Flaherty 2012). Deviations towards the positive and negative values imply enrichments and depletions in the heavy isotope (Newton 2016). The international standards are PeeDee Belemnite (PDB) and

Vienna PeeDee Belemnite (VPDB) for carbon, and atmospheric nitrogen (AIR) for nitrogen (Fry 2008; Ben-David and Flaherty 2012).

2.1.1 Isotopic fractionation

In general, stable isotope signatures vary among environmental substrates depending on different mechanisms (Kürten et al. 2014). The most important is the isotopic fractionation, usually represented with the symbol Δ (Fry 2008). The simplest equation of fractionation applies to a reaction where a product is formed from a source material (Fry 2008):

$$\Delta = \delta_{SOURCE} - \delta_{PRODUCT}$$

The Δ fractionation values are expressed in positive ‰ units, and are usually quite similar to the simple difference between two δ values (Fry 2008).

The isotope signatures in organisms are the product of the ratios of heavy to light isotopes of the substrates they utilize and the physiological processes (i.e., enzymatic reactions) they employ in assimilating these substrates, for instance, the isotopic fractionations of carbon in plants during photosynthesis, with marked differences between C_3 and C_4 plants (Ben-David and Flaherty 2012). Other factors affecting isotopic signatures of primary producers in terrestrial, marine, and freshwater ecosystems, are soil moisture, temperature, levels of dissolved CO_2 , phytoplankton growth rates, in situ vs allochthonous inputs, precipitation, nitrogen fixation, among others (Michener and Kaufman 2007; Ben-David and Flaherty 2012).

The naturally created spatial and temporal variations in the abundance of heavy and light isotopes in all ecosystems on Earth is in essence a marker system that allows to track the flow of nutrients, species interactions, trophic relations, animal diets, and animal migrations (Ben-David and Flaherty 2012, and references therein).

Animal tissues acquire a natural isotopic label or tag from the environment and prey from which the tissues were synthesised (DeNiro and Epstein 1978; Fry 1981; Ryan et al. 2013), plus some added discrimination factor because of the physiological processes involved in assimilation and excretion (Ben-David and Flaherty 2012). As carbon and nitrogen from producers are passed from one trophic level to the next, their $\delta^{13}C$ and $\delta^{15}N$ values tend to increase due to differential use of heavy and light isotopes during metabolism, with light forms being more easily excreted and the heavy ones accumulated (Peterson and Fry 1987; Ricevuto et al. 2013; Garvey and Whiles 2017).

Hence, the change in $\delta^{13}C$ and $\delta^{15}N$ from source to consumer, also known as trophic enrichment factor ($\Delta^{13}C$ and $\Delta^{15}N$), is the mechanism that crucially underpins the positioning of individuals,

populations and species relative to one another in the bivariate isotopic space ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ plot, typically with $\delta^{13}\text{C}$ on the x-axis and $\delta^{15}\text{N}$ on the y-axis) (Perkins et al. 2014). Normally, $\delta^{13}\text{C}$ change minimally with trophic transfers (usually less than 1 ‰), and because basal sources often differ in their $\delta^{13}\text{C}$ values, it can be used as a source indicator; whereas $\delta^{15}\text{N}$ become more enriched with each trophic transfer (usually around 3.4 ‰), and thus is a trophic level indicator (Post 2002) (Fig. 2.1). Nevertheless, recent controlled experiments and other meta-analyses suggests that these enrichment factors may not be universal. For instance, the range in $\delta^{13}\text{C}$ discrimination in soft tissues for animals of the same species can vary from -1 to 5 ‰ and for $\delta^{15}\text{N}$ from -1 to 8 ‰ (Ben-David and Flaherty 2012, and references therein).

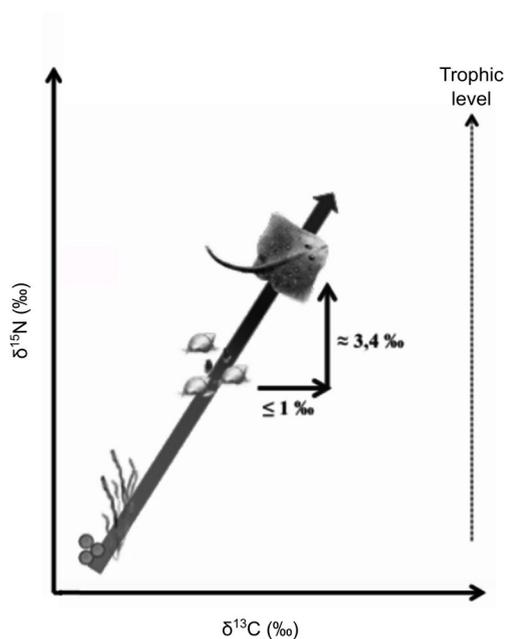


Fig. 2.1 A simplified food chain supported by microphytobenthos and/or coastal macroalgae. Typical enrichment factors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sources/preys and consumers are shown. Modified from: Marine Strategy Framework Directive – Marine food webs (2014-2017), <http://www.dcsmm-d4.fr/signatures-isotopiques-et-contenus-stomacaux?lang=en>

2.1.2 The ‘isotopic niche’ as an approximation of the ecological niche

Stable isotope analysis has the potential to be a powerful integrative measure of foraging niche width (Bearhop et al. 2004) because isotope data is commonly represented as a multidimensional space which records ecological information (e.g., bivariate plots with the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and variance estimates), fitting with the definition of the ecological niche sensu Hutchinson (1957) as ‘a hypervolume in n -dimensional space with environmental variables as axes’, in addition to all other contemporary definitions of the niche after this formulation (Newsome et al. 2007). The ‘isotopic niche’ or ‘ δ -space’ is comparable to the n -dimensional space that contains what ecologists refer to as the niche, because an animal’s chemical composition is directly influenced by what it consumes as well as the habitat in which it lives, represented in the ‘bionomic’ and ‘scenopoetic’ axes sensu Hutchinson (1978), which refer to

biotic and abiotic factors, respectively (e.g., resources and habitat) (Newsome et al. 2007). Some patterns in δ -values used to examine bionomic and scenopoetic dimensions of ecological niche space are shown in Table 2.1.

Table 2.1 Selected patterns in δ -values (with focus on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) used to examine scenopoetic and bionomic dimensions of ecological niche. Synthesized from Newsome et al. (2007)

Gradient	Isotope system	High δ -values	Low δ -values	Scenopoetic	Bionomic
Trophic level	$\delta^{13}\text{C} / \delta^{15}\text{N}$	High levels	Low levels		✓
C3/C4 vegetation	$\delta^{13}\text{C}$	C4 plants	C3 plants		✓
Marine-terrestrial	$\delta^{13}\text{C} / \delta^{15}\text{N}$	Marine	Terrestrial	✓	✓
Benthic-pelagic	$\delta^{13}\text{C}$	Benthic	Pelagic	✓	✓
Eutrophication	$\delta^{15}\text{N} / \delta^{13}\text{C}$	Polluted	Pristine	✓	
Oxic-anoxic	$\delta^{13}\text{C} / \delta^{15}\text{N}$	Oxic	Anoxic	✓	
Methanogenesis	$\delta^{13}\text{C}$	Photosynthetic	Methanogenic	✓	

Isotopic niches are thus defined exactly as a consumer's isotopic variance with a dimension determined by the number of isotope systems employed (Yeakel et al. 2016, and references therein). This definition increases the possibility for applying quantification tools for the niche, rather than the large and ultimately immeasurable construct of the n -dimensional hypervolume, which in essence encapsulates a huge amount of ecological complexity that is challenging to parameterise (Reid et al. 2016; Yeakel et al. 2016).

Isotopic niches have been used to investigate the consequences of habitat fragmentation, landscape heterogeneity, ecosystems' connectivity through ecotones and biological invasions on food webs, as well as species coexistence, resource use throughout ontogeny, evolutionary diversification, changes in food availability, and individual responses to seasonal environments (Musseau et al. 2015; Yeakel et al. 2016, and references therein).

In recent years, Layman et al. (2007) and Jackson et al. (2011) have contributed significantly to the efforts in quantifying and inferring different characteristics of the isotopic niche at the level of populations and even communities by examining the dispersion of stable isotope values in the δ -space. Layman's metrics (2007), based on Euclidean methods, include the total area of a convex polygon (convex hull) encompassing all species within a community (used as a measure of trophic diversity), and other related metrics (e.g., mean nearest neighbour distance) that further characterize spacing among individual data points in isotopic space, providing additional insight into trophic diversity and species packing within communities (Layman et al. 2012). Jackson et al.

(2011) reformulated Layman's metrics in a more sophisticated Bayesian framework (Stable Isotope Bayesian Ellipses in R, SIBER) to calculate and to depict isotopic niches based on multivariate ellipses (more details about this method are shown in section 2.2.2.2). These ellipses are more robust to differences in sample sizes for the quantification of the isotopic niche than the convex hull area, and allow making statistically strong comparisons among isotopic areas and overlap compared to the convex hulls, which do not account for uncertainty associated with sampling because only a point estimate is produced (Jackson et al. 2011; Rossman et al. 2016).

Nevertheless, either the Bayesian approach or the convex-hull-based quantitative analysis may be more appropriate with respect to a particular question of interest and/or the nature of the underlying data set and, in some cases, utilization of both of these analytical approaches may be desirable to reveal different aspects of trophic structure (Layman et al. 2012). For instance, the convex hull approach is powerful because it incorporates each individual sampled and thus includes information about every part of isotopic niche space occupied, whereas the Bayesian approach is targeted at niche widths of "typical" members in a population, which could be viewed as the core isotopic niche (Jackson et al. 2011; Layman et al. 2012). More details about these approaches are discussed in the next section.

2.2 Isotope-based methods

2.2.1 Stable isotope mixing models (SIMMs)

The use of the stable isotopic composition of consumers and their foods to make inferences about the composition of the animal's assimilated diet is accomplished by the use of isotopic mixing models to convert the isotopic data into estimates of food source contributions from the various components of an animal's diet (Phillips 2012; Phillips et al. 2014).

Initially, some limitations of these mixing models were: 1) they only provided point estimates for dietary contributions, with no uncertainty levels specified to account for variability in consumer or food isotopic values, measuring error, etc., 2) they did not account for elemental concentrations among food sources for estimating dietary composition; and 3) they could only partition the dietary proportions of two or three food sources based on the use of one or two isotopes, respectively, otherwise the models were mathematically underdetermined and there was no unique solution (Phillips and Gregg 2003; Phillips et al. 2014). Although some of these sources of variation and uncertainty were individually addressed by some models like IsoError (Phillips and Gregg 2001), IsoConc (Phillips and Koch 2002), and IsoSource (Phillips and Gregg 2003), more recently, Bayesian mixing models have allowed flexible model specification in a rigorous statistical framework to incorporate some or all of these features, or more (e.g., variability in

isotope values and discrimination factors; concentration dependence; larger number of sources; hierarchical variance structure) (Phillips et al. 2014; Vander Zanden et al. 2016).

Bayesian mixing models estimate diet proportions using a flexible likelihood-based structure, which allows for the incorporation of variability in consumer and prey isotope values and covariate information (reviewed in deVries et al. 2016; Stock and Semmens 2016).

The Bayesian approach to stable isotope mixing models is advantageous because it allows to: 1) explicitly account for uncertainty in isotope values when estimating the contribution of sources to an isotope mixture, 2) characterize uncertainty in estimates of source contributions based on underlying uncertainty in the mixture and source isotope values, and 3) include prior knowledge in the analysis (Semmens and Moore 2008).

In contrast with frequentist statistics, in which parameters are fixed quantities, the true value of a parameter in Bayesian statistics can be thought of as being a random variable to which a probability distribution is assigned, which is known as ‘prior information’ (Stevens 2009). A prior distribution is specified for the estimated parameter (i.e., the diet proportions of each source/prey type), and reflects knowledge of a system before (prior to) the analysis (deVries et al. 2016). Once it is incorporated into the analysis, the prior information is updated by the data (the likelihood) (Parnell et al. 2010; deVries et al. 2016). The incorporation of external (prior) information into the Bayesian approach narrows the precision of estimated dietary proportions (Parnell et al. 2010). This prior information may be vague or informative, e.g. corresponding to the volume of existing knowledge regarding *a priori* knowledge about the diet of an animal (Parnell et al. 2010).

Among the stable isotope Bayesian mixing models created during this decade (around seven, see Phillips et al. 2014), SIAR (Stable Isotope Analysis in R, Parnell et al. 2010) and MixSIR (Semmens and Moore 2008) have been widely used (Vander Zanden et al. 2016). SIAR (used in this thesis) has recently halted and the new MixSIAR GUI (graphical user interface) (Stock and Semmens 2013) provides a collaboration between SIAR and MixSIR, while the mixing model components of SIAR are still available as an R package called *simmr* (Vander Zanden et al. 2016).

The SIAR likelihood function is structured in the following way (Parnell et al. 2010; Stock and Semmens 2016):

$$X_{ij} \sim N \left(\sum_k p_k (\mu_{jk} + \lambda_{jk}), \left[\sum_k p_k^2 (\omega_{jk}^2 + \tau_{jk}^2) \right] + \sigma_j^2 \right)$$

where:

X_{ij} = tracer value j of mixture (consumer) i ,

p_k = (diet) proportion of source k (estimated by model),

μ_{jk} = source k mean for tracer j ,

λ_{jk} = mean trophic discrimination factor or trophic enrichment factor (TDF, TEF) for tracer j on source k ,

ω_{jk}^2 = source k variance for tracer j ,

τ_{jk}^2 = discrimination factor variance for tracer j on source k , and

σ_j^2 = residual error term per tracer.

A natural prior distribution for p_k is the Dirichlet, a generalisation of the Beta distribution (Parnell et al. 2010). The Dirichlet-distributed default prior used by SIAR is designed to be vague so that the results are primarily influenced by the data (Parnell et al. 2010). Thus, the SIAR model sets each of the Dirichlet parameters or α values to 1 (Parnell et al. 2010; Parnell et al. 2013). Nevertheless, SIAR allows to specify prior information on the mean proportions (that sum to 1) for each dietary source and a standard deviation for the first of these proportions (Parnell et al. 2010).

Model fitting is via Markov chain Monte Carlo (MCMC), which produces simulations of plausible dietary proportions after taking into account the data and the prior information, known as posterior distributions, representing a true probability density for the parameters of interest (Parnell et al. 2010).

SIAR also includes capability for inclusion of concentration dependence by adding the concentration of element j in source k (q_{jk}) into the model (Parnell et al. 2010).

2.2.2 Metrics used to characterise isotopic niche widths

2.2.2.1 Convex hull area (total area of the convex hull, TA)

The total area of the convex hull (TA) represents a measure of the total amount of niche space occupied and is a proxy for the total extent of trophic diversity within a community or population as it encompasses all species or individuals analyzed in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space (Layman et al. 2007). It is influenced by species with extreme positions on either the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ axis (or both), and thus typically is correlated to some degree to the spread of these values (Layman et al.

2007).

Layman et al. (2007) proposed this metric as a tool for measuring trophic diversity in food webs based on techniques applied in the field of ecomorphology that have quantified position of species in “morphospace” (typically derived from principal component analysis of a suite of morphological characteristics), and on the initial approach of the ‘convex hull volume’ advocated by Cornwell et al. (2006) as a trait-based test for habitat filtering which provides a n -dimensional measure of the space occupied by species in a community.

A further application was proposed by Villéger et al. (2008a), whom described a similar method to quantify functional richness of communities (reviewed by Podani 2009).

The convex hull algorithm determines the most extreme point (vertices), links them to build the convex hull, and finally calculates the area inside (Villéger et al. 2008a). According to Cornwell et al. (2006), if in an n -dimensional trait space we find two individuals/species, one with trait values $(a_1, a_2 \dots a_n)$ and the other with trait values $(b_1, b_2 \dots b_n)$, then for any value t with $0 \leq t \leq 1$, an individual/species with trait values

$$[ta_1 + (1 - t)b_1, ta_2 + (1 - t)b_2 \dots ta_n + (1 - t)b_n]$$

will also be within the convex hull. For example, when $t = 0.5$, the above statement translates to: for any two individuals/species a and b in the trait space, the individual/species whose trait values are the means of a and b will also be in the estimated trait space (Cornwell et al. 2006).

2.2.2.2 Stable isotope Bayesian ellipses

More recently, the Bayesian approach of Jackson et al. (2011), Stable Isotope Bayesian Ellipses in R (SIBER), has been widely applied to analyse stable isotope data in the context of isotopic niche. This approach is based on ‘standard ellipses’ (containing c. 40 % of the data regardless of sample size, Batschelet 1981), which are multivariate metrics that account for different sources of uncertainty, and allow robust comparison to be made 1) between the same taxonomic species or functional groups and 2) among multiple groups (e.g., different foraging guilds or entire communities) (Jackson et al. 2011).

The analysis makes the assumption that the isotope data under consideration is adequately described by a multivariate normal distribution MVN (Jackson et al. 2011). This distribution is an extension of the univariate normal distribution, in which the height of the curve (Y) is plotted against the variable (X), and the highest point of the symmetrical curve is at the mean of X (Zar 1999, Fig. 2.2a). The simplest multivariate case is where there are two variables (X and Y) plotted

with three dimensions (Z , X , and Y) (Zar 1999). The three dimensional bivariate normal curve rises like a hill above a plain (formed by the two variables X and Y), and the highest point of the curve is at the means of X and Y (Zar 1999, Fig. 2.2b). This three-dimensional distribution can be depicted with two dimensions using contour lines (e.g., small planes passing through it parallel to the X - Y plane, Fig. 2.2b), delineating an ellipse if the standard deviations of X and Y are not equal or a circle if they are equal (Zar 1999). If the plot of the multivariate distribution is viewed from directly above, the depicted ellipse would have the largest size formed nearest the tails of the distribution (Zar 1999).

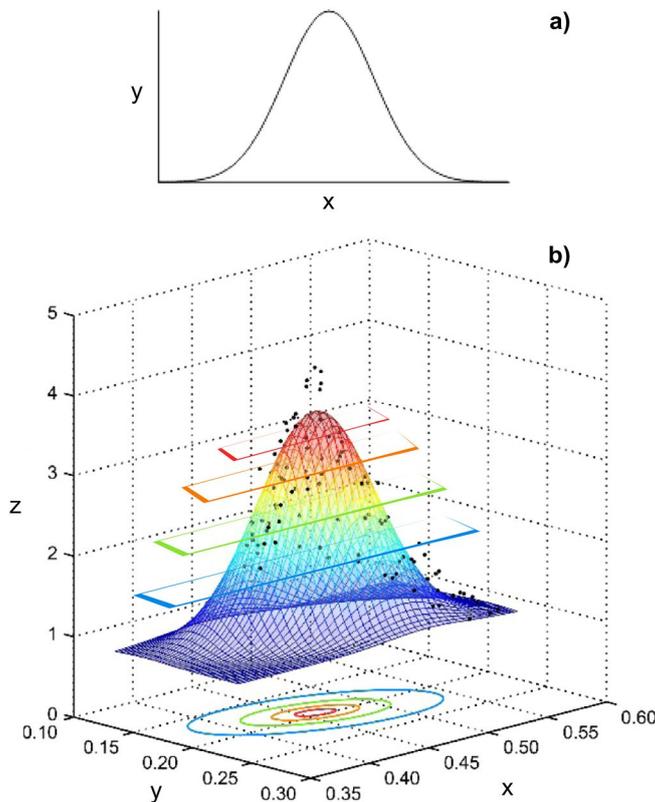


Fig. 2.2 a) Univariate normal distribution, b) Bivariate normal distribution, where X and Y have different standard deviations. The distribution is crossed by intersecting planes parallel to the X - Y plane, and its bidimensional representation is depicted with the ellipses (contour lines) defined by the intersecting planes. Fig. b was modified from Choi and Suk (2016), <https://www.osapublishing.org/oc/abstract.cfm?URI=oe-24-25-28945>

The standard ellipse is underpinned by its associated covariance matrix $\left(\Sigma = \begin{bmatrix} \sigma_x^2 & cov(x,y) \\ cov(y,x) & \sigma_y^2 \end{bmatrix} \right)$ which defines its shape and size, and the means of the X and Y define its location (Jackson et al. 2011). The eigenvalues and eigenvectors of Σ give the lengths of the semi-major axis (a) and the semi-minor axis (b), and the angle between the semi-major axis and the x -axis (Jackson et al. 2011; Reid et al. 2016). Plotting is done via the computation of the area of the resultant ellipse (SEA, Standard Ellipse Area) which is given by $SEA = \pi ab$ (Jackson et al. 2011). An important feature of SIBER is that the point estimate SEA, after an application of a small sample size correction (SEA_c), is shown to be insensitive to bias associated with sample size (Jackson et al. 2011).

It is straight forward to estimate the covariance matrix of the data using Bayesian inference, by which vague normal priors are assigned to the means, and a vague Inverse-Wishart prior is used for Σ (Jackson et al. 2011). The posterior estimate of Σ is then simulated using Markov Chain Monte Carlo (MCMC) by combining the priors and the likelihoods with a set of k iterative draws (Jackson et al. 2011). For each of these k draws, posterior values of the means μ_x and μ_y and covariance matrix Σ value are returned, and this process is repeated for all simulated values producing a range of probable values for the calculated metric (e.g., area, referred to as the Bayesian Standard Ellipse Area, SEA_B) reflecting the uncertainty in the estimated Σ (Jackson et al. 2011). Qualitatively similar to bootstrapping techniques, the Bayesian approach returns a distribution (the posterior SEA_B) representing estimates of SEA that reflect uncertainty arising from the sampling process, and in this manner, the resultant ellipses can be compared quantitatively (Jackson et al. 2011).

Chapter III

— Spatial Food Web Analysis —

Differences in food web structure of mangroves and freshwater marshes: evidence from stable isotope studies in the Southern Gulf of Mexico

Alejandra Sepúlveda-Lozada, Manuel Mendoza-Carranza,
Matthias Wolff, Ulrich Saint-Paul, Alejandro Ponce-Mendoza

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Abstract

Tropical coastal habitats like marshes, mangroves, and submerged grasses comprise diverse plant and animal communities and a certain degree of connectivity with other ecosystems. We compared the food web structure of a fringing mangrove-seagrass habitat and three fluvio-lagoons with marsh-eelgrass and mangrove-bare sediments during a dry season in Terminos Lagoon and Centla Wetlands, Southern Gulf of Mexico. Analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes in tissues of aquatic consumers, primary producers, and other carbon sources, in combination with isotope-based Bayesian methods, were performed to determine the main food sources and the isotopic niche of the consumers' communities. Consumers in the mangrove-seagrass site showed high dependence on phytoplankton (average contribution 31 %), macroalgae (20 %) and organic matter derived from seagrasses (17 %). In the fluvio-lagoons, consumers showed high dependence on marginal vegetation (16–46 %). Phytoplankton and mangrove epiphytes comprised other important resources at these sites (with contributions of 24–44 %). The isotopic niche of consumers from the fringing mangrove-seagrass site did not overlap with those from the fluvio-lagoons. Moreover, despite the predominance of generalist consumers in all sites, differences in their isotopic niche area were observed, with consumers from the marsh-eelgrass site showing the narrowest. This suggests that consumer resource availability greatly differs in these habitats. Our results provide valuable information that help increase our understanding about the trophic structure in these important estuarine systems.

Keywords: stable isotopes, mangroves, seagrasses, Bayesian methods, Centla Wetlands, Terminos Lagoon

3.1 Introduction

Marshes, mangroves, and seagrasses have been recognized as important habitats for fishes and invertebrates (Yáñez-Arancibia et al. 1993; Stribling and Cornwell 1997; Nagelkerken and van der Velde 2004), harboring a high species diversity by virtue of their physical structure and high primary production rates (Laegdsgaard and Johnson 2001; Moncreiff and Sullivan 2001; Rozas and Minello 2006). Knowledge about the linkages between sources of primary production and lower and higher trophic-order consumers is fundamental for the understanding of the structure and function of these complex and dynamic ecosystems (Hobson et al. 2002; Mancera-Pineda 2003; Mazumder 2013).

Most studies related to energy fluxes in estuarine ecosystems of the southern Gulf of Mexico have shown that detritus is the base of the food webs (Manickchand-Heileman et al. 1998a, b; Vega-Cendejas and Arreguín-Sánchez 2001; Rivera-Arriaga et al. 2003). These studies have mainly been carried out in Terminos Lagoon and the adjacent continental platform and do not account for small scale habitat variability and site differences in regards to vegetation assemblages, productivities, resource abundances, and the degree of connectivity, which are factors influencing the utilization of resources by aquatic consumers (Mancera-Pineda 2003; Bouillon et al. 2004; Vaslet et al. 2012).

The use of stable isotope ratios (e.g., $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) has greatly helped to recognize the relative importance of different resources for aquatic consumers within different sections of estuarine systems. For instance, it has been useful to identify the major role of phytoplankton, macroalgae, seagrasses, and epiphytes in fringing mangrove habitats interlinked with seagrasses, compared to more enclosed systems, where riparian sources are more important as they remain in residence due to limited exchange with adjacent ecosystems (Bouillon et al. 2004; Kieckbusch et al. 2004; Thimdee et al. 2004). Stable isotope analysis has also helped to identify the importance of phytoplankton and terrestrial detritus in habitats contrasting in terms of resource availability and turbidity (Abrantes et al. 2013). Moreover, it has provided indication about consumers' feeding strategies, dietary changes with size, trophic niche width, and migratory behavior, which end up shaping the structure of aquatic food webs (Fry 1981; Polis et al. 1997; Bearhop et al. 2004).

Stable isotope analysis is mainly based on differences in the stable isotope values of different primary producers and the predictable isotopic fractionation or enrichment between consumers and their food (e.g., in average $<1\text{‰}$ for $\delta^{13}\text{C}$, and $1.4\text{--}3.4\text{‰}$ for $\delta^{15}\text{N}$) (Post 2002; McCutchan et al. 2003; Vanderklift and Ponsard 2003). Recently, the application of this technique has expanded with the use of Bayesian mixing models like SIAR (Stable Isotope Analysis in R, Parnell et al. 2010), allowing to fit probabilities to isotopic data and to obtain confidence intervals (Bayesian

credible intervals) of estimated dietary composition of consumers (Parnell et al. 2010; Hopkins III and Ferguson 2012; Vaslet et al. 2012). Moreover, the Bayesian approach SIBER (Stable Isotope Bayesian Ellipses in R) of Jackson et al. (2011) to the original metrics proposed by Layman et al. (2007), has allowed to obtain measures of the isotopic niche width (indicative of resource use and trophic niche breadth, Bearhop et al. 2004) of both community members and entire communities. The application of these methods in a range of aquatic ecosystems has great potential to identify large-scale patterns in food web organization across different ecosystem types (Abrantes et al. 2014).

The aim of this study was to compare the aquatic food web structure of four sites differing in vegetation cover and location (distance to the open sea and influence by freshwater input) within Terminos Lagoon and Centla Wetlands, in the Southern Gulf of Mexico, during a dry season. The study sites were: (1) a mangrove channel interlinked with seagrasses in a barrier island, (2) a fluvio-lagoon characterized by beds of the American eelgrass *Vallisneria americana* surrounded by freshwater marsh vegetation, (3) and (4) two fluvio-lagoons with bare sediments surrounded by mangroves and marsh vegetation. The zone where the mangrove channel is located is dominated by phytoplankton production (Knoppers 1994; de la Lanza and Lozano 1999), whereas the river-influenced area is characterized by an extensive coverage of emergent hydrophytes (Guerra-Martínez and Ochoa-Gaona 2006), and high mangrove productivity (Day et al. 1987).

We incorporated analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes from the tissues of potential basal resources and consumers with isotope-based Bayesian methods to (1) depict the isotopic composition of the food web constituents, (2) estimate the trophic level of consumers, (3) identify resident and transient fishes based on their isotopic values and data from the literature, (4) identify the relative importance of different basal resources for consumers, and (5) quantify the isotopic niche of the consumers from each site and the degree of isotopic overlap between the communities.

We followed two hypotheses: (1) Consumers from the river-influenced habitats (fluvio-lagoons) rely more on marginal vegetation including mangroves, while the importance of mangrove-derived carbon in the barrier island site (fringing mangrove) is negligible, and other resources like phytoplankton and seagrass epiphytes are of major importance; (2) The isotopic niches of consumers from the fluvio-lagoons show a high overlap, indicating similar habitat and resource use. In contrast, the isotopic niche of consumers from the fringing mangrove site differs from the isotopic niche of consumers from the fluvio-lagoons, indicating different habitat and resource use.

3.2 Materials and methods

Study area

Terminos Lagoon and Centla Wetlands comprise a special area for Wildlife Protection and a Biosphere Reserve, respectively (Yáñez-Arancibia et al. 2009), with a jointly surface of 1,008,854 ha in the southwestern Yucatan Peninsula (Rivera-Monroy and Twilley 1996; Vega 2005, Fig. 3.1). The climate is humid tropical with three distinct seasons (“dry” —February to May—, “rainy” —June to September—, and “nortes” or winter storms —October to February—); annual rainfall ranges from 1,100 to 2,000 mm; and mean annual temperatures exceed 25 °C (Phleger and Ayala-Castañares 1971; Yáñez-Arancibia and Sánchez-Gil 1986; Rivera-Monroy et al. 2011). The area is drained by the Grijalva–Usumacinta Delta, the second most important in North and Central America after the Mississippi (Yáñez-Arancibia et al. 2009).

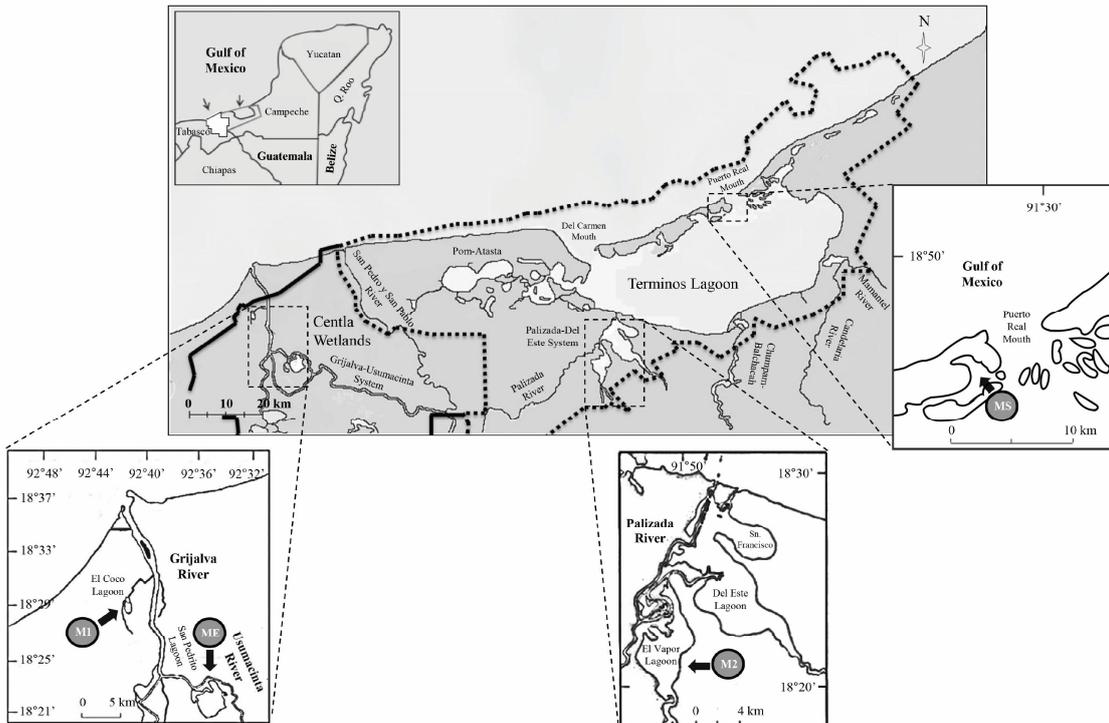


Fig. 3.1 Location of Terminos Lagoon and Centla Wetlands, and sampling sites: mangrove-seagrass (MS), marsh-celgrass (ME), mangrove-bare sediment sites (M1, M2)

Terminos Lagoon connects with the Gulf of Mexico through two mouths or inlets: Puerto Real (eastern) and Carmen (western), one at each end of Isla del Carmen, which is a narrow carbonate sand barrier island that separates the lagoon from the gulf (Day et al. 1982; Kjerfve et al. 1988; Fuentes-Yaco et al. 2001, Fig. 3.1). Tidal range is 0.3–0.7 m, and average salinity ranges from 35 to 36 in areas with strong marine influence to 0–4 in fluvio-lagoon systems (Rivera-Monroy et al.

1998; David and Kjerfve 1998; Yáñez-Arancibia and Day 2006). The circulation pattern is influenced by the predominant easterly trade winds (Graham et al. 1981), which favors a net westward flow most of the year, with a strong net water inflow at Puerto Real Inlet and a net outflow at Carmen Inlet (David and Kjerfve 1998). The river-influenced area at the south and southwestern part of the lagoon receives 70 % or more of river discharge with a maximum contribution from the Palizada river, whereas the northeastern and eastern parts receive about 30 % or less of the river discharge (Yáñez-Arancibia and Day 2006, Table 3.1).

Centla Wetlands connect with the sea through the estuarine mouths of the Grijalva and the San Pedro and San Pablo rivers (Yáñez-Arancibia et al. 2004, Fig. 3.1). The restricted estuarine influence is shown by the dominance of freshwater aquatic angiosperms and a minimum amount of estuarine fauna (Sánchez et al. 2012). Nevertheless, the area provides important habitats for the recruitment of estuarine and marine transient larvae and juveniles (Arévalo-Frías and Mendoza-Carranza 2012).

The study sites comprised a channel with strong marine influence located less than 1 km from the coastal line at the east of the inner littoral of Isla del Carmen, and the fluvio-lagoons San Pedrito, El Coco and El Vapor, connected with the Usumacinta, Grijalva and Palizada rivers, respectively, and located between 13 and 26 km from the coast (Fig. 3.1; Table 3.1). The first site is characterized by interlinked mangrove-seagrass vegetation, with ca. 98–100 % of mangrove coverage along the border, and ca. 1.5 km² of seagrass coverage (mainly *Thalassia testudinum*, but also *Halodule wrightii*) (Table 3.1). This site is denoted hereafter as MS (Fig. 3.1; Table 3.1). San Pedrito Lagoon is mainly characterized by marsh vegetation (ca. 95 % of the border) and the eelgrass *V. americana* (with a coverage of ca. 2.1 km²). This site is denoted hereafter as ME (Table 3.1). El Coco and El Vapor lagoons are characterized by mangroves with an approximate coverage of 100 and 20 %, respectively, and unvegetated bottoms. These sites are denoted hereafter as M1 and M2 (Table 3.1).

Sample collection

Intensive field samplings were conducted at each study site during the dry season of 2009 to obtain representative samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses.

Samples of basal resources included phytoplankton, leaves from marginal vegetation and submerged aquatic vegetation (SAV), macroalgae, epiphytic algae, leaf mangrove detritus, coarse woody debris, sediments, suspended particulate organic matter (SPOM), fine particulate organic matter (FPOM), and flocculated organic matter (Floc). For all samples/ species, three replicates were taken when possible. Phytoplankton and SPOM were collected using a cascade filtering

Table 3.1 Description of the study sites in Terminos Lagoon and Centla Wetlands

	MS Mangrove-seagrass (channel-barrier island)	ME Marsh-eelgrass (San Pedrito lagoon)	M1 Mangrove-bare sediments (El Coco lagoon)	M2 Mangrove-bare sediments (El Vapor lagoon)
Location	Inner littoral of Isla del Carmen, Terminos Lagoon	Centla Wetlands	Centla Wetlands	Palizada Del-Este System, Terminos Lagoon
Distance from the coast (km)	< 1 ^a	26 ^a	13 ^a	25 ^a
Surface (km ²)	~1.60 ^a	13.6 ^b	1.52 ^b	22.7 ^c
Connectivity	Connected directly with Terminos Lagoon	Connected with the Usumacinta River by two main channels	Connected with the Grijalva River by one channel	Connected with the Palizada River and Terminos Lagoon
Depth (m), dry season	1.05 ^a	0.90 ^a	1.10 ^a	2.10 ^a
Transparency (%), dry season	67 ^a	67 ^a	54 ^a	29 ^a
Salinity (ups), dry season	39.5 ^a	4.5 ^a	6 ^a	2.5 ^a
Approximated river discharge or net freshwater inflow (m ³ s)	4 ^d	3,723 ^e	3,723 ^e	288 ^d
Vegetation coverage along the border (%)	Mangroves (~98-100) ^{f, g}	Marsh (~95); Low-medium forest (~5) ^{f, g}	Mangroves (~98); Marsh (~2) ^{f, g}	Mangroves (~20); Marsh (~40); Low-medium forest (~40) ^{f, g}
Submerged aquatic vegetation (SAV) coverage (km ²)	Seagrasses (~1.5) ^h	Eelgrass (~2.1) ⁱ	-	-
Representative plant species ^a	<i>Rhizophora mangle</i> , <i>Avicennia germinans</i> , <i>Laguncularia racemosa</i> , <i>Thalassia testudinum</i> , <i>Halodule wrightii</i>	<i>Vallisneria americana</i> , <i>Phragmites australis</i> , <i>Typha domingensis</i> , <i>Thalia geniculata</i>	<i>Rhizophora mangle</i> , <i>Avicennia germinans</i> , <i>Laguncularia racemosa</i> , <i>Phragmites australis</i>	<i>Rhizophora mangle</i> , <i>Avicennia germinans</i> , <i>Typha domingensis</i> , <i>Phragmites australis</i> , <i>Thalia geniculata</i> , <i>Chrysobalanus icaco</i>

Sources: ^a This study, ^b Rodríguez (2002), ^c CONABIO (2007), ^d Yáñez-Arancibia and Day (2006) (data for the eastern part of Terminos Lagoon and the Palizada river, dry season discharge), ^e Day et al. (2003) (data for the Grijalva-Usumacinta River system, combined discharge), ^f CONABIO (2008), ^g INEGI (2000), ^h Google Earth[®] images, ⁱ Mendoza-Carranza et al. (2010)

device with four piled plankton nets (20, 63, 120 and 500 μm), where large volumes of water were filtered by hand using a 7 l container. Retained fractions were 20 μm (phytoplankton) and 120 and 63 μm (SPOM). Green leaves from the most representative vegetation species were clipped directly from the plants. Macroalgae were collected manually. Epiphytes adhered to SAV and mangrove roots were scraped from the surfaces to obtain composite samples (Hoeinghaus et al. 2007). Leaf detritus and coarse woody debris were collected with colanders and by hand. Sediment was collected to a depth of 10 cm (Winemiller et al. 2007). FPOM was collected by lightly rinsing the flocculated material on submerged vegetation and stems of marginal vegetation through a 63 μm plankton net, and retaining the smaller than 63 μm fraction (Hoeinghaus et al. 2007). Floating Flocc (consisting e.g., on diatoms, bacteria and organic fragments aggregated with inorganic material, Eisma 1993; Petticrew et al. 2011) was collected with the surface water. The Flocc was then separated from the surface water and stored. The collected Flocc consisted of macroflocs (of up to 1–5 cm, Precali et al. 2005).

Consumers included zooplankton, macro-invertebrates (mollusks and crustaceans) and fishes. Zooplankton samples were taken from nocturnal tows of 5 min with a conic net of 500 μm and a light trap. Fishes were collected with different gears (beach seine, beam trawl and gillnet) to obtain representative samples of the fish diversity at each site, although additional individuals were obtained from local artisanal fishermen (Mendoza-Carranza et al. 2010). Bivalves, gastropods and crustaceans were collected by hand and while sampling fishes (Mendoza-Carranza et al. 2010). All samples were stored on ice in the field and frozen upon return to the laboratory (Hoeinghaus et al. 2007).

Laboratory work

Water samples for phytoplankton, SPOM and FPOM were filtered onto pre-combusted (450 °C, 24 h) glass fiber filters (GF/C filters) with a nominal pore-size of 1.2 μm . Epiphytic filamentous algae were rinsed with distilled water and consolidated onto pre-combusted filters (Hoeinghaus et al. 2007). Plant leaves and macroalgal thalli were cut into small pieces and rinsed with distilled water. Coarse detritus samples were rinsed with distilled water over a colander to remove the fine detritus fraction (Hoeinghaus et al. 2007).

Zooplankton samples were examined microscopically, and representative taxa were identified, isolated and consolidated onto pre-combusted filters using forceps (Hoeinghaus et al. 2007). The zooplankton groups were processed whole (Letessier et al. 2012). For macro-consumers, muscle tissue was used as it is less variable in its isotopic composition than other tissues (Pinnegar and Polunin 1999; Yokoyama et al. 2005; German and Miles 2010). For fishes, a skinless and boneless muscle sample (ca. 5–10 g fresh weight) was excised from the dorsum (for armored

catfishes, muscle samples were taken from the elongate base of the caudal fin), and in the case of the smallest size classes (<3 cm total length), a composite sample of individuals of approximately the same size was taken by combining pure muscle tissue from multiple individuals (Garcia et al. 2007; Hoeninghaus et al. 2007). For crustaceans and mollusks, the abdominal and foot muscle, respectively, were removed to form individual or composite samples according to the size of the specimens (Hoeninghaus and Davis 2007; Hoeninghaus et al. 2007).

All samples were dried at 60 °C for at least 48 h in sterile Petri dishes (Hoeninghaus et al. 2007). The dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials (Mendoza-Carranza et al. 2010). Subsamples were weighted to the nearest 0.01 mg and pressed into Ultra-Pure tin capsules (Costech, Valencia, CA) to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with a mass spectrometer. Results were expressed in delta notation (parts per thousand deviation from a standard) based on the formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen (Hoeninghaus et al. 2007; Mendoza-Carranza et al. 2010).

Data analyses

Bi-plots of $\delta^{15}\text{N}$ against $\delta^{13}\text{C}$ values of basal resources and consumers were used to visualize the food web structure at each site and the differences in isotopic values of basal resources and consumers among sites. The trophic levels (TL) of consumers were calculated using the formula:

$$TL = \lambda + (\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{baseline}})/3.4$$

where λ is the trophic level of a primary consumer chosen to represent the base of the food web (λ has a value of “2” for primary consumers), $\delta^{15}\text{N}_{\text{predator}}$ is the $\delta^{15}\text{N}$ value of the consumer being evaluated, $\delta^{15}\text{N}_{\text{baseline}}$ is the average $\delta^{15}\text{N}$ value of the consumers used to estimate the base of the food web (in this case mollusk species), and 3.4 is the per trophic level fractionation of nitrogen according to Post (2002). The feeding guilds of consumers were assigned based on the literature and a cluster analysis using the Ward’s minimum variance method was performed with the trophic level estimates to assess whether the aggrupation based on the literature coincided with the estimations from this study. Non-parametric Kruskal–Wallis and Mann–Whitney tests with a 5 % level of significance (Zar 1996), were performed to compare the mean isotopic values among guilds within each site. In order to determine the possible habitat use of the collected fish species, a cluster analysis (Ward’s minimum variance method) was performed based on their $\delta^{13}\text{C}$ and

$\delta^{15}\text{N}$ values. The ecological guilds of fish species were assigned based on the literature, and we assessed whether the species clustering was consistent with these classifications.

Moreover, a SIAR mixing model (Parnell et al. 2010) was run for each site to estimate the percent contribution of selected basal resources (Table 3.2) to the diet of consumers' feeding guilds. Resources with similar isotopic values were pooled for analyses. SIAR incorporates variability into the input parameters, such as trophic enrichment factors (TEFs), and it deals with external (prior) information not connected to isotopic uncertainty, further narrowing the precision of estimated dietary proportions (Parnell et al. 2010). The TEFs used here were those proposed by Post (2002) for $\delta^{13}\text{C}$ ($0.40 \pm 1.30 \text{ ‰}$) and $\delta^{15}\text{N}$ ($3.40 \pm 1.00 \text{ ‰}$), since they matched with preliminary TEF estimates from this study ($0.45 \pm 0.68 \text{ ‰}$ for $\delta^{13}\text{C}$ and of $3.47 \pm 0.57 \text{ ‰}$ for $\delta^{15}\text{N}$; Sepúlveda-Lozada et al. unpublished data). Dietary proportions, known as posterior distributions, were obtained via a Markov-chain Monte Carlo (MCMC) simulation, after taking into account the data and the prior information (Parnell et al. 2010).

Finally, the SIBER routine of SIAR (Jackson et al. 2011) was used to estimate standard ellipse areas (SEA, standard ellipse area; SEA_c , the small sample size corrected standard ellipse area; and SEA_B , Bayesian standard ellipse area, with ‰^2 units) to depict the isotopic niche width of the consumers' communities and to make comparisons based on the percentage of niche sharing (SEA_c overlap) and niche size (SEA_B) (Jackson and Britton 2013; Abrantes et al. 2014). The standard ellipses contain c. 40 % of the data regardless of sample size (Batschelet 1981), instead of encompassing all data in the isotopic space like the total area of the convex hull (TA) proposed by Layman et al. (2007). Differences in niche area were evaluated using Bayesian inference to estimate the posterior distribution of SEA (SEA_B), based on the combination of available data (e.g., SEA_c) and prior information (e.g., non-informative) through a MCMC simulation (Jackson et al. 2011; Ryan et al. 2013). Moreover, the TA for each community was obtained to complement the previous information.

Mollusks, crustaceans, and fishes, were pooled per site to run the SIBER analysis of the four sampled communities. The inclusion of different taxonomic groups in the analysis can be feasible as the trophic structure of nekton communities in the area of study (as observed from the mouth of the Grijalva River towards Terminos Lagoon and Isla del Carmen) is rather similar due to a species replacement for either low or high trophic values or to the presence of some abundant and widespread species with low and high trophic levels, as well as to the dominance in biomass of species with intermediate trophic levels at the regional scale (e.g., Ariid fishes like *Cathorops melanopus* and *Ariopsis felis*, and Portunid crabs like *Callinectes similis*) (Villéger et al. 2008b). Moreover, by including these taxonomic groups it is also possible to have a good representation of low trophic levels in all systems, mainly represented by mollusk and crustacean species

(Villéger et al. 2008b).

3.3 Results

A total of 40 primary producers among marginal vegetation (36 species), SAV (three species, including submerged grasses), and macroalgae (one species), together with 68 consumer taxa (49 fish species, 11 crustaceans, 8 mollusks) were collected (Annex I, Resource 1). Higher fish and invertebrate species richness was found in ME and M1 with 28 and 32 species, respectively, and the lowest in MS and M2 with 23 and 26 species, respectively.

Isotopic values of food web constituents

$\delta^{13}\text{C}$ values of primary producers ranged from -33.2 to -9.37 ‰, with the most enriched values in MS (Fig. 3.2, Annex I, Resource 1). Marsh plants and mangroves were $\delta^{13}\text{C}$ depleted, with values from -32.4 to -25.1 ‰ (Fig. 3.2). Phytoplankton had similar $\delta^{13}\text{C}$ values to those of marginal vegetation in ME, M1 and M2, and only in MS showed the most enriched value (-12.5 ‰, Fig. 3.2). *V. americana*, *T. testudinum* and *H. wrightii*, showed the most enriched $\delta^{13}\text{C}$ values in ME and MS, with values from ca. -22 to -10 ‰ (Fig. 3.2). Epiphytes from *Rhizophora mangle* showed variable $\delta^{13}\text{C}$ values (-33.2 to -22.4 ‰), with the most enriched values in M1 and M2 (Fig. 3.2). Epiphytes from *T. testudinum* and *V. americana* had $\delta^{13}\text{C}$ values of -16.5 and -21.8 ‰, respectively (Fig. 3.2).

Leaf mangrove detritus in M1 and M2 (-29.7 to -28.1 ‰) reflected the composition of mangrove leaves (Fig. 3.2). Detritus in MS was $\delta^{13}\text{C}$ enriched (-19.6 ‰) as it was composed of a mixture of mangrove and seagrass leaves (Fig. 3.2). Coarse woody debris and FPOM from coarse debris in M1 and M2 (-28.8 to -26.2 ‰), showed similar $\delta^{13}\text{C}$ values to those of the marginal vegetation (-32.4 to -26.1 ‰, Fig. 3.2). SPOM from M1 showed similar $\delta^{13}\text{C}$ values to those of *R. mangle* leaves (-29.1 to -28.3 and -29.2 to -28.1 ‰, respectively, Fig. 3.2). FPOM from *T. testudinum* leaves (-8.6 to -8.46 ‰) and Floc (-9.85 ‰) in MS, were comparable with the $\delta^{13}\text{C}$ values of seagrass leaves (-9.52 to -9.37 ‰, Fig. 3.2).

Most of the consumers from ME, M1 and M2 showed similar $\delta^{13}\text{C}$ values to those of marginal vegetation (Fig. 3.2, Annex I, Resource 1). In the case of MS, the $\delta^{13}\text{C}$ values of consumers had a strong relationship with the values of phytoplankton, seagrass epiphytes, macroalgae, and Floc. Consequently, the most enriched $\delta^{13}\text{C}$ values of consumers were observed in MS (Fig. 3.2).

$\delta^{15}\text{N}$ values of basal resources varied between -2.22 and 9.03 ‰, with the most depleted values in MS (Fig. 3.2). $\delta^{15}\text{N}$ values of consumers ranged from 1.31 to 12.9 ‰, and the lowest $\delta^{15}\text{N}$ values were also found in MS (Fig. 3.2).

Trophic levels and consumers' feeding guilds

The studied food webs consisted of three to four trophic levels including the basal resources (MS consisted of four trophic levels, and ME, M1 and M2 of three, Fig. 3.2). Consumers with the lowest trophic levels were mainly mollusks, however, some crustaceans showed low trophic levels (e.g., in MS and M1, Fig. 3.2). Intermediate trophic levels included most of the species, especially crustaceans and fishes (Fig. 3.2). Highest trophic levels were dominated by fish only (Fig. 3.2). Mean trophic levels of consumers ranged between 1.88 and 3.00, and based on this data it was possible to reclassify the collected species into pre-defined trophic categories based on the literature (Fig. 3.3, Annex I, Resource 2). References used to assign the feeding guilds per species are shown in Annex I, Resource 1. Overall, periphyton-macrophyte feeders (gastropods), deposit and non-selective filter feeders (bivalves), and herbivores (crustaceans and fishes) had the lowest trophic positions; detritivores, planktivores and omnivores (gastropods, crustaceans and fishes) intermediate positions; and zoobenthivores and piscivores (fishes) the highest positions (Fig. 3.3, Annex I, Resource 2).

At the site level, planktivore crustaceans in MS (e.g., *Xiphopenaeus kroyeri* and *Brachyura* larvae) showed $\delta^{15}\text{N}$ depleted values compared to omnivores (e.g., *C. similis*, *Acanthostracion quadricornis*, *Archosargus rhomboidalis*, *Gerres cinereus*, *A. felis*), zoobenthivores (e.g., *Achirus lineatus*, *Batrachoides goldmani*, *Cichlasoma urophthalmum*) and piscivores (e.g., *Cynoscion nebulosus*, *Lutjanus griseus*, *Elops saurus*), the last with the highest mean $\delta^{15}\text{N}$ value ($p < 0.05$) (Fig. 3.2). Planktivores (e.g., *Lucifer faxoni*) also showed depleted $\delta^{13}\text{C}$ values in comparison to other feeding guilds ($p < 0.05$) (Fig. 3.2). Nevertheless, piscivores like *E. saurus* also had a depleted $\delta^{13}\text{C}$ value (Fig. 3.2).

In ME, consumers with the lowest $\delta^{15}\text{N}$ values ($p < 0.05$) were non-selective filter bivalves (*Lampsilis tampicoensis*, *Rangia flexuosa*, *Polymesoda arctata*), periphyton-macrophyte grazers (e.g., *Pomacea flagellata*), and herbivore cichlids (e.g., *Paraneetroplus synspilus*), followed by detritivores (e.g., *Paraneetroplus bifasciatus*), planktivores (e.g., *Brachyura* larvae), and omnivores (e.g., *Macrobrachium acanthurus*, *Penaeus duorarum*, *Callinectes rathbunae*, *Rocio octofasciata*), with intermediate values ($p < 0.05$). Planktivores like *Anchoa* sp. and *Gobiomorus dormitor* larvae, showed high $\delta^{15}\text{N}$ values (Fig. 3.2), although zoobenthivores (e.g., *Cichlasoma salvini*, *Thorichthys helleri*, *Thorichthys meeki*, *B. goldmani*, *Rhamdia quelen*) and piscivores (e.g., *Centropomus undecimalis*, *Petenia splendida*) had the highest $\delta^{15}\text{N}$ values among all groups ($p < 0.05$) (Fig. 3.2). Non-selective filter feeders showed the most depleted $\delta^{13}\text{C}$ values among all consumers ($p < 0.05$) (Fig. 3.2).

In M1, the herbivore crab *Aratus pisonii* showed the most depleted $\delta^{15}\text{N}$ values among all consumers ($p < 0.05$), followed by omnivores (e.g., Tanaidacea, *P. duorarum*, *C. rathbunae*, *Pterygoplichthys pardalis*, *Astyanax aeneus*, *Atherinella alvarezi*), detritivores (e.g., *Dorosoma anale*, *Dorosoma petenense*), and zoobenthivores (e.g., *C. urophthalmum*, *A. lineatus*, *B. goldmani*, *G. dormitor*, *Citharichthys spilopterus*, *Trinectes maculatus*), with similar and intermediate $\delta^{15}\text{N}$ values ($p > 0.05$) (Fig. 3.2). Planktivores with low to intermediate $\delta^{15}\text{N}$ values were Brachyura, *G. dormitor*, and Penaeidae larvae, whereas *Anchoa mitchilli*, *Anchoa hepsetus* and *Brevoortia gunteri* showed high $\delta^{15}\text{N}$ values (Fig. 3.2). Piscivores (e.g., *P. splendida*, *C. undecimalis*, *Oligoplites saurus*, *Strongylura marina*) had the highest $\delta^{15}\text{N}$ values ($p < 0.05$). With regard the $\delta^{13}\text{C}$ values, detritivores showed the most depleted values; omnivores intermediate values; and herbivores, planktivores, zoobenthivores and piscivores, enriched values ($p < 0.05$) (Fig. 3.2).

In M2, consumers at the base of the food web were the periphyton-macrophyte grazer *P. flagellata* (with the lowest $\delta^{15}\text{N}$ values, $p < 0.05$), together with the non-selective filter bivalves *L. tampicoensis* and *Rangia cuneata* (with the lowest $\delta^{13}\text{C}$ values, $p < 0.05$), and the detritivores *Thiara tuberculata* and *Oreochromis niloticus* (Fig. 3.2). Herbivores (e.g., *Ctenopharyngodon idella*), omnivores (e.g., *P. pardalis*, *M. acanthurus*), planktivores (e.g., *Poecilia mexicana*), zoobenthivores (e.g., *C. urophthalmum*, *R. quelen*) and piscivores (e.g., *Parachromis managuensis*) showed a high overlap in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values ($p > 0.05$). Planktivores with high $\delta^{15}\text{N}$ values at this site were *A. mitchilli* and *B. gunteri* (Fig. 3.2).

Overall, omnivores and zoobenthivores comprised the most representative guilds in terms of number of species (Annex I, Resource 2). These groups also included abundant species, e.g., zoobenthivore Cichlidae (*C. salvini* and *T. helleri* in ME), omnivore Gerreidae (*G. cinereus* in MS and *Diapterus rhombeus* in M1) and Atherinidae (*A. alvarezi* in M2). Planktivore Engraulidae were also abundant (*A. mitchilli* in M2).

In all sites, omnivore and zoobenthivore Ariid catfishes were high trophic level predators, e.g., *Bagre marinus* in MS, *R. quelen* in ME, *Cathorops aguadulce* in M1, and *A. felis* in M2 (Fig. 3.2).

Resident and transient fish species

The 49 fish species found in the study sites, most of which consisted of juveniles, included 27 transient and 22 resident species (the ecological guilds per species are shown in Annex I, Resource 1). A cluster analysis based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, grouped fishes into three groups (Fig. 3.4). The first group mainly consisted of marine transient species from MS, with enriched $\delta^{13}\text{C}$ values; the second group of marine transients found in ME, M1, and M2, with

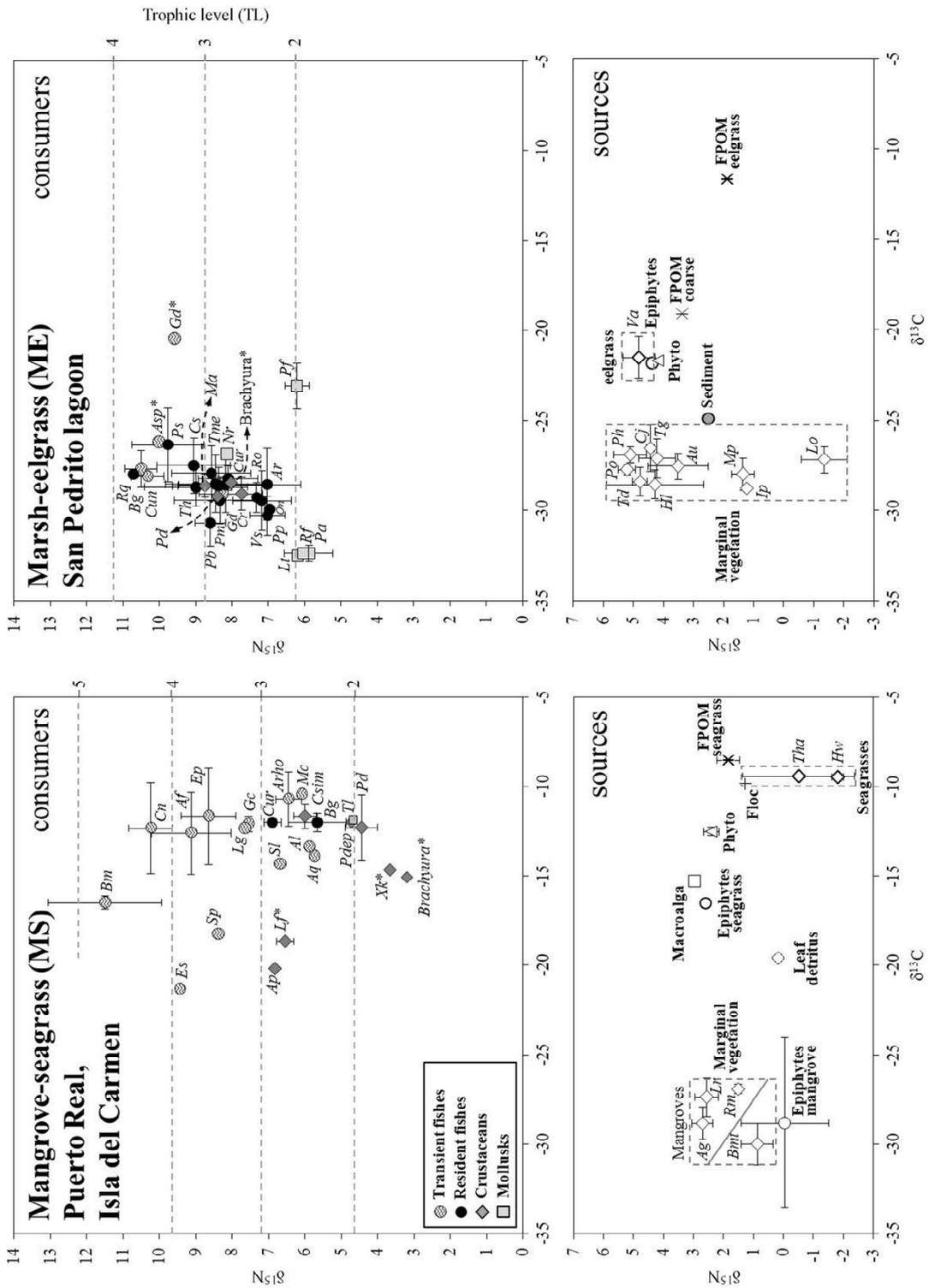


Fig. 3.2 Bi-plots with mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm\text{SD}$) of consumers and basal resources per site. *Gray dotted lines* in the bi-plots of consumers depict the trophic levels in each site. Species identities, isotope values, ecological guilds (for fishes) and feeding guilds (for all consumers) are shown in Annex I (Resource 1). Species marked with *asterisk* refer to larval stages

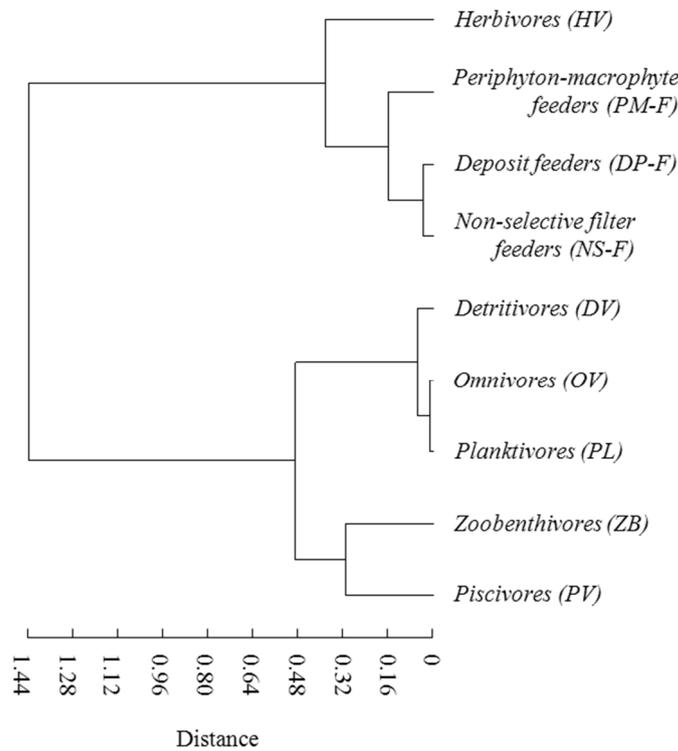


Fig. 3.3 Hierarchical clustering of consumers' feeding guilds based on the mean trophic level per guild. Values per feeding guild and species are shown in Annex I (Resource 2)

intermediate $\delta^{13}\text{C}$ values; and the third group of freshwater residents from ME and M2, with the most depleted $\delta^{13}\text{C}$ values (Fig. 3.4). Most of the fishes from the sites with SAV (mainly in the first and third group of the cluster), showed the lowest $\delta^{15}\text{N}$ values, indicating their predominance in the low trophic level in these sites (Fig. 3.4).

Relationships between consumers and basal resources

According to the isotope bi-plots, most of the consumers in MS were related to the isotopic values of phytoplankton, the red macroalga *Acanthophora spicifera*, seagrass epiphytes, and Floc (Fig. 3.2). Similarly, SIAR results suggested that phytoplankton, seagrass sources (leaves, FPOM from leaves, Floc), seagrass epiphytes, and the red macroalga, contributed significantly to the diet of the consumers (Table 3.2). Phytoplankton showed the greatest contribution (average 31 %), especially for omnivores and zoobenthivores (with up to 80 % contribution, see 95 % Bayesian credible intervals BCI, Table 3.2). Mangroves (leaves) and their epiphytes, together with detritus, contributed much less to the diet of the consumers, with a jointly contribution of 18 % (Table 3.2).

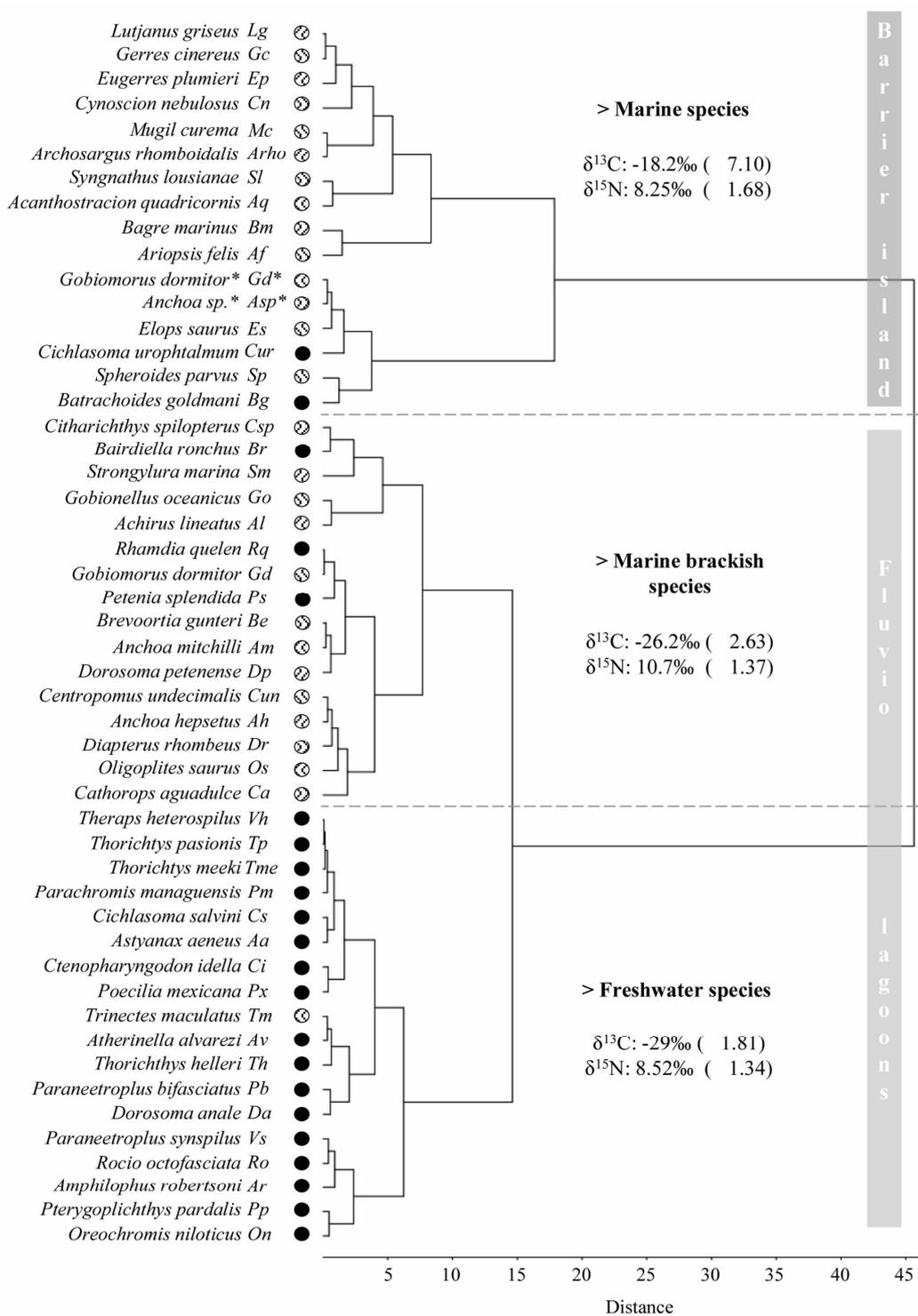


Fig. 3.4 Hierarchical clustering of the collected 49 fish species based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values¹. *Pattern filled circles* transient fishes. *Black filled circles* resident fishes. *Asterisks* refer to larval stages

¹ The number in parentheses denotes standard deviation

In ME, most consumers were related to the isotopic values of marginal vegetation, particularly the widely spread *Typha domingensis* and *Phragmites australis* (Fig. 3.2). SIAR results confirmed the high contribution of marginal plants to the diet of consumers (average 46 %), especially for omnivores and zoobenthivores (average 78–95 %), followed by piscivores and herbivores (average 43–44 %, Table 3.2). Sediment was important for non-selective filter feeders (average 41 %). *V. americana*, epiphytes and phytoplankton showed in general a lower importance (average 13–15 %), but their contribution was higher for detritivores and planktivores (average 19–28 %) which relied evenly upon marsh plants (average 28–31 %, Table 3.2). Periphyton-macrophyte feeders relied evenly upon sediments and marsh plants (average 24–25 %, Table 3.2).

In M1, most consumers' isotopic values were related to SPOM, phytoplankton, and FPOM from coarse debris (Fig. 3.2). However, SIAR results showed that mangrove epiphytes had the highest contribution to the diet of consumers (average 44 %), especially for piscivores (average 70 %, Table 3.2). Detritivores, omnivores, planktivores and zoobenthivores also depended primarily upon epiphytes (95 % BCI: 17–63 %, Table 3.2). Phytoplankton was the second resource in order of importance (average 24 %), and seemed to be evenly used by herbivores, detritivores, omnivores, planktivores and zoobenthivores (average 24–29 %, Table 3.2). Mangrove leaves and marsh plants, together with detritus, showed a lower contribution (average 16 %, Table 3.2).

In M2, most consumers were related to marginal vegetation, especially to the marsh plants *P. australis*, *T. domingensis* and *Cladium jamaicense*, and to the mangrove species *R. mangle* (Fig. 3.2). Detritivores, planktivores and zoobenthivores (e.g., *D. petenense*, *P. mexicana*, *R. quelen*) were also related to FPOM from coarse debris (Fig. 3.2). SIAR results confirmed that marginal vegetation contributed significantly to the diet of consumers (average 40 %), with a higher importance for non-selective filter feeders (average 67 %; 95 % BCI: 34–94 %), followed by omnivores and zoobenthivores (average 45–47 %, Table 3.2). Detritus (mixture of mangrove leaves and FPOM from coarse debris) was the second resource in order of importance (average 28 %), especially for omnivores (average 38 %, Table 3.2). Detritivores and periphyton-macrophyte feeders relied evenly on marginal vegetation, detritus, mangrove epiphytes and phytoplankton (average 21–29 %, Table 3.2).

Isotopic niches of consumers' communities

The most evident difference among the communities was the isotopic niche position of consumers from MS and the consumers from ME, M1 and M2 (Fig. 3.5a).

Consumers from ME, M1 and M2 showed a high overlap in their SEA_c (26.3–85.2 %), suggesting a high overlap in their isotopic niche (Table 3.3, Fig. 3.5a). The overlapped areas of these communities were characterized by shared omnivore species like *M. acanthurus*, *P. duorarum*, *C. rathbunae*, *A. alvarezi*, *A. aeneus*, and *P. pardalis*; and zoobenthivore species like *A. lineatus*, *B. goldmani*, *C. salvini*, *C. urophthalmum*, *R. quelen* and *T. helleri*. Consumers from ME and M2 showed the highest isotopic niche overlap (60.5–85.2 %, Table 3.3, Fig. 3.5a), with shared low trophic level species like *L. tampicoensis*, *P. flagellata*, *P. synspilus* and *T. heterospilus*. The SEA_c correspondent to MS had no overlap with the fluvio-lagoons (Table 3.3).

The isotopic niche size, based on the Bayesian estimate of the standard ellipse areas (SEA_B), was larger for the consumers from MS and M1 compared to the consumers from ME and M2 (Fig. 3.5b). Consumers from ME had the most compact ellipse and thus the narrowest isotopic niche (Fig. 3.5a, b, Table 3.3).

In terms of the total area of the convex hull (TA), a higher overlap was also observed among consumers from ME, M1 and M2 (Fig. 3.5a). Nevertheless, the TAs of these sites overlapped with the TA of MS (Fig. 3.5a) through species with extreme isotopic values in these habitats like *E. saurus*, *Anchoa sp.* larvae, and *G. dormitor* larvae.

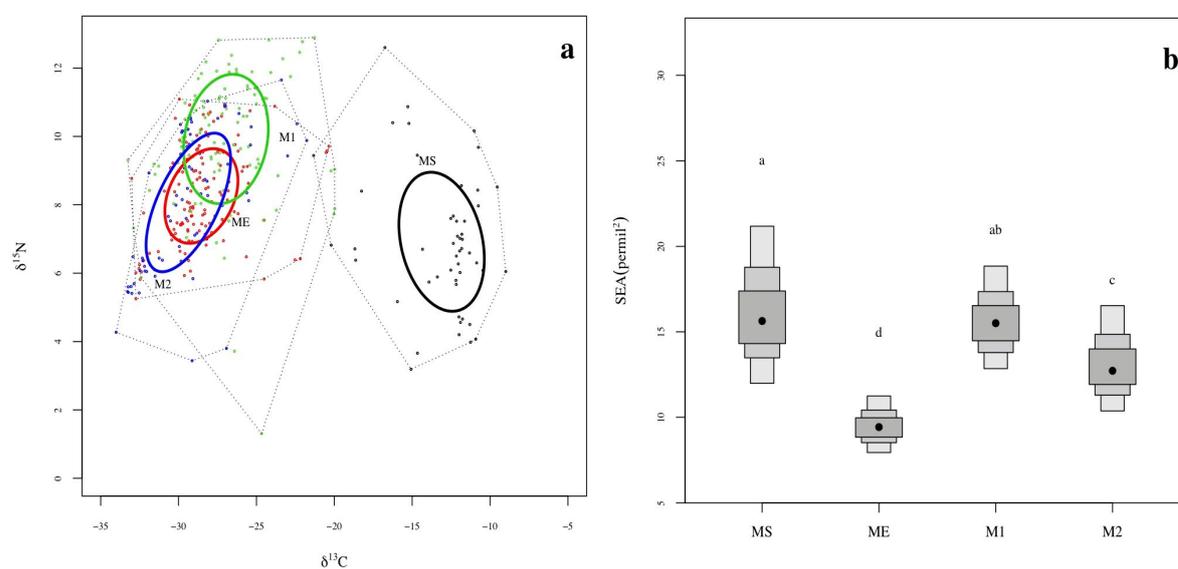


Fig. 3.5 a $\delta^{13}C$ and $\delta^{15}N$ values of consumers from all sites. *Solid lines* small sample size corrected standard ellipse areas (SEA_c). *Dotted lines* convex hull areas (TA). **b** Density plot of the Bayesian standard ellipse areas (SEA_B). *Black points* modes. *Boxes* 50, 75 and 95 % BCI from dark gray to light gray. *Letters above boxes* statistical differences with a $p < 0.0001$

Table 3.2 Average contributions (95 % BCI, Bayesian credible interval) of basal resources to consumers' feeding guilds, and average contribution per source per site obtained with SIAR

Site	Trophic Guild	Contribution of basal resources (%)					
		Mangrove & Epiphytes	Detritus (Leaves)	Red Macroalga	Phytoplankton	Seagrasses sources ^m	Epiphytes (seagrass leaves)
MS ^a	OV ^e	1.95 (0-5.47)	3.36 (0-9.40)	20.2 (0- 43.3)	42.5 (8.7-78.1)	21.4 (1- 40.2)	10.6 (0-26.8)
	PL ^f	17.5 (1.58-31.6)	16.6 (0-32.3)	16.4 (0-31.8)	16.6 (0-31.7)	16.1 (0.2-30.5)	16.7 (0-32.3)
	ZB ^g	2.03 (0-5.59)	3.16 (0-9.18)	25.9 (0-50.9)	44.4 (12.4-80)	11.3 (0-28.7)	13.3 (0-32.9)
	PV ^h	12.2 (0-26.6)	14.4 (0-30.3)	18.9 (0-35.9)	19.2 (0-36.1)	17.4 (0-33.1)	17.9 (0-34.2)
	Av. per source	8.42	9.38	20.4	30.7	16.6	14.6
	<hr/>						
ME ^b		Marsh plants	Sediment	FPOM (coarse debris)	Phytoplankton	Eelgrass & Epiphytes	
	NS-F ⁱ	22.7 (0.43-42.2)	40.7 (13.0-71.5)	16.2 (0-36.3)	11.6 (0-29.4)	8.80 (0-23.1)	
	PM-F ^j	24.8 (1.64-43.5)	23.9 (0.43-44.4)	16.5 (0-34.3)	17.8 (0-36.1)	17.0 (0-34.9)	
	HV ^k	43.7 (13.2-79.4)	15.8 (0-34.5)	7.80 (0-23.3)	15.1 (0-35.2)	17.7 (0-37.8)	
	DV ^l	28.1 (0.1-54.7)	11.7 (0-30.5)	10.8 (0-28.3)	21.0 (0-42.6)	28.4 (0.2-54.7)	
	OV	77.8 (51.7-97.7)	7.10 (0-19.0)	2.40 (0-7.05)	5.60 (0-18.3)	7.11 (0-24.3)	
	PL	31.3 (3.54-58.5)	16.0 (0-35.3)	11.3 (0-28.5)	19.1 (0-39.1)	22.3 (0.1-42.5)	
	ZB	95.4 (91.1-99.0)	1.60 (0-4.66)	0.70 (0-1.88)	1.10 (0-3.10)	1.20 (0-3.40)	
	PV	43.2 (8.69-84.4)	16.8 (0-37.7)	8.50 (0-24.7)	14.9 (0-35.8)	16.6 (0-38.6)	
	Av. per source	45.9	16.7	9.26	13.3	14.9	
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M1 ^c		Mangroves & Marsh plants	Detritus ⁿ	Mangrove epiphytes	Phytoplankton		
	HV	24.6 (0-48.0)	24.2 (0-47.5)	26.5 (0.4-48.4)	24.6 (0-48.4)		
	DV	17.1 (0-38.4)	17.8 (0-38.9)	38.1 (23.5-53.1)	26.9 (0-53.1)		
	OV	17.7 (0-38.3)	20.9 (0-41.3)	32.6 (17.1-48.2)	28.8 (0-55.5)		
	PL	16.0 (0-37.0)	15.2 (0-35.3)	44.8 (26.7-63.5)	24.0 (0-48.0)		
	ZB	12.1 (0-30.0)	12.4 (0-30.5)	49.8 (36.5-62.3)	25.7 (0.1-50.6)		
	PV	8.20 (0-20.3)	7.80 (0-20.2)	70.5 (52.3-87.6)	13.5 (0-33.5)		
	Av. per source	15.9	16.4	43.7	23.9		
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M2 ^d		Mangroves & Marsh plants	Detritus ^o	Mangrove epiphytes	Phytoplankton		
	NS-F	66.7 (34.3-94.1)	9.90 (0-29.1)	4.50 (0-13.1)	18.9 (0-45.3)		
	PM-F	28.3 (0.1-53.7)	25.2 (0-49.2)	20.8 (0-43.2)	25.7 (0-49.7)		
	HV	32.8 (0.6-62.1)	30.8 (0.7-56.0)	13.6 (0-35.0)	22.8 (0-46.5)		
	DV	23.6 (0-46.3)	29.1 (0-56.4)	23.7 (0-46.1)	23.5 (0-46.5)		
	OV	45.0 (7.5-85.5)	38.5 (0.9-74.4)	4.00 (0-11.6)	12.5 (0-34.5)		
	PL	35.7 (2.5-65.7)	32.2 (0-61.5)	10.0 (0-28.1)	22.1 (0-46.5)		
	ZB	46.9 (11.1-85.4)	32.8 (0.2-62.7)	5.40 (0-16.6)	14.8 (0-38.4)		
Av. per source	39.8	28.4	11.7	20.1			

^a Mangrove-seagrass; ^b Marsh-eelgrass; ^c Mangrove-bare sediments; ^d Mangrove-bare sediments; ^e Omnivores; ^f Planktivores; ^g Zoobenthivores; ^h Piscivores; ⁱ Non-selective filter feeders; ^j Periphyton-macrophyte feeders; ^k Herbivores; ^l Detritivores; ^m seagrass leaves + FPOM from seagrass leaves + Floc; ⁿ mangrove leaves + coarse woody debris + FPOM from coarse debris + SPOM; ^o mangrove leaves + FPOM from coarse debris

Table 3.3 Standard ellipse area (SEA), small sample size corrected standard ellipse area (SEA_c), total area of the convex hull (TA), and percentage overlap in SEA_c between pairs of sites

Sites	SEA (‰ ²)	SEA _c (‰ ²)	TA	SEA _c overlap (%) with ME	SEA _c overlap (%) with M1	SEA _c overlap (%) with M2
MS ^a	16.6	16.9	73.9	0	0	0
ME ^b	9.57	9.64	56.9	-	26.3	60.5
M1 ^c	15.8	15.9	102	43.5	-	34.2
M2 ^d	13.4	13.6	61.2	85.2	29.1	-

^a Mangrove-seagrass; ^b Marsh-eelgrass; ^c Mangrove-bare sediments; ^d Mangrove-bare sediments

3.4 Discussion

Isotopic composition of basal resources

The habitat differences observed in terms of basal $\delta^{13}\text{C}$ values, depicted a gradient from the northeast of Terminos Lagoon (MS) with enriched $\delta^{13}\text{C}$ values to the river-influenced habitats in the southwest (ME, M1, M2), with depleted $\delta^{13}\text{C}$ values. Raz-Guzmán and de la Lanza (1991) also reported different isotopic zones in Terminos Lagoon, with more depleted $\delta^{13}\text{C}$ values in sites with important fluvial input, and enriched values in the northeast saline area. This spatial variability in $\delta^{13}\text{C}$ has been found in other tropical and subtropical systems (Deegan and Garritt 1997; Chanton and Lewis 2002; Nyunja et al. 2009). One explanation for this is the variability in $\delta^{13}\text{C}$ values of dissolved inorganic carbon (DIC) in marine (of up to +1.7 ‰) and freshwater habitats (~ -14 ‰) (Bouillon et al. 2007).

Most of the observed isotopic values in basal resources coincided with ranges reported in the literature. The $\delta^{13}\text{C}$ values of phytoplankton corresponded with ranges reported for freshwater-estuarine (ca. -29.8 to -22 ‰) and marine phytoplankton (~ -15 ‰, Fry and Wainright 1991; Fogel et al. 1992; Deegan and Garritt 1997). *A. spicifera* had a similar $\delta^{13}\text{C}$ value to that reported for C₄ red algae in the northeast part of Terminos Lagoon (-17.2 ‰, Raz-Guzmán and de la Lanza 1991). *T. testudinum* and *H. wrightii* had values within the range reported for these intermediate C₃-C₄ seagrass species (-13.5 to -5.2 ‰, Beer and Wetzel 1982; Harrigan et al. 1989; Fourqurean et al. 2005).

V. americana showed typical values of C₃-CAM intermediate plants and coincided with values reported for *V. gigantea* and *Vallisneria* spp. (-27.6 to -17.1 ‰, Keeley and Sandquist 1992; Boon and Bunn 1994; Barret 2007). Terrestrial vegetation, including mangroves, showed $\delta^{13}\text{C}$ values characteristic of C₃ plants (-34.3 to -23 ‰, Raz-Guzmán and de la Lanza 1991). Epiphytes from

R. mangle fell within the $\delta^{13}\text{C}$ range reported by Fry et al. (1982) and Giarrizzo et al. (2011) (-34.7 to -19.5 ‰). Epiphytes from *T. testudinum* and *V. americana* also showed similar $\delta^{13}\text{C}$ values to those reported in the literature (-16.7 to -10.5 and -29.8 to -22 ‰, respectively, Kieckbusch et al. 2004; Boon and Bunn 1994). Mangrove leaf detritus had similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to those documented for yellow and detrital Red mangrove leaves (-30.5 to -27.3 and -0.6 to 13.6 ‰, respectively, Fry and Smith III 2002).

Trophic levels and consumers' feeding guilds

The number of trophic levels in the study sites (three to four levels) coincided with findings from studies carried out in the Monkey River Basin in Belize (Winemiller et al. 2010²), the inner littoral of Isla del Carmen in Terminos Lagoon (Rivera-Arriaga et al. 2003), and Centla Wetlands (Mendoza-Carranza et al. 2010). In this study, the interlinked mangrove-seagrass habitat MS showed the highest number of trophic levels, suggesting a high diversity of resources and consumers' types.

Omnivores and zoobenthivores were the most representative guilds in terms of number of species and abundance, as observed for fishes. This coincides with previous studies highlighting that estuarine fishes are characterized by omnivory, broad dietary overlap, and the ability to exploit temporary peaks of prey (Ley et al. 1994; Layman and Silliman 2002). On the other hand, the high abundance of the planktivore *A. mitchilli* in M2 (El Vapor lagoon) in the Palizada-Del Este System, contiguous to Terminos Lagoon, coincides with studies identifying this species as one of the most important in terms of abundance in this river-influenced area (Vera-Herrera et al. 1988; Ayala-Pérez et al. 1997). This marine transient species uses the Palizada-Del Este System, the Terminos Lagoon and the continental platform for feeding, growing and reproduction, respectively (Ayala-Pérez et al. 1997).

Potential use of basal resources by consumers

Our results sustain the hypothesis that in the fringing mangrove habitat interconnected with seagrasses (MS), mangrove-derived carbon is of limited importance, and that phytoplankton, macroalgae, seagrass-derived carbon and seagrass epiphytes play a major role in sustaining secondary production, as revealed in previous studies (Kieckbusch et al. 2004; Thimdee et al. 2004; Nyunja et al. 2009). Also in this site, some planktivore and piscivore species showed intermediate isotopic values between $\delta^{13}\text{C}$ enriched and depleted resources (Fig. 3.2). Planktivore species included *X. kroyeri*, *L. faxoni*, and *Brachyura* larvae. These taxa have a complex life cycle characterized by a continuous migration from and to the open sea, and a short residence time

² Errata: The correct year of publication of this reference is 2011

within estuaries (Dall et al. 1990; Pile et al. 1996), with bay environments lying on migration routes where transitory species converge from several isotopically distinct feeding grounds (Fry 1981). This could explain the $\delta^{13}\text{C}$ values found for these taxa. The marine transient fish *E. saurus* also showed intermediate $\delta^{13}\text{C}$ values between basal resources with enriched and depleted $\delta^{13}\text{C}$ values. Marine transient fishes are characterized by a high mobility across the estuarine realm, and a greater isotopic variation compared to non-migratory species (Fry et al. 1999, 2003; Herzka et al. 2002; Ray 2005). Recent migrants (which act as a conduit of organic matter export) are distinguishable from those that have resided in coastal areas for sufficiently long time to equilibrate to the new foods (Litvin and Weinstein 2004; Herzka 2005).

In contrast to the findings in MS, marginal marsh plants in ME were of significantly higher importance for consumers, especially for resident omnivores and zoobenthivores. Sediments comprised an important resource for filter-feeding bivalves (which can also pedal feed on sedimentary particles, McMahon and Bogan 2001) and periphyton-macrophyte feeders (gastropods, Table 3.2). These mollusks may play an important role in transferring energy from terrestrial to aquatic ecosystems due to the consumption of terrestrial organic matter accumulated in the sediments, most likely from vascular plants (Antonio et al. 2010). Interestingly, the $\delta^{13}\text{C}$ values of the bivalves of this site showed much more depleted values (ca. -32.5 ‰) than sediments (ca. -25 ‰, Fig. 3.2). A possible explanation for this can be the consumption of methane oxidizing bacteria (MOB) due to preferential use of CH_4 in sediments (with $\delta^{13}\text{C}$ values from -36 to -58 ‰ in river-dominated estuaries), reflecting upstream inputs of biogenic CH_4 (Sansone et al. 1999; Kohzu et al. 2004; Eller et al. 2005). The possibility of methane being an important resource in fresh water food webs has only been proposed recently (Eller et al. 2005). This represents an opportunity to evaluate this issue in our study area. On the other hand, despite the high biomass of *V. americana* in ME (174.2–217.7 g dry m^{-2} , Sánchez et al. 2012), our results revealed that its contribution to the feeding of consumers during the sampling period was negligible, which coincides with other findings in the area (Mendoza-Carranza et al. 2010).

In M1, marginal vegetation and detritus (FPOM from coarse debris and SPOM) comprised the less assimilated food, contradicting our assumption that these resources could be the most important in fueling secondary production in this site. Nevertheless, some consumers appeared to make use of these and other resources, like the crab *A. pisonii*, suggesting opportunistic feeding behavior (Table 3.2). Mangrove epiphytes and phytoplankton were the most important resources for consumers at this site. The high $\delta^{15}\text{N}$ value observed for the epiphytes (9.03 ‰) could be related to the efficient removal of nitrate (NO_3^-) from the water column (Dudley et al. 2001). Nitrate rich material such as sewage is characterized by high $\delta^{15}\text{N}$ values (Kuramoto and Minagawa 2001; Wada 2009). Positive correlations between $\delta^{15}\text{N}$ values of stream water NO_3^- and

percent of agricultural land-use within a given catchment have also been reported (Harrington et al. 1998). As a result, it is possible that mangrove epiphytes in M1 constitute an important sink for anthropogenic inputs of NO_3^- (as observed for benthic primary producers in other studies, e.g., Dudley et al. 2001), but this deserves further consideration.

In M2, marginal plants and detritus showed the highest contribution for consumers, especially for non-selective filter feeders, omnivores and zoobenthivores, whereas phytoplankton and mangrove epiphytes had a lower contribution. The highly depleted $\delta^{13}\text{C}$ values of bivalves, gastropods, and fishes like *P. synspilus*, *O. niloticus*, and *P. pardalis*, suggest the pertinence of considering the role of other potential resources with depleted $\delta^{13}\text{C}$ values like MOB in further studies.

Isotopic niches of consumers' communities

In accordance to our second hypothesis, the degree of isotopic niche overlap of the communities suggests the high affinity among the river-influenced communities ME, M1, and M2, in comparison to the marine community MS. This can be explained by the habitat-derived differences in stable isotope values, foraging behavior of individuals, and their ultimate use of resources based on factors like resource availability (Bearhop et al. 2004; Flaherty and Ben-David 2010).

The consumers from ME, M1 and M2 were mainly composed of freshwater resident species, followed by marine-brackish transient species. Omnivores and zoobenthivores were abundant at these sites, occupying the shared isotopic area of the three communities. Consumers from ME and M2 appeared to greatly depend on highly available material derived from marginal vegetation, especially from the abundant emergent hydrophytes, but also mangroves. Just in Centla Wetlands, the coverage of emergent hydrophytes in the marshlands, dominated by *T. domingensis* and *Thalia geniculata* (tular-popal vegetation), comprises 183,932 ha (Guerra-Martínez and Ochoa-Gaona 2006). On the other hand, riverine mangroves in association with fluvio-lagoon systems are very productive areas, generating large amounts of litterfall ($1,252 \text{ g m}^{-2} \text{ year}^{-1}$) compared to fringe mangroves from the inner littoral of Isla del Carmen ($835 \text{ g m}^{-2} \text{ year}^{-1}$) (Day et al. 1987). This may influence the importance of these resources for consumers in these sites.

In M1, consumers depended more on mangrove epiphytes and phytoplankton, and to a lesser extent on marginal vegetation. M1 is located downstream of the confluence zone of the Grijalva and Usumacinta rivers, known as Tres Brazos, near to the small city of Frontera. This area is threatened by the increasing construction of roads and channels, agriculture and livestock expansion, oil activity, among other factors (Guerra-Martínez and Ochoa-Gaona 2006). As previously mentioned, the high $\delta^{15}\text{N}$ values, especially found in mangrove epiphytes, may be

attributed to input materials with high $\delta^{15}\text{N}$ values, which are propagated to the aquatic food webs (Kuramoto and Minagawa 2001; Abrantes et al. 2013; Connolly et al. 2013). High $\delta^{15}\text{N}$ values in basal resources and consumers were also observed in ME and M2, suggesting that these river-influenced habitats are subject to nitrogen rich inputs, which can be related to the degree of perturbation and hypereutrophication observed in the drainage areas of the Grijalva and Usumacinta rivers (Salcedo et al. 2012).

It has been observed that the ecological condition of river catchments can affect environmental parameters such as turbidity and primary productivity, which in turn affect trophic structure in downstream estuaries, e.g., high concentrations of total suspended solids (TSS) may limit aquatic primary productivity, and thus food webs may be based on terrestrial sources from the catchment (Abrantes et al. 2014). This is likely to occur in the Grijalva–Usumacinta system, with concentrations of TSS of up to 153 mg L^{-1} during the dry season (Albarran-Melze et al. 2009), although as previously mentioned, mangrove epiphytes and phytoplankton can play an important role, as observed in M1. Presumably, inputs from the Grijalva river into M1 may enhance aquatic productivity up to certain point due to high nutrient inputs, but these may be accompanied by an increase in suspended solids, increasing turbidity and limiting aquatic productivity (Abrantes et al. 2013).

In MS, consumers showed a high dependence on phytoplankton, macroalgae and seagrass sources. This may be attributed to the high production in these near shore waters close to seagrass beds and mangroves as a consequence of stimulatory effects by high nutrient levels and humic substances (Day et al. 1982). The inner littoral of Isla del Carmen presents high phytoplankton productivity, with an annual average of $803 \text{ mgC m}^{-3} \text{ h}^{-1}$, and maximum peaks of productivity in April ($1,660 \text{ mgC m}^{-3} \text{ h}^{-1}$) and June ($882.2 \text{ mgC m}^{-3} \text{ h}^{-1}$) (de la Lanza and Lozano 1999). The highest seagrass biomass and productivity also generally occur during the dry season when water transparency is the highest (Reyes et al. 1994). This clear environment (TSS concentration during the dry season oscillates between 0.015 and 0.018 mg L^{-1} , Herrera-Silveira et al. 2002) may allow for a range of aquatic producers to occur, supporting consumers with different trophic ecologies (Abrantes et al. 2013, 2014). Nevertheless, despite the different set of resources used by consumers in this habitat, a distinct preference for phytoplankton was found. This coincides with previous observations highlighting that Terminos Lagoon is a phytoplankton based lagoon, which despite the existence of other primary producers like seagrasses and macroalgae, their contribution to total areal production is very low in comparison to phytoplankton (Knoppers 1994).

Despite the differences observed in the isotopic position of the communities, as previously mentioned, omnivores (transient and resident) dominated in almost all habitats. This suggests that

Terminos Lagoon and Centla Wetlands provide favorable habitats to marine transient and resident species, mostly benthic-pelagic omnivores (Villéger et al. 2012). These species can feed on a large variety of prey and move across the ecosystem depending on abiotic conditions (Villéger et al. 2012). In contrast, herbivore sedentary species typically dominant in seagrass meadows are marginal as these habitats are becoming scarce (Villéger et al. 2010). *V. americana* is also disappearing from Centla Wetlands, and the reasons behind this have not been documented (Sánchez et al. 2007). This is of special importance in terms of conservation, and highlights the importance of the spatial heterogeneity of the area, which enhances that many more species coexist regionally (Kneitel and Chase 2004).

Another concern is the overlap in habitat use of native species and the introduced Amazon sailfin catfish *P. pardalis* in river-influenced areas of Centla Wetlands and Terminos Lagoon, which suggests some potential for competitive interactions (Mendoza-Carranza et al. 2010). Other introduced species in the area are the Nile tilapia *O. niloticus*, the Grass carp *C. idella*, and the Red-rimmed melania *T. tuberculata* (Mendoza-Carranza et al. 2010; Sánchez et al. 2012). These introduced species were found in our study sites (specifically the fluvio-lagoons), and further studies should consider the use of resources by these species and by native aquatic fauna.

In terms of the isotopic niche size, consumers from ME showed the narrowest isotopic niche. This may indicate more selective feeding upon the highly available material derived from terrestrial vegetation, in spite of the presence of other basal resources like phytoplankton and epiphytes of *V. americana*.

Final remarks

To conclude, in accordance to the hypotheses, it was observed that aquatic consumers in river-influenced habitats (fluvio-lagoons) of Centla Wetlands and Terminos Lagoon rely more on marginal vegetation resources, although mangrove epiphytes and phytoplankton also play an important role in these food webs. On the other hand, it was observed a negligible contribution of mangrove-derived carbon to consumers in the interlinked mangrove-seagrass habitat (barrier island) in comparison to phytoplankton, macroalgae and seagrass sources.

Consumers from the fluvio-lagoon sites showed a high overlap in their isotopic niche, mainly due to their resemblance in isotopic position or habitat use, and community structure, whereas consumers from the fringing mangrove-seagrass habitat showed a different isotopic position. Moreover, the isotopic niche area of the consumers' communities differed, suggesting that resource availability may greatly differ across the studied sites.

Further studies should consider additional information to make more robust comparisons among

contrasting habitats in this area, including estimates of food availability, nutrient fluxes, and hydrological characteristics of the sites (e.g., water residence time).

Our results are a snapshot of the food web structure of different estuarine habitats during the dry season. However, a between season comparison is necessary to enhance our understanding of the structure and dynamics of these spatially and temporally complex ecosystems (Mendoza-Carranza et al. 2010).

It would be also suitable to collect other potential basal resources (e.g., microphytobenthos, MOB, dissolved organic carbon) in the study area, and to employ methods like fatty acid biomarkers and stomach content analysis to complement the resolution given by stable isotopes (Connolly et al. 2004; Winemiller et al. 2007). Moreover, future work should validate which $\delta^{15}\text{N}$ baselines are the most appropriate for the calculation of trophic levels (e.g., mollusks were good baseline indicators in ME and M2, but zooplankton or crustaceans could be probably more appropriate in sites like MS and M1).

The comparison of the food web structure in different habitats of Terminos Lagoon and the neighboring Centla Wetlands with the use of stable isotopes has as yet been poorly addressed (Raz-Guzmán and de la Lanza 1991; Mendoza-Carranza et al. 2010). More studies in the area using this technic would allow for comparative results and would provide valuable information of these important but highly threatened estuarine systems.

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Chapter IV

— Seasonal Food Web Analysis —

Flood pulse induced changes in isotopic niche and resource utilization of consumers in a Mexican floodplain system

Alejandra Sepúlveda-Lozada, Ulrich Saint-Paul, Manuel Mendoza-Carranza, Matthias Wolff, Alejandro Yáñez-Arancibia

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Abstract

Tropical coastal ecosystems of the southern Gulf of Mexico including marshes, mangroves and seagrasses of Centla Wetlands and Terminos Lagoon (Grijalva-Usumacinta delta) are known to host a high diversity of aquatic consumers. Nevertheless, the limited research focusing on the energy fluxes that sustain consumers has as yet neither considered the strong seasonality of these systems, nor the linkage of the trophic flow patterns with ecosystem functioning. The present work analyses and compares stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of consumers during the dry and rainy season at different wetland sites to determine their resource utilization. The sites compared comprise three fluvio-lagoons and a coastal mangrove creek that differ in vegetational characteristics, distance to the sea, and freshwater input. The results support the hypothesis that a larger isotopic niche breadth of consumers prevails during the rainy season, when resource availability is supposedly higher. This translates into an increase in resource use diversification by consumers and corroborates the flood pulse concept (FPC), which can be particularly applied to those habitats with high riverine influence in the study area (e.g., fluvio-lagoons). However, the FPC alone cannot be applied to understand the main factors influencing the fate and utilization of basal resources in areas interacting more actively with the sea, and therefore further extensions and/or complementary conceptual approaches considering marine systems highly interconnected with coastal floodplains should be considered.

Keywords: isotopic niche breadth, resource use, seasonality, Centla Wetlands, Terminos Lagoon, Mexico

4.1 Introduction

The coastal and estuarine system is a mosaic of interconnected habitats (Sheaves 2009) with mangroves and marshes being some of the most distinctive (Rountree and Able 2007; Davis et al. 2012). Adjacent to mangroves, seagrasses often form extensive beds in clear, shallow waters (McKee 2012b). The links between these ecosystems and fisheries production is based on the fact that they serve as nursery grounds, provide shelter, protect from predators, and supply a rich food source (Kathiresan 2014).

In the southern tropical portion of the Gulf of Mexico, these ecosystems are well represented in the Centla Wetlands floodplain and the neighbouring Terminos Lagoon, which occupy major portions of the Grijalva-Usumacinta delta. In this area river discharge is the second highest in the Gulf of Mexico after the Mississippi River (Yáñez-Arancibia et al. 2009, 2013a). These wetlands are known to host a high diversity of aquatic species, particularly juvenile stages, some of which sustain the multispecies fishery of the adjacent continental platform (Yáñez-Arancibia and Sánchez-Gil 1986; Gracia 1989; Yáñez-Arancibia et al. 2013b). Nevertheless, little is known in terms of energy fluxes and the structure of aquatic food webs in the habitat continuum from the continental shelf to fringing mangrove-seagrass areas up to the more inland freshwater-dominated sites with mangrove and marsh vegetation. Moreover, the research in this regard has not taken into account the strong seasonal variability in the area, particularly in terms of precipitation and freshwater discharge (e.g., Manickhand-Heileman et al. 1998ab; Rivera-Arriaga et al. 2003; Mendoza-Carranza et al. 2010).

In highly dynamic systems like these, energetic pulsing can be linked to primary productivity pulses and seasonal changes in the contribution of different energy sources driving the food webs. The pulsing idea means that coastal systems are structured and sustained by a hierarchical series of overlapping energetic forces or pulsing events that vary on spatial and temporal scales (Yáñez-Arancibia et al. 2013b). The pioneer concept referring to this was the flood pulse concept (FPC) of Junk et al. (1989) (updated version in Junk and Wantzen 2004), based on long-term observations of the Amazon and Mississippi rivers. The concept highlights that the flood pulse is the driving force in river-wetland systems, with most secondary production being attributed to the high in situ aquatic and riparian production. This concept also states that food supply during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic organisms (Junk et al. 1989; Junk and Wantzen 2004). Thus, the seasonal shifts in resource availability and the reliance upon a wider variety of resources by aquatic consumers during the flood phase can be strongly associated with habitat changes due to the flood pulse (Wantzen et al. 2002).

The present work, based on stable isotope analysis, aims to understand the aquatic food web dynamics in different habitats of Centla Wetlands and Terminos Lagoon during two contrasting periods of precipitation and freshwater discharge, namely the dry and rainy seasons.

Our specific objectives were as follows: 1) to describe seasonal food web structures in terms of the isotopic values of the basal resources and consumers in four different habitats of Centla Wetlands and Terminos Lagoon, 2) to assess the seasonal changes in isotopic niche breadth of mollusks, crustaceans, and fishes, as representative groups of aquatic consumers of the study sites, and 3) to identify seasonal changes in relation to the relative contribution of basal resources to the diet of consumers.

We tested two hypotheses: 1) for the majority of consumers, a larger niche breadth is observed during the rainy season, when basal resources contributing to their diets are more diverse and overall productivity is higher; 2) the flood pulse would be the main driving force of the energetic changes in the studied communities.

4.2 Materials and methods

Study area

The RAMSAR sites Centla Wetlands (with many distributary channels and ca. 110 lentic ecosystems) and Terminos Lagoon (connected to the sea by two inlets at each extreme of ‘Del Carmen’ barrier island) comprise a Biosphere Reserve ‘BR’ (302,706 ha) and a Protected Area for Flora and Fauna ‘PAFF’ (706,147 ha), in a microtidal region (0.3 to 0.7 m) along Tabasco and Campeche, Southern Gulf of Mexico (Kjerfve 1986; INE 1997, 2000; Sánchez et al. 2007; McKee 2012b; Medina-Gómez et al. 2015) (Fig. 4.1). The two sites constitute major portions of the Grijalva-Usumacinta system, the second most important delta in North and Central America after the Mississippi, with a combined discharge into the Gulf of Mexico of 3,000 to 4,700 m³ s⁻¹ (Yáñez-Arancibia et al. 2009). This estuarine complex comprises a terrigenous-clastic environment at the west and a calcareous region at its eastern extreme (Yáñez-Arancibia et al. 2007; Medina-Gómez et al. 2015). The climate is humid tropical with a mean annual temperature higher than 25°C and an annual rainfall from 1,200 to more than 3,000 mm (Yáñez-Arancibia et al. 2009; Rivera-Monroy et al. 2011). There are three distinct seasons: dry (March to May), rainy (June to October, heavy rains), and ‘nortes’ (November to February, intermediate rains with strong northerly winds) (Espinal et al. 2007; Yáñez-Arancibia et al. 2009). The second and third seasons are considered in general as a rainy period. During this time, particularly from September to December, there is the highest water discharge and sediment load in the lower reaches of the

Grijalva and Usumacinta (Muñoz-Salinas and Castillo 2015). There, the volume of water increases by about 50 % (e.g., Centla Wetlands) (Sánchez et al. 2007).

The study sites comprised the fluvio-lagoons San Pedrito, El Vapor, and El Coco (hereafter S1, S2, and S3), connected with the Usumacinta, Palizada, and Grijalva rivers, and located 26, 25, and 13 km from the coast, respectively, in the two protected areas; and one creek located less than 1 km from the coast at the east of the inner littoral of Del Carmen Island in Terminos Lagoon (hereafter S4) (Fig. 4.1). S1 is characterized by marsh vegetation (ca. 95 % of the border) and the eelgrass *Vallisneria americana* (with a coverage of ca. 2.1 km²). S2 and S3 are characterized by riverine-basin mangrove forest with an approximate coverage of 20 % and 100 %, respectively, as well as by marsh vegetation, low semi-deciduous forest, and unvegetated bottoms. In S2, the submerged plant *Cabomba palaeformis* was only found in the rainy season. S4 is an interlinked fringing mangrove-seagrass habitat with approximated mangrove coverage of 98 to 100 % along the border, and seagrass coverage (*Thalassia testudinum* and *Halodule wrightii*) of ca. 1.5 km².

Some physico-chemical and hydrological characteristics of the study sites per season are shown in Table 4.1.

Table 4.1 Changes in water depth, salinity, total suspended solids, rainfall, freshwater inflow and wind patterns in the study sites between the dry and rainy season

	S1		S2		S3		S4	
	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
Depth (m)	0.90 ^a	1.60 ^a	2.00 ^a	2.10 ^a	1.10 ^a	1.30 ^a	1.05 ^a	1.21 ^a
Salinity	4.5 ^a	2 ^a	2.5 ^a	0 ^a	6 ^a	4 ^a	39.5 ^a	23 ^a
TSS (mg L ⁻¹)	31.01 ^b	13.67 ^b	0.025 ^c	0.020 ^c	31.01 ^b	13.67 ^b	0.018 ^c	0.018 ^c
Total rainfall (mm)	68.5 ^d	1904.5 ^d	114.9 ^d	1857 ^d	68.5 ^d	1904.5 ^d	22.1 ^d	936.4 ^d
Net freshwater inflow (m ³ s ⁻¹)	770 ^e	4,390 ^e	288 ^f	480 ^f	770 ^e	4,390 ^e	4 ^f	158-200 ^f
Winds	SE ^g	NE ^g	SE ^g	NE ^g	SE ^g	NE ^g	SE ^g	NE ^g

^a This study, ^b Albarran-Melze et al. (2009), ^c Herrera-Silveira et al. (2002) (mean values from the rainy and ‘nortes’ season for the eastern inner littoral of Del Carmen Island and southwest part of Terminos Lagoon), ^d CONAGUA precipitation data 2009-2010 for Tres Brazos (reference for S1, S3), Palizada (S2), and Isla Aguada (S4), smn.coangua.gob.mx, ^e Ortiz-Zamora et al. (2002) (values for the Grijalva-Usumacinta system), ^f Yáñez-Arancibia and Day (2006) (values for the eastern part of Terminos Lagoon and the Palizada river), ^g Yáñez-Arancibia et al. (2007)

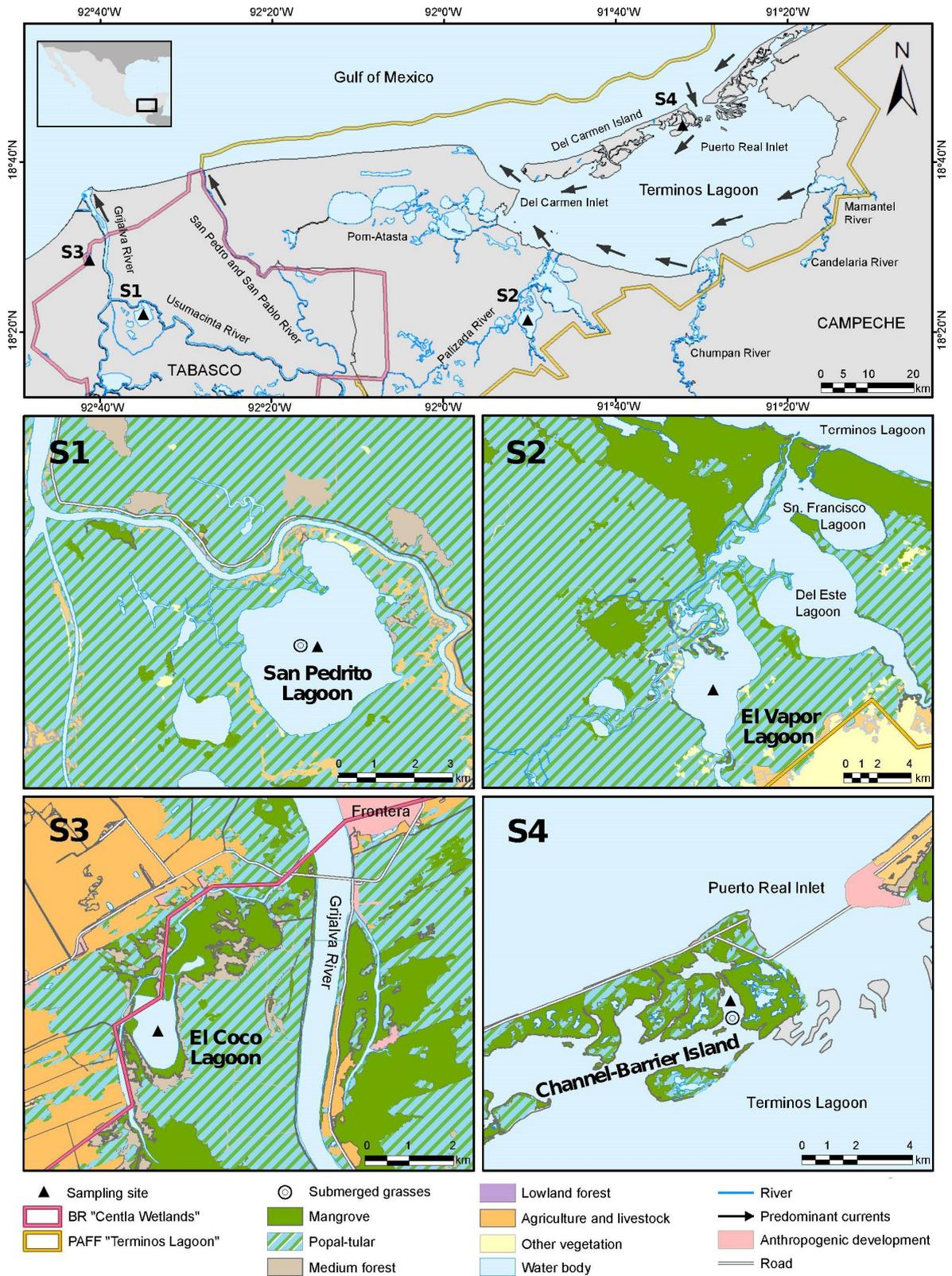


Fig. 4.1 Location of Centla Wetlands and Terminos Lagoon, and sampling sites with main vegetation types: S1 (marsh-elgrass), S2 (marsh-mangrove), S3 (mangrove), S4 (mangrove-seagrass). Other vegetation types and land uses are shown. Sources of information: INEGI (2002), Guerra-Martínez and Ochoa-Gaona (2006), CONABIO (2013a, b), CONANP (2014), and field observations. Cartographic specifications: Geographic Coordinate System GCS, geodetic datum WGS84

Sample collection and processing

Field samplings were conducted during April and May of 2009 (dry season) and November and December of 2010 (rainy season under the influence of ‘nortes’).

Samples for stable isotope analyses of basal resources included seston, benthic algae (Rhodophyta –*Acanthophora spicifera*– and cyanobacteria –gelatinous colonies presumably of Rivulariaceae–), submerged aquatic vegetation ‘SAV’ (*T. testudinum*, *H. wrightii*, *V. americana*, *C. palaeformis*), floating vegetation (e.g., free floating, free floating submerged, and floating leaved-rooted), marginal vegetation (22 C₃ species including mangroves, marsh plants, and low-medium flooded forest shrubs and trees; and one C₄ Poaceae grass), and epiphytic algae from SAV and mangrove roots. Other basal resources included detrital mangrove leaves, sediments from vegetated and non-vegetated bottoms, fine particulate organic matter (on the surface of seagrass leaves – FPOMs–, eelgrass leaves –FPOMe– and coarse woody material –FPOMc–), and flocculated organic matter consisting of macroflocs of up to 5 cm (Floc). The identity and number of samples of the collected basal resources are shown in Annex II (Resource 1). In regard to the fine particulate organic matter component, we will only focus on FPOMc throughout the results and discussion. Consumers mainly included zooplankton, macro-invertebrates (mollusks, crustaceans) and fishes. Additionally, some samples of insects were collected during the rainy season in the fluvio-lagoons.

Seston was collected using a cascade-filtering device with four plankton nets (20, 63, 120 and 500 µm), where large volumes of water were filtered by hand. Retained fractions were >20 µm, >63 µm and >120 µm. Fine particulate organic matter was collected by lightly rinsing the flocculated material on submerged vegetation and woody stems of marginal vegetation through a 63 µm plankton net, and retaining the smaller than 63 µm fraction (Hoeinghaus et al. 2007). Flocculated organic matter was collected with the surface water and then separated from the water using a fine mesh colander. Leaves from plant species were clipped directly and algae were collected by hand. Epiphytes adhered to leaves of submerged grasses and mangrove roots were obtained from the surfaces using a scalpel and forceps to obtain composite samples (Moncreiff and Sullivan 2001; Sheaves et al. 2007; Wilson 2010). Detrital mangrove leaves, made up of dark brown to black leaf fragments, were collected with colanders. Sediment was collected with a Petite Ponar Grab to a depth of 10 cm.

Zooplankton samples were taken from nocturnal tows of 5 minutes with a conic net of 500 µm mesh size, and a light trap. Fishes were collected during day and night with different gears (beach seine, beam trawl, gillnet, dip net) to collect representative samples of the fish diversity at each

site (Mendoza-Carranza et al. 2010). Additional individuals were also obtained from local fishermen. Bivalves, gastropods, and crabs were collected while sampling fishes and by hand. Insects were collected at night with a light trap consisting of a white cotton sheet tied up with a rope between two shrubs or trees and with a white light lamp in the front (Schauff 1986; Steiner and Häuser 2010), but they were also incidentally caught while using the conical plankton net and the beam trawl. All samples were stored on ice in the field and then frozen upon return to the laboratory (Hoeinghaus et al. 2007).

Processing of samples prior to drying followed standard methods for basal resources (Hoeinghaus et al. 2007), zooplankton (Hoeinghaus et al. 2007; Letessier et al. 2012), insects (Zambrano et al. 2010), mollusks, crustaceans, and fishes (Garcia et al. 2007; Hoeinghaus and Davis 2007; Hoeinghaus et al. 2007).

All samples were dried at 60°C for at least 48 hrs in sterile Petri dishes (Hoeinghaus et al. 2007). Dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials (Hoeinghaus et al. 2007; Mendoza-Carranza et al. 2010). Subsamples were weighted to the nearest 0.01 mg and pressed into Ultra-Pure tin capsules (Costech, Valencia, CA) for the determination of stable isotope ratios of carbon and nitrogen at the Analytical Chemistry Laboratory, University of Georgia, Athens, GA, using a Carlo Erba NA 1500 CHN analyzer coupled to a Finnigan Delta-C continuous flow mass spectrometer. Isotopic ratios were expressed in delta notation (δ) as parts per thousand (‰) relative to the standards Pee Dee Belemnite (PDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$, according to the equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The analytical precision was based on the standard deviation of two secondary standards (bovine and poplar, $n=104$) analyzed every 12 samples throughout each run. The precision across all runs ranged from ± 0.08 to 0.15 ‰ for $\delta^{13}\text{C}$, and from ± 0.08 to 0.30 ‰ for $\delta^{15}\text{N}$.

Data analyses

Differences in isotopic values of basal resources and consumers across sites and seasons, as well as among selected items (14 basal resources, main taxonomic groups of consumers and feeding guilds) were represented graphically with beanplots, which provide density shape estimations based on the Sheather-Jones method (Venables and Ripley 2002). Graphs were done with the R-package “beanplot” (Kampstra 2008). The non-parametric Kruskal-Wallis H -test for multiple comparisons and Bonferroni-corrected Mann-Whitney U -tests for post hoc comparisons were used to test for significant differences as the data did not satisfy the assumptions of normality and

variance homogeneity required for an ANOVA (Zar 2010). The Bonferroni-corrected p value threshold used to declare significance was calculated as $p < 0.05 / (\text{number of tests})$ (Moeller et al. 2013).

In the case of consumers, feeding guilds were assigned based on literature for the collected species and mainly included: non-selective filter feeders (NSF), periphyton-macrophyte feeders (PMF), herbivores (HV), detritivores (DV), omnivores (OV), zoobenthivores (ZB), planktivores (PL) and piscivores (PV) (see Annex II, Resource 2). Two unidentified gastropod mollusks and one crustacean species (*Alpheus sp.*) from S4, as well as insects from the fluvio-lagoons were not classified into feeding guilds in this study. Thus, the isotopic data of the latter were analysed exclusively with the pooled data. Ecological guilds related with the habitat requirements and migratory behaviour of fishes, were also assigned based on literature.

Isotopic niches per group of consumer and their seasonal variation per site were investigated with Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al. 2011) within the package SIAR (Parnell et al. 2010) for R software, first by examining the dispersion of the raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the isotopic space with the sample size-corrected standard ellipse area (SEAc), which only gives one data point and is used for graphical representations of the ellipses, and then by estimating the Bayesian SEA (SEA_B) and corresponding 95 % credible intervals to quantify uncertainty in core isotopic niche areas (Hinke et al. 2015; Reid et al. 2016). SEA_B were calculated using Markov chain Monte Carlo simulation with 10^4 iterations for each case (Jackson et al. 2011). This method allows a direct probabilistic interpretation of the differences in SEA_B , rather than the traditional frequentist test of a null-hypothesis (Fleming et al. 2015). Here, the isotopic niche comparisons were based on the probabilities from pairwise tests that the SEA_B in the dry season is smaller than the SEA_B in the rainy season ($\text{SEA}_{\text{dry}} < \text{SEA}_{\text{rainy}}$). Standard ellipses were expressed in units of per mil squared (‰^2), as they represent the amount of areal space occupied by the consumers in the bivariate $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ space (Elliott Smith et al. 2015).

Furthermore, a Bayesian stable isotope mixing model SIAR (Stable Isotope Analysis in R, Parnell et al. 2010) was run for each study site and season (in total eight models) to estimate the distribution of possible contributions of selected resources to the diet of most consumers' feeding guilds. Additionally, insects were integrated as a group alone in the models for the rainy season. The inputs to the models were the mean isotopic values of basal resources and their standard errors, elemental concentrations of basal resources and their standard errors, trophic enrichment factors (TEFs) with their standard errors, and replicate samples of consumer isotopic values (Parnell et al. 2010; Le Pape et al. 2013). The TEFs were those proposed by Post (2002) for $\delta^{13}\text{C}$ ($0.4 \pm 1.3 \text{‰}$) and $\delta^{15}\text{N}$ ($3.4 \pm 1.0 \text{‰}$). The models include five to six basal resources, some of which consisted of a single sample (e.g., seston, eelgrass epiphytes, fine particulate organic matter,

mangrove epiphytes, mangrove detrital leaves, seagrass epiphytes, benthic algae). In such cases, the single isotopic values were used as means in the source input tables, and instead of using standard deviations of zero, there were added reported standard deviations for the same or related resources in Mendoza-Carranza et al. (2010), Vaslet et al. (2012), and Claudino et al. (2015). By using imputed standard deviations, there is added a variability component for sampling error and prior information on the standard deviations of the sources, reflecting the complexity and variation usually found in ecological systems (D. Phillips, pers. comm. 2015; R. Inger, pers. comm. 2015; A. Parnell, pers. comm. 2016). The models were based on 500,000 iterations, thinned by 15, except for the models of S2 and S4 in the rainy season, which were run with 200,000 iterations. The number of iterations according to the SIAR's convergence diagnosis was acceptable. The data used for each model are shown in Annex II (Resource 3).

4.3 Results

$\delta^{13}C$ and $\delta^{15}N$ values of basal resources

A total of 343 samples of basal resources were collected in the four study sites during the two sampling periods, with $\delta^{13}C$ and $\delta^{15}N$ values ranging from -41.6 to -5.5 ‰ and -2.9 to 9.0 ‰, and global medians of -28.0 ‰ and 3.3 ‰, respectively (Fig. 4.2a, b). $\delta^{13}C$ values varied significantly among sites, with resources from S4 and S1 showing the highest values compared to S2 and S3 (Fig. 4.2a). The median $\delta^{15}N$ values in S1, S2 and S3 were higher than in S4 (Fig. 4.2b).

High $\delta^{13}C$ values in S4 were due to the presence of seagrasses, marine seston, seagrass epiphytes, benthic algae and flocculated organic matter, which spanned some of the highest values overall (range -19.0 to -9.0 ‰) (Fig. 4.3a). In S1, eelgrass leaves and sediment from an eelgrass carpet, followed by eelgrass epiphytes, also spanned $\delta^{13}C$ values above the global median of -28.0 ‰ (Fig. 4.3a). In all fluvio-lagoons, some samples of freshwater-estuarine seston and fine particulate organic matter also spanned higher $\delta^{13}C$ values than the global median (Fig. 4.3a). Basal resources with $\delta^{13}C$ values mostly below the global median comprised C_3 marginal vegetation (e.g., *Chrysobalanus icaco* and *Mimosa pigra* with low values, and marsh plants like *Thalia geniculata*, *Cladium jamaicense* and *Phragmites australis* with higher values), detrital mangrove leaves, floating vegetation (e.g., *Utricularia sp.* with a low value, and *Eichhornia crassipes*, *Salvinia spp.*, and *Pistia stratiotes*, with higher values), and mangrove epiphytes (e.g., red filamentous algae with lower values and green filamentous algae with higher values) (Fig. 4.3a).

In most cases, $\delta^{13}C$ values of basal resources were higher in the dry than in the rainy season, but significant seasonal differences were only observed in the case of seagrasses (Fig. 4.3a). Nevertheless, eelgrass epiphytes (with a single sample per season) and mangrove epiphytes also

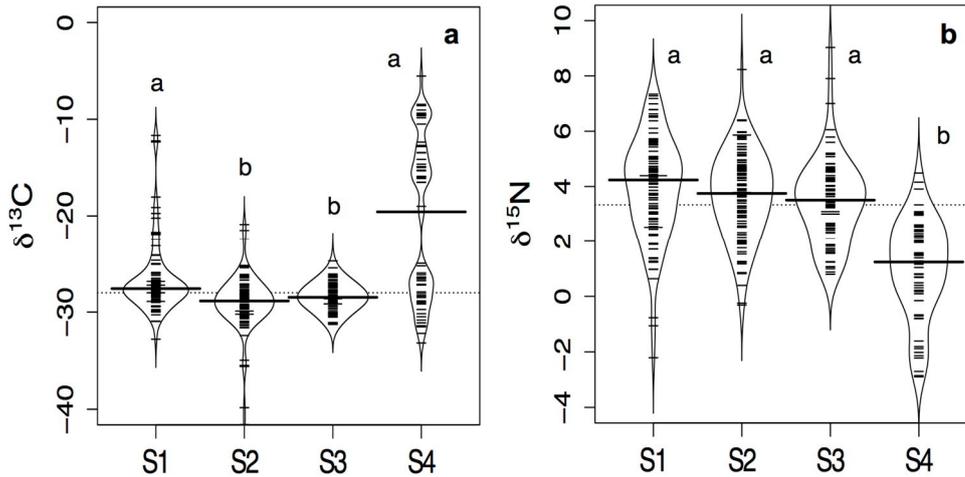


Fig. 4.2 Beanplots of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ values (b) of pooled basal resources per site. Dashed line overall median, horizontal black lines medians for each case. $a > b$, significant differences ($p < 0.01$ after Bonferroni correction)

showed higher values in the dry than in the rainy season, with differences of up to 9.1 ‰ (Fig. 4.3a). Marine and freshwater-estuarine seston, benthic algae, eelgrass, fine particulate organic matter, and detrital mangrove leaves still showed this trend, but with smaller differences of up to 2.5 ‰ (Fig. 4.3a). It is possible that a reduced number of samples in some cases did not allow finding significant statistical differences between seasons. In contrast, sediment from an eelgrass carpet in S1 showed markedly lower values in the dry (median of ca. -25.0 ‰) than in the rainy season (-12.3 ‰) (Fig. 4.3a).

Basal resources with $\delta^{15}\text{N}$ values distributing mostly below the global median (3.3 ‰) were seagrasses, flocculated organic matter, mangrove epiphytes (mainly red filamentous algae), detrital mangrove leaves and benthic algae, followed by marine seston, and sediment from an eelgrass carpet (Fig. 4.3b). Intermediate to high $\delta^{15}\text{N}$ values mainly corresponded to marginal vegetation, fine particulate organic matter, freshwater-estuarine seston, floating vegetation, and eelgrass leaves (Fig. 4.3b). The minimum and maximum $\delta^{15}\text{N}$ values were found in seagrasses (-2.9 ‰) and green filamentous mangrove epiphytes (9.0 ‰), respectively. *V. americana* leaves also had one of the highest $\delta^{15}\text{N}$ values overall (7.3 ‰). No seasonal differences in $\delta^{15}\text{N}$ values were found for any basal resource (Fig. 4.3b).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among main groups of consumers and feeding guilds

A total of 722 samples of consumers showed $\delta^{13}\text{C}$ values from -37.0 to -9.0 ‰ and a global median of -28.5 ‰. All consumer identities per feeding guild and main taxonomic group, together with their median isotopic values per site and season are shown in Annex II (Resource 2).

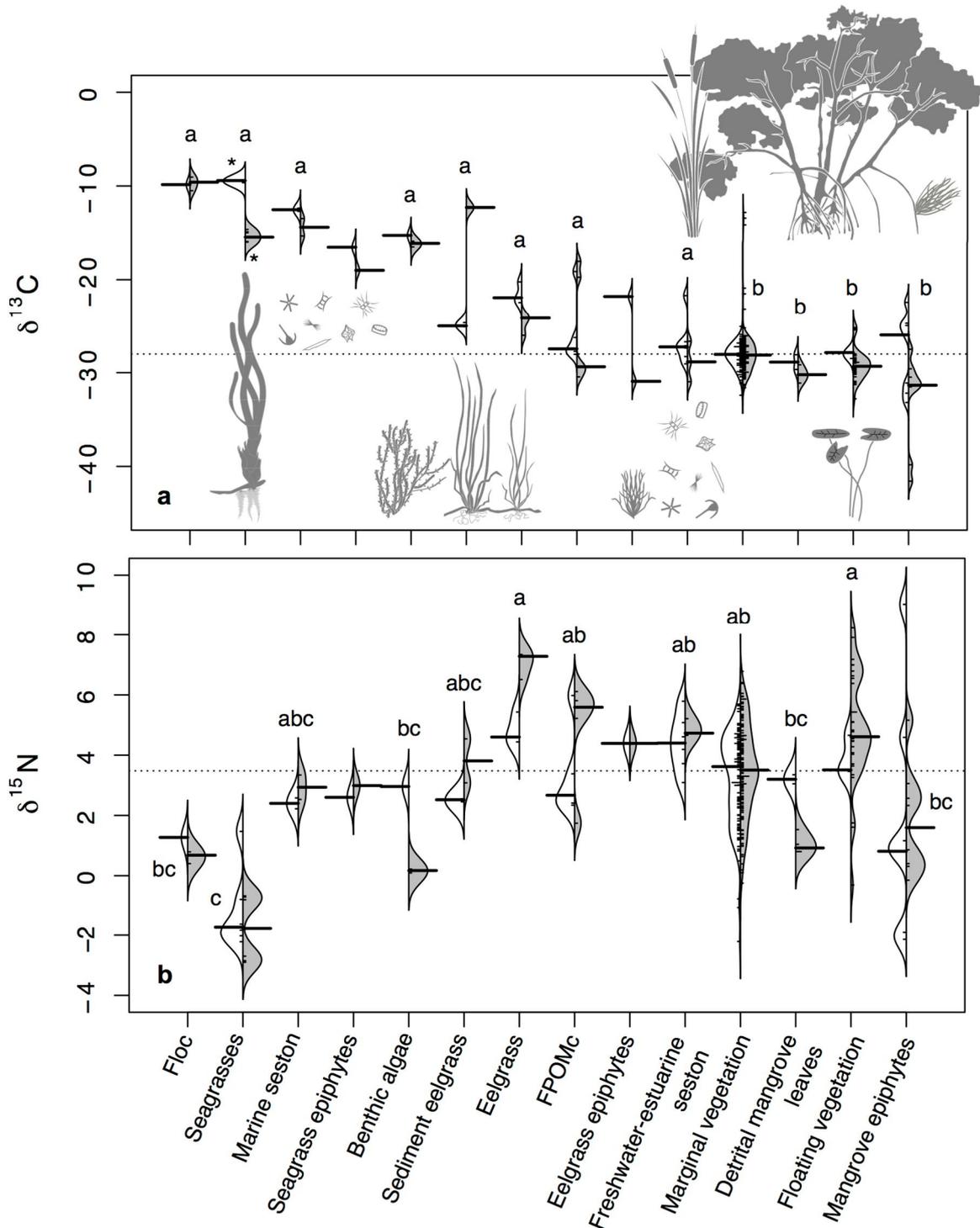


Fig. 4.3 Beanplots of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ values (b) of main basal resources per season (white dry, gray rainy). Dashed line overall median, horizontal black lines medians for each case. $a > b > c$, significant differences among resources with sample number higher than 3 ($p < 0.001$ after Bonferroni correction). Shared letters similarity. Asterisks seasonal differences per resource type ($p < 0.05$). Primary producer's images authored by T. Saxby, J. Woerner and D. Kleine, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

Among the main groups of consumers, mollusks showed the lowest median $\delta^{13}\text{C}$ value (-33.0 ‰) compared to crustaceans (-27.0 ‰) and fishes (-28.0 ‰) (Fig. 4.4a). As expected, non-selective filter feeders (mainly bivalves) showed the lowest $\delta^{13}\text{C}$ values, followed by periphyton-macrophyte feeders (gastropods), herbivores (sesarimid crab, fishes), detritivores (gastropod, isopods, fishes), and omnivores (amphipods, tanaidaceans, shrimps, crayfish, crabs, fishes), with intermediate values; and zoobenthivores (fishes), planktivores (mainly crab and shrimp larvae, and fishes), and piscivores (fishes), with the highest values (Fig. 4.4b). Omnivores, zoobenthivores, and planktivores showed the highest number of taxa with 30, 22, and 17, respectively (Annex II, Resource 2), as well as some of the most abundant species overall like the fishes *Cichlasoma salvini* and *Anchoa mitchilli* in S1 and S2, as well as *Diapterus rhombeus*, *Diapterus auratus*, and *Eucinostomus gula*, together with the shrimp *Farfantepenaeus duorarum* in S3 and S4.

Consumers from all the sites showed a wide range of $\delta^{15}\text{N}$ values from -2.3 to 14.0 ‰ and a global median of 8.2 ‰. The lowest median values were found for mollusks (6.0 ‰) followed by crustaceans (7.0 ‰), and the highest for fishes (8.8 ‰) (Fig. 4.4c). Among feeding guilds, non-selective filter feeders and periphyton-macrophyte feeders showed the lowest median $\delta^{15}\text{N}$ values (ca. 6.0 ‰) compared to herbivores, detritivores, omnivores, zoobenthivores, and planktivores (8.0 to 9.0 ‰) (Fig. 4.4d). Piscivores had the highest median $\delta^{15}\text{N}$ value overall (9.8 ‰) (Fig. 4.4d).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of main groups of consumers among sites and seasons

Among sites, mollusks, crustaceans, and fishes showed lower $\delta^{13}\text{C}$ values in S1, S2, and S3 than in S4 (Fig. 4.5a-c). Details per feeding guild can be consulted in Annex II (Resource 2).

In most cases, median $\delta^{13}\text{C}$ values of consumers were higher in the dry than in the rainy season, remarkably in S4 and in the case of fishes (Fig. 4.5c). In S4, shared fish species between seasons largely contributing to this difference included marine transients like *Mugil curema* (-32.5 to -10.5 ‰), *Archosargus rhomboidalis* (-26.2 to -11.3 ‰), and *Cynnoscion nebulosus* (-33.2 to -11.0 ‰), and the estuarine resident *Cichlasoma urophthalmum* (-30.7 to -11.9 ‰) (Annex II, Resource 2). Some estuarine and marine transient species collected exclusively in the dry season contributing to high $\delta^{13}\text{C}$ values were *Ariopsis felis* (-11.8 ‰), *Eugerres plumieri* (-10.7 ‰), *Acanthostracion quadricornis* (-13.9 ‰), and *Lutjanus griseus* (-12.4 ‰); whereas species collected exclusively in the rainy season contributing to low $\delta^{13}\text{C}$ values were *Bairdiella ronchus* (-31.9 ‰) and *Caranx latus* (-33.0 ‰) (Annex II, Resource 2).

Noteworthy, in S1, S2, and S3, some crustaceans and fishes showed higher median $\delta^{13}\text{C}$ values in the rainy than in the dry season (Fig. 4.5b-c). Species contributing greatly to this variability were

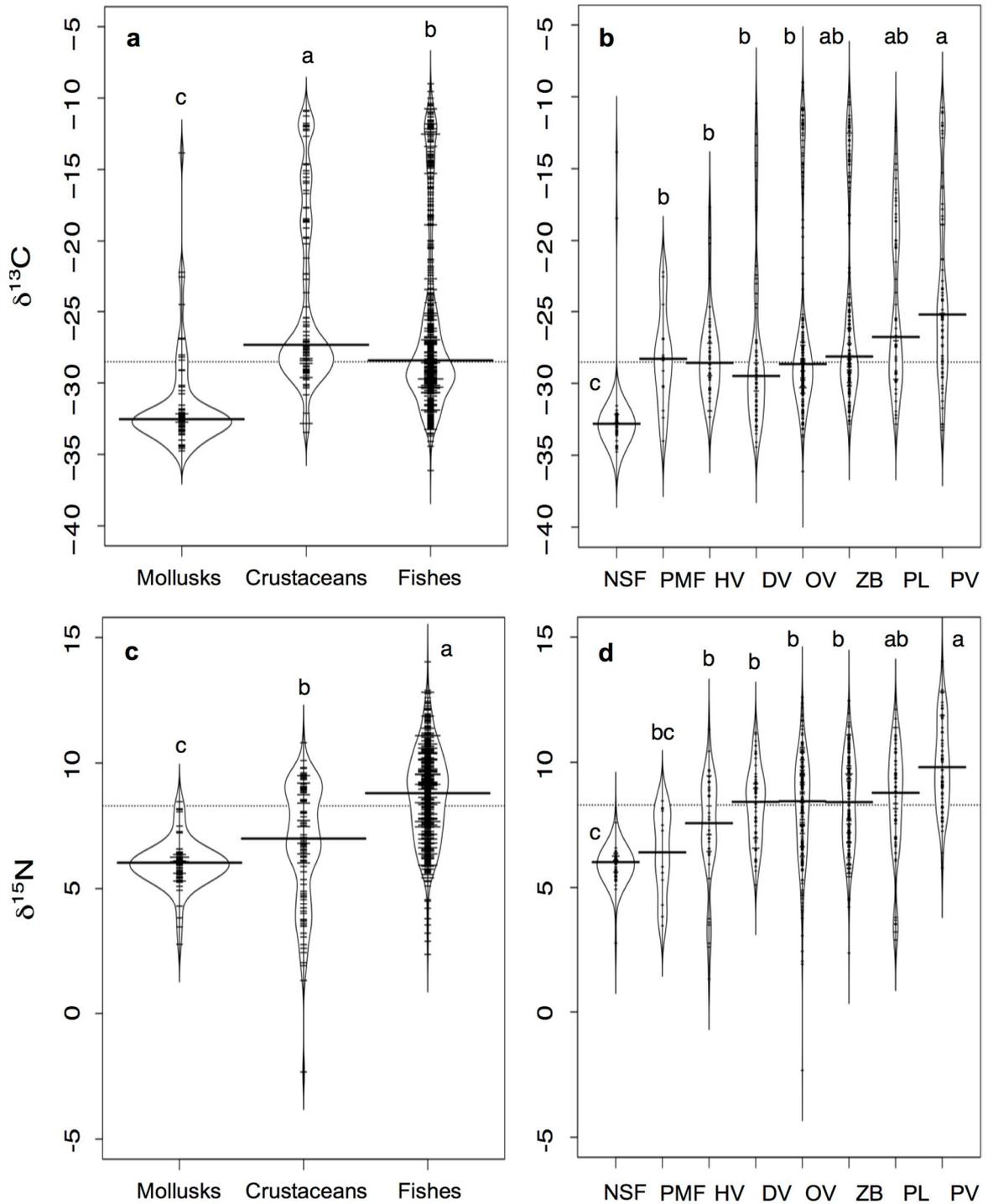


Fig. 4.4 Beanplots of $\delta^{13}\text{C}$ (a-b) and $\delta^{15}\text{N}$ values (c-d) of consumers per main taxonomic group and feeding guild. *NSF* non-selective filter feeders, *PMF* periphyton-macrophyte feeders, *HV* herbivores, *DV* detritivores, *OV* omnivores, *ZB* zoobenthivores, *PL* planktivores, *PV* piscivores. Dashed line overall median, horizontal black lines medians for each case. $a > b > c$, significant differences ($p < 0.17$ and < 0.002 after Bonferroni correction). Shared letters similarity

the shrimp *F. duorarum* in S3 (-27.7 to -12.3 ‰); the freshwater resident fishes *Pterygoplichthys pardalis* (-30.0 to -14.7 ‰), *Thorichthys pasionis* (-29.1 to -10.4 ‰), *Thorichthys helleri* (-28.4 to -15.4 ‰), *C. salvini* (-27.3 to -11.8 ‰), and *Petenia splendida* in S1 (-25.6 to -11.8 ‰); and the estuarine transient *A. felis* in S2 (-23.4 to -16.3 ‰) (Annex II, Resource 2). Fish species collected exclusively in the rainy season contributing to the observed high $\delta^{13}\text{C}$ values in these sites were the marine transients *A. rhomboidalis*, *Prionotus scitulus*, *M. curema*, *Caranx hippos*, *C. latus*, *C. nebulosus*, and *L. griseus* in S2 and S3 (-18.7 to -11.0 ‰) (Annex II, Resource 2).

In regard to $\delta^{15}\text{N}$, higher values were found in S1, S2, and S3, compared to S4, mainly in the case of crustaceans (Fig. 4.5d-f). Seasonal differences in $\delta^{15}\text{N}$ median values were particularly marked in S3 in the case of crustaceans and fishes, as well as in S2 in the case of crustaceans, with higher values in the dry than in the rainy season (Fig. 4.5e-f). Species from S3 showing higher $\delta^{15}\text{N}$ median values in the dry than in the rainy season comprised the crab *Callinectes rathbunae* (8.9 and 6.5 ‰), the shrimp *F. duorarum* (9.4 and 2.0 ‰), and the fishes *Dorosoma anale* (9.0 and 6.9 ‰), *Dorosoma petenense* (10.8 and 7.4 ‰), *T. helleri* (10.6 and 7.2 ‰), and *Centropomus undecimalis* (11.9 and 9.8 ‰) (Annex II, Resource 2). In S2, the shrimp *Macrobrachium acanthurus* showed a higher median $\delta^{15}\text{N}$ value in the dry than in the rainy season (9.1 and 7.3 ‰) (Annex II, Resource 2).

Seasonal changes in the isotopic niche of consumers and in the contribution of basal resources

The isotopic niches of mollusks in S1 and S2, according to the SEAc estimations were ca. 3 times bigger in the dry compared to the rainy season (9.7 and 4.5 ‰², and 3.0 and 1.5 ‰², respectively) (Fig. 4.6, Mollusks S1-S2a). The sizes of the ellipses varied significantly between seasons, based on the corresponding posterior estimates of the standard ellipse areas (SEA_B) and the pairwise tests comparing these distributions (see the density plots with the SEA_B modes and associated uncertainty in Fig. 4.6, Mollusks S1-S2b). No seasonal comparisons for this group were done in S3 and S4 due to a small number of samples. Crustaceans in all sites showed isotopic niches ca. 2 to 4.5 times bigger in the rainy season compared to the dry season, with values of 7.2 vs. 1.6 ‰² in S1, 3.8 vs. 0.8 ‰² in S2, 26.5 vs. 10.3 ‰² in S3, and 23.3 vs. 10.9 ‰² in S4 (Fig. 4.6, Crustaceans S1-S4a). In all cases, the probabilities that $\text{SEA}_{\text{dry}} < \text{SEA}_{\text{rainy}}$ ranged from 83 to 100 % (Fig. 4.6, Crustaceans S1-S4b). Fishes in all sites also showed isotopic niches ca. 1.6 to 4.6 times bigger in the rainy season compared to the dry season, with values of 39.4 vs. 8.49 ‰² in S1, 29.3 vs. 10.4 ‰² in S2, 22.2 vs. 13.9 ‰² in S3, and 49.5 vs. 12.5 ‰² in S4 (Fig. 4.6, Fishes S1-S4a). In all cases, the probabilities that $\text{SEA}_{\text{dry}} < \text{SEA}_{\text{rainy}}$ ranged from 99 to 100 % (Fig. 4.6, Fishes S1-S4b). In the case of crustaceans, the highest increment in isotopic niche in the rainy season was observed in S1 and S2, and in the case of fishes in S1 and S4.

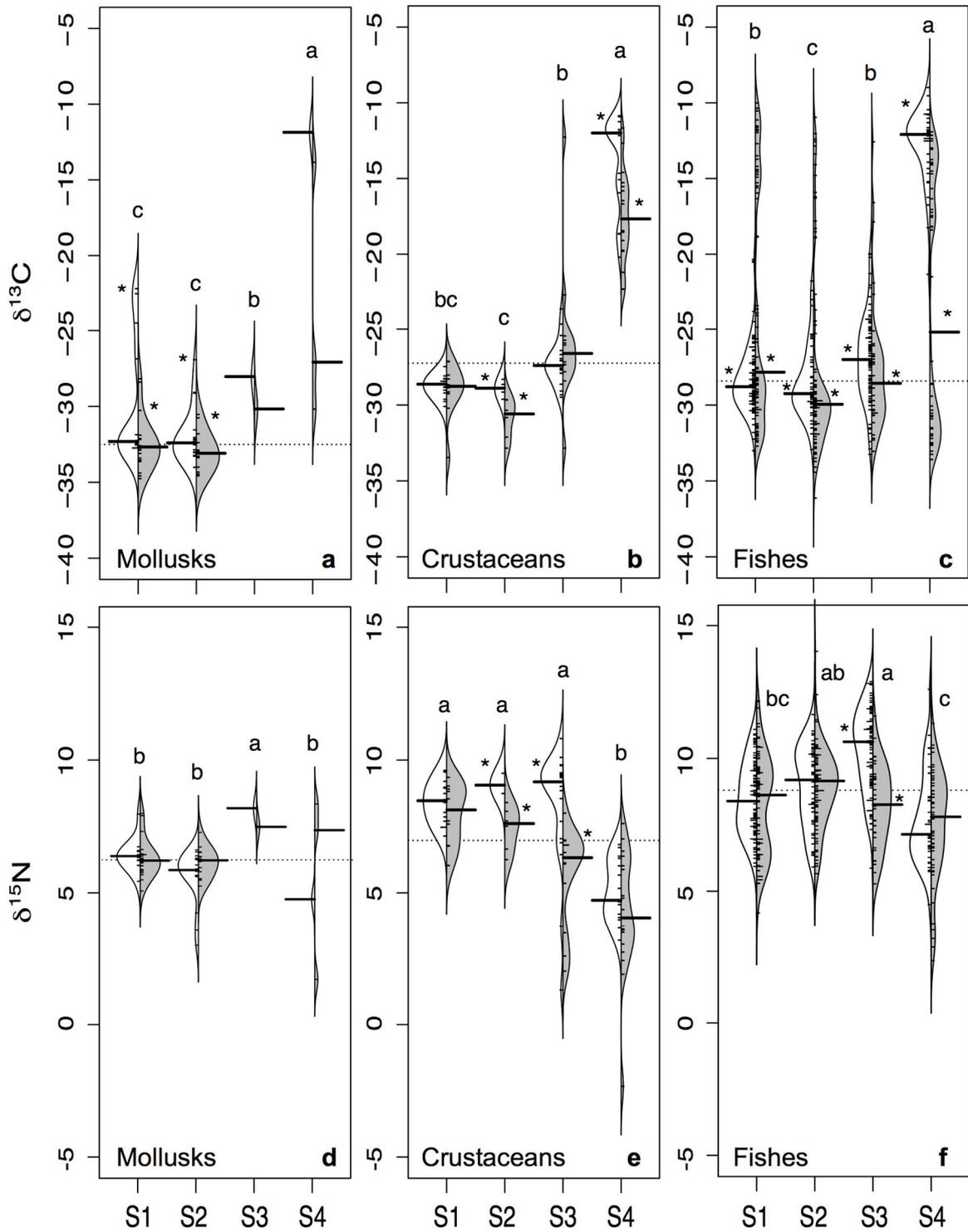


Fig. 4.5 Beanplots of $\delta^{13}\text{C}$ (a-c) and $\delta^{15}\text{N}$ values (d-f) of consumers per main taxonomic group, site and season (white dry, gray rainy). Dashed line overall median, horizontal black lines medians for each case. $a > b > c$, significant differences among sites ($p < 0.01$ after Bonferroni correction). Shared letters similarity. For mollusks, a letter in S3 was placed for qualitative comparison. Asterisks seasonal differences per site ($p < 0.05$)

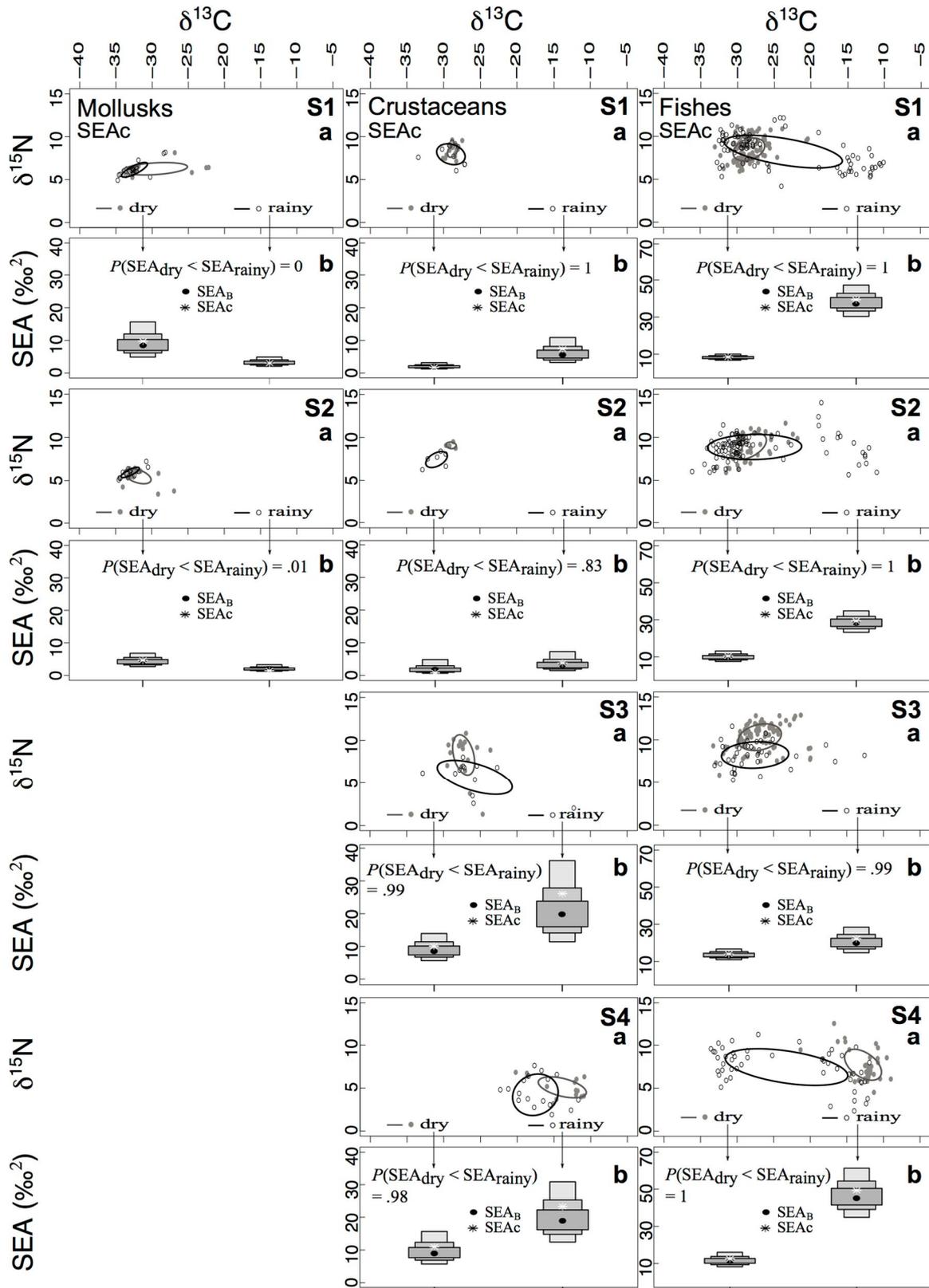


Fig. 4.6 Stable isotope bi-plots with small sample size corrected standard ellipse areas (SEAc) of mollusks, crustaceans, and fishes in the dry and rainy season per study site (a), and density plots with the respective Bayesian standard ellipse areas (SEAB) (b). Black points in the density plots modes of SEAB. Boxes 50, 75 and 95 % BCI (Bayesian credible intervals) of SEAB. Asterisks point estimates of SEAc. Statistical probabilities ($\text{SEA}_{\text{dry}} < \text{SEA}_{\text{rainy}}$) are based on a $p < 0.0001$

In regard to the seasonal changes in S1, marsh vegetation in the dry season constituted the most important resource for consumers (overall mean contribution = 52 %), particularly for omnivores like *C. rathbunae*, *F. duorarum* and *M. acanthurus* (mean = 80 %, 95 % credible interval = 64 to 95 %), and zoobenthivores like *C. urophthalmum*, *C. salvini*, *T. helleri*, *Thorichthys meeki*, *Gobiomorus dormitor*, *Batrachoides goldmani*, and *Rhamdia quelen* (mean = 93 %, 95 % credible interval = 86 to 98 %) (Table 4.2). In this season, marsh vegetation was also important for planktivores (e.g., *Brachyura* larvae, *Amphilophus robertsoni*), herbivores (e.g., *Paraneetroplus synspilus*), detritivores (e.g., *Paraneetroplus bifasciatus*), and piscivores (e.g., *Parachromis managuensis*, *C. undecimalis*) (with a contribution of up to 83 %) (Table 4.2). For non-selective filter feeder bivalves (*Cyrtonaias tampicoensis*, *Polymesoda arctata*, *Rangia flexuosa*), the most important resource comprised sediment from a *V. americana* carpet (mean = 49 %, 95 % credible interval = 19 to 79 %) (Table 4.2). In the rainy season, sediment from a *V. americana* carpet, seston, and epiphytes from *V. americana*, contributed with 22 to 26 % to all consumers (Table 4.2). Among these resources, sediment from a *V. americana* carpet had a high contribution for zoobenthivore species (mean = 85 %, 95 % credible interval = 70 to 96 %). Epiphytes from *V. americana* and seston showed a higher importance for non-selective filter feeder bivalves and herbivores (with means ranging from 26 to 45 %, and 95 % credible intervals from 43 to 77 %) (Table 4.2). *Utricularia sp.*, which was exclusively found in the rainy season and was not included in the SIAR model to keep the same number of basal resources in the models of the two seasons, also seemed to represent an important resource to herbivore and planktivore fishes.

In S2, marsh vegetation in the dry season, together with fine particulate organic matter and detrital mangrove leaves had a high importance for consumers, the latter particularly for non-selective filter feeder bivalves (*C. tampicoensis*, *Rangia cuneata*) (mean = 63 %, 95 % credible interval = 30 to 89 %) (Table 4.2). Seston and mangrove epiphytes showed a lower importance during this season (Table 4.2). In the rainy season, fine particulate organic matter considerably increased its importance, particularly for omnivores (mean = 59 %, 95 % credible interval = 31 to 86 %) including species like *C. rathbunae* and *Astyanax aeneus* (Table 4.2). Detrital mangrove leaves remained important to non-selective filter feeders (mean = 46 %, 95 % credible interval = 25 to 64 %) (Table 4.2). Mangrove epiphytes also comprised an important feeding resource for non-selective filter feeders (mean = 30 %, 95 % credible intervals = 17 to 44 %) and insects like Ephemeroptera (*Ephoron sp.* larvae, *Brachycercus sp.*), Coleoptera (*Tropisternus sp.*) and Odonata (*Phyllocycla sp.*, *Libellula sp.* larvae) (mean = 35 %, 95 % credible intervals = 20 to 51 %) (Table 4.2). The submerged plant *C. palaeformis* (not included in the SIAR model for the rainy season) also seemed to be related with the latter two groups of consumers (Table 4.2).

Table 4.2 Mean contributions (with corresponding low and high 95 % Bayesian credible intervals, BCI) of basal resources to the consumers analysed with SIAR per study site and season. Sample sizes of basal resources (n=dry; rainy) and consumers used in the models are shown. *NSF* non-selective filter feeders, *HV* herbivores, *DV* detritivores, *OV* omnivores, *PL* planktivores, *ZB* zoobenthivores, *PV* piscivores

Guild		Contribution of basal resources (%)					
S1		Marsh vegetation (n=15; 15)	Seston (n=1; 1)	SAV (eelgrass) (n=3; 3)	Epiphytes (eelgrass) (n=1; 1)	Sediment (eelgrass) (n=3; 2)	
Dry	NSF (n=8)	17 (0-36)	12 (0-31)	9 (0-24)	13 (0-30)	49 (19-79)	
	HV (n=12)	47 (18-80)	14 (0-32)	8 (0-24)	14 (0-31)	17 (0-34)	
	DV (n=9)	46 (16-80)	13 (0-30)	19 (0-41)	13 (0-30)	9 (0-22)	
	OV (n=25)	80 (64-95)	6 (0-16)	3 (0-8)	6 (0-15)	5 (0-13)	
	PL (n=11)	32 (9-57)	19 (0-37)	16 (0-35)	19 (0-37)	14 (0-30)	
	ZB (n=49)	93 (86-98)	2 (0-7)	1 (0-3)	3 (0-8)	1 (0-3)	
	PV (n=9)	49 (20-83)	15 (0-37)	11 (0-29)	16 (0-38)	9 (0-26)	
	Overall mean	52	12	9	12	15	
Rainy	Insects (n=6)	21 (0-41)	23 (0-42)	14 (0-31)	24 (0-46)	18 (0-37)	
	NSF (n=17)	5 (0-17)	45 (19-77)	2 (0-5)	43 (13-66)	5 (0-14)	
	HV (n=9)	18 (0-37)	34 (11-58)	12 (0-27)	26 (5-43)	10 (0-26)	
	OV (n=32)	23 (0-44)	22 (1-40)	13 (0-27)	20 (1-35)	22 (0-40)	
	PL (n=4)	18 (0-37)	23 (0-44)	21 (0-42)	22 (0-42)	16 (0-35)	
	ZB (n=26)	6 (0-15)	3 (0-10)	1 (0-3)	5 (0-11)	85 (70-96)	
	PV (n=14)	16 (0-34)	12 (0-30)	33 (10-56)	15 (0-33)	24 (0-46)	
	Overall mean	15	23	14	22	26	
S2		Marsh vegetation (n=15; 15)	Mangrove detrital leaves (n=1; 1)	Seston (n=1; 1)	Epiphytes (mangrove) (n=1; 4)	FPOMc (n=1; 2)	
Dry	NSF (n=14)	13 (0-33)	63 (30-89)	10 (0-26)	5 (0-15)	9 (0-24)	
	HV (n=7)	26 (1-49)	23 (1-42)	17 (0-34)	12 (0-28)	22 (0-42)	
	DV (n=7)	22 (0-41)	17 (0-35)	19 (0-37)	20 (0-37)	22 (0-42)	
	OV (n=20)	39 (10-69)	11 (0-32)	11 (0-31)	4 (0-12)	35 (4-64)	
	PL (n=7)	27 (1-50)	20 (0-41)	19 (0-38)	11 (0-28)	23 (0-46)	
	ZB (n=11)	34 (4-63)	18 (0-39)	15 (0-34)	6 (0-20)	27 (1-51)	
	Overall mean	27	25	15	10	23	
Rainy	Insects (n=10)	10 (0-25)	26 (5-45)	12 (0-27)	35 (20-51)	17 (0-33)	
	NSF (n=11)	7 (0-18)	46 (25-64)	7 (0-18)	30 (17-44)	10 (0-23)	
	DV (n=17)	30 (3-55)	12 (0-28)	24 (1-42)	7 (0-18)	27 (1-48)	
	OV (n=44)	12 (0-31)	5 (0-13)	21 (0-40)	3 (0-9)	59 (31-86)	
	PL (n=8)	14 (0-33)	15 (0-31)	27 (1-48)	4 (0-9)	40 (9-74)	
	ZB (n=16)	27 (0-51)	5 (0-16)	23 (0-45)	3 (0-9)	42 (8-78)	
	Overall mean	17	18	19	14	32	
S3		Marsh vegetation (n=6; 12)	Mangrove detrital leaves (n=1; 2)	Seston (n=4; 1)	Epiphytes (mangrove) (n=1; 1)	FPOMc (n=3; 1)	
Dry	HV (n=3)	22 (0-41)	18 (0-36)	20 (0-39)	19 (0-36)	21 (0-40)	
	DV (n=15)	13 (0-30)	33 (9-60)	22 (1-40)	19 (11-28)	13 (0-30)	
	OV (n=30)	11 (0-26)	34 (17-53)	21 (1-38)	23 (17-29)	11 (0-27)	
	PL (n=12)	17 (0-35)	11 (0-29)	22 (0-41)	31 (19-45)	19 (0-37)	
	ZB (n=29)	15 (0-32)	15 (0-30)	27 (4-47)	30 (23-37)	13 (0-30)	
	PV (n=15)	14 (0-32)	11 (0-25)	19 (0-40)	40 (29-52)	16 (0-37)	
	Overall mean	15	20	22	27	16	
Rainy	Insects (n=4)	22 (0-40)	24 (0-46)	19 (0-37)	14 (0-33)	21 (0-40)	
	HV (n=7)	25 (1-46)	18 (0-36)	21 (0-40)	17 (0-34)	19 (0-39)	
	DV (n=7)	26 (1-48)	18 (0-34)	24 (1-44)	16 (0-31)	16 (0-34)	
	OV (n=19)	26 (3-47)	14 (0-30)	24 (0-45)	20 (3-34)	16 (0-33)	
	ZB (n=6)	22 (0-41)	15 (0-32)	23 (0-43)	23 (2-40)	17 (0-35)	
	PV (n=3)	23 (0-43)	16 (0-34)	22 (0-43)	22 (0-40)	17 (0-36)	
	Overall mean	24	17	22	19	18	
S4		Mangrove org. matter ^a (n=8; 1)	Seston (n=2; 2)	SAV (seagrass) (n=6; 6)	Benthic algae (n=1; 3)	Epiphytes (mangrove) (n=5; 3)	Epiphytes (seagrass) (n=1; 1)
Dry	OV (n=25)	1 (0-3)	40 (3-82)	22 (2-40)	22 (0-46)	2 (0-24)	13 (0-31)
	PL (n=4)	12 (0-25)	18 (0-34)	20 (2-34)	19 (0-35)	13 (0-28)	18 (0-35)
	ZB (n=14)	1 (0-3)	42 (3-80)	9 (0-26)	32 (0-64)	2 (0-4)	14 (0-35)
	PV (n=5)	11 (0-26)	19 (0-37)	19 (0-35)	21 (0-39)	11 (0-26)	19 (0-36)
	Overall mean	6	30	17	24	7	16
Rainy	OV (n=13)	5 (0-13)	23 (0-45)	19 (0-37)	19 (0-38)	6 (0-16)	28 (8-50)
	PL (n=17)	16 (0-30)	17 (0-33)	14 (0-29)	16 (0-31)	15 (0-30)	22 (5-39)
	ZB (n=24)	27 (5-48)	16 (0-35)	4 (0-12)	7 (0-18)	12 (0-30)	34 (15-54)
	PV (n=4)	18 (0-34)	17 (0-33)	14 (0-29)	15 (0-31)	16 (0-33)	20 (1-37)
	Overall mean	17	18	13	14	12	26

^a For the models of S4, refers to fresh mangrove leaves in the dry season, and to mangrove detrital leaves in the rainy season

In S3, mangrove epiphytes, followed by seston and detrital mangrove leaves constituted the most important resources for consumers in the dry season (Table 4.2). Mangrove epiphytes were more important for zoobenthivores (e.g., *G. dormitor*, *Citharichthys spilopterus*, *B. ronchus*), planktivores (Penaeidae larvae), and piscivores (e.g., *Strongylura marina*) (means = 30 to 40 %, 95 % credible intervals = 19 to 52 %). Detrital mangrove leaves accounted for the higher contribution to detritivores (e.g., *D. anale*, *D. petenense*) and omnivores (e.g., *F. duorarum*, *C. rathbunae*, *Cathorops aguadulce*) (means = 33 and 34 %, 95 % credible intervals = 9 to 60 % and 17 to 53 %, respectively). During the rainy season, marsh vegetation and seston constituted the resources with higher importance, particularly for detritivores (e.g., *D. petenense*), and omnivores (e.g., *Atherinella alvarezii*, *D. auratus*) (means = 24 to 26 %, 95 % credible intervals = 1 to 48 %). Detrital mangrove leaves, mangrove epiphytes, and fine particulate organic matter (with overall means of 17 to 19 %) had lower contributions to these guilds (Table 4.2). Nevertheless, detrital mangrove leaves had a higher importance for insects (mean = 24 %, 95 % credible interval = 0 to 46 %) (Table 4.2).

In the marine site S4, seston and benthic algae comprised the resources with the most important contributions for the consumers in the dry season (means = 24 to 30 %) (Table 4.2). Omnivores (e.g., *F. duorarum*, *Callinectes similis*, *A. quadricornis*, *Gerres cinereus*, *A. felis*) and zoobenthivores (e.g., *Opsanus beta*, *Achirus lineatus*, *C. urophthalmum*) showed up to 82 % dependence on these resources (see 95 % credible intervals in Table 4.2). Seagrasses and their epiphytes followed in order of importance and had a maximum contribution (up to 40 %) for omnivores (e.g., *A. rhomboidalis*); whereas mangrove leaves and mangrove epiphytes showed a negligible importance (means = 6 to 7 %) (Table 4.2). During the rainy season, seagrass epiphytes showed the highest contributions for the consumers (mean = 26 %), particularly omnivores (e.g., *Clibanarius vittatus*, *E. gula*) and zoobenthivores (e.g., *Sphoeroides parvus*) (means = 28 and 34 %, 95 % credible intervals = 8 to 50 % and 15 to 54 %, respectively) (Table 4.2). Seston and mangrove detrital leaves followed in order of importance (means = 17 to 18 %), with contributions of up to 45 and 48 % to omnivores like *Bagre marinus*, *D. auratus*, and *G. cinereus*, and zoobenthivores like *C. urophthalmum* and *S. parvus*, respectively (Table 4.2).

4.4 Discussion

We hypothesized that for the majority of consumers, a larger niche breadth would be observed in the rainy season than in the dry season, when more resources are available. At all study sites, a larger isotopic niche of crustaceans and fishes was observed in the rainy season, supporting this hypothesis. This, compared to higher species packing and trophic redundancy in the dry season, translates into a higher trophic diversification and lower trophic redundancy in the rainy season (Layman et al. 2007; Abrantes et al. 2014), particularly in habitats with high structural complexity

like S1 and S4, which are characterized by marsh-eelgrass and mangrove-seagrass vegetation, respectively.

The seminal proposal of the FPC by Junk et al. (1989) highlighted that food supply during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic animals in floodplains. During the low water period, reduction in food supply would limit the aquatic fauna (Junk et al. 1989; Junk and Wantzen 2004). Other studies in Brazil (e.g., Wantzen et al. 2002; Corrêa and Uieda 2007; Figueiredo et al. 2014), Costa Rica (Winemiller 1993), and West Africa³ (Abrantes et al. 2014), have confirmed this trend.

The results from the SIBER and SIAR approaches indicated an increase in resource use diversification by most consumers in the rainy season and helped to corroborate, for the habitats with high riverine influence in the study area (e.g., the fluvio-lagoons S1, S2, and S3), our second hypothesis stating that the flood pulse concept (FPC) would be the main driving force of the energetic changes in the studied communities. For the humid tropic Grijalva-Usumacinta system, with 2,934.1 km² of areas prone to flooding and with an increment of water volume by about 50 % during the rainy season (Sánchez et al. 2007), an important lateral exchange of water, nutrients and organisms is expected as stated by the FPC (Junk et al. 1989; Junk and Wantzen 2004). As also stated by the FPC (Junk et al. 1989; Junk and Wantzen 2004), in situ aquatic production (e.g., seston, mangrove epiphytes) and riparian production (e.g., marsh vegetation, detrital mangrove leaves) played an important role in the studied floodplain food webs. Nonetheless, sediment accumulated in a *V. americana* carpet and fine particulate organic matter, constituted other important resources, particularly in the more inland sites S1 and S2. On the other hand, the FPC alone cannot be applied to understand the main factors influencing the fate and utilization of basal resources in areas interacting more actively with the sea (e.g., S4), and therefore, in order to understand the complex dynamics in terms of energy flow within these ecosystems, further extensions including marine systems highly interconnected with coastal floodplains and/or complementary conceptual approaches should be considered.

In all sites, the relative contribution of basal resources across sites and seasons appears to be highly dependent on the habitat setting (e.g., connectivity, vegetation types and cover), environmental factors (e.g., salinity), physical forces (e.g., floods, winds), and primary productivity pulses, which highly influence prey availability. Fig. 4.7 provides a conceptual figure exemplifying the seasonal changes in the contribution of different resources to the aquatic consumers along the gradient from freshwater influenced sites (S1, S2, and S3, between 26 and

³ Errata: East Africa

13 km from the coast) to the marine influenced site (S4, less than 1 km from the coast) in the extensive floodplain system of Centla Wetlands and the large interconnected Terminos Lagoon. Below, the main trends observed per study site are discussed.

In S1, marsh vegetation (the predominant plant community therein) was the dominant resource for consumers in the dry season (mean contribution of 52 % for all consumers, Fig. 4.7), particularly for omnivore and zoobenthivore species (with up to 98 % importance, see specific contribution for the feeding guilds in Table 4.2). The eelgrass *V. americana*, seston, eelgrass epiphytes, and sediment from a *V. americana* carpet, showed a lower importance for all consumers (mean contributions from 9 to 15 %, Fig. 4.7), although sediment appeared to be the most important resource for non-selective filter feeder bivalves. In the rainy season, the contribution of marsh vegetation to the consumers reduced by 3.5 times (overall mean of 15 %), while the importance of *V. americana*, eelgrass epiphytes and seston increased from 1.5 times to almost the double (14 to 23 %, Fig. 4.7). Also, the importance of sediment from a *V. americana* carpet almost doubled in the rainy season (mean of 26 %, Fig. 4.7). This denote changes in productivity pulses, leading to a differentiated importance of different primary producers to the food web from one season to another, as well as changes in the contribution of sediment to the food web with changing hydrological conditions. Interestingly, while most omnivore species relied on resources with depleted $\delta^{13}\text{C}$ values in the rainy season (e.g., marsh vegetation, seston), the introduced catfish *P. pardalis* was the only species from this guild showing a considerably spread in the use of resources from depleted (-32.1 to -27.6 ‰) to enriched $\delta^{13}\text{C}$ values (-14.9 to -11.6 ‰), the latter being related with the values of sediment from a *V. americana* carpet. Important native cichlid fishes with zoobenthivore and piscivore guilds like *C. salvini*, *C. urophthalmum*, *T. helleri*, *T. passionis*, and *P. splendida*, overlapped with the enriched $\delta^{13}\text{C}$ values of *P. pardalis*. This spread in the use of resources relates with the considerably bigger isotopic niche of fishes in S1 in the rainy season (Fig. 4.6). It remains unclear which enriched ^{13}C source in the vegetated sediments could account to the feeding of these fishes, although there is evidence that with the advent of the wet season, the increased mobilization of organic carbon from C_4 -enriched areas (dominated by C_4 grasses or C_4 crops) leads to relatively ^{13}C -enriched particulate organic carbon pools (Bunn et al. 1997; Marwick et al. 2014, and references therein). This could occur along the Usumacinta river at the time of the highest average freshwater discharge and sediment suspended load, particularly during September and October (Muñoz-Salinas and Castillo 2015), although this is still an issue that needs to be assessed. According to the FPC, the organic matter produced within the floodplain under regular flood pulses is expected to be more important than the importation of organic matter from upstream (river continuum concept –RCC- of Vannote et al. 1980) (Junk et al. 1989; Junk and Wantzen 2004). However, a single extreme flooding can flush out considerable amounts of organic matter (e.g., 80 % of the annual transport

of particulate organic matter) and may limit in situ productive processes and access by aquatic animals (Junk et al. 1989; Junk and Wantzen 2004, and references therein).

In S2, marsh vegetation and detrital mangrove leaves played an important role in the food web in the dry season (overall mean contributions of 27 and 25 %, Fig. 4.7), particularly for omnivores and zoobenthivores (with up to 69 % contribution) and for non-selective filter feeders (up to 89 %), respectively. Mangrove epiphytes, seston, and fine particulate organic matter showed lower contributions during this season (means of 10 to 15 %, Fig. 4.7), although the latter constituted an important resource for omnivores. In the rainy season, the contribution of marsh vegetation and detrital mangrove leaves to the consumers decreased by 1.6 and 1.4 times, respectively, whereas the importance of fine particulate organic matter increased more than two-fold (mean of 32 % for all consumers, Fig. 4.7). This type of fine particulate organic matter, as mentioned previously, was obtained from the surface of submerged woody material, and this substrate is more critical to retaining sediments and POM than previously recognized (Eggert et al. 2012). In the rainy season, seston and mangrove epiphytes also increased in importance by ca. 1.4 times (means of 19 and 14 % for all consumers, respectively, Fig. 4.7). The latter seemed to be particularly important for insects, including adult and larval stages of Ephemeroptera, Coleoptera and Odonata (with up to 51 % contribution, Fig. 4.7). Some of these insects have been observed to feed on periphyton, C₃ macrophytic sources, and small invertebrates (De Marco and Latini 1998; Puig 1999; Molina et al. 2011). The majority of these insects are collector-gatherers and generalists (De Marco and Latini 1998; Zilli et al. 2008), and therefore they could play an important trophic link between mangrove epiphytes and consumers with higher trophic levels in this site.

In S3, mangrove epiphytes, seston, and detrital mangrove leaves (with mean contributions of 27, 22, and 20 %, respectively), were the most important resources for all consumers in the dry season (Fig. 4.7). While mangrove epiphytes and seston had a higher importance for planktivores, zoobenthivores and piscivores (with maximum contributions from 37 to 52 %), detrital mangrove leaves showed the highest contributions for detritivores and omnivores (up to 53 and 60 %). Fine particulate organic matter and marsh vegetation showed the lowest contributions in the dry season (means of 16 and 15 %, respectively, Fig. 4.7). Nevertheless, in the rainy season, marsh vegetation increased in importance 1.6 times (mean contribution of 24 % for all consumers, Fig. 4.7). The importance of fine particulate organic matter also increased slightly during the rainy season (mean of 18 %); seston kept the same overall importance (mean of 22 %); and detrital mangrove leaves and mangrove epiphytes decreased in importance by 1.2 and 1.4 times, respectively (means of 17 and 19 %, Fig. 4.7). The observed seasonal differences in the contribution of detrital mangrove leaves and mangrove epiphytes may be due to changes in litterfall dynamics and in the productivity and availability of these resources. In the case of

mangrove detrital leaves, there is evidence from a study in the coastal lagoon of Mecocan, Tabasco, that higher leaf fall of the Black mangrove *Avicennia germinans* takes place during the dry season (López-Portillo and Ezcurra 1985). This could account for a higher availability of detrital leaf material in S3 in this season. Nevertheless, as the mangrove forest in S3 is a mixed community composed by *A. germinans*, *Rhizophora mangle* and *Laguncularia racemosa*, it would be necessary to compare the litterfall production and quality of these three species in further studies. Evidence from the literature suggests that *Rhizophora* shows lower litter decomposition rate and higher nitrogen immobilization than *Avicennia*, as a result of a higher C:N ratio (Yáñez-Arancibia et al. 1998). For this reason, *A. germinans*, with its faster decomposition and higher nitrogen content, has been suggested to represent an important source of organic matter (Barroso-Matos et al. 2012).

In S4, the main basal resources for the aquatic consumers in the dry season were seston (mean of 30 %) and benthic algae (mean of 24 %), whereas in the rainy season, the main basal resources for the consumers were seagrass epiphytes (mean of 26 %, Fig. 4.7). It is noteworthy that mangrove organic matter, with negligible contributions to the consumers in the dry season (mean of 6 %), increased in importance by ca. 3 times in the rainy season (mean of 17 %, Fig. 4.7). This may be explained by the fact that mangrove forests in the inner littoral of Del Carmen Island are periodically flooded during the rainy and ‘nortes’ season as the strong north winds increase water levels in the lagoon (Rivera-Monroy et al. 1998). Under these conditions, high export rates of particulate nitrogen and dissolved organic nitrogen (DON) from the fringe forest to the water column also take place (Rivera-Monroy et al. 1995). This effluent of DON can form the bulk of derived N available to surrounding seagrasses and epiphytes (Hyndes et al. 2012). As the uptake rate of N by epiphytic algae is greater than that of seagrass leaves, the former might benefit from higher nitrogen inputs in the water column compared to seagrasses, which obtain much of their nutrients from the sediments (Dixon 2004; Hyndes et al. 2012). With this, the higher importance of seagrass epiphytes for consumers in the rainy season might be related to an increase in their availability due to higher nutrient levels in the water column. Another potential factor positively influencing the epiphytic algae biomass is the increase in water exchange (Dixon 2004). Seagrasses, on the contrary, grow best at lower exchange rates that allow nutrient concentrations to be drawn down, slowing algal growth. In Terminos Lagoon, seagrasses and benthic algae generally show the highest biomass and productivity during the dry season when water transparency is the highest (Day et al. 1982; Reyes et al. 1994). The latter can explain the higher importance of benthic macroalgae (*A. spicifera*) and seagrasses for the food web in the dry season (Fig. 4.7).

4.5 Conclusions

In line with our expectations, the results support the hypothesis that a larger isotopic niche breadth of consumers prevails during the rainy season, when resource availability is higher. This translates into an increase in resource use diversification by consumers and corroborates the FPC, which can be particularly applied to those habitats with high riverine influence in the study area (e.g., fluvio-lagoons). Nevertheless, the FPC alone cannot be applied to understand the main factors influencing the fate and utilization of basal resources in areas interacting more actively with the sea. Therefore, additional conceptual frameworks or hypotheses should be taken into account for an in-depth understanding about the influence of other factors relating to the structure of aquatic food webs and energy fluxes in this important ecological system. For example, the ‘coastal flooding’ influenced by the ‘nortes’ winds in S4 seems to be an important driver in this site by inundating mangrove forests, which in turn has been found to be an important cause of the release of significant amounts of particulate N and DON to the adjacent waters (Rivera-Monroy et al. 1995, 1998).

Our results provide a valuable basis to recognize that food webs in the studied habitats are complex and very dynamic, and to stress the relevance of marshes, mangroves and SAV for the aquatic fauna in Centla Wetlands and Terminos Lagoon. The mentioned types of vegetation are relevant at different spatio-temporal scales and sustain important multiple functions and ecosystem services. This is particularly relevant considering the degradation of these ecosystems and the progressively and alarming disappearance of *V. americana* in the study area. Techniques like stomach content analysis and fatty acid biomarkers would greatly help to validate the possible energy flux from these resources to consumers. Moreover, the large spread in the isotopic niche of consumers in complex interlinked habitats suggests the importance of these habitats in providing a high diversity of resources and consumer types.

Also, the observed high $\delta^{15}\text{N}$ values of some basal resources (e.g., *V. americana* in S1 and mangrove epiphytes in S3) may reflect the influence of land derived N and eutrophication (Gooday et al. 2009). This coincides with the hypereutrophication condition reported in S1 (San Pedrito Lagoon), S3 (El Coco Lagoon), and other water bodies of Centla Wetlands (Salcedo et al. 2012). Thus, it would be important to consider in detail the relationship between $\delta^{15}\text{N}$ of algae and macrophytes with the actual nutrient levels in water and sediments, the potential sources of eutrophication, and the potential effects in food webs.

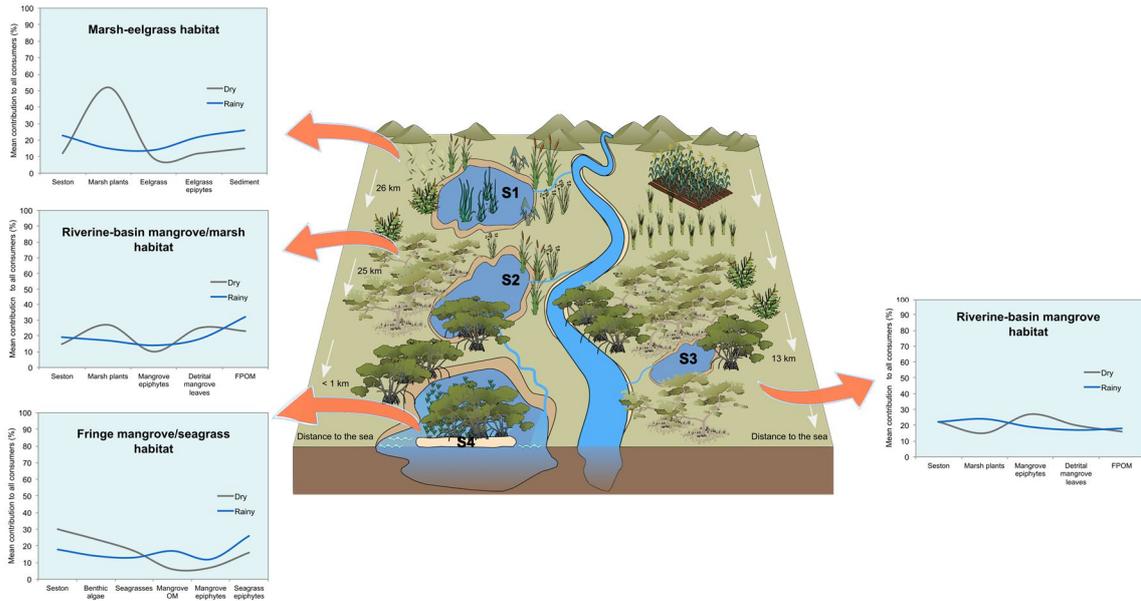


Fig. 4.7 Conceptual figure illustrating the seasonal changes in overall mean percentage contributions of basal resources to the aquatic consumers in the study sites. Overall means were obtained from the individual mean contributions of the resources to each feeding guild analysed and sum 100 % (see also Table 4.2). This image, depicting the case of a floodplain and an interconnected coastal lagoon with different vegetation settings and influenced by different environmental forces, was elaborated based on image templates authored by T. Saxby, D. Kleine, J. Hawkey and J. Thomas, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

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Chapter 5

— Connectivity —

Fish assemblage connectivity between marine and low salinity mangrove habitats in the southern Gulf of Mexico: insights from stable isotope analysis

In preparation

Abstract

Animal movements can be boosted by seasonal resource pulses, the physical connectivity across ecosystems, and the self migratory traits of the species. Freshwater inflow has been suggested to create conditions of high-quality habitat available for exploitation by consumers that rapidly assemble to flooded habitats, even migratory species capable to tolerate sub-optimal conditions to exploit resources. In this study, we aimed to assess if the connectivity of fish assemblages in two spatially separated mangrove habitats in a tropical lagoon-estuarine system (Terminos Lagoon), which differ in terms of marine (MAR) and freshwater (FRW) influences, increases during the period of highest river discharge and availability of resources (rainy season, under the simultaneous strong effect of northerly winds –*nortes*–). The MAR and FRW fish communities were first compared with the Chao's estimator (Chao-Jacc-Est) of abundance-based similarity index per season. Then, stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in muscle tissue were used to calculate the entire isotopic niche of the communities (total area of the convex hull, TA), as well as the core isotopic niches of all the collected marine-estuarine and freshwater species from the two sites and their overlap per season (with multivariate ellipse-based metrics). The results indicate a considerably increase in the number of marine species in FRW in the rainy season, and consequently an increase in the similarity between the fish assemblages, compared to the dry season (Chao-Jaccard estimates of 0.072 ± 0.04 and 0.022 ± 0.039 for the rainy and dry season, respectively). In relation to this, the core and entire isotopic niches of the fish assemblages did not overlap in the dry season, but considerably did so in the rainy season (with overlaps of 2.09 to 13.1 %, and 67 to 69 %, respectively). These results highlight the importance of seasonal environmental forces, particularly of rains, in enhancing the movement of fishes from marine to low salinity habitats in Terminos Lagoon, and the importance of fish migrations in linking these habitats.

Keywords: fish migration, habitat use, isotopic niche overlap, rainy season, winds, Terminos Lagoon

5.1 Introduction

Mangroves are iconic coastal ecosystems that have been widely assumed to provide nursery habitat functions for juvenile fishes and to support local fisheries (Sheridan and Hays 2003). Nevertheless, any advantage accruing from the utilisation of mangroves, in the case of many fish species, has to be set in the context of connectivity with other habitats (Sheaves 2005). For instance, the mangrove-seagrass-coral reef continuum comprises important inter-linked support areas for fishes (Berkström 2012). Also, often interconnected with mangroves are freshwater marshes and forested wetlands, but fish movements across these habitats has been underappreciated despite their exceptional ecological value in the entire wetland landscape (Yáñez-Arancibia et al. 1988; Rehage and Loftus 2007; Ewel 2010). In the neotropical realm, these habitats are well represented in areas influenced by large rivers like in the Florida Everglades, the Terminos Lagoon in southern Gulf of Mexico, the Magdalena Delta in the Caribbean coast of Colombia, and the Orinoco Delta in Venezuela, to give some examples (Conde 2001; Restrepo et al. 2016).

Understanding whether and how communities differ among these habitats and the movement of individuals among them (connectivity) is crucial to determine habitat value and bears important management and conservation implications (França 2011; López-Duarte et al. 2012).

Freshwater inflow is one of the most influential pulses affecting community structure and function in estuaries because under predictable flood pulse regimes it delivers resources to large expanses of estuarine habitat, and also makes high-quality habitats available for exploitation by resident consumers and marine higher-order consumers able to tolerate sub-optimal conditions to exploit resources (Odum et al. 1995; Piazza and La Peyre 2012).

In Terminos Lagoon, studies have shown that habitat utilization by fishes is highly driven by the pattern of river discharge and the influence of northerly winds (*nortes*), which also relate to pulses of primary production and food availability (Yáñez-Arancibia et al. 1980; Yáñez-Arancibia et al. 1988; Ayala-Pérez 2006). The combined effect of these conditions, the high diversity of fish species, and the variety of habitats that fishes utilize from the adjacent continental shelf to marine mangrove-seagrass areas and low-salinity fluvial lagoons with bordering mangroves and freshwater marshes (Yáñez-Arancibia et al. 1988; Sirot et al. 2015), make this system a very interesting ecological setting to address the topic of fish assemblage connectivity. To date, the view of multispecies connectivity between different habitats has as yet been little studied (Yáñez-Arancibia and Lara-Domínguez 1988; Ayala-Pérez 2006; Sánchez-Gil et al. 2009).

The objective of this study is to assess the degree of connectivity between the fish assemblages

from two habitats in Terminos Lagoon, a marine mangrove-seagrass area (MAR) and a low-salinity fluvial lagoon (FRW). We hypothesize that the connectivity between fish assemblages increases during the rainy season under the influence of *nortes*.

As research approach, we analysed stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in the muscle tissue of fish specimens from the two habitats, because isotopic signatures in animal tissues reflect those of local food webs or of the aquatic habitats in which they have resided. They thus help to trace the origin or movement of organisms (Boutton 1991; Gillanders 2009). Moreover, the use of stable isotope metrics based on the overlap and areal estimation of the isotopic space of the communities (Layman et al. 2007; Jackson et al. 2011), has been shown instrumental to determine the degree of connectivity between the assemblages. We also assessed the species composition and size distribution patterns of the fish communities, to better understand the seasonal changes as linked to the observed connectivity patterns.

5.2 Materials and methods

Study area

Terminos Lagoon (18.5–18.8 °N, 91.3–91.9 °W), located in a microtidal region at the southwest of the Yucatan Peninsula, has an ellipsoidal shape in an east west direction, a surface of 2500 km², a maximum length of 75 km and a width of 35 km (Gullian and Aguirre-Macedo 2009; Contreras et al. 2014; Medina-Gómez et al. 2015). Its mean depth is 3.5 m, and it is separated from the Gulf of Mexico by the calcareous island ‘Del Carmen’ and its two inlets: Carmen Inlet in the west, and Puerto Real Inlet in the east (Yáñez-Arancibia and Day 1982; Ramos-Miranda et al. 2005) (Fig. 5.1). The tropical climate in the area is characterized by three distinct seasons: the classical dry and rainy seasons, from March to May and from June to September, respectively, and the *nortes* season from October to February, characterized by a decrease of the temperatures and by intermediate rains with strong northerly winds with speeds higher than 12 m s⁻¹ (Espinal et al. 2007; Yáñez-Arancibia et al. 2009; Contreras et al. 2014; Sirot et al. 2015). During the *nortes* period, seawater penetrates into the lagoon through both inlets (Mancilla-Peraza and Vargas-Flores 1980; Graham et al. 1981).

Extensive mangrove forests bordering the lagoon and seagrass beds are common in clear water areas (Gonneea et al. 2004). Fluvial lagoon systems at the mouth of the rivers entering the lagoon (the Palizada, the Candelaria, and the Chumpan) comprise a turbid, freshwater, low-salinity mangrove-marsh complex (Yáñez-Arancibia and Day 1982; Yáñez-Arancibia et al. 1988). Our study sites along this habitat continuum were two shallow sites (with depths from 1.05 to 2.10 m): 1) ‘MAR’, a marine fringing mangrove/*Thalassia testudinum* habitat located at the eastern part of

the inner littoral of Del Carmen Island, and 2) ‘FRW’, a freshwater mangrove-marsh habitat in ‘El Vapor Lagoon’, influenced by the Palizada River at the southwestern portion of the lagoon (Fig. 5.1).

During the sampling in the dry season of 2009 and rainy season of 2010, the total rainfall varied from 22.1 to 936 mm in MAR, and from 115 to 1857 mm in FRW (CONAGUA, smn.conagua.gob.mx). Published freshwater inflow data positively correlate to the seasonal differences in precipitation, e.g., from 4 to 158 m³ s in MAR, and from 288 to 480 m³ s in FRW (Yáñez-Arancibia and Day 2006). Salinity correlated negatively to these parameters, and varied from 39.5 to 23 psu in MAR, and from 2.5 to 0 in FRW, in the dry and rainy season, respectively.

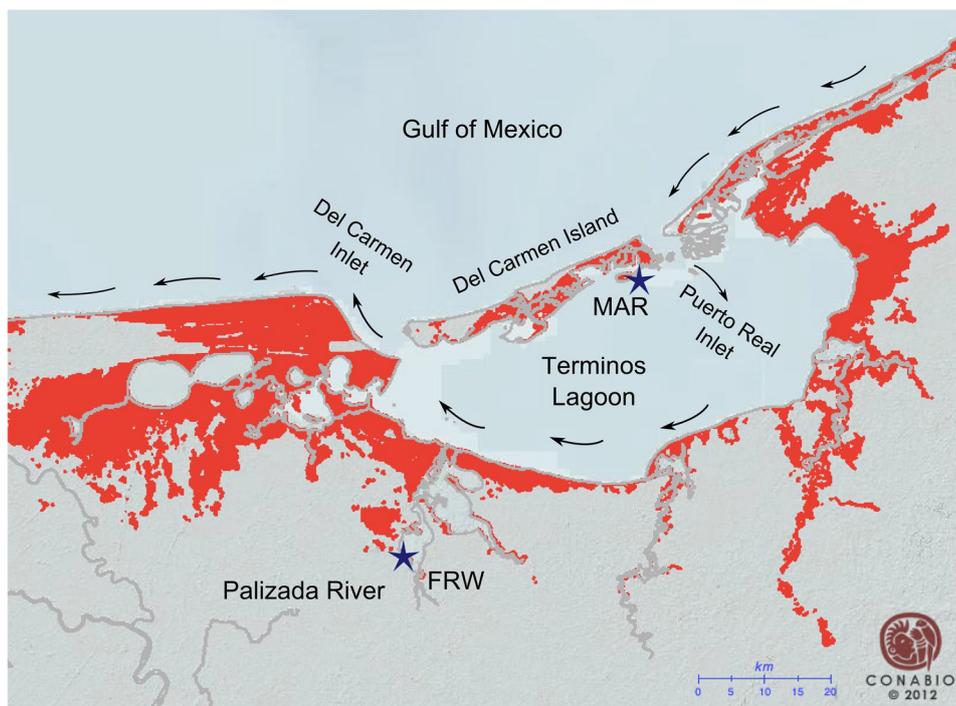


Fig. 5.1 Terminos Lagoon and sampling sites marked with stars: MAR, in the southeastern portion of Del Carmen Island; and FRW, influenced by the Palizada river. The arrows indicate the predominant currents. During the *nortes* season marine water also penetrates the system through the western inlet. The color red indicates the mangrove distribution in the area. Adapted from: <http://www.conabio.gob.mx/informacion/gis/>, based on mangrove distribution data in Mexico for 2010 (CONABIO 2013c). The use of this material and its adaptation is allowed based on the creative commons license 2.5 Mexico (CC BY-NC 2.5 MX)

Sampling and processing

1207 fishes were collected with multiple gears in MAR and FRW to obtain representative samples of the fish diversity at each site (Table 5.1).

In the laboratory, the collected specimens were identified to the species level, counted, and measured (total length in cm), and 227 individuals were used for stable isotope analyses.

Table 5.1 Gears used to collect fish species at the study sites and their characteristics

Fishing gears	Characteristics
Beach seine ¹	Length=9 m, mesh size=13 mm in the lateral wings and 5 mm in the codend, swept area= ca. 62 m ²
Beam trawl ^{1,2}	Mouth width=1.2 m, mouth height=0.8 m, codend mesh=10 mm, swept area= ca. 420 m ²
Gillnet ^{1,2}	Length=65 m, width=2.5 m, mesh size=1.5 inches, set over 3 hrs.
Spoon ¹	Mouth width=0.40 m, mouth height=0.40 m
Ichthyoplankton net ²	Mouth diameter=50 cm, mesh size=500µm

¹ Diurnal sampling, ² nocturnal sampling

Processing of samples for stable isotope analysis prior drying followed standard methods according to Garcia et al. (2007), Hoeninghaus and Davis (2007), and Hoeninghaus et al. (2007). All samples were dried at 60°C for at least 48 hrs in sterile Petri dishes (Hoeninghaus et al. 2007). Dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials (Hoeninghaus et al. 2007; Mendoza-Carranza et al. 2010). Subsamples were weighed to the nearest 0.01 mg and pressed into Ultra-Pure tin capsules (Costech, Valencia, CA) for the determination of stable isotope ratios of carbon and nitrogen, using a Carlo Erba NA 1500 CHN analyzer coupled to a Finnigan Delta-C continuous flow mass spectrometer. Isotopic ratios were expressed in delta notation (δ) as part per thousand (‰) relative to the standards Pee Dee Belemnite (PDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$, according to the equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

Data analysis

The ecological guilds related with the habitat requirements and migratory behaviour of the collected fish species were assigned based on literature. These guilds included marine, estuarine, freshwater, and anadromous species. Euryhaline species were also identified from the literature.

In order to assess the degree of similarity between the fish assemblages of MAR and FRW per season, we calculated the Chao-Jaccard-Est Abundance-based estimator (\hat{J}_{abd} , Chao et al. 2005) in EstimateS 9.1.0 (Colwell 2013), based on total abundances from all gears. The Chao-Jaccard-Est Abundance-based estimator is based on the number of shared species (corrected for unseen species), with a potential range from 0 (no shared species) to 1 (Chao et al. 2005; Chao et al. 2006; Kidwell 2007). Standard errors were computed by a bootstrap procedure with 200

resamples (Chao et al. 2005; Colwell 2013).

The size-structure of the fish communities was analysed with relative frequency histograms based on different length classes (total length in cm) to examine fish size patterns within communities per season. Juvenile and adult stages were recognized based on published length at first maturity data, consisting of one of the following information: L_m for females, males, or mixed sexes; the size range for sexual maturity; or the minimum size at maturity (references are found at the bottom of Table 5.2).

To assess the degree of isotopic overlap between the fish assemblages per season, we first used the total area of the convex hull (TA) proposed by Layman et al. (2007) as a measure of the combined spread of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in each fish community, giving indication of the entire isotopic niche encompassed by all fish species (and their mean isotopic values) within each site, and accounting for the total extent of trophic diversity. The total area of this metric was estimated for each community per season and was expressed in units of per mil squared (‰^2). The overlap between the convex hulls of the two sites was also calculated per season and expressed in % of the overlapped areas. Calculations were done with SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011) within the package SIAR (Stable Isotope Analysis in R, Parnell et al. 2010) for R software.

To further assess the fish assemblages' connectivity, and as the total area of the convex hull (TA) is very dependent on sample size, multivariate standard ellipses (expressed in ‰^2 units) and their overlap were calculated for the previously identified 'marine-estuarine' and 'freshwater' species per season with SIBER (Jackson et al. 2011), by examining the dispersion of the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the species in the isotopic space with the sample size-corrected standard ellipse area (SEAc). Standard ellipses contain c. 40 % of the data regardless of sample size (Batschelet 1981), instead of encompassing all data in the isotopic space like the total area of the convex hull (TA) of Layman et al. (2007), and therefore, they provide a measure of the mean core isotopic niche of the groups being studied (Jackson et al. 2012; Layman et al. 2012).

5.3 Results

Composition and similarity of the fish assemblages

The 1207 fish specimens collected in MAR and FRW pertained to 59 species and 34 families.

In the dry season, 15 species were caught in MAR and 21 in FRW, out of which three marine and estuarine species, all of them euryhaline, were found in the two sites (*Achirus lineatus*, *Ariopsis felis*, *Cichlasoma urophthalmum*) (Table 5.2). The Chao-Jaccard-Est Abundance-based estimator

revealed a similarity among fish assemblages in the dry season of 0.022 (\pm 0.039), concordant with the low number of shared species. During this season, 80 % of the species in MAR were of marine origin and 20 % estuarine. In FRW, 62 % of the species were of freshwater origin, 19 % estuarine, and 19 % marine.

In the rainy season, 26 species were caught in MAR and 31 in FRW, out of which seven marine and estuarine species, five of them euryhaline, were found at the two sites (*Archosargus rhomboidalis*, *Caranx latus*, *C. urophthalmum*, *Cynoscion nebulosus*, *Diapterus auratus*, *Mugil curema*, *Prionotus scitulus*) (Table 5.2). The Chao-Jaccard-Est Abundance-based estimator revealed a similarity among fish assemblages of 0.072 (\pm 0.04). In MAR, 73 % of the species were of marine origin, 23 % estuarine, and 4 % anadromous. In FRW, the proportion of marine species increased and equated the proportion of freshwater species (42 % and 48 %, respectively), whereas 10 % were estuarine species.

Accounting for the two sampling periods, the shared species between MAR and FRW reached 14, and included the above mentioned species, but also five additional marine and estuarine species that were either found in the dry season in MAR and in the rainy season in FRW (*Bagre marinus*, *Elops saurus*, *Lutjanus griseus*), or in the dry season in FRW and in the rainy season in MAR (*Poecilia mexicana*, *Anchoa mitchilli*) (Table 5.2). From these species, four were euryhaline (Table 5.2).

Moreover, other marine species were found in the FRW site in the rainy season, including *Caranx hippos*, *Megalops atlanticus*, *Strongylura marina*, and *Trinectes maculatus*, all of them euryhaline. These species were not found in MAR (Table 5.2).

General aspects of the size-structures

In MAR, the size class of 5 to 10 cm, sampled with beam trawl, dominated the fish community in the dry season. *C. urophthalmum* was the most abundant species of this size class and one of the most abundant species in the community ($>$ 10 % of relative abundance) (Annex III, Resource 1). Larger size classes of up to 45 cm were captured with beam trawl and gillnet (Fig. 5.2), including species of 11 families (Table 5.2). The proportion of juvenile and adult fishes in this season was of 56 and 44 %, respectively. In the rainy season, there was a clear predominance of the size class of 0 to 5 cm, sampled with ichthyoplankton net, beach seine and beam trawl (Fig. 5.2). 84 % of the fishes in this season comprised juveniles, with species like *Eucinostomus gula* and *D. auratus* showing the highest relative abundance overall ($>$ 10 % of relative abundance, Annex III, Resource 1) (Fig. 5.2).

Table 5.2 Sample size (n), total length range (TL, cm), and *LS* life stage (J, juveniles; A, adults; U, unknown) of the marine-estuarine and freshwater fishes collected in MAR and FRW, together with their seasonal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean and standard dev.). Euryhaline species are marked with *. References at the bottom

		Dry season						Rainy season								
		n	TL cm	LS	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd	n	TL cm	LS	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd	
MARINE-ESTUARINE SPP.																
Site MAR																
1.	Achiridae	<i>Achirus lineatus</i> ^{1,*}	1	12.5	A	-13.4		5.9	1	4.9	A	-12.5		5.8		
2.	Ariidae	<i>Ariopsis felis</i> ^{2,*}	3	27.6 - 31.9	A	-12.6	2.3	9.1	1.1							
2.	Ariidae	<i>Bagre marinus</i> ^{3,*}	2	27.8 - 28.8	J	-16.5	0.4	11.5	1.6							
3.	Batrachoididae	<i>Opsanus beta</i> ^{4,*}	4	8.6 - 15.5	J/A	-12.0	0.5	5.7	0.8	1	14.6	A	-13.0		5.6	
4.	Carangidae	<i>Caranx latus</i> ^{5,*}								1	18.3	J	-33.0		9.2	
5.	Centropomidae	<i>Centropomus parallelus</i> ^{6,*}								2	7.3 - 18.7	J	-16.9	0.8	8.1	1.2
6.	Cichlidae	<i>Cichlasoma urophthalmum</i> ^{7,*}	7	4.2 - 8.4	J	-12.0	0.2	6.9	0.2	12	3.9 - 18.5	J/A	-30.7	1.4	7.9	1.3
7.	Clupeidae	<i>Harengula jaguana</i> ^{8,*}	2							2	7.6 - 8.7	J/A	-17.9	0.4	8.0	0.2
8.	Cyprinodontidae	<i>Floridichthys carpio</i> ^{9,*}								3	6.5 - 7.0	A	-12.8	1.0	3.5	0.3
9.	Elopidae	<i>Elops saurus</i> ^{10,*}	1	27.0	J	-21.3		9.4								
10.	Engraulidae	<i>Anchoa mitchilli</i> ^{11,*}								2	4.0 - 4.2	J	-16.4	1.0	9.1	0.5
10.	Engraulidae	<i>Anchoa sp.</i> ^{11,*}								1	ca. 1	J	-21.5		10.4	
11.	Gerreidae	<i>Diapterus auratus</i> ^{12,*}								1	17.0	A	-13.0		6.8	
11.	Gerreidae	<i>Eucinostomus gula</i> ^{12,*}								1	2 - 6.9	J	-16.2	3.0	7.5	1.2
11.	Gerreidae	<i>Eugerres plumieri</i> ^{12,*}	3	16.7 - 19.0	J/A	-11.7	2.7	8.6	0.7							
11.	Gerreidae	<i>Gerres cinereus</i> ^{12,*}	3	6.4 - 8.0	J	-12.1	0.4	7.5	0.0	1	18.0	A	-11.9		8.0	
12.	Gobiidae	<i>Gobionellus oceanicus</i> [*]								1	3.2	U	-14.0		2.3	
13.	Haemulidae	<i>Orthoprichthys chrysoptera</i> ^{13,*}								1	18.0	J	-31.6		8.6	
14.	Lutjanidae	<i>Lutjanus griseus</i> ^{8,*}	1	23.0	J	-12.4		7.7								
15.	Mugilidae	<i>Mugil curema</i> ^{8,*}	1	33.0	A	-10.5		6.1		3	28.0 - 31.5	A	-32.4	0.2	6.2	1.0
16.	Ostraciidae	<i>Acanthostracion quadricornis</i> ¹⁴	1	5.4	J	-13.9		5.7								
17.	Paralichthyidae	<i>Citharichthys spilopterus</i> ^{15,*}								1	7.2	J	-14.7		6.6	
18.	Poeciliidae	<i>Poecilia mexicana</i> ¹⁶								1	2.7	J	-17.2		2.9	
19.	Sciaenidae	<i>Bairdiella ronchus</i> ^{8,*}								1	13.0	J	-31.9		7.8	
19.	Sciaenidae	<i>Cynoscion nebulosus</i> ^{17,*}	3	35.0 - 38.0	A	-12.4	2.5	10.2	0.6	1	33.5	A	-33.3		9.3	
20.	Sparidae	<i>Archosargus rhomboidalis</i> ¹⁸	3	5.6 - 16.9	J/A	-10.7	1.5	6.5	0.4	2	12.0 - 13.7	A	-26.2	1.4	10.1	1.8
20.	Sparidae	<i>Lagodon rhomboides</i> ^{19,*}								3	14.7 - 18.5	A	-32.1	1.5	9.9	0.5
21.	Syngnathidae	<i>Syngnathus louisianae</i> [*]	1	27.4	U	-14.3		6.7								
22.	Tetraodontidae	<i>Sphoeroides parvus</i> [*]	1	20.0	U	-18.3		8.4		2	11.8 - 14.5	U	-24.4	8.7	7.9	1.6
22.	Tetraodontidae	<i>Sphoeroides testudineus</i> ^{20,*}								1	4.3	J	-13.1		5.7	
23.	Triglidae	<i>Prionotus scitulus</i> ²¹	1							1	19.6	A	-13.8		9.8	
23.	Triglidae	<i>Prionotus tribulus</i> ²²								1	3.2	J	-14.5		6.0	
Site FRW																
1.	Achiridae	<i>Achirus lineatus</i> ^{1,*}	1	3.7	J	-28.2		8.7								
1.	Achiridae	<i>Trinectes maculatus</i> ^{23,*}								1	14.0	A	-30.4		9.4	
2.	Ariidae	<i>Ariopsis felis</i> ^{2,*}	1	13.6	J	-23.4		11.7		1	30.0	A	-16.3		10.0	
2.	Ariidae	<i>Bagre marinus</i> ^{3,*}								2	26.5 - 41.5	J/A	-28.0	0.5	10.3	0.3
24.	Belontiidae	<i>Strongylura marina</i> ^{24,*}								1	27.8	A	-29.6		10.1	
4.	Carangidae	<i>Caranx hippos</i> ^{25,*}								2	19.4 - 19.8	J	-18.7	0.3	13.2	1.2
4.	Carangidae	<i>Caranx latus</i> ^{5,*}								2	20.9 - 22.7	J	-17.3	1.5	10.1	0.5
5.	Centropomidae	<i>Centropomus undecimalis</i> ^{26,*}	1	28.2	J	-25.3		10.3								
6.	Cichlidae	<i>Cichlasoma urophthalmum</i> ^{7,*}	3	14.8 - 21.0	A	-29.3	0.6	8.0	1.8	1	17.1	A	-30.2		7.3	
7.	Clupeidae	<i>Brevoortia gunteri</i> [*]	1	2.5	U	-27.5		10.5								
25.	Eleotridae	<i>Gobiomorus dormitor</i> ^{27,*}	1	n.m.		-29.9		9.4		2	2.8 - 30.4	J/A	-29.6	1.6	9.0	0.2
9.	Elopidae	<i>Elops saurus</i> ^{10,*}								1	42.3	J	-29.5		8.8	
10.	Engraulidae	<i>Anchoa mitchilli</i> ^{11,*}	3	2.6 - 2.7	J	-27.4	0.6	11.0	0.1							
11.	Gerreidae	<i>Diapterus auratus</i> ^{12,*}								3	9.7 - 11.6	J	-31.4	1.2	10.9	0.5
14.	Lutjanidae	<i>Lutjanus griseus</i> ^{8,*}								4	23.0 - 31.0	J/A	-15.5	3.3	8.9	1.6
26.	Megalopidae	<i>Megalopsis atlanticus</i> ^{28,*}								3	32.0 - 36.4	J	-32.3	0.9	7.8	0.3
15.	Mugilidae	<i>Mugil curema</i> ^{8,*}								3	30.0 - 32.0	A	-13.6	1.1	6.7	1.1
18.	Poeciliidae	<i>Poecilia mexicana</i> ¹⁶	2	4.4 - 6.3	A	-27.7	2.9	8.3	0.1							
19.	Sciaenidae	<i>Cynoscion nebulosus</i> ^{17,*}								1	34.5	A	-12.0		8.8	
20.	Sparidae	<i>Archosargus rhomboidalis</i> ¹⁸								1	14.0	A	-11.0		5.9	
23.	Triglidae	<i>Prionotus scitulus</i> ²¹								2	19.0 - 20.2	A	-15.0	1.3	9.7	0.5
FRESHWATER SPP.																
Site FRW																
27.	Atherinopsidae	<i>Atherinella alvarezii</i>	6	2.0 - 5.83	U	-29.5	0.3	10.3	0.2	2	4.4 - 5.0	U	-31.3	0.3	8.5	0.2
28.	Characidae	<i>Astyanax aeneus</i> ¹⁶	7	5.1 - 7.5	A	-28.5	1.9	8.4	1.3	7	3.1 - 7.2	J/A	-30.3	1.4	8.7	0.7
6.	Cichlidae	<i>Amphilophus robertsoni</i>								2	3.8 - 17.0	U	-30.2	0.7	9.0	1.9
6.	Cichlidae	<i>Cichlasoma salvini</i>	2	11.0 - 15.7	U	-29.2	1.4	7.5	0.7	1	3.5	U	-32.8		8.8	
6.	Cichlidae	<i>Oreochromis niloticus</i> ⁸	1	21.5	A	-32.9		6.5		1	18.0	J	-34.4		6.9	
6.	Cichlidae	<i>Parachromis managuensis</i> ²⁹	1	18.7	A	-30.7		7.7								
6.	Cichlidae	<i>Paraneotroplus synspilus</i> ³⁰	2	10.2 - 10.8	J	-31.1	0.1	6.4	0.0	3	6.9 - 16.5	J/A	-31.2	1.2	8.1	1.6
6.	Cichlidae	<i>Theraps heterospius</i> ³¹	4	8.5 - 11.0	J	-29.3	2.1	8.7	1.1	1	8.2	J	-31.9		7.7	
6.	Cichlidae	<i>Thorichthys helleri</i>	3	9.7 - 10.5	U	-29.5	0.3	9.9	0.6	5	4.7 - 12.1	U	-28.7	2.1	9.9	0.5
6.	Cichlidae	<i>Thorichthys pisonis</i>								1	15.0	U	-31.5		6.3	

Table 5.2 continued

		Dry season							Rainy season						
		n	TL cm	LS	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd	n	TL cm	LS	$\delta^{13}\text{C}$	sd	$\delta^{15}\text{N}$	sd
6. Clupeidae	<i>Dorosoma anale</i>	1	24.8	U	-28.6		8.3								
6. Clupeidae	<i>Dorosoma petenense</i> ³²	4	6.1 - 18.5	J/A	-24.2	3.6	10.0	0.4	10	6.0 - 23.0	J/A	-28.9	4.6	8.7	1.0
29. Cyprinidae	<i>Ctenopharyngodon idella</i> ⁸	1	28.5	J	-27.2		8.0								
30. Hemiramphidae	<i>Hyporhamphus mexicanus</i>								9	11.0 - 29.0	U	-30.2	0.4	9.0	0.8
31. Heptapteridae	<i>Rhamdia quelen</i> ³³	2	14.4 - 20.6	J	-26.8	1.9	9.0	1.0							
32. Ictaluridae	<i>Ictalurus furcatus</i>								8	9.0 - 15.5	U	-30.0	1.1	9.5	0.4
33. Loricariidae	<i>Pterygoplichthys pardalis</i> ³⁴	2	15.8 - 16.5	J	-31.0	0.7	6.7	1.1	5	17.8 - 28.0	J	-33.8	1.4	6.2	0.3
18. Poeciliidae	<i>Gambusia sexradiata</i> ³⁵	6	2.1 - 4.1	A	-29.7				6	2.1 - 4.1	A	-29.7	0.4	9.5	0.3
34. Synbranchidae	<i>Ophisternon aenigmaticum</i> ³³	3	10.9 - 16.5	J	-25.1				3	10.9 - 16.5	J	-25.1	11.0	8.5	1.3
ANADROMOUS SPP.															
Site MAR															
21. Syngnathidae	<i>Microphis lineatus</i> ³⁶								1	6.8	J	-13.9		4.6	

Life stages' references according to data of length at first maturity: ¹ Morales-López (2007), ² Yáñez-Arancibia and Lara-Domínguez (1988), ³ Pinheiro et al. (2006), ⁴ Nagata (2013), ⁵ García-Cagide et al. (1994), ⁶ Gómez-Ortiz et al. (2011), ⁷ Caso-Chávez et al. (1986), ⁸ Froese and Pauly (2016), ⁹ Serafy et al. (2007), ¹⁰ Santos-Martínez and Arboleda (1993), ¹¹ Ayala-Pérez et al. (1997), ¹² Aguirre-León and Yáñez-Arancibia (1986), ¹³ Hildebrand and Cable (1930), ¹⁴ Ruiz et al. (1999), ¹⁵ Dias et al. (2005), ¹⁶ Soto-Galera (2006), ¹⁷ Brown-Peterson (2003), ¹⁸ Chavance et al. (1986), ¹⁹ Nelson (2002), ²⁰ Rocha et al. (2002), ²¹ Ross (1980), ²² McEachran and Fechhelm (2005), ²³ Mansueti and Pauly (1956), ²⁴ Hardy (1978), ²⁵ Thompson and Munro (1974), ²⁶ Perera-García et al. (2011), ²⁷ Bachelier et al. (2004), ²⁸ Crabtree et al. (1997), ²⁹ PREPAC (2006), ³⁰ Aguilar-Ontiveros (1996), ³¹ Cu-Sarmiento and Arreguín-Sánchez (1997), ³² Shelton (1972), ³³ Lorán-Núñez et al. (2006), ³⁴ Wakida-Kusunoki and Amador-del Ángel (2011), ³⁵ Arriaga and Schlupp (2013), ³⁶ Miranda-Marure (2004)

* References for eurihalinity: Ayala-Pérez et al. (1997), Castro-Aguirre et al. (1999), Martínez-Palacios and Ross (1992), Bussing (2002), Schultz and McCormick (2013), Ayala-Pérez et al. 2015, Carpenter (2001)

In FRW, the size class of 0 to 5 cm dominated the fish community in the dry season (Fig. 5.2). This was composed of individuals captured with ichthyoplankton net and beach seine, and was mainly represented by *A. mitchilli* (marine), *Atherinella alvarezii* (freshwater), and *Brevoortia gunteri* (marine), the former two the most abundant in the dry season (> 10 % of relative abundance, Annex III, Resource 1). Size classes from 5 to 30 cm, including freshwater species from six families, as well as marine and estuarine fishes from five families (Table 5.2), were captured with beach seine, beam trawl and gillnet, and showed abundances lower than 10 %. In this season, the proportion of juvenile and adult stages was of 85 and 15 %, respectively. In the rainy season, individuals from 0 to 5 cm were still predominant (Fig. 5.2) and were mainly represented by *Astyanax aeneus* (freshwater), which accounted for one of the highest abundances overall (> 10 % of relative abundance, Annex III, Resource 1). Nevertheless, in comparison with the dry season, the abundance of individuals of up to 30 cm increased considerably (Fig. 5.2).

Within the class of 20 to 25 cm, *Dorosoma petenense* (freshwater) accounted for a high abundance, as well as overall in the community (Annex III, Resource 1). Additionally, three more classes from 30 to 45 cm appeared in this season (Fig. 5.2), represented by marine fishes like *B. marinus*, *C. latus*, *L. griseus*, *M. atlanticus*, and *M. curema*. The proportion of juveniles and adults in this season was of 45 and 55 %, and highlight the approximated fourfold increase in adult stages compared to the dry season.

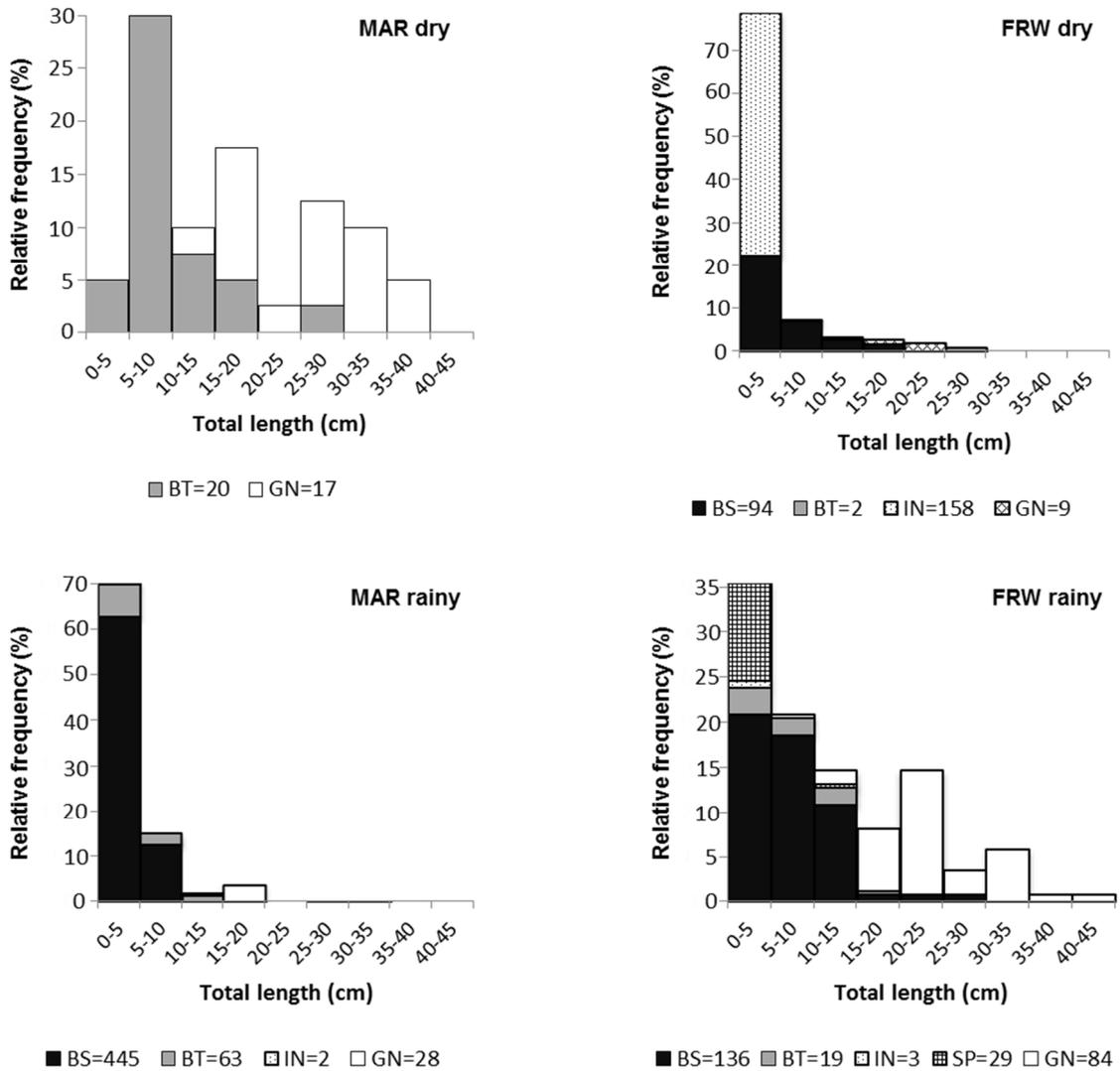


Fig. 5.2 Size frequency histograms of the fish collected in MAR (left panel) and FRW (right panel) with different gears. The total *n* per gear is shown. *BS* beach seine, *BT* beam trawl, *IN* ichthyoplankton net, *SP* spoon, *GN* gillnet

Stable isotope variability of the fish assemblages

In the dry season, fishes from MAR spanned enriched $\delta^{13}\text{C}$ values from -21.3 to -8.99 ‰ in a negatively skewed multimodal distribution with a mean of -12.8 ‰ (see beanplot and its blue colored area in Fig. 5.3a). In FRW, isotopic data spanned depleted $\delta^{13}\text{C}$ values from -32.9 to -21.8 ‰ in a positively skewed multimodal distribution with a mean of -28.5 ‰ (see beanplot and its green colored area in Fig. 5.3a). The difference between the mean $\delta^{13}\text{C}$ values of MAR and FRW spanned 15.7 ‰.

In the rainy season, the variation in $\delta^{13}\text{C}$ values within the two sites increased considerably, and also showed a multimodal pattern, but clustered into two main large set of values, one with depleted and another one with enriched values (beanplot in Fig. 5.3b). In MAR, values ranged

from -33.6 to -11.9 ‰, and the mean was -23.2 ‰ (see beanplot and its blue colored area in Fig. 5.3b); and in FRW, values ranged from -36.1 to -11.0 ‰, and the mean was -27.6 ‰ (see beanplot and its green colored area in Fig. 5.3b). The difference between the mean $\delta^{13}\text{C}$ values of MAR and FRW in this season spanned 4.4 ‰.

$\delta^{15}\text{N}$ was less variable than $\delta^{13}\text{C}$, spanning values in the dry season from 4.5 to 12.6 ‰ in MAR, and from 5.91 to 11.65 ‰ in FRW, and mean values of 7.44 and 10.4 ‰, respectively, with a difference of 2.96 ‰. In the rainy season, values ranged from 2.35 to 11.32 ‰ in MAR, and from 5.66 to 14.0 ‰ in FRW, with means of 6.94 and 8.81 ‰, respectively, and a difference of 1.87 ‰.

Connectivity between fish assemblages: insights from isotope-based metrics

In the dry season, the convex hull of all the species collected in MAR had a total area (TA) of 34.8 ‰², and the convex hull of the species in FRW, 21.0 ‰². Both convex hulls were well separated from each other (0 overlap), highlighting the contrasting $\delta^{13}\text{C}$ isotopic signatures of the communities (see convex polygons in Fig. 5.3a). In the rainy season, the convex hulls for the species in MAR and FRW increased by 3.5 and 5.6 times, with areas of 121 and 118 ‰², respectively. The increment in area in MAR was towards low $\delta^{13}\text{C}$ values, and in FRW towards high $\delta^{13}\text{C}$ values. This was related with the high overlap between the convex hulls of MAR and FRW in the rainy season (67 to 69 %) (see convex polygons in Fig. 5.3b).

In the dry season, the SEAc of the marine-estuarine fishes (from both sites) had a big and elongated area of 37.4 ‰² compared to the small and compact SEAc of 7.60 ‰² of the freshwater fishes (only from FRW) (see ellipses in Fig. 5.3a). No overlap between the SEAc's of the marine-estuarine and freshwater fishes was observed in the dry season (see ellipses in Fig. 5.3a), despite eight marine-estuarine species were found in FRW in this season (*A. lineatus*, *A. mitchilli*, *A. felis*, *B. gunteri*, *Centropomus undecimalis*, *C. urophthalmum*, *Gobiomorus dormitor*, and *P. mexicana*) (Table 5.2). In the rainy season, the SEAc of the marine-estuarine fishes (from both sites) was of 53.0 ‰² (1.4 times bigger than in the dry season) and the SEAc of the freshwater fishes (only from FRW) remained small and compact with an area of 6.95 ‰² (see ellipses in Fig. 5.3b). In this season, the number of marine-estuarine species in FRW doubled to 16 (*A. rhomboidalis*, *A. felis*, *B. marinus*, *C. latus*, *C. hippos*, *C. urophthalmum*, *C. nebulosus*, *D. auratus*, *E. saurus*, *G. dormitor*, *L. griseus*, *M. atlanticus*, *M. curema*, *P. scitulus*, *S. marina*, *T. maculatus*), and the overlap between the SEAc's of the marine-estuarine and freshwater fishes was of 2.09 to 13.1 % (see ellipses in Fig. 5.3b).

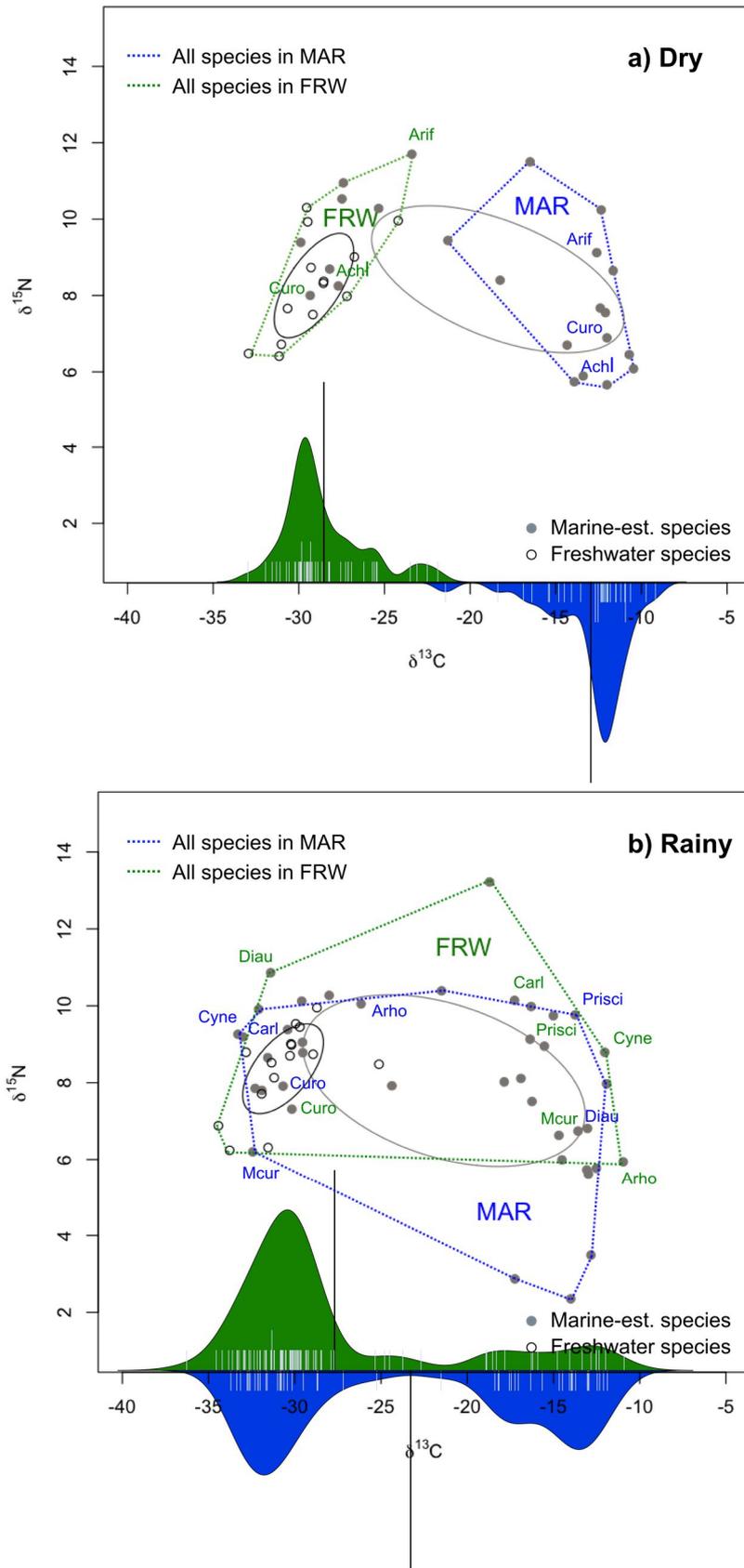


Fig. 5.3 Individual mean isotopic values of the fish species (circles) collected in MAR (blue) and FRW (green) and the distribution of $\delta^{13}\text{C}$ values depicted with beanplots in the dry (a) and rainy season (b) *Polygons* convex hulls delimiting the isotopic niche of all the species in each site, *Ellipses* standard ellipse areas (SEAc) depicting the core isotopic niche of marine-estuarine and freshwater species from the two sites. *Shared species* per season are shown with the abbreviations: Achl, *Achirus lineatus*; Arif, *Ariopsis felis*; Carl, *Caranx latus*; Curo, *Cichlasoma urophthalmum*; Cyne, *Cynoscion nebulosus*; Diau, *Diapterus auratus*; Mcur, *Mugil curema*; Prisci, *Prionotus scitulus*

5.4 Discussion

In this study, the species richness in MAR and FRW was higher in the rainy season under the influence of *nortes* (with 26 and 31 species, respectively) compared to the dry season (15 and 21, respectively), reinforcing previous observations in Terminos Lagoon emphasizing a higher diversity during this period (Yáñez-Arancibia et al. 1988; Ramos-Miranda et al. 2005).

Remarkable was the twofold increase in the marine-estuarine component in FRW during the rainy season. This corroborates previous observations stressing the higher immigration of marine species into Terminos Lagoon during this season (Ramos-Miranda et al. 2005), likely due to the influence of rainfall through the resultant freshwater runoff, which promote primary productivity and food supply (Day et al. 1982; Gracia and Soto 1990).

Based on a two-dimensional hydrodynamic model for Terminos Lagoon of Kjerfve et al. (1988), Medina-Gómez et al. (2015) also highlight the water-level setup along the landward margin when the model is forced by the 6–10 m s⁻¹ northwesterly winds accompanied by rains during the winter storms, in which southward flow is opposing the main river flow. This may represent the controlling factor responsible both for increasing the water residence time within the fluvio-lagoon systems and favoring phytoplankton assimilation and biomass development under high N/P ratio conditions in the *nortes* wind regime (Medina-Gómez et al. 2015).

Enhanced plankton food supply amplifies abundances of zooplankton (Cloern and Jassby 2012), and zooplankton is an important intermediate component in food webs, acting as a trophic link between small particles (e.g. microalgae and detritus) and fishes (Schwamborn et al. 2001).

In front of the coastal zone where Terminos Lagoon is located, the observed high zooplanktonic biomass and ichthyoplankton densities make evident that neritic and coastal communities are associated with highly productive systems subjected to important continental water discharge, which comprise nutrient-rich coastal fronts and suitable areas for larval feeding and growth (Flores-Coto et al. 2009). The seasonal variation in larval abundance, with highest values during the rainy period (and lowest during dry conditions), agree with the time of highest continental water discharge from June to November (Flores-Coto et al. 2009 and references therein). Under the *nortes* influence, these communities can also be restricted to a narrow margin contiguous to the littoral (Flores-Coto et al. 2009).

Highest ichthyoplankton densities have been recorded near the Carmen Inlet most of the year (Sánchez-Velasco et al. 1996; Sanvicente-Añorve et al. 2000). Advection, food quality, response of plankton to aggregation, and tidal-induced currents (at a finer scale), may act as some of the mechanisms responsible for distribution patterns, while juvenile movement (e.g., into Terminos

Lagoon habitats) is mainly behaviourally mediated (Sanvicente-Añorve et al. 2000 and references therein). Amongst the most representative families near the Carmen Inlet in terms of abundance are Engraulidae (e.g., *A. mitchilli*), Gobiidae, Clupeidae (e.g., *Brevoortia gunteri*), Scianidae (e.g., *C. nebulosus*) and Gerreidae (Sanvicente-Añorve et al. 2000). In this study, marine members from the Engraulidae (*A. mitchilli*, dry season), Clupeidae (*B. gunteri*, dry season), Scianidae (*C. nebulosus*, rainy season), and Gerreidae families (*D. auratus*, rainy season) were found in the oligohaline site FRW within the Palizada Del-Este system, which freshwater discharge directly influences the Carmen Inlet.

The other marine and estuarine fishes found in FRW, comprising members of the families Achiridae (*A. lineatus*, dry season; *T. maculatus*, rainy season), Ariidae (*A. felis*, *B. marinus*, rainy season), Belonidae (*S. marina*, rainy season), Carangidae (*C. hippos* and *C. latus*, rainy season), Centropomidae (*C. undecimalis*, dry season), Cichlidae (*C. urophthalmum*, dry and rainy season), Eleotridae (*G. dormitor*, dry and rainy season), Elopidae (*E. saurus*, rainy season), Lutjanidae (*L. griseus*, rainy season), Megalopidae (*M. atlanticus*, rainy season), Mugilidae (*M. curema*, rainy season), Sparidae (*A. rhomboidalis*, rainy season), and Triglidae (*P. scitulus*, rainy season), have already been reported in the Palizada Del-Este system, or more generally, in the southwestern part of Terminos Lagoon and the west coast of Campeche by Yáñez-Arancibia et al. (1985, 1988), Ayala-Pérez (2006), Ayala-Pérez et al. (2012), and Amador del Ángel et al. (2012, 2015).

Some of the marine species found in FRW in this study, comprise populations exclusive from the deltaic (western) province off Terminos Lagoon that are estuarine dependent (*A. mitchilli*, *C. hippos*, *C. undecimalis*, *Prionotus sp.*), whereas others are common to both the deltaic (western) and carbonate (eastern) provinces off Terminos Lagoon and are estuarine dependent (*A. rhomboidalis*, *A. felis*, *B. marinus*, *A. lineatus*, *T. maculatus*, *C. latus*) (Yáñez-Arancibia et al. 1985). These species are considered as estuarine dependent because the recruits (young fish) utilize the Terminos Lagoon and adjacent estuarine areas (Pauly and Yáñez-Arancibia 2012) for protection, feeding and growth, and later migrate to the sea to mature and be recruited by the adult population (Tapia-García et al. 1988). Other species categorized as estuarine-dependent in the southern Gulf of Mexico (Campeche Bay) are *C. nebulosus* and *B. gunteri* (Flores-Coto et al. 2004; Sanvicente-Añorve et al. 2011). Many others, like *E. saurus*, *M. atlanticus*, *M. curema*, *S. marina*, *D. auratus*, *G. dormitor*, and *L. griseus* are marine transient species, which usually breed at sea and only a small portion of the overall population uses the lagoon (Bravo-Núñez and Yáñez-Arancibia 1979; Sanvicente-Añorve et al. 2011). Others, like *C. urophthalmum* are estuarine resident species (Miller 1966).

Related with the core hypothesis of this work, results allowed to confirm that similarity and connectivity of fish assemblages between marine (MAR) and freshwater (FRW) habitats in

Terminos Lagoon increase at times of higher river discharge and the influence of *nortes*, whereas similarity and connectivity decreases in the dry season. This was ought to the considerably increase in the number of marine species in FRW in the rainy season (as discussed above), and to the higher amount of shared species between the marine and freshwater sites during this time.

In each site, the Convex hull areas (TA) were considerably larger in the rainy season. This, compared to higher species packing and trophic redundancy in the dry season, translates into a higher trophic diversification and lower trophic redundancy in the rainy season (Layman et al. 2007; Abrantes et al. 2014). The latter particularly applies in the case of MAR, where fishes had a wide range of $\delta^{13}\text{C}$ values in the rainy season (between -33.6 and -11.9 ‰) in accordance with the $\delta^{13}\text{C}$ values of basal resources including mangroves, detrital mangrove leaves, epiphytes, seston and seagrasses (-31.5 to -5.54 ‰, see Chapter IV), giving indication that different potential sources of organic matter sustained biomass production (López-Rasgado et al. 2016). In the dry season, fishes in MAR showed a contrasting smaller and narrow TA, with $\delta^{13}\text{C}$ values ranging from -21.3 to -8.99 ‰.

It is important to mention that TA is influenced by species with extreme positions on either the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ axis (or both), and thus typically is correlated to some degree with the span of these values (Layman et al. 2007). Here, we make special emphasis in the variability in $\delta^{13}\text{C}$ values, as it was considerably large across seasons, and because $\delta^{13}\text{C}$ values are generally used to evaluate foraging habitats (DeNiro and Epstein 1978).

In FRW, the same phenomenon of a compressed and a large isotopic niche was observed for the fish species in the dry and rainy season, with $\delta^{13}\text{C}$ values ranging from -32.9 to -21.8 ‰ and -36.1 to -11 ‰, respectively, but the cause of the considerable expansion of the isotopic niche of fishes in the latter season (resources spanned $\delta^{13}\text{C}$ signatures from -41.6 to -21 ‰, see Chapter IV) was the penetration of marine species with extreme enriched positions along the $\delta^{13}\text{C}$ axis (-18.3 to -11 ‰). These marine species were recognized as recent migrants (e.g., *A. rhomboidalis*, *C. latus*, *C. nebulosus*, *M. curema*, *P. scitulus*). Recent migrants are distinguishable from those that have resided in the area for sufficiently long time to equilibrate to the new foods (Litvin and Weinstein 2004; Herzka 2005).

The information provided by the convex hull areas (TA) is ecologically relevant as they illustrate how a shrinkage and expansion in isotopic niche is coupled to contrasting seasonal influences and availability of resources in the area, as well as the role of species with extreme isotopic values, for instance, the marine species migrating into freshwater fluvio-lagoon habitats of Terminos Lagoon (FRW). These transitory species export energy from these habitats to Terminos Lagoon and consequently to the Campeche Bay through their movements (Amezcuca-Linares and Yáñez-

Arancibia 1980).

Nevertheless, the overlap of the convex hull areas (TA) between the MAR and FRW sites, based on all the species found in each site, can mask and overestimate the real connectivity between habitats and fish assemblages. For instance, the strong bimodality in the $\delta^{13}\text{C}$ values of fishes from MAR in the rainy season, and thus the bigger TA of the community, was due to the emergence of two isotopically contrasting trophic pathways within this vegetated complex mangrove-seagrass habitat: one based on seagrass epiphytes and the other on detrital mangrove leaves (see Chapter IV). Both pathways and the species associated to them had ^{13}C -enriched and ^{13}C -depleted values, respectively, influencing the large isotopic area of the fish community during the rainy season, compared to the smaller area in the dry season, when resources with ^{13}C -enriched values like seston and benthic macroalgae were predominant (see Chapter IV). With this, the high overlap between the TA's of MAR and FRW in the rainy season (67-69 %), does not necessarily implies connectivity between the fish assemblages, but it does the considerable expansion in the TA of FRW towards ^{13}C -enriched values in the rainy season (represented by marine migrants).

A further approach to assess the connectivity between the fish assemblages consisted in the estimation of the sample size-corrected standard ellipse area (SEAc) of all the marine-estuarine and freshwater species collected from the two sites and their overlap. These ecological guilds better represent the origin of the species and not strictly the sampling site.

In the dry season, no overlap between the SEAc of these groups was found despite eight marine-estuarine species were found in FRW (*A. felis*, *C. urophthalmum*, *Gobiomorus dormitor*, *A. mitchilli*, *Brevoortia gunteri*, *Centropomus undecimalis*, *A. lineatus*, and *P. mexicana*). This is probable due to the standard ellipses contain c. 40 % of the data regardless of sample size (Batschelet 1981), instead of encompassing all data in the isotopic space like the total area of the convex hull (TA) (Jackson et al. 2011). Noteworthy, the marine and estuarine species found in FRW in the dry season were isotopically on par with the signatures of the freshwater fish species and basal resources therein, indicating that these species make use of the freshwater habitats connected with Terminos Lagoon during the dry season as feeding areas, as observed in the case of *A. mitchilli* in a previous study (Ayala-Pérez et al. 1997).

In the rainy season, the number of marine-estuarine species in FRW doubled to 16, and the half (*C. urophthalmum*, *G. dormitor*, *M. atlanticus*, *E. saurus*, *Trinectes maculatus*, *B. marinus*, *Strongylura marina*, *D. auratus*) were isotopically on par with the $\delta^{13}\text{C}$ values of freshwater species and the basal resources in this site. The other half were identified as recent migrants, indicating that during the rainy season there is a higher inflow of marine visitors which most

likely make use of the freshwater habitats for feeding. The observed overlap between the SEAc's of the marine-estuarine and freshwater fishes in the rainy season, together with the increase in isotopic niche area of the marine-estuarine species by 1.4 times, corroborates the hypothesis that connectivity of fish assemblages between marine (MAR) and freshwater (FRW) habitats in Terminos Lagoon increases at times of higher river discharge and the influence of *nortes* winds.

5.5 Conclusions

The results of this study helped to confirm the hypothesis that similarity and connectivity of fish assemblages between marine (MAR) and freshwater (FRW) habitats in Terminos Lagoon increase at times of higher river discharge and the influence of *nortes* winds, whereas similarity and connectivity decrease in the dry season.

Remarkable was the twofold increase in the marine-estuarine component in FRW during the rainy season, likely due to the influence of rainfall and the resultant freshwater runoff, which promotes primary productivity and food supply (Day et al. 1982; Gracia and Soto 1990).

The mentioned results corroborate previous studies stressing the higher immigration of marine species into Terminos Lagoon during the rainy season (Yáñez-Arancibia et al. 1988; Ramos-Miranda et al. 2005). The effect of the *nortes* winds by enhancing intrusion of salt water into the lagoon has also been related with the movement of marine species such as snappers (Lutjanidae) into the system (Ramos Miranda et al. 2005).

There has been suggested that there is preferential use of the fluvio-lagoon habitats during the wet season and of mangrove-seagrass habitats during the dry season, which coincide with periods of high primary productivity of these areas (Yáñez-Arancibia et al. 1988). Under highly productive conditions, the influx of freshwater species in the oligohaline portion of the estuary may enhance estuarine fish abundance and richness, and should provide an important prey source for marine predators (Rehage and Loftus 2007).

The ecological importance of the fluvio-lagoon systems associated with Terminos Lagoon as nursery and/or feeding areas for various fish populations has been recognized since the 80's (Amezcu-Linares and Yáñez-Arancibia 1980), but there has been a large gap of time without paying enough attention to the ecological role, value, and changes of these habitats with respect other habitats within the complex Terminos Lagoon system. The use of stable isotope analysis in this study proved to be beneficial in the understanding about the habitat use and movement of fish species.

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Chapter VI

General Discussion

General Discussion

The objective of this work was to analyze the food web dynamics, as well as the connectivity of fish assemblages, across important spatial and temporal scales in tropical coastal ecosystems of the southern Gulf of Mexico (Centla Wetlands and Terminos Lagoon), where marshes, mangroves and seagrasses are conspicuous, and in some instances, interconnected.

Specifically assessed were:

- 1) The food web structure and contribution of different basal resources for aquatic consumers in sites differing in geomorphology, distance to the sea and vegetational characteristics.
- 2) The seasonal shifts in food web structure, dietary contribution of resources and consumers' isotopic niche width.
- 3) The connectivity of fish assemblages in spatially separated habitats under contrasting seasonal conditions.

The related hypotheses were:

- 1) The importance of riparian-derived carbon for aquatic consumers highly depends on habitat geomorphology (predicted to be higher in 'more enclosed' vs 'more open' habitats) and on availability of basal resources.
- 2) Larger consumers' isotopic niches in the rainy season are induced by energetic pulsing events like the riverine pulse (flood pulse concept).
- 3) The connectivity between fish assemblages of marine and low-salinity habitats increases in the rainy-*nortes* season as higher food availability enhances fish migration towards productive river-influenced habitats.

In the following sections, the main findings and their relation to each of the mentioned issues are discussed.

6.1 General patterns of isotopic variability and food web structure

6.1.1 Basal resources

Habitat differences in terms of $\delta^{13}\text{C}$ values depicted a gradient from the northeast marine-influenced area of Terminos Lagoon with enriched $\delta^{13}\text{C}$ values to the river-influenced habitats with depleted $\delta^{13}\text{C}$ values. Raz-Guzmán and de la Lanza (1991) also reported different isotopic zones in Terminos Lagoon, with more depleted $\delta^{13}\text{C}$ values in sites with important fluvial input, and enriched values in the northeast area. This spatial variability in $\delta^{13}\text{C}$ has been found in other tropical and subtropical systems (Deegan and Garritt 1997; Chanton and Lewis 2002; Nyunja et al. 2009), and can be attributed to the $\delta^{13}\text{C}$ values of dissolved inorganic carbon (DIC) along salinity gradients (up to +1.7 ‰ in seawater and ca. -14 ‰ in estuarine-freshwater), and differences between aquatic primary producers that fix CO_2 or HCO_3^- (Maberly et al. 1992; Cloern et al. 2002; Bouillon et al. 2007, 2011). Another factor influencing $\delta^{13}\text{C}$ values is the photosynthetic carbon metabolism which largely differentiates C_3 from C_4 plants (O’Learly 1981; Anderson and Fourqurean 2003).

Habitat differences based on $\delta^{15}\text{N}$ values showed an inverse pattern to that observed with $\delta^{13}\text{C}$. The highest $\delta^{15}\text{N}$ values were characteristic of the fluvio-lagoon habitats, and the lowest of the fringe mangrove site. The large variability in $\delta^{15}\text{N}$ values observed in primary producers can be influenced by physiology or the contributions of various N sources to plant N-uptake (Marshall et al. 2007). Low $\delta^{15}\text{N}$ values close to 0 ‰ are often attributed to N_2 fixation (Lepoint et al. 2004). Thus, the low $\delta^{15}\text{N}$ values observed for seagrasses and benthic algae (cyanobacteria) may be due to the influence of ^{15}N -depleted inorganic N originating in N_2 fixation (Liu et al. 1996). High $\delta^{15}\text{N}$ values, as those found in *Vallisneria americana* and in some riparian marsh plants, can be related with the assimilation of inorganic N from aquatic sediments where microbial mineralization and nitrification/denitrification produce ^{15}N -enriched inorganic N (Cline and Kaplan 1975). Anthropogenic sources of dissolved inorganic N (DIN), like wastewater and manure typically enriched in ^{15}N (Bouillon et al. 2011), could be another factor influencing high $\delta^{15}\text{N}$ values in *V. americana* and in mangrove epiphytes (e.g., 7.34 and 9.03 ‰, respectively). The characteristically low $\delta^{15}\text{N}$ values of some species of riparian vegetation can be attributed to natural sources of DIN such as precipitation and soil-derived N, which are typically depleted in ^{15}N (Bouillon et al. 2011), while in other cases it may be due to N_2 fixation activity (dos Reis et al. 2010).

The increase and decrease in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of basal resources respectively during the rainy season could reveal a significant influence of a high flow of nutrient sources and important ^{13}C -depleted continental inputs, as well as the fixation of biogenic CO_2 provided by decomposition

processes that are more accelerated in this season (Carlier et al. 2007; Lima et al. 2010; Olin et al. 2013a).

6.1.2 Consumers

Mollusks, crustaceans and fishes constituted the main groups of consumers sampled in the two seasons, although insects were also collected in the rainy season. Insects included taxa from the orders Blattodea, Coleoptera, Diptera, Hemiptera, Ephemeroptera and Odonata. Mollusks included five species from the class Bivalvia, and five from the class Gastropoda. Crustaceans included 17 taxa among which decapod (e.g., Penaeidae, Palaemonidae, Portunidae, Sesarmidae) and pericarid groups (amphipods, isopods, tanaids) were the most representative. Fishes comprised 69 species grouped into 34 families, among which Cichlidae, Gerreidae and Engraulidae were the most important in terms of species diversity and/or abundance.

Consumers from the fluvio-lagoons San Pedrito (Centla Wetlands), El Coco (Centla Wetlands) and El Vapor (Terminos Lagoon) were primarily freshwater and estuarine species, followed by marine transient fauna. In the fringe mangrove site, marine species dominated the community, followed by estuarine species.

Omnivore, zoobenthivore and planktivore feeding guilds, in order of importance, showed the highest number of taxa, as well as some of the most abundant species overall like the shrimp *Farfantepenaeus duorarum*, and the fishes *Diapterus rhombeus*, *Diapterus auratus*, *Eucinostomus gula* (fringe mangrove site and El Coco); *Cichlasoma salvini* (San Pedrito); and *Anchoa mitchilli* (El Vapor).

Previous studies in Centla Wetlands and Terminos Lagoon stress the importance of these ecosystems to benthic-pelagic omnivore species (Sánchez et al. 2012; Villéger et al. 2012), while other studies highlight that estuarine fishes are typically characterized by omnivory, and the availability of species to exploit temporary peaks of prey (Ley et al. 1994; Layman and Silliman 2002). The high abundance of the planktivore *A. mitchilli* in El Vapor within the Palizada-Del Este System contiguous to Terminos Lagoon also coincides with studies identifying this marine species as one of the most important in terms of abundance, and its using this portion of the estuary as a feeding/nursery area (Vera-Herrera et al. 1988; Ayala-Pérez et al. 1997).

With regard the stable isotope values among consumers groups, mollusks showed the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared to crustaceans and fishes. Following this trend, the lowest trophic levels (based on $\delta^{15}\text{N}$ data) were observed for mollusks; intermediate levels for most species, especially crustaceans and fishes; and the highest for fishes.

Three to four trophic levels (including the basal resources) were observed in the studied sites during the two seasons which corresponds to findings from studies carried out in the Monkey River Basin in Belize (Winemiller et al. 2011), the inner littoral of Isla del Carmen in Terminos Lagoon (Rivera-Arriaga et al. 2003) and Centla Wetlands (Mendoza-Carranza et al. 2010). The structurally complex fringe mangrove site interconnected with seagrasses showed the highest number of trophic levels, suggesting a high diversity of resources and consumer types.

Omnivore Ariid catfishes were high trophic level predators like *Bagre marinus* and *Ariopsis felis* in the fringe mangrove site and El Vapor (with trophic levels of 3.7 to 4.3). Other fishes with high trophic levels were *Cynnoscion nebulosus* in the fringe mangrove site (3.5 to 3.9), *Caranx hippos* in El Vapor and San Pedrito (3.7 to 4.4), *Centropomus undecimalis* in San Pedrito (with a maximum trophic level of 3.5), and *Strongylura marina* in El Coco (3 to 3.3).

Across sites, the isotopic values of the consumers generally followed the trends observed for the basal resources with higher $\delta^{13}\text{C}$ values in the fringe mangrove site compared to the river-influenced habitats, while the inverse was found in the case of $\delta^{15}\text{N}$.

The notorious isotopic variability in the rainy season towards more depleted $\delta^{13}\text{C}$ values in the marine site, and towards more enriched $\delta^{13}\text{C}$ values in the fluvio-lagoons suggests a shift in prey availability and/or prey preferences, as well as changes in foraging location (Perga et al. 2005; Madurell et al. 2008; Kim et al. 2012). For instance, as discussed later, the higher number of consumers with enriched $\delta^{13}\text{C}$ values in the fluvio-lagoons indicates that a considerable number of marine species enter these habitats during the rainy season (e.g., *F. duorarum*, *A. felis*, *Archosargus rhomboidalis*, *Prionotus scitululus*, *Mugil curema*, *C. hippos*, *Caranx latus*, *C. nebulosus*, *Lutjanus griseus*).

6.2 Importance of riparian-derived carbon for the aquatic fauna

Since the late 70's and 80's, Odum et al. (1979), Odum (1980), and Nixon (1980), indicated that the most important factor determining the extent of carbon movement is likely to be the degree of openness of the estuarine system to the open sea (reviewed in Connolly et al. 2005). Carbon movement within estuaries is expected to be higher in systems having restricted connectivity and exchange with open coastal waters than those open to the sea (Odum et al. 1979, reviewed in Connolly et al. 2005). Therefore, geomorphometry represents a key factor determining whether there is outwelling (Odum et al. 1979; Odum 1980).

Studies in more recent years, like those of Mancera-Pineda (2003), Bouillon et al. (2004), and Vaslet et al. (2012), have affirmed the importance of assessing the utilization of riparian-derived carbon in mangrove ecosystems across different coastal settings. These studies have pointed out

that utilization patterns indeed vary depending on the geomorphological setting, with higher utilization of riparian carbon being observed in river-dominated, basin and pond settings compared to fringe, island and overwash settings.

In this study, results from Chapter III and IV (manuscripts I and II) confirmed the prediction that higher dietary contributions of riparian-derived carbon are found in ‘more enclosed’ fluvio-lagoons compared to the ‘more open’ fringe mangrove site, corresponding with findings in the aforementioned studies.

In the fringe mangrove site, mangrove-derived carbon was of limited importance, particularly in the dry season (with a maximum dietary contribution of up to 26 % according to the SIAR mixing model results from chapter IV used as reference hereon); whereas seston, macroalgae and seagrass-derived carbon, in order of importance, played a major role in sustaining secondary production (with maximum contributions of 40 to 82 %). This corresponds with observations that at interlinked mangrove-seagrass ecosystems, the dominant carbon sources mainly derived from seagrass, their associated epiphytic community and macroalgae, and that mangrove-derived organic matter contributes only marginally to the overall food web (Nyunja et al. 2009). The investigations of Bouillon et al. (2004) in different geomorphological settings in Kenya, India and Sri Lanka also point out that in sites with significant inputs of aquatic sources, use of mangrove carbon is rather limited on a community basis compared to systems with less material exchange with adjacent waters, where the relative importance of mangroves is higher. Thus, the availability of autotrophic food plays an important role in the energy flow within estuaries (Abrantes et al. 2015; Claudino et al. 2015).

In this regard, the importance of aquatic primary producers as food sources in the fringe mangrove site may relate with the high productivity values of such producers. For instance, high phytoplankton productivity has been reported for the inner littoral of Isla del Carmen with an annual average of $803 \text{ mgC m}^{-3} \text{ h}^{-1}$, and maximum peaks in April ($1,660 \text{ mgC m}^{-3} \text{ h}^{-1}$) and June ($882.2 \text{ mgC m}^{-3} \text{ h}^{-1}$) (de la Lanza and Lozano 1999). The highest biomass and productivity of benthic algae and seagrasses also generally occur during the dry season when water transparency is highest (Day et al. 1982; Reyes et al. 1994). The conditions of low turbidity may allow for a range of aquatic producers to occur, supporting consumers with different trophic ecologies (Abrantes et al. 2013, 2014). However, the remarkable preference on phytoplankton coincides with previous observations that Terminos Lagoon is a phytoplankton-based lagoon in spite of the presence of other primary producers like seagrasses and macroalgae whose contribution to total areal production is low in comparison to phytoplankton (Knoppers 1994).

Contrasting with the above, in the ‘more enclosed’ fluvio-lagoons, riparian-derived carbon was of

higher importance for the aquatic consumers. For example, marsh vegetation in San Pedrito contributed up to 95 and 98 % of the diet of omnivore and zoobenthivore species respectively; whereas detrital mangrove leaves contributed up to 89 % to non-selective filter feeders in El Vapor, and up to 60 % to detritivores in El Coco.

The importance of riparian-derived carbon in the latter sites can be related with the high availability of riparian resources, presumably due to elevated ratios of wetland area to open water (Mancera-Pineda 2003), in addition to higher litterfall production of riverine mangroves than fringing mangroves (1,252 and 835 g m⁻² year⁻¹ respectively, Day et al. 1987).

Careful interpretations of the importance of riparian-derived carbon as a basal resource are necessary so as not to overestimate it, and not to attribute a direct link of this basal resource with consumers. Most food web studies are biased towards metazoan consumers, and ignore isotopic heterogeneity at the base as well as concepts such as the microbial loop (Middelburg 2014). Thus, while direct assimilation of riparian organic matter and its detritus may not be that common because consumers often lack the digestive enzymes necessary to process it, assimilation of microbial epifauna that coats this material may be a major route of energy (Belicka et al. 2012, and references therein).

Organic matter in particulate and dissolved organic form from the watershed and upstream systems can also be consumed directly or indirectly via bacteria by many consumers in aquatic ecosystems (Middelburg 2014, and references therein). Here sediments were observed comprising another important resource for filter-feeding bivalves with contributions of up to 79 % in San Pedrito during the dry season. These mollusks may play an important role in transferring energy from terrestrial to aquatic ecosystems due to the consumption of terrestrial organic matter accumulated in the sediments, most likely from vascular plants (Antonio et al. 2010). Nevertheless, bivalves showed considerably more ¹³C-depleted values (ca. -32.5 ‰) than sediments (ca. -25 ‰). A possible explanation for this can be the consumption of methane oxidizing bacteria (MOB) due to preferential use of CH₄ in sediments with δ¹³C values from -36 to -58 ‰ in river-dominated estuaries (Sansone et al. 1999; Kohzu et al. 2004; Eller et al. 2005).

6.3 Changes in the contribution of resources and consumers' isotopic niche width under contrasting seasonal conditions

Chapter IV (manuscript II) mainly focused on assessing the seasonal changes in the contribution of basal resources to consumers, in addition to the changes in consumers' isotopic niche width.

The periodic drought and flooding events characteristic of the dry and rainy seasons, particularly in the river-influenced zones of the Grijalva-Usumacinta delta, with 2,934.1 km² of areas prone to flooding (Sánchez et al. 2007), may have a strong influence in the energetic resource pulsing from one season to the other.

As it has been observed that seasonal shifts in resource availability, and the reliance upon a wider variety of resources by aquatic consumers during the flood phase can be strongly associated with habitat changes during the flood pulse (Wantzen et al. 2002), results were expected to follow predictions of the flood pulse concept (FPC) (Junk et al. 1989; Junk and Wantzen 2004). The FPC (Junk et al. 1989; Junk and Wantzen 2004) states that food supply during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic organisms. It highlights the importance of the lateral-mediated transfer of energy, materials and organisms in floodplain ecosystems (Junk et al. 1989; Junk and Wantzen 2004). Contrary to the river-continuum concept (RCC) of Vannote et al. (1980), the FPC predicts that organic matter from upstream origins is insignificant for floodplain production relative to organic material produced and consumed locally. Therefore, most secondary production is attributed to the high in situ aquatic and riparian production. However, the FPC also recognizes that extreme flooding can flush out considerable amounts of organic matter (Junk et al. 1989; Junk and Wantzen 2004, and references therein).

Results from this study confirmed that the isotopic niche width of the majority of aquatic consumers (e.g., crustaceans and fishes) increases during the rainy season when freshwater discharge and resource availability are higher.

The relevance of the lateral linkages in floodplain ecosystems was specifically manifested with the high contribution of riparian-derived carbon for most or some groups of consumers in the fluvio-lagoon sites after the rainy season (beginning of the dry season) when the receding water potentially carries out the riparian organic matter into the water bodies (Gasith and Resh 1999). The most notorious case was observed in San Pedrito where marsh vegetation had a mean overall importance of 52 % for all consumers, and maximum contributions ranging between 57 and 98 % for most consumers (herbivore, detritivore, omnivore, planktivore, zoobenthivore and piscivore species). The mean overall importance of marsh vegetation in the dry season exceeded that of the other resources (seston, eelgrass, epiphytes and sediment) by 3.5 to ca. 6 times, thus having a disproportionate importance in the food web of this habitat. Nevertheless, as discussed in the previous section, a high dependency on sediment for filter-feeder bivalves was also observed in San Pedrito.

Compared to San Pedrito, riparian-derived carbon in the fluvio-lagoons El Vapor and El Coco

showed lower mean overall contributions for consumers in the dry season, although these contributions were significant within each of these sites. For example, from all the basal resources analyzed in El Vapor (marsh vegetation, detrital mangrove leaves, seston, epiphytes and fine particulate organic matter), marsh vegetation and detrital mangrove leaves had the highest mean overall importance for consumers (25 and 27 %), and maximum contributions of 63 to 69 % for zoobenthivore/omnivore species, and 89 % for non-selective filter feeders respectively. In El Coco, detrital mangrove leaves constituted one of the most important resources together with mangroves epiphytes and seston, showing a mean overall importance of 20 %, and highest upper limit contributions of 53 to 60 % for omnivore and detritivore species respectively.

These results suggest that fluvio-lagoons in the area may act as sinks of derived organic carbon from the dominant riparian C₃ vegetation particularly after the rainy season. According to Roach (2013), terrestrial C₃ plants can subsidize aquatic consumers after periods of high discharge or leaf litterfall that increase the amount of terrestrial material in the particulate organic matter pool. This riparian organic matter, as mentioned, is potentially carried into the water bodies by the receding flood water (Gasith and Resh 1999). In addition, observations near the study area (in the coastal lagoon of Mecoacan, Tabasco) highlight that higher mangrove leaf fall (*Avicennia germinans*) takes place during the dry season (López-Portillo and Ezcurra 1985).

The above findings indicate that few resources were dominant in the food webs of the fluvio-lagoon habitats during the dry season (e.g., riparian-derived carbon). In contrast with this, basal resources in the rainy season contributed more evenly to the diet of the consumers. This translates into an increase in resource use diversification by consumers, and corroborates the FPC in these ecosystems. Studies in Brazil (e.g., Wantzen et al. 2002; Corrêa and Uieda 2007; Figueiredo et al. 2014), Costa Rica (Winemiller 1993) and east Africa (Abrantes et al. 2014) have confirmed this increase in resource use diversification by consumers during the wet period.

In San Pedrito, the overall mean importance of marsh vegetation for consumers in the rainy season was reduced by 3.5 times from 52 to 15 %, while the importance of *V. americana*, eelgrass epiphytes and seston nearly doubled from 14 to 23 %. Also, the mean importance of sediment from a *V. americana* carpet almost doubled from 15 to 26 %, especially for zoobenthivore fishes (maximum contribution of 96 %). In El Vapor, the mean contribution of marsh vegetation and detrital mangrove leaves decreased, whereas the importance of fine particulate organic matter increased 1.4 times from 23 to 32 % for all consumers. Mangrove epiphytes and seston also increased in overall importance by ca. 1.4 times from 10-15 to 14-19 %. In El Coco, the mean importance of fine particulate organic matter increased slightly from 16 to 18 %; seston kept the same overall importance of 22 %; and detrital mangrove leaves and mangrove epiphytes decreased in importance by 1.2 and 1.4 times from 20-27 % to 17-19 %.

The above denotes changes in productivity pulses, leading to a differentiated weight in the importance of different primary producers to the food webs from one season to the other, as well as changes in the contribution of resources like sediment and fine particulate organic matter potentially transported from upstream areas. The latter resources increased in importance at the time of highest freshwater discharge and sediment suspended load. This can be attributed to the effect of strong flooding during the high-discharge periods associated with the rainy season that can flush out considerable amounts of organic matter (e.g., 80 % of the annual particulate organic matter transport, and 84 % of the annual total suspended matter transport) via the mobilization of surface soil layers and/or river bank sediments (Junk et al. 1989; Junk and Wantzen 2004, and references therein; Tamooch et al. 2014).

Interestingly, sediments accumulated in a *V. americana* carpet in San Pedrito during the rainy season, showed enriched $\delta^{13}\text{C}$ values (-14.9 to -11.6 ‰) to which several native cichlid fishes and the introduced Amazon sailfin catfish *Pterygoplichthys pardalis* related isotopically. The origin of such ^{13}C -enriched material in the vegetated sediments is unclear, and merits further consideration. Evidence from studies in other systems suggest that with the advent of the wet season, the increased mobilization of organic carbon from C_4 -enriched areas (dominated by C_4 grasses or C_4 crops) leads to relatively ^{13}C -enriched particulate organic carbon pools (Bunn et al. 1997; Marwick et al. 2014, and references therein).

In contrast with the above findings for the fluvio-lagoon sites, where the FPC seems to apply well, the factors influencing the fate and utilization of basal resources in the fringe mangrove site are different. Therefore, additional or complementary conceptual frameworks to the FPC should be taken into account for a better understanding about the main factors driving the energy fluxes in coastal floodplains, as well as in adjacent marine habitats subjected to other influences.

For instance, the fringe mangrove site is not subjected to riverine influence, but the ‘coastal flooding’ influenced by the *nortes* winds seems to be an important driver of ecosystem changes in this area by keeping the mangrove forests inundated, which under these conditions release significant amounts of particulate N and dissolved organic N (DON) to the adjacent waters, enhancing primary productivity (Rivera-Monroy et al. 1995, 1998).

Similar to the other study sites, environmental pulses lead to a differentiated importance of resources from one season to the next, and a larger isotopic niche width of consumers also prevailed during the rainy season. The main basal resources in the dry season were seston (mean of 30 %) and benthic algae (mean of 24 %) with maximum contributions ranging from 64 to 82% for zoobenthivore and omnivore species. In the rainy season, seagrass epiphytes were the most important source (mean of 26 %) with maximum contributions of 50 to 54 % for these feeding

guilds. Mangrove organic matter, with negligible contributions to the consumers in the dry season (mean of 6 %), increased in importance by ca. 3 times in the rainy season (mean of 17 %) with a maximum contribution of 48 % for zoobenthivore fish.

The higher importance of seagrass epiphytes for consumers in the rainy season might be related to an increase in their availability due to higher nutrient levels in the water column. For instance, the effluent of DON from the inundated mangrove forest (Rivera-Monroy et al. 1995) can form the bulk of derived N available to surrounding seagrasses and epiphytes (Hyndes et al. 2012). As the uptake rate of N by epiphytic algae is greater than that of seagrass leaves, the former might benefit from higher N inputs in the water column compared to seagrasses which obtain much of their nutrients from the sediments (Dixon 2004; Hyndes et al. 2012). Another potential factor positively influencing the epiphytic algae biomass is the increase in water exchange (Dixon 2004). Seagrasses, on the contrary, grow best at lower exchange rates that allow nutrient concentrations to be drawn down, slowing algal growth. In Terminos Lagoon, seagrasses and benthic algae generally show the highest biomass and productivity during the dry season when water transparency is the highest (Day et al. 1982; Reyes et al. 1994). The latter can explain the higher importance of benthic macroalgae (*Acanthophora spicifera*) and seagrasses for the food web in the dry season.

6.4 Connectivity of fish assemblages

Results from Chapter V allowed confirming that connectivity of fish assemblages between marine and low-salinity habitats in Terminos Lagoon (e.g., fringe mangrove site and El Vapor) increases at times of higher river discharge and the influence of *nortes*, whereas connectivity decreases in the dry season.

One of the observations that supported this hypothesis was the twofold increase in the number of marine species in El Vapor in the rainy season. This coincides with studies stressing that higher immigration of marine species into Terminos Lagoon takes place during this season (Ramos-Miranda et al. 2005) likely due to the influence of rainfall through the resultant freshwater runoff, which increases primary productivity and food supply (Day et al. 1982; Gracia and Soto 1990).

The total area of the convex hull (TA) metric used to evaluate the isotopic niche area encompassing all the species sampled per site indicated a considerable expansion of the niche during the rainy season at the two sites. In the fringe mangrove site, the enlarged isotopic niche indicates the different potential sources of organic matter sustaining biomass production during the rainy season (López-Rasgado et al. 2016), corresponding with the SIAR results (previous section). This translates into a higher trophic diversification and lower trophic redundancy in the

rainy season, compared to higher species packing and trophic redundancy in the dry season (Layman et al. 2007; Abrantes et al. 2014).

In El Vapor, the same phenomenon of a compressed and large isotopic niche was observed for the fish species in the dry and rainy season, but the cause of the considerable expansion in the latter season was the intrusion of marine species with extreme enriched positions along the $\delta^{13}\text{C}$ axis (-18.3 to -11 ‰). These marine species (e.g., *A. rhomboidalis*, *C. latus*, *C. nebulosus*, *M. curema*, *P. scitulus*) were recognized as recent migrants, distinguishable from those that have resided in the area for a long time and have equilibrated to the new foods (Litvin and Weinstein 2004; Herzka 2005).

The information provided by TA is ecologically relevant as it illustrates how a shrinkage and expansion in isotopic niche is related to contrasting seasonal influences and availability of resources in the area, as well as the role of species with extreme isotopic values, e.g., the marine species migrating into low-salinity habitats of Terminos Lagoon. These species play an important role by exporting energy from these habitats to Terminos Lagoon and subsequently to the Campeche Bay through their movements (Amezcuca-Linares and Yáñez-Arancibia 1980).

Nevertheless, the overlap of TA between the fringe mangrove site and El Vapor in the rainy season (from 67 to 69 ‰) can mask and overestimate the real connectivity between habitats and fish assemblages. For instance, the strong bimodality in the $\delta^{13}\text{C}$ values of fishes from the marine site in the rainy season, and the big TA of the community, indicate the emergence of two isotopically contrasting trophic pathways within this habitat (one based on seagrass epiphytes and the other on detrital mangrove leaves per results from Chapter IV) and not precisely the movement of marine species into the freshwater zone.

A further approach to assess the connectivity between fish assemblages consisted of the estimation of sample size-corrected standard ellipse areas (SEAc) of all the marine-estuarine and freshwater species from the two sites and their overlap. These ecological guilds better represent the origin of the species, and not strictly the sampling site.

In the dry season, no overlap between the SEAc of these groups was found despite eight marine-estuarine species found in the freshwater site El Vapor (*A. felis*, *Cichlasoma urophthalmum*, *Gobiomorus dormitor*, *A. mitchilli*, *Brevoortia gunteri*, *C. undecimalis*, *Achirus lineatus*, and *Poecilia mexicana*). This is probably due to the standard ellipses containing ca. 40 % of the data regardless of sample size (Batschelet 1981). Noteworthy is the fact that marine and estuarine species were isotopically on par with the freshwater fish species and basal resources therein, indicating that these species make use of the low-salinity habitats of Terminos Lagoon potentially

as feeding areas, as observed in the case of *A. mitchilli* (Ayala-Pérez et al. 1997).

In the rainy season, the number of marine-estuarine species in El Vapor doubled to 16, and one half (*C. urophthalmum*, *G. dormitor*, *Megalops atlanticus*, *Elops saurus*, *Trinectes maculatus*, *B. marinus*, *S. marina*, *D. auratus*) were isotopically on par with the $\delta^{13}\text{C}$ values of freshwater species and the basal resources in this site. The other half were identified as recent migrants, indicating that during the rainy season there is an important inflow of marine visitors which most likely make use of this habitat for feeding. The observed overlap between the SEAc's of the marine-estuarine and freshwater fishes in the rainy season, together with the increase in isotopic niche area of the marine-estuarine species by 1.4 times, corroborates the hypothesis that connectivity of fish assemblages between marine and freshwater habitats in Terminos Lagoon increases at times of higher river discharge and the influence of *nortes* winds, but the mechanisms driving fish movements at the species level still need to be studied and analyzed.

Chapter VII

Conclusions and Outlook

Conclusions and Outlook

The corroboration of this work's primary assumptions bolsters the core hypothesis that the importance of riparian-derived carbon for aquatic consumers in coastal marshes and mangrove ecosystems in the Southern Gulf of Mexico is highly variable across spatial scales, and that the periodic dry and wet conditions in the area drive the major changes in resource availability, and the connectivity of aquatic food webs.

Results add some evidence to the still poorly resolved issue of the balance of contributions from different basal resources to consumers in tropical systems (Abrantes et al. 2015), and specifically to the importance of riparian-derived carbon which has been found controversial but also of certain relevance depending on the attributes of the systems under study (Mancera-Pineda 2003; Bouillon et al. 2004; Vaslet et al. 2012; Claudino et al. 2015). Moreover, this study contributes to the comprehension of seasonal influences on coastal food webs which is crucial in understanding the dynamic function of coastal ecosystems, as well as in elucidating the adaptive nature of complex ecological systems (Abrantes et al. 2015; Yeakel et al. 2016). Finally, emphasis is given to the importance of habitat heterogeneity and seasonal environmental forces, particularly rain, in enhancing the connectivity of fish assemblages through freshwater runoff in river-influenced areas, making these sites attractive feeding areas for an array of marine species migrating into these productive systems. However, the role that wind exerts on this connectivity merits further consideration.

The relevance of lateral linkages in floodplain ecosystems (fluvio-lagoons), as stated by the FPC, was also recognized through the high contribution of riparian-derived carbon for abundant aquatic consumers (e.g., omnivore and zoobenthivore species) after the rainy season, when the receding water carries out this organic matter into the water bodies. More investigation of the potential role of insects in linking riparian and aquatic food webs is still needed (Mendoza-Carranza et al. 2010). During the rainy season, it was observed that riparian-derived carbon in the fluvio-lagoons comprised one of the resources with highest importance for insects (adult and larval stages of Ephemeroptera, Coleoptera, Hemiptera and Odonata). Despite the contribution of this resource to insects barely surpassing 50 %, its importance still needs to be evaluated in the dry season.

This work also contends that other resources presumably transported from upstream areas (longitudinal connectivity) are important in the floodplain ecosystems associated with Terminos Lagoon and in Centla Wetlands during the time of highest freshwater discharge (sediments and fine particulate organic matter).

In general, the findings from this work broaden the understanding of the dynamic role coastal vegetated habitats play in sustaining food webs and facilitating cross-habitat utilization, although it must be carefully considered the synergistic interaction of these functions with species behavior (Vaslet et al. 2012; Reis-Filho et al. 2016).

Considering that the human uses of coastal ecosystems depend on the nature of their ecological functions and services, and that direct and indirect anthropogenic activities on these ecosystems have a feedback effect on their processes and functions (Twilley et al. 1992), studies about energy fluxes in coastal vegetated habitats can serve as a baseline to reinforce their conservation and management in the face of diverse external and internal impacts (Mendoza-Carranza et al. 2010).

For example, some of the most important impacts threatening the sustainability of the Centla Wetlands Biosphere Reserve and the Terminos Lagoon protected area include species introductions, overfishing, oil and gas exploration and extraction, pollution, agriculture, livestock expansion, delta subsidence and/or relative sea-level rise, and wetland burns (Guerra-Martínez and Ochoa-Gaona 2006; Mendoza-Carranza et al. 2010; Lara-Domínguez et al. 2013).

Some results from this study already give indications of the potential degradation of these ecosystems. The elevated $\delta^{15}\text{N}$ values of some basal resources (e.g., *V. americana* and mangrove epiphytes in San Pedrito and El Coco) may reflect the influence of land derived N and eutrophication (Gooday et al. 2009). This coincides with the hypereutrophication condition reported in San Pedrito, El Coco and other water bodies of Centla Wetlands (Salcedo et al. 2012).

Another issue is the overlap in habitat use, and apparently of resources, of native species and the introduced Amazon sailfin catfish in the river-influenced areas which suggests potential for competitive interactions (Mendoza-Carranza et al. 2010; this study). Other introduced species like the Nile tilapia *Oreochromis niloticus*, the Grass carp *Ctenopharyngodon idella* and the Red-rimmed melania *Thiara tuberculata* were found in the fluvio-lagoon sites, and further research should evaluate the use of resources by these species and by native aquatic fauna.

It also remains unclear, and therefore constitutes another topic for further research, what the origin of the ^{13}C -enriched organic matter in sediments accumulating in *V. americana* carpets is, particularly during the rainy season. Future studies should also evaluate the effects of hydrology and water level changes on food assimilation and connectivity patterns in order to mitigate these impacts over estuarine communities (Abrantes et al. 2008; Claudino et al. 2015).

The use of stable isotopes for the approach of these topics can be beneficial as they serve as indicators of eutrophication ($\delta^{15}\text{N}$) to assess water quality in aquatic ecosystems (Cole et al. 2004), provide information on the origin of carbon sources and eventual external carbon subsidies

(Van den Meersche et al. 2009), and also serve as a temporally integrative tool to analyze the trophic interactions between native and non-native species, and to determine the ecological effects of these interactions (Cucherousset et al. 2012).

At a broader scale of analysis of food web organization and dynamics, stable isotope analysis is useful as it allows the measurement of entire food webs and constitutes a versatile tool for approaching questions related with niche shifts, migration patterns, resource use, among other issues (Middelburg 2014, and references therein).

Moreover, statistical models and quantitative metrics based on stable isotope data, as the ones applied in this thesis, are rapidly increasing in sophistication, allowing for the identification of general patterns of trophic organization and comparisons between systems and sampling periods (Abrantes et al. 2014; Phillips et al. 2014). These tools can be applied, for example, to compare food web structure before and after impactful events, or to monitor recovery after rehabilitation (Abrantes et al. 2014).

To be sure, in order to gain a more robust understanding of the response of populations and communities to environmental changes and disturbances, a combination of approaches is necessary.

For connectivity studies, the combination of stable isotope-based metrics (e.g., Convex hull areas and standard ellipse-based metrics) with passive acoustic telemetry and fatty acid biomarkers (Rosenblatt and Heithaus 2011; Santos-Carvalho et al. 2015; Every et al. 2017) seems promising in broadening the understanding of cross-habitat movements (e.g., between marine and estuarine/freshwater habitats). The expansion of niche-based metrics to three dimensions by including a third isotope like $\delta^{34}\text{S}$ affords another potential means to generate better estimates of how animals use their environments, which in turn can be reinforced by GIS-derived or morphometric data (Rossman et al. 2015, 2016). Also in this vein, the application of compound-specific stable isotope analysis to analyze amino acid (AA) $\delta^{13}\text{C}$ values from fish otoliths has been proven to be a powerful tool for dietary reconstruction and for tracking movement of fishes across isoscapes (McMahon et al. 2011).

With regard to the use of stable isotope mixing models, certain conditions and caveats need to be kept in mind including:

- The existence of unsampled sources compromising the validity of the results
- The influence of the geometry of the mixing space determining constrained or diffuse distributions of source contributions
- The appropriate selection of trophic enrichment factors (TEFs)

- Knowledge of isotope turnover rates of the consumer tissue sampled for an accurate interpretation of isotopic analyses (Madigan et al. 2012; Olin et al. 2013b; Abrantes et al. 2014; Phillips et al. 2014).

Because mixing models are sensitive to variation in trophic enrichment factors, sensitivity analysis is recommended by running additional models with different TEFs to determine if different scenarios would lead to different results regarding the contribution of resources to consumers (Abrantes et al. 2015). These models are best used in conjunction with other methods of dietary analysis that help ensure that all possible prey items are included in the models (reviewed in deVries et al. 2016).

Promising developments in stable isotope modeling invoke the use of prey abundance data to weight source estimates in model posterior distributions (Yeakel et al. 2011), the incorporation of DNA analysis data into model prior distributions to constrain dietary estimates (Chiaradia et al. 2014), and the incorporation of hierarchical population structure and other continuous covariates in the estimation of consumer diets (Stock and Semmens 2013) (reviewed in Phillips et al. 2014).

Also, the simultaneous application of stable isotope tools and mass-balance ecosystem models like ECOPATH can be used to provide more accurate information on the structure and function of ecosystems, and can be useful to validate results (Navarro et al. 2011).

Another exciting application is the recently developed functional framework of Cucherousset and Villéger (2015) to quantitatively assess multiple aspects of isotopic diversity by including the abundance of organisms in the food webs, allowing stable isotopes to serve as ecological indicators and as an efficient tool for assessing community changes following disturbances.

Final remarks

The present thesis illustrates that aquatic food webs in tropical coastal ecosystems in the Southern Gulf of Mexico (Centla Wetlands and Terminos Lagoon) are spatially and temporally complex.

Marshes, mangroves and seagrasses therein are conspicuous, and in some instances interconnected, enhancing the landscape heterogeneity and ecosystem services of the coastal region. These vegetated ecosystems provide important habitats for resident freshwater and estuarine aquatic fauna, as well as for marine transient species. Their role as feeding areas via riparian-derived carbon assimilation by aquatic consumers from the abundant marsh and mangrove vegetation, or via the contribution of other aquatic resources, varies across spatial and temporal scales. While the variation at the spatial scale has to do with factors like geomorphology, distance to the sea and availability of resources at each site, the temporal

variation (at the seasonal scale) relates with flood pulses (river-influenced areas) and the effect of winds (marine-influenced area).

The use of stable isotope analysis coupled with Bayesian modeling approaches (SIAR and SIBER) and the Layman's convex hull metric proved to be beneficial in identifying the observed spatial and temporal trends, as well as the connectivity of fish assemblages.

With these findings, the present work contributes to the body of research looking to address the level of contributions from different basal resources to consumers in tropical coastal regions, and the importance of riparian-derived carbon to the aquatic faunal communities in varied ecosystems and under contrasting seasonal influences.

This work represents the first effort in addressing these issues in two interconnected and priority coastal ecosystems in the Southern Gulf of Mexico, the Centla Wetlands and Terminos Lagoon, which historically have been studied separately. Previous studies related to energy fluxes and the structure of aquatic food webs in each of these areas have underestimated the range of environmental settings within the coastal region including the low-salinity portions of these systems, and little attention has been given to the influence of strong seasonal forces in the dynamics of aquatic food webs (e.g., Romo-Ríos 2013).

The results from this study provide an important knowledge base about the structure and dynamics of aquatic food webs in these spatially and temporally complex ecosystems. By considering the major seasonal forces in these systems, which are freshwater pulses and winds, this study also contributes to the understanding of the influence of these particular forces in coastal ecosystems of the area. This knowledge, together with analysis of the habitat value of different habitats in terms of the diversity of resources available for a high number of consumer types can have important management and conservation implications, particularly in the face of degrading forces on these vulnerable ecosystems.

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Annex

Annex I. Supplement material for Chapter III

Resource 1 Sample size (n) and mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SD) of fishes, crustaceans, mollusks, primary producers and other basal resources collected at the interlinked mangrove-seagrass (a), marsh- eelgrass (b), and mangrove-bare sediment habitats (c, d). Mean total length (cm Total length \pm SD) is provided for fishes, crustaceans and mollusks. Ecological guilds are provided for fishes, and feeding guilds are provided for all consumers (references at the bottom of the Table). * and Z: zooplankton samples. *: composite samples. Number of *: number of composite samples.

Species / Keys / Ecological & Feeding guilds				a) Mangrove-seagrass (MS)			
				n	Total length	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
FISHES							
<i>Acanthostracion quadricornis</i>	<i>Aq</i>	MT ¹	OV ⁴⁰	1	5.40	-13.9	5.74
<i>Achirus lineatus</i>	<i>Al</i>	MT ²	ZB ³⁴	1	12.5	-13.4	5.89
<i>Archosargus rhomboidalis</i>	<i>Arho</i>	MT ³	OV ⁴¹	3	12.7 (6.16)	-10.7 (1.52)	6.45 (0.35)
<i>Ariopsis felis</i>	<i>Af</i>	ET ³	OV ⁴²	3	30.0 (2.21)	-12.6 (2.31)	9.12 (1.09)
<i>Bagre marinus</i>	<i>Bm</i>	MT ⁴	OV ⁴²	2	28.3 (0.71)	-16.5 (0.36)	11.50 (1.56)
<i>Batrachoides goldmani</i>	<i>Bg</i>	ER ⁵	ZB ⁴⁷	4	12.2 (2.83)	-12.0 (0.52)	5.66 (0.80)
<i>Cichlasoma urophthalmum</i>	<i>Cur</i>	ER ⁵	ZB ⁴⁹	7	6.50 (1.41)	-12.0 (0.21)	6.89 (0.24)
<i>Cynoscion nebulosus</i>	<i>Cn</i>	MT ²	PV ⁵⁶	3	36.9 (1.68)	-12.3 (2.54)	10.20 (0.60)
<i>Elops saurus</i>	<i>Es</i>	MT ²	PV ⁵⁷	1	27.0	-21.3	9.44
<i>Eugerres plumieri</i>	<i>Ep</i>	MT ⁴	OV ⁴⁴	3	17.9 (1.15)	-11.6 (2.68)	8.65 (0.75)
<i>Gerres cinereus</i>	<i>Gc</i>	MT ³	OV ⁴⁴	3	7.30 (0.82)	-12.1 (0.44)	7.55 (0.04)
<i>Lutjanus griseus</i>	<i>Lg</i>	MT ⁴	PV ⁴⁶	1	23.0	-12.4	7.67
<i>Mugil curema</i>	<i>Mc</i>	MT ²	DV ²⁴	1	33.0	-10.5	6.08
<i>Sphoeroides parvus</i>	<i>Sp</i>	MT ²	ZB ⁵¹	1	20.0	-18.2	8.40
<i>Syngnathus louisianae</i>	<i>Sl</i>	MT ²	ZB ⁵²	1	27.4	-14.3	6.70
CRUSTACEANS							
<i>Aratus pisonii</i>	<i>Ap</i>		HV ¹⁸	1	3.70	-20.2	6.82
<i>Callinectes similis</i>	<i>Csim</i>		OV ³⁵	3	11.40 (4.56)	-11.6 (0.70)	5.99 (0.32)
Brachyura	Brachyura*		PL ²⁶	Z*		-15.1	3.19
<i>Lucifer faxoni</i>	<i>Lf*</i>		PL ²⁷	Z**		-18.7 (0.04)	6.54 (0.23)
<i>Panoplax depressa</i>	<i>Pdep</i>		OV ³⁷	12*	1.51 (0.21)	-12.0	4.72
<i>Penaeus duorarum</i>	<i>Pd</i>		OV ³⁸	6	7.37 (1.10)	-12.3 (1.84)	4.44 (0.45)
<i>Xiphopenaeus kroyeri</i>	<i>Xk*</i>		PL ²⁹	Z*		-14.7	3.66
MOLLUSKS							
<i>Tellina lineata</i>	<i>Tl</i>		DP-F ¹²	3*	1.80 (0.53)	-11.9	4.67
PRIMARY PRODUCERS							
<i>Acanthophora spicifera</i>	Macroalga			1		-15.3	2.96
<i>Avicennia germinans</i>	<i>Ag</i>			3		-28.8 (0.91)	2.70 (0.36)
<i>Batis maritima</i>	<i>Bmt</i>			2		-30.0 (1.17)	0.87 (0.53)
<i>Epiphytic algae (mangrove)</i>				2		-29.5 (3.80)	4.73 (1.46)
<i>Epiphytic algae (seagrass)</i>				1		-16.5	2.60
<i>Halodule wrightii</i>	<i>Hw</i>			3		-9.5 (0.14)	-1.81 (0.20)
<i>Laguncularia racemosa</i>	<i>Lr</i>			3		-27.4 (1.05)	2.56 (0.40)
Phytoplankton	Phyto			2		-12.5 (0.24)	2.40 (0.26)
<i>Rhizophora mangle</i>	<i>Rm</i>			2		-26.9 (0.26)	1.51 (0.02)
<i>Thalassia testudinum</i>	<i>Tha</i>			3		-9.4 (0.08)	-0.52 (1.86)
OTHER CARBON SOURCES							
Leaf detritus (mangrove-seagrass)				1		-19.6	0.18
FPOM (seagrass)				2		-8.5 (0.10)	1.84 (0.38)
Flocculated organic matter	Floc			1		-9.9	1.27

Resource 1 continued

Species / Keys / Ecological & Feeding guilds				b) Marsh-eelgrass (ME)					
				n	Total length	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
FISHES									
<i>Amphilophus robertsoni</i>	<i>Ar</i>	FR ⁵	PL ³¹	6	12.8 (2.94)	-28.5 (2.00)	7.03 (0.94)		
<i>Anchoa sp.</i>	<i>Asp</i> *	MT ⁶	PL ³⁰	Z ^x		-26.2	10.00		
<i>Astyanax aeneus</i>	<i>Aa</i>	FR ⁷	OV ²³	11 ^{xxx}	5.97 (1.33)	-27.9 (1.54)	8.57 (1.10)		
<i>Batrachoides goldmani</i>	<i>Bg</i>	ER ⁵	ZB ⁴⁷	3	20.4 (4.14)	-27.7 (1.00)	10.50 (0.44)		
<i>Centropomus undecimalis</i>	<i>Cun</i>	MT ⁴	PV ⁵⁵	2	41.0 (4.24)	-28.1 (0.02)	10.30 (0.45)		
<i>Cichlasoma salvini</i>	<i>Cs</i>	FR ⁵	ZB ⁴⁸	11	8.81 (4.19)	-27.5 (1.54)	9.05 (1.01)		
<i>Cichlasoma urophthalmum</i>	<i>Cur</i>	ER ⁵	ZB ⁴⁹	6	13.7 (6.74)	-28.2 (0.67)	8.11 (0.81)		
<i>Gobiomorus dormitor</i> *	<i>Gd</i> *	ET ⁷	ZB ³³	Z ^{xxx}	~1.5	-20.4 (0.10)	9.60 (0.09)		
<i>Gobiomorus dormitor</i>	<i>Gd</i>	ET ⁷	ZB ³³	3	32.5 (3.07)	-29.1 (0.17)	8.27 (0.63)		
<i>Oreochromis niloticus</i>	<i>On</i>	FR ⁸	DV ²³	1	14.0	-29.9	6.97		
<i>Parachromis managuensis</i>	<i>Pm</i>	FR ⁷	PV ⁵⁹	2	19.8 (4.38)	-29.4 (1.32)	8.33 (1.26)		
<i>Paraneetroplus bifasciatus</i>	<i>Pb</i>	FR ⁵	DV ²³	8	8.35 (1.72)	-30.7 (1.28)	8.60 (0.42)		
<i>Paraneetroplus synspilus</i>	<i>Vs</i>	FR ⁵	HV ²¹	8	11.5 (3.19)	-29.4 (1.65)	7.18 (0.80)		
<i>Petenia splendida</i>	<i>Ps</i>	FR ⁵	PV ²¹	5	18.7 (11.7)	-26.3 (2.05)	9.77 (0.99)		
<i>Pterygoplichthys pardalis</i>	<i>Pp</i>	FR ⁸	OV ⁴⁵	6	17.3 (7.90)	-30.3 (1.08)	7.02 (0.48)		
<i>Rhamdia quelen</i>	<i>Rq</i>	FR ⁷	ZB ²³	1	11.7	-28.0	10.70		
<i>Rocio octofasciata</i>	<i>Ro</i>	FR ⁵	OV ²¹	2	9.80 (0.14)	-29.3 (0.84)	7.33 (0.12)		
<i>Theraps heterospilus</i>	<i>Vh</i>	FR ⁵	HV ²⁰	6	11.3 (3.40)	-28.5 (1.55)	8.18 (1.29)		
<i>Thorichthys helleri</i>	<i>Th</i>	FR ⁵	ZB ²³	9	8.88 (4.55)	-28.7 (1.08)	8.99 (1.42)		
<i>Thorichthys meeki</i>	<i>Tme</i>	FR ⁵	ZB ⁴⁸	9	9.19 (1.89)	-28.6 (1.00)	8.36 (1.28)		
<i>Thorichthys pansionis</i>	<i>Tp</i>	FR ⁵	ZB ⁵³	7	8.21 (3.27)	-28.5 (1.59)	8.45 (1.38)		
CRUSTACEANS									
Brachyura	Brachyura*		PL ²⁶	Z ^x		-28.4	8.03		
<i>Callinectes rathbunae</i>	<i>Cr</i>		OV ³⁵	16	4.15 (3.99)	-29.1 (0.93)	7.73 (0.57)		
<i>Macrobrachium acanthurus</i>	<i>Ma</i>		OV ³⁶	9	5.97 (2.33)	-28.6 (0.64)	8.75 (0.75)		
<i>Penaes duorarum</i>	<i>Pd</i>		OV ³⁸	1	6.00	-29.2	8.40		
MOLLUSKS									
<i>Lampsilis tampicoensis</i>	<i>Lt</i>		NS-F ¹³	4	7.65 (0.97)	-32.5 (0.20)	6.19 (0.15)		
<i>Polymesoda arctata</i>	<i>Pa</i>		NS-F ¹⁴	3	5.03 (0.59)	-32.4 (0.44)	5.88 (0.67)		
<i>Rangia flexuosa</i>	<i>Rf</i>		NS-F ¹⁵	1	4.30	-32.4	6.04		
<i>Neritina reclivata</i>	<i>Nr</i>		PM-F ¹⁶			-26.9	8.14		
<i>Pomacea flagellata</i>	<i>Pf</i>		PM-F ¹⁷	3		-23.1 (1.26)	6.21 (0.33)		
PRIMARY PRODUCERS									
<i>Acrostichum aureum</i>	<i>Au</i>			3		-27.5 (0.71)	3.51 (1.00)		
<i>Cladium jamaicense</i>	<i>Cj</i>			3		-26.6 (1.30)	4.43 (0.12)		
<i>Epiphytic algae (V. americana)</i>				1		-21.8	4.39		
<i>Hymenocallis littoralis</i>	<i>Hl</i>			3		-28.6 (0.80)	4.28 (1.61)		
<i>Ipomoea purpurea</i>	<i>Ip</i>			1		-28.8	1.23		
<i>Ludwigia octovalvis</i>	<i>Lo</i>			3		-27.2 (0.72)	-1.35 (0.76)		
<i>Mimosa pigra</i>	<i>Mp</i>			3		-28.0 (0.88)	1.35 (0.37)		
<i>Phragmites australis</i>	<i>Ph</i>			3		-26.9 (0.46)	5.10 (0.54)		
Phytoplankton	Phyto			1		-21.7	4.19		
<i>Pontederia sagittata</i>	<i>Po</i>			3		-27.7 (0.27)	5.21 (0.28)		
<i>Thalia geniculata</i>	<i>Tg</i>			3		-27.1 (1.07)	4.22 (0.62)		
<i>Typha domingensis</i>	<i>Td</i>			3		-28.4 (0.77)	4.78 (0.24)		
<i>Vallisneria americana</i>	<i>Va</i>			3		-21.5 (1.16)	4.82 (0.53)		
OTHER CARBON SOURCES									
FPOM (from coarse debris)				1		-19.1	3.38		
FPOM (eelgrass)				1		-11.7	1.88		
Sediment				3		-24.9 (0.23)	2.50 (0.05)		

Resource 1 continued

Species / Keys / Ecological & Feeding guilds				c) Mangrove-bare sediments (M1)						
				n	Total length		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
FISHES										
<i>Achirus lineatus</i>	<i>Al</i>	MT ²	ZB ³⁴	1	6.10		-29.6		9.99	
<i>Anchoa hepsetus</i>	<i>Ah</i>	MT ²	PL ³⁰	9 ^x	3.67	(0.48)	-26.8		12.1	
<i>Anchoa mitchilli</i>	<i>Am</i>	MT ⁶	PL ³⁰	13 ^x	3.73	(0.34)	-27.3		11.7	
<i>Anchoa sp.</i>	<i>Asp</i> [*]	MT ⁶	PL ³⁰	Z ^{xx}			-20.1	(0.16)	9.01	(0.03)
<i>Astyanax aeneus</i>	<i>Aa</i>	FR ⁷	OV ²³	2 ^x	7.00	(0.14)	-25.6		8.50	
<i>Atherinella alvarezii</i>	<i>Av</i>	FR ⁷	OV ²³	11 ^{xxxx}	6.59	(0.62)	-26.0	(0.20)	9.82	(0.38)
<i>Bairdiella ronchus</i>	<i>Br</i>	ER ⁹	ZB ⁴⁶	28 ^{xxx}	4.10	(2.76)	-25.5	(0.82)	11.6	(0.29)
<i>Batrachoides goldmani</i>	<i>Bg</i>	ER ⁵	ZB ⁴⁷	1	11.6		-28.6		10.2	
<i>Brevoortia gunteri</i>	<i>Be</i>	MT ²	PL ³²	26 ^{xxx}	3.66	(0.35)	-26.7	(0.88)	11.3	(0.03)
<i>Cathorops aguadulce</i>	<i>Ca</i>	ET ¹⁰	OV ⁴²	4	20.4	(3.36)	-28.6	(0.27)	11.7	(0.46)
<i>Centropomus undecimalis</i>	<i>Cun</i>	MT ⁴	PV ⁵⁵	35 ^{xxx}	4.08	(1.64)	-26.4	(0.50)	11.8	(0.03)
<i>Cichlasoma urophthalmum</i>	<i>Cur</i>	ER ⁵	ZB ⁴⁹	2	21.3	(8.06)	-25.2	(2.16)	7.69	(0.22)
<i>Citharichthys spilopterus</i>	<i>Csp</i>	MT ²	ZB ⁵⁰	27 ^{xxxx}	4.75	(1.77)	-25.2	(0.87)	10.9	(0.14)
<i>Diapterus rhombeus</i>	<i>Dr</i>	MT ²	OV ⁴³	52 ^{xxx}	4.13	(0.90)	-27.3	(0.38)	11.8	(0.40)
<i>Dorosoma anale</i>	<i>Da</i>	FR ⁷	DV ²²	9	12.6	(2.67)	-30.1	(2.24)	8.96	(0.66)
<i>Dorosoma petenense</i>	<i>Dp</i>	FT ⁴	DV ²³	6	10.5	(2.06)	-28.3	(1.14)	10.6	(0.72)
<i>Gobiomorus dormitor</i>	<i>Gd</i>	ET ⁷	ZB ³³	3	12.1	(1.61)	-25.0	(1.04)	10.7	(0.36)
<i>Gobiomorus dormitor</i> [*]	<i>Gd</i> [*]	ET ⁷	ZB ³³	Z ^{xx}	~1.5		-20.0	(0.04)	7.81	(0.11)
<i>Gobionelus oceanicus</i>	<i>Go</i>	MT ²	ZB ³⁴	14 ^x	4.14	(1.63)	-24.6	(0.16)	8.04	(0.80)
<i>Oligoplites saurus</i>	<i>Os</i>	MT ²	PV ⁵⁸	2 ^x	4.9	(2.40)	-27.4		12.8	
<i>Parachromis managuensis</i>	<i>Pm</i>	FR ⁷	PV ⁵⁹	3	21	(0.93)	-27.9	(2.06)	8.51	(1.04)
<i>Petenia splendida</i>	<i>Ps</i>	FR ⁵	PV ²¹	1	18.2		-25.1		11.2	
<i>Pterygoplichthys pardalis</i>	<i>Pp</i>	FR ⁸	OV ⁴⁵	3	34.7	(2.75)	-31.9	(1.37)	7.07	(1.10)
<i>Strongylura marina</i>	<i>Sm</i>	MT ²	PV ⁶⁰	5	22.8	(6.75)	-22.7	(1.13)	12.5	(0.48)
<i>Thorichthys helleri</i>	<i>Th</i>	FR ⁵	ZB ²³	6	9.18	(2.74)	-28.5	(1.81)	10.4	(0.76)
<i>Trinectes maculatus</i>	<i>Tm</i>	MT ²	ZB ⁵⁴	5	5.70	(0.71)	-29.4	(0.35)	9.82	(0.30)
CRUSTACEANS										
<i>Aratus pisonii</i>	<i>Ap</i>		HV ¹⁸	8 ^{xxx}	1.98	(0.37)	-25.9	(1.07)	3.5	(2.13)
Brachyura	Brachyura [*]		PL ²⁶	Z ^x			-26.7		7.69	
<i>Callinectes rathbunae</i>	<i>Cr</i>		OV ³⁵	2	12.1	(2.47)	-28.2	(1.80)	8.93	(2.66)
<i>Callinectes similis</i>	<i>Csim</i>		OV ³⁵	1	13.2		-25.4		9.16	
Penaeidae	Penaeidae [*]		PL ²⁸	Z ^x			-23.6		8.85	
<i>Penaeus duorarum</i>	<i>Pd</i>		OV ³⁸	24 ^{xxxxx}	5.79	(3.55)	-27.9	(0.72)	9.67	(0.41)
Tanaidacea	Tanaidacea [*]		OV ³⁹	Z ^x			-27.6		6.89	
MOLLUSKS										
<i>Neritina reclivata</i>	<i>Nr</i>		PM-F ¹⁶				-28.0		8.46	
PRIMARY PRODUCERS										
<i>Acrostichum aureum</i>	<i>Au</i>			3			-27.2	(0.75)	2.83	(1.42)
<i>Eichornia crassipes</i>	<i>Ec</i>			3			-28.0	(0.39)	3.88	(0.68)
Epiphytic algae (mangrove)				1			-24.7		9.03	
<i>Hydrocotyle umbellata</i>	<i>Hu</i>			3			-28.7	(0.41)	1.96	(1.25)
<i>Hymenocallis littoralis</i>	<i>Hl</i>			3			-29.9	(1.28)	3.52	(0.70)
<i>Laguncularia racemosa</i>	<i>Lr</i>			3			-28.0	(0.37)	1.65	(0.15)
<i>Phragmites australis</i>	<i>Ph</i>			3			-27.4	(0.46)	3.32	(1.83)
Phytoplankton	Phyto			2			-27.2	(0.17)	5.2	(0.84)
<i>Rhizophora mangle</i>	<i>Rm</i>			3			-28.8	(0.64)	3.65	(1.08)
<i>Typha domingensis</i>	<i>Td</i>			3			-28.2	(0.49)	4.12	(0.19)
OTHER CARBON SOURCES										
FPOM (from coarse debris)				3			-27.7	(0.29)	2.47	(0.17)
Leaf detritus (mangroves)				1			-29.7		3.35	
Coarse woody debris				1			-28.8		2.57	
SPOM				2			-28.7	(0.56)	4.08	(1.41)

Resource 1 continued

Species / Keys / Ecological & Feeding guilds				d) Mangrove-bare sediments (M2)					
				n	Total length	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
FISHES									
<i>Achirus lineatus</i>	<i>Al</i>	MT ²	ZB ³⁴	3 ^x	3.67 (0.31)	-28.2		8.69	
<i>Anchoa mitchilli</i>	<i>Am</i>	MT ⁶	PL ³⁰	100 ^{xxx}	2.65 (0.28)	-27.4	(0.51)	11.00	(0.06)
<i>Ariopsis felis</i>	<i>Af</i>	ET ³	OV ⁴²	1	13.6	-23.4		11.60	
<i>Astyanax aeneus</i>	<i>Aa</i>	FR ⁷	OV ²³	14	5.68 (0.98)	-28.9	(1.35)	8.73	(0.98)
<i>Atherinella alvarezii</i>	<i>Av</i>	FR ⁷	OV ²³	87 ^{xxxxxx}	2.68 (1.00)	-29.6	(0.29)	10.30	(0.14)
<i>Brevoortia gunteri</i>	<i>Be</i>	MT ²	PL ³²	28 ^x	2.49 (0.24)	-27.5		10.50	
<i>Centropomus undecimalis</i>	<i>Cun</i>	MT ⁴	PV ⁵⁵	1	28.2	-25.3		10.30	
<i>Cichlasoma salvini</i>	<i>Cs</i>	FR ⁵	ZB ⁴⁸	2	13.3 (3.32)	-29.2	(1.40)	7.49	(0.70)
<i>Cichlasoma urophthalmum</i>	<i>Cur</i>	ER ⁵	ZB ⁴⁹	3	18.9 (3.58)	-29.3	(0.57)	8.00	(1.79)
<i>Ctenopharyngodon idella</i>	<i>Ci</i>	FR ⁸	HV ¹⁹	1	28.5	-27.2		7.98	
<i>Dorosoma anale</i>	<i>Da</i>	FR ⁵	DV ²²	1	24.8	-28.6		8.32	
<i>Dorosoma petenense</i>	<i>Dp</i>	FT ⁴	DV ²³	5	12.9 (6.38)	-25.3	(3.98)	9.99	(0.36)
<i>Gobiomorus dormitor</i> *	<i>Gd</i> *	ET ⁷	ZB ³³	Z ^x	~1.5	-29.9		9.39	
<i>Oreochromis niloticus</i>	<i>On</i>	FR ⁸	DV ²³	1	21.5	-32.9		6.48	
<i>Parachromis managuensis</i>	<i>Pm</i>	FR ⁷	PV ⁵⁹	1	18.7	-30.7		7.66	
<i>Paraneetroplus synspilus</i>	<i>Vs</i>	FR ⁵	HV ²¹	2	10.5 (0.42)	-31.1	(0.15)	6.41	(0.04)
<i>Poecilia mexicana</i>	<i>Px</i>	ER ¹¹	PL ³⁴	2	5.35 (1.34)	-27.7	(2.93)	8.25	(0.14)
<i>Pterygoplichthys pardalis</i>	<i>Pp</i>	FR ⁸	OV ⁴⁵	2	16.2 (0.49)	-31.0	(0.70)	6.72	(1.14)
<i>Rhamdia quelen</i>	<i>Rq</i>	FR ⁷	ZB ²³	2	17.5 (4.38)	-26.7	(1.95)	9.01	(1.05)
<i>Theraps heterospilus</i>	<i>Vh</i>	FR ⁵	HV ²⁰	4	9.2 (1.20)	-29.3	(2.08)	8.73	(1.13)
<i>Thorichthys helleri</i>	<i>Th</i>	FR ⁵	ZB ²³	3	10.1 (0.40)	-29.5	(0.33)	9.93	(0.55)
CRUSTACEANS									
<i>Macrobrachium acanthurus</i>	<i>Ma</i>		OV ³⁶	4	9.2 (1.38)	-28.9	(0.58)	9.09	(0.31)
MOLLUSKS									
<i>Thiara tuberculata</i>	<i>Tt</i>		DV ²⁵	x	5.08 (2.15)	-29.1		5.84	
<i>Lampsilis tampicoensis</i>	<i>Lt</i>		NS-F ¹³	17	3.8 (0.35)	-32.7	(0.39)	5.66	(0.36)
<i>Pomacea flagellata</i>	<i>Pf</i>		PM-F ¹⁷	3	2.19 (0.69)	-30.0	(3.63)	3.84	(0.42)
<i>Rangia cuneata</i>	<i>Rc</i>		NS-F ¹⁵	8 ^{xx}		-31.9	(0.36)	6.08	(0.02)
PRIMARY PRODUCERS									
<i>Cladium jamaicense</i>	<i>Cj</i>			3		-28.2	(0.30)	4.50	(0.39)
Epiphytic algae (mangrove)				1		-22.4		4.59	
<i>Hymenocallis littoralis</i>	<i>Hl</i>			3		-30.1	(0.30)	3.92	(0.12)
Creeping plant (no identified)	<i>n.i.</i>			2		-26.5	(0.01)	1.97	(1.10)
<i>Ipomea tiliacea</i>	<i>It</i>			1		-29.9		0.82	
<i>Chrysobalanus icaco</i>	<i>Cco</i>			3		-30.4	(1.73)	1.80	(0.51)
<i>Pachira aquatica</i>	<i>Pq</i>			3		-29.5	(1.07)	2.09	(0.14)
Poaceae	<i>Pce</i>			3		-28.4	(0.87)	4.70	(0.85)
<i>Phragmites australis</i>	<i>Ph</i>			3		-28.0	(0.49)	4.31	(0.48)
Phytoplankton	Phyto			1		-26.7		3.72	
<i>Rhizophora mangle</i>	<i>Rm</i>			3		-30.4	(0.58)	3.72	(0.58)
<i>Thalia geniculata</i>	<i>Tg</i>			3		-27.0	(0.81)	4.08	(0.53)
<i>Typha domingensis</i>	<i>Td</i>			3		-28.1	(0.78)	3.77	(0.58)
OTHER CARBON SOURCES									
FPOM (from coarse debris)				1		-26.2		5.98	
Leaf detritus (mangroves)				1		-28.1		3.05	

Ecological guilds: FR, freshwater resident; ER, estuarine resident; FT, freshwater transient; ET, estuarine transient; MT, marine transient. References (see also page): ¹Yáñez-Arancibia and Lara-Domínguez (1983), ²Sanvicente-Añorve et al. (2011), ³Vaslet et al. (2012), ⁴Nordlie (2003), ⁵Miller (1966), ⁶Ayala-Pérez et al. (1997), ⁷Winemiller et al. (2011), ⁸Muchlisin (2012), ⁹Reyes et al. (1994), ¹⁰Froese and Pauly (2012), ¹¹Gómez-González et al. (2012).

Feeding guilds: DP-F, deposit feeders; NS-F, non-selective filter feeders; PM-F, periphyton-macrophyte feeders; HV, herbivores; DV, detritivores; PL, planktivores; OV, omnivores; ZB, zoobenthivores; PV, piscivores. References: ¹²Arruda et al. (2003), ¹³Burlakova and Karatayev (2010), ¹⁴Gracia and Díaz (2002), ¹⁵LaSalle and de la Cruz (1985), ¹⁶Lane (1991), ¹⁷Ruehl (2010), ¹⁸Beever III et al. (1979), ¹⁹Cudmore and Mandrak (2004), ²⁰Gutiérrez-Franco (2012), ²¹Valtierra-Vega and Schmitter-Soto (2000), ²²Smoot and Findlay (2010), ²³Pease (2010), ²⁴Elliot et al. (2007), ²⁵Sánchez et al. (2012), ²⁶Hinz et al. (2001), ²⁷Lee et al. (1992), ²⁸Harvey et al. (2002), ²⁹Fehlauer and Freire (2002), ³⁰Allen et al. (1995), ³¹Froese and Pauly (2012), ³²Castillo-Rivera et al. (1996), ³³Bachelier et al. (2004), ³⁴Barletta and Blaber (2007), ³⁵Gómez-Luna et al. (2009), ³⁶Albertoni et al. (2003), ³⁷This study, according to the obtained trophic level, ³⁸Odum and Heald (1972), ³⁹Macdonald et al. (2010), ⁴⁰Vega-Cendejas et al. (1994), ⁴¹Nagelkerken et al. (2006), ⁴²Kobelkowsky and Castillo-Rivera (1995), ⁴³Chaves and Otto (1998), ⁴⁴Arenas-Granados and Acero (1992), ⁴⁵Martelo et al. (2008), ⁴⁶Vega-Cendejas and Arreguín-Sánchez (2001), ⁴⁷Gosline (1996), ⁴⁸Cochran (2008), ⁴⁹Martínez-Palacios and Ross (1988), ⁵⁰Castillo-Rivera et al. (2000), ⁵¹Moncreiff and Sullivan (2001), ⁵²Motta et al. (1995), ⁵³Artigas (2006), ⁵⁴Derrick and Kennedy (1997), ⁵⁵Ferreira and Petrere Jr. (2009), ⁵⁶Ruehl (2004), ⁵⁷Nagelkerken and van der Velde (2004), ⁵⁸Randall (1967), ⁵⁹Barlow (1974), ⁶⁰Murdy et al. (1997).

Resource 2 Mean trophic level (\pm SD) of consumers' feeding guilds and species within feeding guilds (pooled data from the four study sites). * Refers to zooplankton.

Feeding guild	n	Trophic level	Min	Max
DEPOSIT FEEDERS (DP-F)	1	2	2	2
MOLLUSKS	1			
<i>Tellina lineata</i>	1	2	2	2
NON-SELECTIVE FILTER FEEDERS (NS-F)	22	2.04 (0.14)	1.70	2.27
MOLLUSKS	22			
<i>Lampsilis tampicoensis</i>	15	2.05 (0.11)	1.92	2.27
<i>Polymesoda arcuata</i>	3	1.89 (0.20)	1.70	2.09
<i>Rangia cuneata</i>	3	2.17 (0.01)	2.16	2.17
<i>Rangia flexuosa</i>	1	1.93	1.93	1.93
PERIPHYTON-MACROPHYTE FEEDERS (PM-F)	8	1.88 (0.37)	1.39	2.55
MOLLUSKS	8			
<i>Neritina reclinata</i>	2	2.28 (0.39)	2	2.55
<i>Pomacea flagellata</i>	6	1.75 (0.28)	1.39	2.04
HERBIVORES (HV)	23	2.27 (0.77)	-0.10	3.23
CRUSTACEANS	4			
<i>Aratus pisonii</i>	4	1.14 (1.17)	-0.10	2.63
FISHES	19			
<i>Ctenopharyngodon idella</i>	1	2.73	2.73	2.73
<i>Theraps heterospilus</i>	8	2.79 (0.40)	2.20	3.23
<i>Paraneetroplus synspilus</i>	10	2.27 (0.21)	1.90	2.69
DETRITIVORES (DV)	32	2.55 (0.41)	1.88	3.43
FISHES	31			
<i>Dorosoma anale</i>	10	2.22 (0.28)	1.88	2.83
<i>Dorosoma petenense</i>	10	2.90 (0.39)	2.23	3.43
<i>Mugil curema</i>	1	2.41	2.41	2.41
<i>Oreochromis niloticus</i>	2	2.25 (0.06)	2.21	2.28
<i>Paraneetroplus bifasciatus</i>	8	2.69 (0.12)	2.44	2.80
MOLLUSKS	1			
<i>Thiara tuberculata</i>	1	2.10	2.10	2.10
PLANKTIVORES (PL)	34	2.60 (0.58)	1.56	3.62
CRUSTACEANS	7			
Brachyura*	3	1.95 (0.50)	1.56	2.52
<i>Lucifer faxoni</i> *	2	2.55 (0.07)	2.50	2.60
Penaeidae*	1	2.11	2.11	2.11
<i>Xiphopenaeus kroyeri</i> *	1	1.70	1.70	1.70
FISHES	27			
<i>Anchoa hepsetus</i>	1	3.07	3.07	3.07
<i>Anchoa mitchilli</i>	4	3.44 (0.32)	2.96	3.62
<i>Anchoa sp.</i> *	3	2.48 (0.55)	2.16	3.11
<i>Amphilophus robertsoni</i>	6	2.22 (0.27)	1.94	2.69
<i>Brevoortia gunteri</i>	5	2.92 (0.33)	2.61	3.48
<i>Gobiomorus dormitor</i> *	6	2.62 (0.63)	1.79	3.14
<i>Poecilia mexicana</i>	2	2.80 (0.04)	2.78	2.83

Resource 2 continued

Feeding guild	n	Trophic level	Min	Max
OMNIVORES (OV)	100	2.61 (0.54)	1.24	4.33
CRUSTACEANS	43			
<i>Callinectes rathbunae</i>	6	2.33 (0.40)	1.58	2.69
<i>Callinectes similis</i>	4	2.34 (0.12)	2.21	2.48
<i>Macrobrachium acanthurus</i>	13	2.83 (0.24)	2.35	3.17
<i>Panoplax depressa</i>	1	2.01	2.01	2.01
<i>Penaeus duorarum</i>	18	2.19 (0.23)	1.80	2.63
Tanaidacea*	1	1.54	1.54	1.54
FISHES	57			
<i>Acanthostracion quadricornis</i>	1	2.31	2.31	2.31
<i>Archosargus rhomboidalis</i>	3	2.52 (0.10)	2.41	2.60
<i>Ariopsis felis</i>	4	3.43 (0.36)	3.11	3.80
<i>Astyanax aeneus</i>	11	2.72 (0.42)	2.01	3.52
<i>Atherinella alvarezi</i>	10	3.04 (0.48)	2.35	3.47
<i>Bagre marinus</i>	2	4.01 (0.46)	3.69	4.33
<i>Cathorops aguadulce</i>	4	2.95 (0.13)	2.77	3.09
<i>Diapterus rhombeus</i>	3	2.99 (0.18)	2.79	3.15
<i>Eugerres plumieri</i>	3	3.17 (0.22)	2.97	3.41
<i>Gerres cinereus</i>	3	2.85 (0.01)	2.84	2.86
<i>Pterygoplichthys pardalis</i>	11	2.07 (0.38)	1.24	2.59
<i>Rocio octofasciata</i>	2	2.31 (0.04)	2.29	2.34
ZOOBENTHIVORES (ZB)	103	2.67 (0.37)	1.73	3.48
FISHES	103			
<i>Achirus lineatus</i>	3	2.58 (0.31)	2.36	2.93
<i>Bairdiella ronchus</i>	4	2.99 (0.14)	2.87	3.18
<i>Batrachoides goldmani</i>	8	2.68 (0.51)	1.95	3.36
<i>Cichlasoma salvini</i>	13	2.78 (0.29)	2.27	3.25
<i>Cichlasoma urophthalmum</i>	18	2.53 (0.36)	1.73	3.34
<i>Citharichthys spilopterus</i>	4	2.74 (0.04)	2.69	2.78
<i>Gobiomorus dormitor</i>	6	2.63 (0.14)	2.48	2.80
<i>Gobionelus oceanicus</i>	3	2.07 (0.29)	1.73	2.26
<i>Rhamdia quelen</i>	3	3.12 (0.27)	2.81	3.31
<i>Sphoeroides parvus</i>	1	3.10	3.10	3.10
<i>Syngnathus louisianae</i>	1	2.60	2.60	2.60
<i>Thorichthys helleri</i>	18	2.80 (0.40)	2.16	3.48
<i>Thorichthys meeki</i>	9	2.62 (0.38)	2.20	3.13
<i>Thorichthys pasionis</i>	7	2.64 (0.41)	2.06	3.37
<i>Trinectes maculatus</i>	5	2.40 (0.09)	2.28	2.51
PISCIVORES (PV)	31	3.00 (0.45)	1.81	3.82
FISHES	31			
<i>Centropomus undecimalis</i>	8	3.10 (0.16)	2.99	3.40
<i>Cynoscion nebulosus</i>	3	3.64 (0.18)	3.47	3.82
<i>Elops saurus</i>	1	3.40	3.40	3.40
<i>Lutjanus griseus</i>	1	2.88	2.88	2.88
<i>Oligoplites saurus</i>	1	3.28	3.28	3.28
<i>Parachromis managuensis</i>	6	2.31 (0.42)	1.81	2.87
<i>Petenia splendida</i>	6	2.99 (0.27)	2.72	3.36
<i>Strongylura marina</i>	5	3.19 (0.14)	2.97	3.30

The references used to assign the feeding guilds to each species were referred in Resource 1

Refereres for Annex I (Resource 1)

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Annex II. Supplement material for Chapter IV

Resource 1 Number of samples of basal resources per category and species (n.i. denotes not identified), in each sampling site and season

	Dry				Rainy				Total
	S1	S2	S3	S4	S1	S2	S3	S4	
Marine seston				2				2	4
Estuarine-freshwater seston	1	1	4		1	1	1		9
Marginal vegetation									
C ₃ plants									
<i>Avicennia germinans</i>				3			3	3	9
<i>Laguncularia racemosa</i>			3	3			3	3	12
<i>Rhizophora mangle</i>		3	3	2		3	3	3	17
<i>Acrostichum aureum</i>	3		3		3	3			12
<i>Batis maritima</i>				2				3	5
<i>Chrysobalanus icaco</i>		3				3			6
<i>Cladium jamaicense</i>	3	3			3	3	3		15
<i>Dalbergia brownei</i>					3				3
Herbaceous plant n.i.		2							2
<i>Hydrocotyle umbellata</i>			3			3	3		9
<i>Hymenocallis littoralis</i>	3	3	3		3	1			13
<i>Ipomoea purpurea</i>	1								1
<i>Ipomoea tilacea</i>		1	3			3			7
<i>Ludwigia octovalvis</i>	3					3			6
<i>Mimosa pigra</i>	3				3	3			9
Herbaceous plant n.i.					3		3		6
<i>Pachira aquatica</i>		3			3	3			9
<i>Phragmites australis</i>	3	3	3		6	3	6		24
Poaceae n.i.		3				2			5
<i>Pontederia sagittata</i>	3					3			6
<i>Senna hayesiana</i>					3				3
<i>Thalia geniculata</i>	3	3			3	3			12
<i>Typha domingensis</i>	3	3	3		3	3	3		18
C ₄ plants									
Poaceae n.i.								3	3
Seagrasses									
<i>Halodule wrightii</i>				3				3	6
<i>Thalassia testudinum</i>				3				3	6
Eelgrass									
<i>Vallisneria americana</i>	3				3				6
Other SAV									
<i>Cabomba palaeformis</i>						3			3
Floating vegetation (free floating, free floating submerged, & floating leaved-rooted)									
<i>Eichhornia crassipes</i>			3		3	3	3		12
<i>Nelumbo lutea</i>						3			3
<i>Pistia stratiotes</i>					3	3	3		9
<i>Salvinia auriculata</i>						3	3		6
<i>Salvinia minima</i>					3				3
<i>Utricularia sp.</i>					1				1
Benthic algae									
<i>Acanthophora spicifera</i>				1					1
Cyanobacteria								3	3
Epiphytes									
Mangrove roots		1	1	5		4	1	3	15
Seagrass leaves				1				1	2
Eelgrass leaves	1				1				2
Leaf mangrove detritus		1	1	1		1	2	1	7

Resource 1 continued

	Dry				Rainy				Total
	S1	S2	S3	S4	S1	S2	S3	S4	
Coarse woody debris			1			1	1		3
Fine particulate organic matter on the surface of									
Seagrass leaves (FPOMs)				2				1	3
Eelgrass leaves (FPOMe)	1								1
Coarse debris (FPOMc)	1	1	3		2	2	1		10
Flocculated organic matter (Floc)				1				3	4
Sediment									
Seagrass bed								1	1
Eelgrass bed	3				2				5
Non-vegetated bottoms					1	4	1		6
Total									343

Resource 2 Median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feeding guilds and constituent species (divided into main taxonomic groups) per site and season (species not classified into feeding guilds are shown at the end of the table). The total number of samples (n Tot) per each species across sites and seasons is shown, together with the number of compound samples obtained from the total in parenthesis. Ecological guilds are shown for fishes in the column 'EG' (*A* anadromous, *FR* freshwater resident, *FT* freshwater transient, *ER* estuarine resident, *ET* estuarine transient, *MT* marine transient). All references for feeding and ecological guilds are denoted by superscripts.

		$\delta^{13}\text{C}$								$\delta^{15}\text{N}$								n Tot
		S1		S2		S3		S4		S1		S2		S3		S4		
EG		Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	
Deposit-feeders (DPF)									-11.9								4.7	1
Mollusks	<i>Tellina lineata</i> ¹								-11.9								4.7	1
Non-selective filter feeders (NSF)		-32.5	-32.9	-32.5	-33.3				-18.2	6.1	5.9	5.9	6.0				4.9	
Poriphera	Poriphera ²								-18.2								4.9	3
Mollusks	Bivalvia larvae ²								-13.8								2.7	1 (1)
Mollusks	<i>Cyrtoneaias tampicoensis</i> ³	-32.5	-33.4	-32.9	-33.3					6.2	5.8	5.6	5.7					29 (2)
Mollusks	<i>Polymesoda arctata</i> ⁴	-32.5	-32.6							5.8	6.2							9
Mollusks	<i>Rangia cuneata</i> ⁵		-33.1	-32.2	-33.6						5.9	6.1	6.2					10 (3)
Mollusks	<i>Rangia flexuosa</i> ⁵	-32.4								6.0								1
Crustaceans	<i>Balanus sp.</i> ²		-33.5						-18.4		7.6						6.4	2 (2)
Periphyton-macrophyte feeders (PMF)		-23.5	-29.3	-29.1	-32.4	-28.0	-30.2			6.4	7.7	3.8	5.6	8.5	7.5			
Mollusks	<i>Neritina reclivata</i> ⁶	-26.9	-28.4			-28.0	-30.2			8.1	8.1			8.5	7.5			6 (6)
Mollusks	<i>Pomacea flagellata</i> ⁷	-22.5	-30.3	-29.1	-32.4					6.4	5.3	3.8	5.6					8
Herbivores (HV)		-29.5	-28.7	-29.5	-31.9	-26.4	-26.0	-20.2	-18.7	7.2	9.4	8.0	8.3	3.7	6.5	6.8	3.2	
Crustaceans	<i>Aratus pisonii</i> ⁸					-26.4	-25.9	-20.2	-18.7					3.7	3.5	6.8	3.2	9 (3)
Fishes	<i>Ctenopharyngodon idella</i> ⁹			-27.2			-22.6						8.0		6.5			2
Fishes	<i>Paraneetroplus synspilus</i> ¹⁰			-31.1	-31.9		-27.6			7.1	8.8	6.4	8.9		8.7			21
Fishes	<i>Theraps heterospilus</i> ¹¹			-29.2	-31.9		-28.6			8.1	9.6	9.1	7.7		8.3			13
Detritivores (DV)		-30.0	-28.7	-28.6	-30.5	-28.6	-30.3	-10.5	-24.9	8.6	8.8	9.4	7.8	9.2	7.6	6.1	6.5	
Mollusks	<i>Thiara tuberculata</i> ¹²			-29.1	-30.8								5.8	6.6				4 (4)
Crustaceans	Isopoda ²								-15.8								6.5	3 (3)

Resource 2 continued

			$\delta^{13}\text{C}$								$\delta^{15}\text{N}$								n Tot	
			S1		S2		S3		S4		S1		S2		S3		S4			
EG			Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy		
Fishes	<i>Dorosoma anale</i> ¹³	FR ⁶³		-28.2	-28.6			-31.3	-30.4			8.7	8.3			9.0	7.0			14
Fishes	<i>Dorosoma petenense</i> ¹⁴	FT ⁶⁴			-22.7	-30.2			-28.2	-30.3			10.0	9.0	10.8	7.4				22 (1)
Fishes	<i>Mugil curema</i> ¹⁵	MT ⁶⁵		-29.1		-13.4			-15.2	-10.5	-32.5		8.9		6.8		8.8	6.1	6.5	12
Fishes	<i>Oreochromis niloticus</i> ¹⁴	FR ⁶²	-29.9		-32.9	-34.4			-33.0			7.0		6.5	6.9		7.0			4
Fishes	<i>Paraneetroplus bifasciatus</i> ¹⁴	FR ⁶³	-30.1									8.7								8
Omnivores (OV)			-29.0	-29.0	-29.4	-30.2	-27.6	-27.8	-11.9	-19.7	7.8	8.3	9.1	8.6	9.6	7.5	6.6	5.9		
Crustaceans	Amphipoda ²																		1.9	1 (1)
Crustaceans	Tanaidacea ²						-27.6									6.9				1 (1)
Crustaceans	<i>Farfantepenaeus duorarum</i> ¹⁶		-29.2					-27.7	-12.3	-11.8	-15.6	8.4				9.4	2.0	4.4	3.1	21 (7)
Crustaceans	<i>Macrobrachium acanthurus</i> ¹⁷		-28.6	-29.0	-28.9	-31.6		-27.3				8.9	8.9	9.1	7.3		8.0			22 (8)
Crustaceans	<i>Procambarus sp.</i> ¹⁸					-32.1									7.5					1 (1)
Crustaceans	<i>Clibanarius vittatus</i> ¹⁹										-19.1								4.4	3
Crustaceans	<i>Libinia emarginata</i> ²⁰										-22.3								-2.3	1
Crustaceans	<i>Panoplax depressa</i> ²¹									-12.0									4.7	1 (1)
Crustaceans	<i>Callinectes rathbunae</i> ²²		-29.0	-27.1		-29.7	-28.2	-27.8			-21.2	7.7	6.8		7.7	8.9	6.5		4.9	16 (1)
Crustaceans	<i>Callinectes sapidus</i> ²²																		4.8	1
Crustaceans	<i>Callinectes similis</i> ²²						-25.4			-11.9					9.2			6.0		4
Fishes	<i>Acanthostracion quadricornis</i> ²³	MT ⁶⁶									-13.9								5.7	1
Fishes	<i>Archosargus rhomboidalis</i> ²⁴	MT ⁶⁷				-11.0					-11.3	-26.2			5.9			6.6	10.0	6
Fishes	<i>Ariopsis felis</i> ²⁵	ET ⁶⁷			-23.4	-16.3				-11.8				11.6	10.0				8.6	5
Fishes	<i>Astyanax aeneus</i> ¹⁴	FR ⁶⁸	-27.9	-29.8	-29.4	-29.9	-25.6	-27.2				8.1	7.0	8.3	8.4	8.5	7.5			22 (8)
Fishes	<i>Atherinella alvarezi</i> ¹⁴	FR ⁶⁸		-29.5	-29.6	-31.3	-25.9	-28.9					10.2	10.3	8.5	10.2	9.3			20 (12)
Fishes	<i>Atherinella sp.</i> ²⁶			-32.0								10.1								1
Fishes	<i>Bagre marinus</i> ²⁵	MT ⁶⁴				-28.0				-16.5				10.3				11.5		4
Fishes	<i>Cathorops aguadulce</i> ²⁵	FT ⁵¹					-28.6									11.8				4
Fishes	<i>Diapterus auratus</i> ²⁷	MT ⁶⁴		-30.3		-31.9		-28.6		-13.0		8.1		10.7		9.9		6.8		6
Fishes	<i>Diapterus rhombeus</i> ²⁸	MT ⁶⁵					-27.3								11.9					3 (3)
Fishes	<i>Eucinostomus gula</i> ²⁷	MT ⁶⁵								-14.1									6.7	1
Fishes	<i>Eugerres plumieri</i> ²⁷	MT ⁶⁴					-26.4	-10.7								10.3	8.5			5
Fishes	<i>Gerres cinereus</i> ²⁷	MT ⁶⁷						-12.1	-11.9								7.5	8.0		4
Fishes	<i>Hyporhamphus mexicanus</i> ³⁰	FR ⁶³		-25.6		-30.2		-26.8				6.0		9.2		8.7				12 (2)
Fishes	<i>Ictalurus furcatus</i> ³¹	FT ⁶⁹				-29.9								9.4						8

Resource 2 continued

		$\delta^{13}\text{C}$								$\delta^{15}\text{N}$								n Tot	
		S1		S2		S3		S4		S1		S2		S3		S4			
EG		Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy		
Fishes	<i>Lagodon rhomboides</i> ²³	MT ⁶⁴							-32.0								9.7	3	
Fishes	<i>Pterygoplichthys pardalis</i> ³²	FR ⁶²	-30.0	-14.7	-31.0	-33.2	-32.4	-30.4		7.2	6.5	6.7	6.2	7.3	6.0			30	
Fishes	<i>Rocio octofasciata</i> ¹⁰	FR ⁶³	-29.3							7.3								2	
Fishes	<i>Theraps lentiginosus</i> ³³	FR ⁷⁰		-31.5							9.1							3	
Planktivores (PL)			-28.4	-32.1	-27.5	-29.7	-26.1	-27.3	-16.9	-17.0	8.0	10.0	10.5	9.4	9.8	7.0	5.0	7.9	
Jellyfish	Jellyfish ³⁴								-24.1									10.1	1 (1)
Crustaceans	Brachyura larvae ³⁵		-28.4				-26.7		-15.1	-16.5	8.0			7.7		3.2	3.5	4 (4)	
Crustaceans	Penaeidae larvae ³⁶						-23.6	-25.4		-16.7				8.8	7.0		7.0	5 (5)	
Crustaceans	<i>Xiphopenaeus kroyeri</i> larvae ³⁷									-14.7						3.7		1 (1)	
Crustaceans	<i>Lucifer faxoni</i> larvae ³⁸									-18.7						6.5		2 (2)	
Fishes	<i>Amphilophus robertsoni</i> ¹⁰	FR ⁶³	-29.2		-30.2					6.8			9.0					8	
Fishes	<i>Anchoa hepsetus</i> ³⁹	MT ⁶⁵				-26.8								12.1				1 (1)	
Fishes	<i>Anchoa mitchilli</i> ³⁹	MT ⁷¹		-32.1	-27.0		-27.3	-32.2		-16.4		10.6	10.9		11.7	10.1		9.1	9 (4)
Fishes	<i>Anchoa sp. larvae</i> ³⁹	MT ⁷¹	-26.2				-20.1		-21.5		10.0			9.0		10.4		4 (4)	
Fishes	<i>Brevoortia gunteri</i> ⁴⁰	MT ⁶⁵			-27.5		-27.2						10.5		11.2			5 (4)	
Fishes	Clupeidae ⁴¹			-32.4								9.5						1	
Fishes	<i>Eucinostomus gula</i> larvae ²⁹	MT ⁶⁵								-18.4							8.3	1 (1)	
Fishes	<i>Floridichthys carpio</i> ⁴²	ER ⁶⁷								-12.4							3.5	3	
Fishes	<i>Gambusia sexradiata</i> ⁴³	FR ⁷²				-29.7							9.4					6 (3)	
Fishes	<i>Gobiomorus dormitor</i> larvae ⁴⁴	ET ⁶⁸	-20.5		-29.9		-20.0				9.6		9.4		7.8			6 (6)	
Fishes	<i>Harengula clupeiola</i> ⁴⁵	MT ⁷³								-17.9							8.0	2	
Fishes	<i>Poecilia mexicana</i> ⁴³	ER ⁷⁴		-31.2	-27.7					-17.2		8.4	8.2				2.9	4	
Zoobenthivores (ZB)			-28.4	-15.0	-29.2	-30.1	-26.2	-30.2	-12.1	-29.7	8.8	6.7	8.7	9.2	10.4	8.6	6.7	7.2	
Fishes	<i>Achirus lineatus</i> ⁴³	MT ⁶⁵			-28.2		-29.6		-13.4	-12.5			8.7		10.0		5.9	5.8	4 (1)
Fishes	<i>Bairdiella ronchus</i> ⁴²	ER ⁷⁵		-31.6			-25.3	-30.7		-31.9		9.5			11.7	11.6		7.8	10 (3)
Fishes	<i>Batrachoides goldmani</i> ^{46a}	ER ⁶³	-27.2				-28.6				10.6				10.2				4
Fishes	<i>Cichlasoma salvini</i> ⁴⁷	FR ⁶³	-27.3	-11.8	-29.2	-32.8					9.1	6.8	7.5	8.8					21
Fishes	<i>Cichlasoma urophthalmum</i> ⁴⁸	ER ⁶³	-28.2	-18.3	-29.2	-30.2	-25.2	-19.2	-11.9	-30.7	7.8	5.2	7.2	7.3	7.7	7.8	7.0	8.0	35
Fishes	<i>Citharichthys spilopterus</i> ⁴⁹	MT ⁶⁵					-24.8			-14.7					11.0			6.6	5 (4)
Fishes	<i>Gobiomorus dormitor</i> ⁴⁴	ET ⁶⁸	-29.1	-17.6		-29.6	-24.5				7.9	6.4		9.0	10.7				10 (1)

Resource 2 continued

			$\delta^{13}\text{C}$								$\delta^{15}\text{N}$								n Tot
			S1		S2		S3		S4		S1		S2		S3		S4		
EG			Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	
Fishes	<i>Gobionellus oceanicus</i> ⁴³	MT ⁶⁵					-24.8								9.2			2.3	4 (3)
Fishes	<i>Microphis lineatus</i> ⁵⁰	A ⁶⁵																4.6	1
Fishes	<i>Ophisternon aenigmaticum</i> ⁵¹	FR ⁷⁶				-31.3							9.2						3 (1)
Fishes	<i>Opsanus beta</i> ^{46b}	MT* ⁶⁴							-12.1	-13.0							5.9	5.6	5
Fishes	<i>Orthoprichthys chrysoptera</i> ²³	MT ⁶⁴																8.6	1
Fishes	<i>Prionotus scitulus</i> ⁵²	MT ⁶⁵				-15.0							9.7					9.8	3
Fishes	<i>Prionotus tribulus</i> ⁵²	ET ⁶⁷																6.0	1
Fishes	<i>Rhamdia quelen</i> ¹⁴	FR ⁶⁸	-28.0		-26.8			-29.7			10.7		9.0			9.0			4
Fishes	<i>Sphoeroides parvus</i> ⁴¹	MT ⁶⁵							-18.2	-24.4							8.4	7.9	3
Fishes	<i>Sphoeroides testudineus</i> ⁴²	MT ⁶⁵								-13.1								5.7	1
Fishes	<i>Syngnathus louisianae</i> ⁵³	MT ⁶⁵								-14.3							6.7		1
Fishes	<i>Thorichthys helleri</i> ¹⁴	FR ⁶³	-28.4	-15.4	-29.3	-28.8	-29.2	-32.3			9.2	5.8	9.8	10.1	10.6	7.2			32
Fishes	<i>Thorichthys meeki</i> ⁴⁷	FR ⁶³	-28.7								7.5								9
Fishes	<i>Thorichthys pasonis</i> ⁵⁴	FR ⁶³	-29.1	-10.4		-31.5					8.3	6.6		6.3					11
Fishes	<i>Trinectes maculatus</i> ⁵⁵	MT ⁶⁵				-30.4	-29.4	-32.0						9.4	9.8	9.2			7
Piscivores (PV)			-28.1	-24.5	-28.0	-18.7	-25.3	-26.0	-12.4	-25.2	9.4	9.6	9.0	8.8	11.9	9.8	9.7	9.1	
Fishes	<i>Caranx hippos</i> ⁴⁵	MT ⁶⁴		-24.1		-18.7						12.1		13.2					5
Fishes	<i>Caranx latus</i> ⁴⁵	MT ⁶⁴				-17.3								10.1				9.2	3
Fishes	<i>Centropomus parallelus</i> ⁵⁶	MT ⁶⁵		-28.7				-25.5		-16.9		9.0				9.1		8.1	5
Fishes	<i>Centropomus undecimalis</i> ⁵⁶	MT ⁶⁴	-28.1	-23.4	-25.3		-26.3	-27.3			10.3	10.4	10.3		11.9	9.8			12
Fishes	<i>Cynoscion nebulosus</i> ⁵⁷	MT ⁶⁵				-12.0				-11.0	-33.2			8.8			10.2	9.3	5
Fishes	<i>Elops saurus</i> ⁵⁸	MT ⁶⁵				-29.5				-21.3				8.8			9.4		2
Fishes	<i>Lutjanus griseus</i> ⁴²	MT ⁶⁴				-15.3				-12.4				8.2			7.7		5
Fishes	<i>Megalops atlanticus</i> ⁴³	MT ⁶⁴		-29.2		-32.8						9.6		7.8					7
Fishes	<i>Oligoplites saurus</i> ⁵⁹	MT ⁶⁵					-27.4								12.8				1
Fishes	<i>Parachromis managuensis</i> ⁶⁰	FR ⁶⁸	-29.4		-30.7		-28.9				8.3		7.7		8.0				6
Fishes	<i>Petenia splendida</i> ¹⁰	FR ⁶³	-25.6	-11.8			-25.1				9.4	6.4			11.2				9
Fishes	<i>Strongylura marina</i> ⁶¹	MT ⁶⁵				-29.6	-22.8							10.1	12.8				6

N Total of species classified into feeding guilds

699

Resource 2 continued

	EG	$\delta^{13}\text{C}$								$\delta^{15}\text{N}$								n Tot
		S1		S2		S3		S4		S1		S2		S3		S4		
		Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	
Samples not classified into feeding guilds																		
Insects	<i>Belostoma sp.</i> (Hemiptera)				-28.8								7.2				1	
Insects	Blattodea															5.1	1	
Insects	<i>Brachycercus sp.</i> (Ephemeroptera)				-34.8								5.7				1 (1)	
Insects	Ceratopogonidae (Diptera)				-33.0								5.8				1	
Insects	Coleoptera		-22.4						-30.1				4.2			3.5	2 (1)	
Insects	Diptera		-30.8										5.2				1 (1)	
Insects	Ephemeroptera		-28.2		-36.1				-26.7				1.1	6.2		6.5	4 (2)	
Insects	<i>Ephoron sp.</i> (Ephemeroptera)				-35.8									6.1			2 (2)	
Insects	Hemiptera		-28.2						-29.4				5.6			4.8	2 (2)	
Insects	Lampyridae (Coleoptera)		-26.5										4.7				1 (1)	
Insects	<i>Libellula sp.</i> (Odonata)				-32.4									7.1			1	
Insects	<i>Phyllocycla sp.</i> (Odonata)				-34.3									6.9			1	
Insects	<i>Tropisternus sp.</i> (Coleoptera)				-33.9									5.7			1	
Insects	Insecta n.i.		-32.2										9.1				1	
Mollusks	Gastropod n.i.								-30.2							7.3	1	
Mollusks	Gastropod n.i.								-27.1							8.7	1	
Crustacean	<i>Alpheus sp.</i>								-11.7							3.6	1	
N Total of species not classified into feeding guilds																	23	
N Total of all species																	722	

* Some populations are permanent residents in estuaries (Nordlie 2003).

Feeding guilds' references: ¹ Arruda et al. (2003), ² Macdonald et al. (2010), ³ Burlakova and Karatayev (2010), ⁴ Gracia and Díaz (2002), ⁵ LaSalle and de la Cruz (1985), ⁶ Lane (1991), ⁷ Ruehl (2010), ⁸ Beaver III et al. (1979), ⁹ Cudmore and Mandrak (2004), ¹⁰ Valtierra-Vega and Schmitter-Soto (2000), ¹¹ Gutiérrez-Franco (2012), ¹² Sánchez et al. (2012), ¹³ Smoot and Findlay (2010), ¹⁴ Pease (2010), ¹⁵ Elliott et al. (2007), ¹⁶ Odum and Heald (1972), ¹⁷ Albertoni et al. (2003), ¹⁸ Dom and Wojdak (2004), ¹⁹ McLaughlin (2015), ²⁰ Aldrich (1972), ²¹ Sepúlveda-Lozada et al. (2015), ²² Gómez-Luna et al. (2009), ²³ Vega-Cendejas et al. (1994), ²⁴ Nagelkerken et al. (2006), ²⁵ Kobelkowsky and Castillo-Rivera (1995), ²⁶ Da Rocha et al. (2008), ²⁷ Arenas-Granados and Acero (1992), ²⁸ Chaves and Otto (1998), ²⁹ Powell and Greene (2000), ³⁰ Collette (2003), ³¹ Eggleton and Schramm Jr. (2004), ³² Martelo et al. (2008), ³³ Conkel (1993), ³⁴ Mills (1995), ³⁵ Hinz et al. (2001), ³⁶ Harvey et al. (2002), ³⁷ Fehrlauer and Freire (2002), ³⁸ Lee et al. (1992), ³⁹ Allen et al. (1995), ⁴⁰ Castillo-Rivera et al. (1996), ⁴¹ Moncreiff and Sullivan (2001), ⁴² Vega-Cendejas and Arreguín-Sánchez (2001), ⁴³ Barletta and Blaber (2007), ⁴⁴ Bachelier et al. (2004), ⁴⁵ Vaslet et al. (2010), ^{46a} Gosline (1996), ^{46b} Schmitter-Soto (1996), ⁴⁷ Cochran (2008), ⁴⁸ Martínez-Palacios and Ross (1988), ⁴⁹ Castillo-Rivera et al. (2000), ⁵⁰ Arrington et al. (2002), ⁵¹ Miller (2009), ⁵² Ross (1977), ⁵³ Motta et al. (1995), ⁵⁴ Artigas (2006), ⁵⁵ Derrick and Kennedy (1997), ⁵⁶ Winemiller and Leslie (1992), ⁵⁷ Ruehl (2004), ⁵⁸ Nagelkerken and van der Velde (2004), ⁵⁹ Randall (1967), ⁶⁰ Barlow (1974), ⁶¹ Murdy et al. (1997). **Ecological guilds' references:** ⁶² Muchlisin (2012), ⁶³ Miller (1966), ⁶⁴ Nordlie (2003), ⁶⁵ Sanvicente-Añorve et al. (2011), ⁶⁶ Yáñez-Arancibia and Lara-Domínguez (1983), ⁶⁷ Vaslet et al. (2012), ⁶⁸ Winemiller et al. (2011), ⁶⁹ Upchurch and Wenner (2008), ⁷⁰ Conkel (1993), ⁷¹ Ayala-Pérez et al. (1997), ⁷² Caballero-Vázquez et al. (2005); ⁷³ CSA International Inc (2009), ⁷⁴ Gómez-González et al. (2012), ⁷⁵ Reyes et al. (1994), ⁷⁶ Macossay-Cortez et al. (2011)

Resource 3 Input data used to run the SIAR models for each study site and sampling period (in total, eight models). For each model there were used four input tables. Note that the tables related with the basal resources additionally include the number of samples per component

S1 – Dry season

1. Sources' stable isotope values

1.

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	-21.7	0.04	4.19	3.73
Eelgrass	3	-21.5	1.16	4.82	0.53
Marsh vegetation	15	-27.3	0.99	4.75	0.52
Eelgrass epiphytes	1	-21.8	5.29	4.39	5.20
Sediment eelgrass	3	-24.9	0.23	2.51	0.05

For samples with n=1 (seston and eelgrass epiphytes), imputed standard deviations (blue color) were additionally included from:

1. Claudino et al. (2015) for seston, from three samples of particulate organic matter (POM) from an upstream site (Mangrove 1, M1) in the Mamanguape River estuary, Paraíba, Brazil, and
2. Mendoza-Carranza et al. (2010) for eelgrass epiphytes, from two samples of epiphytic algae on wood in San Pedrito Lagoon, Centla Wetlands, Mexico.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	1	12.7	0.00	1.66	0.00
Eelgrass	3	36.7	2.82	2.23	0.05
Marsh vegetation	15	41.7	7.96	2.00	0.61
Eelgrass epiphytes	1	13.5	0.00	1.14	0.00
Sediment eelgrass	3	34.9	2.84	2.35	0.19

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	0.4	1.3	3.4	1
Eelgrass	3	0.4	1.3	3.4	1
Marsh vegetation	15	0.4	1.3	3.4	1
Eelgrass epiphytes	1	0.4	1.3	3.4	1
Sediment eelgrass	3	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data):

Grouping variable 1 = non selective filter-feeders (NSF); 2 = herbivores (HV); 3 = detritivores (DV); 4 = omnivores (OV); 5 = planktivores (PL); 6 = zoobenthivores (ZB); 7 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-32.54	6.13	4	-28.44	9.20	6	-28.44	9.54
1	-32.51	6.25	4	-28.63	8.94	6	-28.32	7.74
1	-32.25	6.37	4	-27.47	9.55	6	-28.23	6.82
1	-32.74	6.01	4	-28.81	8.74	6	-29.67	9.25
1	-32.47	5.82	4	-29.02	8.98	6	-29.30	8.05
1	-31.87	6.58	4	-29.21	8.40	6	-29.44	8.08
1	-32.74	5.25	4	-28.26	8.47	6	-26.37	9.76
1	-32.38	6.04	4	-29.62	7.86	6	-29.95	11.09
2	-27.20	7.57	4	-28.29	7.14	6	-28.41	10.64
2	-26.76	8.67	4	-30.10	7.47	6	-26.18	7.74
2	-27.75	10.44	5	-28.44	8.03	6	-25.83	9.11
2	-29.34	6.94	5	-20.46	9.58	6	-27.31	9.15
2	-29.63	5.93	5	-20.53	9.53	6	-26.18	9.57
2	-25.52	8.63	5	-20.34	9.71	6	-25.92	8.98
2	-30.37	7.11	5	-26.17	10.04	6	-26.81	8.41
2	-30.30	7.28	5	-29.13	6.93	6	-28.54	10.21
2	-29.58	6.57	5	-29.12	8.63	6	-27.73	8.77
2	-30.44	6.97	5	-24.51	7.55	6	-27.88	7.19
2	-30.48	7.13	5	-29.36	6.37	6	-30.21	10.53
2	-29.28	7.82	5	-29.24	6.06	6	-29.93	9.89
3	-29.93	6.97	5	-29.91	6.64	6	-28.32	7.85
3	-30.25	8.38	6	-29.07	7.90	6	-27.67	7.67
3	-33.01	8.77	6	-29.24	7.92	6	-28.00	7.46
3	-30.91	8.4	6	-28.89	9.00	6	-29.14	7.68
3	-29.74	8.96	6	-27.24	10.59	6	-27.34	8.37
3	-32.25	7.76	6	-26.98	10.89	6	-28.76	9.64
3	-29.48	8.95	6	-28.83	10.03	7	-28.51	7.44
3	-29.98	8.60	6	-25.65	6.48	7	-30.37	9.22
3	-29.99	8.98	6	-30.52	9.08	7	-28.08	10.65
4	-28.67	7.24	6	-27.24	8.29	7	-28.10	10.01
4	-29.86	7.41	6	-29.19	7.67	7	-25.59	9.12
4	-27.88	8.09	6	-29.08	7.95	7	-28.52	9.37
4	-26.42	7.80	6	-28.64	8.80	7	-28.42	8.71
4	-29.50	9.83	6	-29.29	10.92	7	-23.82	10.88
4	-31.30	6.63	6	-27.97	10.71	7	-25.41	10.75
4	-31.81	6.24	6	-29.74	7.44			
4	-29.04	7.43	6	-27.12	6.95			
4	-29.87	7.42	6	-27.13	9.54			
4	-29.41	7.27	6	-29.41	7.53			
4	-30.20	7.16	6	-28.26	7.38			
4	-29.77	7.47	6	-29.40	7.23			
4	-28.45	7.70	6	-28.25	10.12			
4	-28.09	8.51	6	-29.45	9.33			
4	-28.84	9.61	6	-28.67	9.73			

Resource 3 continued

S1 – Rainy season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	-30.9	3.40	4.73	0.23
Eelgrass	3	-24.7	1.09	7.04	0.46
Marsh vegetation	15	-27.6	0.86	4.43	1.71
Eelgrass epiphytes	1	-30.9	5.29	4.39	5.20
Sediment eelgrass	2	-12.3	0.08	3.81	1.03

For samples with n=1 (seston and eelgrass epiphytes), imputed standard deviations (blue color) were additionally included from:

1. Claudino et al. (2015) for seston, from three samples of particulate organic matter (POM) from a sandy beach site (SB1) in the Mamanguape River estuary, Paraíba, Brazil, and
2. Mendoza-Carranza et al. (2010) for eelgrass epiphytes, from two samples of epiphytic algae on wood in San Pedrito Lagoon, Centla Wetlands, Mexico.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	1	21.6	0.00	4.43	0.00
Eelgrass	3	41.9	14.7	2.49	0.75
Marsh vegetation	15	41.7	5.15	1.85	0.52
Eelgrass epiphytes	1	20.5	0.00	2.03	0.00
Sediment eelgrass	2	5.24	0.85	0.15	0.04

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	0.4	1.3	3.4	1
Eelgrass	3	0.4	1.3	3.4	1
Marsh vegetation	15	0.4	1.3	3.4	1
Eelgrass epiphytes	1	0.4	1.3	3.4	1
Sediment eelgrass	2	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data):

Grouping variable 1 = insects (IN); 2 = non selective filter-feeders (NSF); 3 = herbivores (HV); 4 = omnivores (OV); 5 = planktivores (PL); 6 = zoobenthivores (ZB); 7 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-32.24	9.10	4	-31.96	10.10	6	-23.95	4.18
1	-26.50	4.74	4	-30.30	8.13	6	-15.96	5.77
1	-22.45	4.19	4	-25.64	5.97	6	-15.28	5.56
1	-30.79	5.18	4	-11.58	6.38	6	-15.61	5.43
1	-28.19	1.14	4	-14.58	6.24	6	-14.74	5.93
1	-28.19	5.58	4	-14.73	7.16	6	-13.73	5.56
2	-33.46	7.59	4	-13.50	7.46	6	-14.41	5.93
2	-32.88	6.07	4	-11.85	5.29	6	-31.93	9.56
2	-32.59	5.81	4	-27.62	6.55	6	-25.86	6.82
2	-33.54	6.25	4	-32.06	5.31	6	-10.36	6.61
2	-33.41	5.62	4	-28.41	9.68	6	-11.53	6.19
2	-34.76	4.93	4	-14.91	7.51	6	-10.01	6.96
2	-32.69	6.19	4	-31.53	9.24	6	-16.33	6.39
2	-32.16	5.92	4	-30.50	9.15	6	-18.81	6.34
2	-33.10	5.95	4	-32.03	9.11	7	-24.11	12.17
2	-34.39	5.61	4	-27.12	6.78	7	-23.63	12.14
2	-34.58	5.55	4	-28.29	6.03	7	-24.87	11.90
2	-32.18	6.46	4	-27.15	6.76	7	-28.66	9.05
2	-32.76	6.25	4	-30.21	8.54	7	-23.40	11.19
2	-32.12	6.28	4	-28.03	8.82	7	-18.87	10.45
2	-32.60	6.10	4	-28.67	7.71	7	-29.31	9.02
2	-32.66	5.67	4	-29.14	8.91	7	-26.84	9.08
2	-33.63	5.48	4	-29.26	9.02	7	-31.73	8.41
3	-30.69	11.31	4	-28.87	9.35	7	-30.16	10.26
3	-28.33	9.64	5	-32.21	10.76	7	-28.27	10.17
3	-28.20	9.42	5	-31.94	10.42	7	-11.13	6.38
3	-29.46	8.68	5	-32.43	9.52	7	-11.81	5.78
3	-29.30	8.64	5	-31.24	8.36	7	-11.97	8.56
3	-27.84	9.01	6	-28.63	7.28			
3	-27.53	9.46	6	-31.36	9.48			
3	-28.69	9.46	6	-31.90	9.60			
3	-32.34	6.31	6	-31.78	9.66			
4	-29.83	9.99	6	-11.76	5.43			
4	-32.71	6.96	6	-10.54	6.81			
4	-29.18	6.84	6	-11.63	7.75			
4	-30.30	10.01	6	-14.46	6.77			
4	-31.44	10.18	6	-14.20	7.76			
4	-29.52	10.80	6	-15.49	8.96			
4	-29.14	10.42	6	-10.53	6.81			
4	-28.96	10.02	6	-12.70	6.25			

Resource 3 continued

S2 – Dry season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	-26.7	0.04	3.72	3.73
Marsh vegetation	15	-27.9	0.76	4.27	0.60
Mangrove epiphytes	1	-22.4	5.29	4.59	5.20
Detrital mangrove leaves	1	-28.1	0.20	3.05	0.50
FPOM	1	-26.2	1.01	5.98	4.57

For samples with n=1 (seston, mangrove epiphytes, detrital mangrove leaves, and fine particulate organic matter –FPOM–), imputed standard deviations (blue color) were additionally included from:

1. Claudino et al. (2015) for seston and FPOM, from three samples, respectively, of particulate organic matter (POM) and organic matter in sediment from an upstream site (Mangrove 1, M1) in the Mamanguape River estuary, Paraíba, Brazil,
2. Mendoza-Carranza et al. (2010) for mangrove epiphytes, from two samples of epiphytic algae on wood in San Pedrito Lagoon, Centla Wetlands, Mexico, and
3. Vaslet et al. (2012) for detrital mangrove leaves, from four samples of *Rhizophora mangle* litter from the Indian River Lagoon, Florida.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	1	26.2	0.00	3.43	0.00
Marsh vegetation	15	49.7	12.0	2.43	0.86
Mangrove epiphytes	1	33.4	0.00	2.02	0.00
Detrital mangrove leaves	1	50.5	0.00	3.35	0.00
FPOM	1	9.54	0.00	0.90	0.00

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	0.4	1.3	3.4	1
Marsh vegetation	15	0.4	1.3	3.4	1
Mangrove epiphytes	1	0.4	1.3	3.4	1
Detrital mangrove leaves	1	0.4	1.3	3.4	1
FPOM	1	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data):
 Grouping variable 1 = non selective filter-feeders (NSF); 2 = herbivores (HV); 3 = detritivores (DV); 4 = omnivores (OV); 5 = planktivores (PL); 6 = zoobenthivores (ZB)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-31.55	6.10	4	-29.88	10.35
1	-32.16	6.06	4	-29.77	10.16
1	-32.48	6.07	4	-29.80	10.12
1	-32.33	6.44	4	-28.31	8.74
1	-32.05	6.05	4	-29.62	9.07
1	-32.19	6.20	4	-28.64	9.50
1	-33.28	5.46	4	-29.15	9.04
1	-32.30	6.36	5	-29.89	9.39
1	-33.24	5.60	5	-27.04	10.88
1	-33.23	5.44	5	-27.03	10.94
1	-32.86	5.69	5	-28.14	11.03
1	-33.05	5.61	5	-29.77	8.15
1	-33.00	5.41	5	-25.62	8.35
1	-32.53	5.42	5	-27.48	10.53
2	-27.19	7.98	6	-29.95	6.78
2	-31.25	6.44	6	-28.82	7.17
2	-31.04	6.38	6	-29.25	10.06
2	-28.96	7.11	6	-28.13	8.27
2	-29.46	9.70	6	-25.38	9.75
2	-26.84	9.19	6	-30.17	7.99
2	-31.90	8.93	6	-28.19	7.00
3	-28.57	8.32	6	-28.17	8.69
3	-32.93	6.48	6	-29.32	9.77
3	-22.40	10.37	6	-29.86	9.48
3	-23.00	9.43	6	-29.25	10.55
3	-21.77	9.88			
3	-29.62	10.16			
3	-29.08	5.84			
4	-30.52	7.53			
4	-31.51	5.91			
4	-29.51	7.60			
4	-29.43	8.48			
4	-25.50	8.12			
4	-26.12	10.67			
4	-30.13	8.27			
4	-29.84	6.35			
4	-29.31	9.11			
4	-23.40	11.65			
4	-29.39	10.21			
4	-29.16	10.42			
4	-29.22	10.51			

Resource 3 continued

S2 – Rainy season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	-28.85	0.04	4.66	3.73
Marsh vegetation	15	-27.97	1.20	4.64	1.07
Mangrove epiphytes	4	-35.05	6.75	2.20	0.95
Detrital mangrove leaves	1	-31.11	1.00	1.53	0.10
FPOM	2	-29.91	0.77	5.51	0.42

For samples with n=1 (seston, detrital mangrove leaves), imputed standard deviations (blue color) were additionally included from:

1. Claudino et al. (2015) for seston, from three samples of particulate organic matter (POM) from an upstream site (Mangrove 1, M1) in the Mamanguape River estuary, Paraíba, Brazil, and
2. Vaslet et al. (2012) for detrital mangrove leaves, from six samples of *Rhizophora mangle* litter from the Florida Keys.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	1	12.8	0.00	1.76	0.00
Marsh vegetation	15	48.8	6.58	2.38	0.66
Mangrove epiphytes	4	53.2	18.9	3.11	0.83
Detrital mangrove leaves	1	49.1	0.00	1.46	0.00
FPOM	2	21.7	4.72	1.68	0.03

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	0.4	1.3	3.4	1
Marsh vegetation	15	0.4	1.3	3.4	1
Mangrove epiphytes	4	0.4	1.3	3.4	1
Detrital mangrove leaves	1	0.4	1.3	3.4	1
FPOM	2	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data)

Grouping variable 1 = insects (IN); 2 = non selective filter-feeders (NSF); 3 = detritivores (DV); 4 = omnivores (OV); 5 = planktivores (PL); 6 = zoobenthivores (ZB)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-34.85	5.75	4	-29.12	9.83	4	-30.83	7.71
1	-37.20	5.16	4	-28.66	9.56	4	-29.65	6.65
1	-34.95	7.17	4	-29.63	7.95	5	-30.72	10.37
1	-35.63	6.18	4	-32.47	8.43	5	-29.72	7.65
1	-35.90	5.99	4	-30.07	8.53	5	-29.29	9.35
1	-33.89	5.73	4	-29.92	8.22	5	-30.41	9.20
1	-33.01	5.82	4	-32.08	8.42	5	-29.71	9.56
1	-32.45	7.07	4	-31.11	8.63	5	-29.72	9.34
1	-34.32	6.88	4	-31.59	8.42	5	-29.85	9.38
1	-28.76	7.23	4	-27.65	10.51	5	-29.28	9.91
2	-33.09	6.34	4	-28.37	10.03	6	-32.83	8.79
2	-33.06	6.15	4	-31.90	11.45	6	-30.17	7.31
2	-32.89	6.17	4	-30.04	10.73	6	-30.70	8.94
2	-33.30	5.34	4	-32.26	10.40	6	-28.42	9.16
2	-33.38	5.74	4	-29.99	10.45	6	-31.66	9.24
2	-32.99	6.02	4	-30.17	9.39	6	-12.40	6.98
2	-34.33	5.29	4	-30.75	9.17	6	-31.29	9.23
2	-34.57	5.09	4	-30.45	8.35	6	-15.92	10.13
2	-34.46	5.30	4	-29.82	9.76	6	-14.09	9.36
2	-33.29	6.36	4	-29.61	9.31	6	-28.73	9.25
2	-34.00	5.97	4	-30.59	7.96	6	-30.62	10.37
3	-24.46	10.44	4	-30.14	8.25	6	-30.12	10.43
3	-24.74	8.79	4	-30.20	8.18	6	-28.83	9.54
3	-22.65	9.15	4	-29.72	9.30	6	-25.29	10.14
3	-33.50	9.54	4	-27.83	9.13	6	-31.55	6.31
3	-29.21	7.82	4	-31.09	9.52	6	-30.42	9.38
3	-23.69	7.46	4	-30.66	9.28			
3	-34.09	8.75	4	-29.90	8.97			
3	-31.26	7.16	4	-31.23	9.84			
3	-32.55	9.15	4	-30.00	10.13			
3	-33.24	9.12	4	-29.20	10.11			
3	-13.38	6.80	4	-32.76	6.54			
3	-12.55	7.77	4	-33.12	6.17			
3	-14.80	5.66	4	-36.13	6.04			
3	-34.43	6.88	4	-33.20	6.49			
3	-30.53	6.57	4	-33.72	5.95			
3	-30.76	7.22	4	-30.35	8.40			
3	-31.81	6.07	4	-32.84	6.25			
4	-10.96	5.94	4	-32.12	7.51			
4	-16.30	9.98	4	-29.67	8.07			

Resource 3 continued

S3 – Dry season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	4	-27.9	0.89	4.64	1.14
Marsh vegetation	6	-27.8	0.61	3.72	1.24
Mangrove epiphytes	1	-24.7	5.29	9.03	5.20
Detrital mangrove leaves	1	-29.7	0.20	3.35	0.50
FPOM	3	-27.7	0.29	2.47	0.17

For samples with n=1 (mangrove epiphytes, detrital mangrove leaves), imputed standard deviations (blue color) were additionally included from:

1. Mendoza-Carranza et al. (2010) for mangrove epiphytes, from two samples of epiphytic algae on wood in San Pedrito Lagoon, Centla Wetlands, Mexico, and
2. Vaslet et al. (2012) for detrital mangrove leaves, from four samples of *Rhizophora mangle* litter from the Indian River Lagoon, Florida.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	4	24.1	11.8	2.40	0.77
Marsh vegetation	6	44.6	5.81	2.32	0.64
Mangrove epiphytes	1	40.9	0.00	2.40	0.00
Detrital mangrove leaves	1	48.6	0.00	0.75	0.00
FPOM	3	12.0	0.58	0.90	0.03

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	4	0.4	1.3	3.4	1
Marsh vegetation	6	0.4	1.3	3.4	1
Mangrove epiphytes	1	0.4	1.3	3.4	1
Detrital mangrove leaves	1	0.4	1.3	3.4	1
FPOM	3	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data)

Grouping variable 1 = herbivores (HV); 2 = detritivores (DV); 3 = omnivores (OV); 4 = planktivores (PL); 5 = zoobenthivores (ZB); 6 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-24.67	1.31	3	-29.33	9.45	5	-29.43	10.20
1	-26.41	3.72	3	-29.08	8.55	5	-29.72	9.96
1	-27.06	6.44	3	-27.70	9.82	5	-29.07	9.40
2	-28.56	8.04	3	-27.43	9.20	5	-29.81	9.70
2	-27.10	8.42	3	-27.36	9.52	5	-29.08	9.85
2	-27.70	8.96	3	-27.09	9.79	5	-29.57	9.99
2	-31.51	8.89	3	-28.63	10.1	5	-24.85	9.20
2	-31.87	8.42	3	-27.57	6.89	5	-24.91	9.33
2	-33.25	9.31	4	-27.28	11.74	5	-24.55	7.55
2	-28.05	10.33	4	-26.77	12.11	6	-29.20	7.80
2	-31.28	9.13	4	-28.29	10.55	6	-28.93	8.03
2	-31.59	9.19	4	-25.55	11.39	6	-25.51	9.70
2	-30.04	9.23	4	-27.40	11.09	6	-24.08	11.87
2	-28.94	11.19	4	-27.03	11.39	6	-25.29	11.89
2	-28.10	10.67	4	-20.02	7.73	6	-26.37	11.81
2	-28.39	10.85	4	-19.97	7.88	6	-26.75	11.88
2	-26.98	11.12	4	-20.21	8.99	6	-26.27	11.87
2	-27.20	10.66	4	-19.98	9.04	6	-22.81	11.75
3	-28.74	11.69	4	-26.68	7.69	6	-24.20	12.82
3	-28.24	12.18	4	-23.62	8.85	6	-23.31	12.27
3	-28.53	11.84	5	-23.72	7.84	6	-22.05	12.77
3	-28.85	11.09	5	-26.78	7.53	6	-21.28	12.89
3	-27.35	11.16	5	-24.35	10.66	6	-25.12	11.22
3	-26.60	12.37	5	-26.20	10.41	6	-27.43	12.82
3	-27.55	11.91	5	-24.47	11.12			
3	-25.58	8.50	5	-28.60	10.19			
3	-25.84	10.59	5	-22.22	12.46			
3	-25.61	10.59	5	-25.06	11.41			
3	-26.47	9.75	5	-25.58	11.48			
3	-26.02	9.64	5	-26.29	11.96			
3	-32.41	5.87	5	-24.60	11.09			
3	-30.31	8.03	5	-24.35	11.11			
3	-32.89	7.32	5	-25.00	10.95			
3	-29.49	7.04	5	-26.10	10.82			
3	-26.94	10.81	5	-29.58	10.98			
3	-25.42	9.16	5	-25.02	9.09			
3	-27.61	9.50	5	-29.83	9.85			
3	-27.91	9.40	5	-29.59	10.50			
3	-27.90	9.34	5	-28.40	11.03			
3	-27.37	9.01	5	-28.88	10.76			

Resource 3 continued

S3 – Rainy season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	-26.6	0.04	5.21	3.73
Marsh vegetation	12	-27.8	1.29	3.53	1.27
Mangrove epiphytes	1	-29.6	5.29	5.16	5.20
Detrital mangrove leaves	2	-29.7	0.78	0.80	0.00
FPOM	1	-29.4	1.01	1.74	4.57

For samples with n=1 (seston, mangrove epiphytes, FPOM), imputed standard deviations (blue color) were additionally included from:

1. Claudino et al. (2015) for seston and FPOM, from three samples, respectively, of particulate organic matter (POM) and organic matter in sediment from an upstream site (Mangrove 1, M1) in the Mamanguape River estuary, Paraíba, Brazil, and
2. Mendoza-Carranza et al. (2010) for mangrove epiphytes, from two samples of epiphytic algae on wood in San Pedrito Lagoon, Centla Wetlands, Mexico.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	1	5.95	0.00	0.72	0.00
Marsh vegetation	12	42.9	8.27	1.46	0.72
Mangrove epiphytes	1	25.3	0.00	2.23	0.00
Detrital mangrove leaves	2	41.8	2.33	1.19	0.05
FPOM	1	29.6	0.00	1.18	0.00

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	1	0.4	1.3	3.4	1
Marsh vegetation	12	0.4	1.3	3.4	1
Mangrove epiphytes	1	0.4	1.3	3.4	1
Detrital mangrove leaves	2	0.4	1.3	3.4	1
FPOM	1	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data)

Grouping variable 1 = insects (IN); 2 = herbivores (HV); 3 = detritivores (DV); 4 = omnivores (OV); 5 = zoobenthivores (ZB); 6 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-25.49	5.11	5	-29.71	9.03
1	-26.69	6.51	5	-32.30	7.22
1	-30.06	3.50	5	-31.97	9.22
1	-29.44	4.77	6	-25.12	10.08
2	-22.65	6.54	6	-25.97	8.22
2	-28.57	8.26	6	-27.31	9.80
2	-27.19	8.26			
2	-28.07	9.20			
2	-25.92	2.59			
2	-26.05	3.47			
2	-25.73	5.36			
3	-30.53	7.65			
3	-30.34	6.13			
3	-31.16	7.67			
3	-29.37	7.20			
3	-17.86	9.41			
3	-12.58	8.20			
3	-33.05	7.02			
4	-27.17	7.46			
4	-28.88	9.32			
4	-28.53	9.26			
4	-30.03	8.46			
4	-28.58	9.90			
4	-26.09	10.76			
4	-26.76	9.91			
4	-26.98	8.82			
4	-26.64	8.62			
4	-30.53	5.28			
4	-30.69	6.15			
4	-26.81	5.70			
4	-30.30	6.01			
4	-30.37	6.63			
4	-27.35	8.00			
4	-12.27	2.02			
4	-27.16	6.80			
4	-28.41	6.09			
4	-27.81	6.52			
5	-30.66	11.59			
5	-16.59	7.47			
5	-21.90	8.10			

Resource 3 continued

S4 – Dry season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	2	-12.5	0.24	2.40	0.25
Seagrasses	6	-9.46	0.10	-1.16	1.38
Mangrove epiphytes	5	-29.5	3.76	-0.25	1.62
Seagrass epiphytes	1	-16.5	0.60	2.60	0.90
Benthic algae	1	-15.3	0.40	2.96	0.40
Mangrove leaves (fresh)	8	-27.8	1.14	2.35	0.59

For samples with n=1 (seagrass epiphytes, benthic algae), imputed standard deviations (blue color) were additionally included from:

1. Vaslet et al. (2012) from three samples, respectively, of seagrass epiphytes and algae from the Indian River Lagoon and Florida Keys.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	2	13.5	2.69	1.40	0.27
Seagrasses	6	36.3	2.28	2.76	0.26
Mangrove epiphytes	5	24.8	6.22	2.51	0.73
Seagrass epiphytes	1	25.6	0.00	2.34	0.00
Benthic algae	1	32.1	0.00	2.50	0.00
Mangrove leaves (fresh)	8	46.5	6.16	1.26	0.33

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	2	0.4	1.3	3.4	1
Seagrasses	6	0.4	1.3	3.4	1
Mangrove epiphytes	5	0.4	1.3	3.4	1
Seagrass epiphytes	1	0.4	1.3	3.4	1
Benthic algae	1	0.4	1.3	3.4	1
Mangrove leaves (fresh)	8	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data)

Grouping variable 1 = omnivores (OV); 2 = planktivores (PL); 3 = zoobenthivores (ZB); 4 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-16.75	12.6	3	-12.19	5.79
1	-16.25	10.4	3	-11.30	4.50
1	-15.21	10.38	3	-14.34	6.70
1	-10.79	8.43	4	-11.02	10.16
1	-11.84	8.56	4	-15.28	10.87
1	-8.99	6.05	4	-10.75	9.68
1	-11.32	6.59	4	-21.33	9.44
1	-11.82	6.72	4	-12.36	7.67
1	-14.67	9.45			
1	-10.75	7.97			
1	-9.54	8.52			
1	-12.15	7.52			
1	-11.64	7.52			
1	-12.52	7.60			
1	-13.92	5.74			
1	-12.00	4.72			
1	-10.86	6.30			
1	-11.93	6.02			
1	-12.17	5.67			
1	-11.90	4.56			
1	-10.92	4.07			
1	-11.25	3.98			
1	-11.77	4.66			
1	-11.99	4.20			
1	-15.95	5.17			
2	-18.63	6.38			
2	-18.68	6.71			
2	-14.66	3.66			
2	-15.08	3.19			
3	-18.25	8.40			
3	-13.38	5.89			
3	-11.78	6.99			
3	-11.81	7.14			
3	-12.09	7.08			
3	-11.95	6.65			
3	-11.94	7.02			
3	-12.16	6.50			
3	-12.36	6.87			
3	-12.04	6.27			
3	-12.52	6.09			

Resource 3 continued

S4 – Rainy season

1. Sources' stable isotope values

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	2	-14.4	1.31	2.93	0.57
Seagrasses	6	-15.4	0.63	-1.77	1.15
Mangrove epiphytes	3	-31.1	0.57	0.18	0.30
Seagrass epiphytes	1	-19.0	0.60	2.99	0.90
Benthic algae	3	-16.2	0.31	0.16	0.06
Detrital mangrove leaves	1	-30.2	1.00	1.04	0.10

For samples with n=1 (seagrass epiphytes, detrital mangrove leaves), imputed standard deviations (blue color) were additionally included from:

1. Vaslet et al. (2012), from three samples of seagrass epiphytes from the Indian River Lagoon, and six samples of *Rhizophora mangle* litter from the Florida Keys.

2. Elemental concentrations

Source	n	Mean Total C (%)	SD Total C (%)	Mean Total N (%)	SD Total N (%)
Seston	2	15.4	2.26	1.28	0.67
Seagrasses	6	44.4	1.66	3.10	0.27
Mangrove epiphytes	3	29.3	5.97	3.29	0.80
Seagrass epiphytes	1	55.4	0.00	10.9	0.00
Benthic algae	3	25.8	3.33	3.80	0.49
Detrital mangrove leaves	1	44.3	0.00	1.28	0.00

3. Trophic enrichment factors (TEF's) according to Post (2002)

Source	n	Mean $\delta^{13}\text{C}$ (‰)	SD $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)	SD $\delta^{15}\text{N}$ (‰)
Seston	2	0.4	1.3	3.4	1
Seagrasses	6	0.4	1.3	3.4	1
Mangrove epiphytes	3	0.4	1.3	3.4	1
Seagrass epiphytes	1	0.4	1.3	3.4	1
Benthic algae	3	0.4	1.3	3.4	1
Detrital mangrove leaves	1	0.4	1.3	3.4	1

Resource 3 continued

4. Consumers' stable isotope values (raw data)

Grouping variable 1 = omnivores (OV); 2 = planktivores (PL); 3 = zoobenthivores (ZB); 4 = piscivores (PV)

Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Group	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	-15.67	8.78	3	-30.91	6.19
1	-17.05	9.47	3	-32.65	8.53
1	-21.49	10.39	3	-32.03	7.09
1	-18.40	8.35	3	-30.34	8.66
1	-12.15	3.77	3	-30.77	7.19
1	-12.37	3.19	3	-14.69	6.63
1	-13.96	3.52	3	-14.00	2.35
1	-18.16	8.15	3	-13.94	4.56
1	-17.56	7.89	3	-31.57	8.65
1	-17.24	2.87	3	-13.75	9.76
1	-16.46	3.49	3	-14.51	5.99
1	-16.68	7.03	3	-30.54	9.07
1	-24.11	10.06	3	-18.20	6.78
2	-27.12	11.32	3	-13.07	5.73
2	-25.20	8.79	4	-33.04	9.19
2	-13.03	6.81	4	-17.45	8.97
2	-14.10	6.68	4	-16.34	7.25
2	-11.92	7.97	4	-33.25	9.26
2	-33.59	9.56			
2	-30.69	10.5			
2	-32.02	9.68			
2	-15.28	1.90			
2	-19.74	4.37			
2	-19.10	5.88			
2	-15.54	3.04			
2	-22.30	4.80			
2	-12.67	2.42			
2	-18.55	3.74			
2	-21.20	4.89			
2	-22.32	-2.33			
3	-12.52	5.77			
3	-31.91	7.80			
3	-12.98	5.62			
3	-32.56	10.23			
3	-30.07	7.26			
3	-29.42	7.72			
3	-28.58	8.54			
3	-30.72	8.30			
3	-28.63	9.34			
3	-31.50	5.89			

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Annex III. Supplement material for Chapter V

Resource 1 Fish species grouped per family collected during the two sampling periods in MAR and FRW. The origin of the species is depicted as: ● marine, ● estuarine, ● freshwater, ● anadromous. It is shown the total of individuals captured with all gears (superscripts indicate the gears used) and the relative abundance based on the pooled individuals from all gears per site and season (species with relative abundance >10 % are highlighted)

Family	Species	Dry season				Rainy season			
		MAR		FRW		MAR		FRW	
		Total n	RA (%)	Total n	RA (%)	Total n	RA (%)	Total n	RA (%)
1 Achiridae	1 ● <i>Achirus lineatus</i>	1 ⁴	1.35	3 ¹	0.86	1 ¹	0.2		
	2 ● <i>Trinectes maculatus</i>							1 ²	0.35
2 Ariidae	3 ● <i>Ariopsis felis</i>	3 ⁴	4.05	1 ¹	0.29			1 ⁴	0.35
	4 ● <i>Bagre marinus</i>	2 ⁴	2.7					5 ⁴	1.75
3 Atherinopsidae	5 ● <i>Atherinella alvarezii</i>			88 ^{1,3}	25.1			30 ^{1,2}	10.5
4 Batrachoididae	6 ● <i>Batrachoides goldmani</i>	5 ²	6.76			2 ²	0.4		
5 Belonidae	7 ● <i>Strongylura marina</i>							1 ¹	0.35
6 Carangidae	8 ● <i>Caranx hippos</i>							2 ⁴	0.7
	9 ● <i>Caranx latus</i>					1 ⁴	0.2	2 ⁴	0.7
7 Centropomidae	10 ● <i>Centropomus parallelus</i>					10 ^{1,2}	2.01		
	11 ● <i>Centropomus undecimalis</i>			1 ²	0.29				
8 Characidae	12 ● <i>Astyanax aeneus</i>			17 ¹	4.86			45 ^{1,2,5}	15.7
9 Cichlidae	13 ● <i>Amphilophus robertsoni</i>							2 ^{1,4}	0.7
	14 ● <i>Cichlasoma salvini</i>			2 ⁴	0.57			1 ⁵	0.35
	15 ● <i>Cichlasoma urophthalmum</i>	8 ²	10.8	3 ^{1,4}	0.86	58 ^{2,4}	11.7	4 ^{2,4}	1.4
	16 ● <i>Oreochromis niloticus</i>			1 ⁴	0.29			6 ⁴	2.1
	17 ● <i>Parachromis managuensis</i>			1 ¹	0.29				
	18 ● <i>Paraneetroplus synspilus</i>			2 ¹	0.57			3 ^{1,4}	1.05
	19 ● <i>Theraps heterospilus</i>			4 ¹	1.14			1 ²	0.35
	20 ● <i>Thorichthys helleri</i>			3 ^{1,2}	0.86			10 ^{1,2,4}	3.5
10 Clupeidae	21 ● <i>Thorichthys pasionis</i>							2 ⁴	0.7
	22 ● <i>Brevoortia gunteri</i>			28 ¹	8				
	23 ● <i>Dorosoma anale</i>			1 ⁴	0.29				
	24 ● <i>Dorosoma petenense</i>			5 ¹	1.43			55 ^{1,3,4}	19.2
	25 ● <i>Harengula clupeola</i>					18 ^{1,2}	3.62		
11 Cyprinidae	26 ● <i>Ctenopharyngodon idella</i>			1 ¹	0.29				
12 Cyprinodontidae	27 ● <i>Floridichthys carpio</i>					57 ¹	11.5		
13 Eleotridae	28 ● <i>Gobiomorus dormitor</i>			NC ³				3 ^{2,4}	1.05

Resource 1 continued

Family	Species	Dry season				Rainy season			
		MAR Total n	RA (%)	FRW Total n	RA (%)	MAR Total n	RA (%)	FRW Total n	RA (%)
14	Elopidae	29							
	● <i>Elops saurus</i>	1 ⁴	1.35					1 ⁴	0.35
15	Engraulidae	30		183 ³	52.3	4 ¹	0.8		
	● <i>Anchoa mitchilli</i>					1 ³	0.2		
	● <i>Anchoa sp.</i>					112 ^{1,2}	22.5	3 ²	1.05
16	Gerreidae	32				172 ^{1,3}	34.6		
	● <i>Diapterus auratus</i>								
	● <i>Eucinostomus gula</i>								
	● <i>Eugerres plumieri</i>	3 ⁴	4.05						
	● <i>Gerres cinereus</i>	29 ²	39.2			23 ^{1,2,4}	4.63		
17	Gobiidae	36				2 ²	0.4		
	● <i>Gobionellus oceanicus</i>					1 ⁴	0.2		
18	Haemulidae	37							
	● <i>Orthoprichthys chrysoptera</i>							26 ¹	9.09
19	Hemiramphidae	38							
	● <i>Hyporhamphus mexicanus</i>								
20	Heptapteridae	39		2 ⁴	0.57				
	● <i>Rhamdia quelen</i>								
21	Ictaluridae	40						25 ^{1,2,3}	8.74
	● <i>Ictalurus furcatus</i>							7 ⁴	2.45
22	Loricariidae	41		2 ⁴	0.57				
	● <i>Pterygoplichthys pardalis</i>								
23	Lutjanidae	42						4 ⁴	1.4
	● <i>Lutjanus griseus</i>	2 ⁴	2.7					10 ⁴	3.5
24	Megalopidae	43							
	● <i>Megalops atlanticus</i>								
25	Mugilidae	44				5 ⁴	1.01	3 ⁴	1.05
	● <i>Mugil curema</i>	1 ⁴	1.35						
26	Ostraciidae	45							
	● <i>Acanthostracion quadricornis</i>	1 ²	1.35						
27	Paralichthyidae	46				3 ¹	0.6		
	● <i>Citharichthys spilopterus</i>								
28	Poeciliidae	47		2 ¹	0.57	2 ¹	0.4		
	● <i>Poecilia mexicana</i>							25 ⁵	8.74
	● <i>Gambusia sexradiata</i>								
29	Sciaenidae	49				1 ²	0.2		
	● <i>Bairdiella ronchus</i>								
	● <i>Cynoscion nebulosus</i>	3 ⁴	4.05			1 ⁴	0.2	1 ⁴	0.35
30	Sparidae	51				3 ^{2,4}	0.6	1 ⁴	0.35
	● <i>Archosargus rhomboidalis</i>	13 ^{2,4}	17.6			3 ⁴	0.6		
	● <i>Lagodon rhomboides</i>								
31	Synbranchidae	53						4 ^{2,5}	1.4
	● <i>Ophisternon aenigmaticum</i>								
32	Syngnathidae	54				1 ²	0.2		
	● <i>Microphis lineatus</i>								
	● <i>Syngnathus louisianae</i>	1 ²	1.35						
33	Tetraodontidae	56				2 ^{1,2}	0.4		
	● <i>Sphoeroides parvus</i>	1 ⁴	1.35						
	● <i>Sphoeroides testudineus</i>					10 ¹	2.01		
34	Triglidae	58				1 ⁴	0.2	2 ⁴	0.7
	● <i>Prionotus scitulus</i>								
	● <i>Prionotus tribulus</i>					3 ^{1,2}	0.6		
	Total	74		350		497		286	

¹ Beach seine, ² Beam trawl, ³ Ichthyoplankton net, ⁴ Gillnet, ⁵ Spoon

NC, not counted. References for the ecological guilds of these species are shown in the previous Annex

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Ich, Alejandra Sepúlveda Lozada,

Fedelhören 14, 28203 Bremen,

Matr.-Nr. 2777303

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