



Trophic position and isotopic niche of mangrove fish assemblages at both sides of the Isthmus of Panama

¹ Leibniz Centre for Tropical Marine Research (ZMT),
Fahrenheitstr. 6, 28359 Bremen,
Germany

² Current address: Smithsonian
Tropical Research Institute,
Balboa, Panama

* Corresponding author email:
<lara-stuthmann@web.de>

Lara E Stuthmann ¹ *
Gustavo A Castellanos-Galindo ^{1, 2}

ABSTRACT.—Fishes are important components of marine coastal ecosystems, often represented in food webs as second and third order consumers. Fish trophic positions (TP) in these food webs can vary across ontogeny and accurate estimation can provide insights into the functioning of these ecosystems. Mangrove ecosystem function can also vary depending on local and regional environmental conditions. Panamanian mangroves in the Caribbean Sea and the Pacific Ocean occur under strikingly different environmental conditions after the closure of the Panama Isthmus over 3 mya and likely function differently. Here, we use $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and Bayesian models to calculate the TP and the Convex Hull Area (TA) of the most common fish species inhabiting mangroves of the Gulf of Montijo and Bocas del Toro on the Pacific and Caribbean coasts of Panama, respectively. Thirteen dominant fishes were used for the estimation of TP, eight in the Pacific and five in the Caribbean. Mean TP of the communities was similar but with significantly larger variations in the Caribbean than in the Pacific. Similarly, the TA was larger for the Caribbean fish assemblage than for the Pacific. Both results indicate that trophic modes in the Caribbean fish assemblages are more varied than in the Pacific. With some exceptions, FishBase TP estimates correlated positively with TP stable isotope estimates. Our results suggest that TP and TA are good proxies for mangrove fish communities' trophic modes and that these metrics may vary depending on mangrove environmental settings.



Guest Editor: Amy Y Then

Date Submitted: 15 February, 2019.
Date Accepted: 24 September, 2019.
Available Online: 24 September, 2019.

In the tropics and subtropics, mangrove ecosystems are a common seascape thought to be important for many organisms and coastal ecological processes (Lee et al. 2014). Fishes inside mangroves find refuge and shelter from predators and can also feed from a wide variety of prey items available in these ecosystems (Laegdsgaard and Johnson 2001). As mobile organisms, fishes inhabiting mangroves are important in the exchange of energy between other connected coastal ecosystems like seagrasses, coral reefs, and subtidal soft bottoms, ultimately influencing the tropho-dynamics in these areas (Nagelkerken et al. 2015).

Mangrove ecosystems function differently depending on the local and regional environmental settings (Ewel et al. 1998). The connectivity to other seascapes, the tidal regime, the coastal morphology, and the productivity of the mangrove system are all factors that can affect the way mangrove ecosystems function (Igulu et al. 2014, Castellanos-Galindo and Krumme 2015, Twilley et al. 2018). For example, variability in mangrove flooding patterns, which are related to coastal morphology and tidal regimes, may affect the functional value of mangrove ecosystems for aquatic fauna by regulating the occupation patterns of organisms inside these habitats (Baker et al. 2015).

A strong difference in the type of mangrove settings that can be found in the world is observed in Panama, Central America. The formation of the Central American Isthmus in Panama dramatically changed the environmental conditions of the previously connected Atlantic (Caribbean Sea) and Pacific oceans and consequently determined the type of ecosystems that can be observed in these two marine regions (Leigh et al. 2014). On one side, the mangroves in the Pacific are located in estuarine macrotidal areas with high productivity and no coral reefs in close proximity. On the other side, many Caribbean mangroves occur in carbonate environments surrounded by seagrasses and coral reefs with small tides (<50 cm). These differences in the type of mangrove settings provide the opportunity for interoceanic comparisons on the functioning of mangrove ecosystems, using, for example, stable isotopes to investigate differences in trophic positions of mangrove-associated fauna that are phylogenetically related.

Trophic position (TP) is a useful descriptor of the ecological role of organisms within terrestrial and marine food webs (Vander Zanden and Rasmussen 1999, Post 2002). Its calculation has traditionally relied on the examination of stomach contents (Hyslop 1980). The information on fish TPs has been incorporated in databases like FishBase (Froese and Pauly 2018) where researchers can use TPs in a wide range of analyses intended to uncover ecological patterns. In the last twenty years, the use of stable isotopes, principally $\delta^{15}\text{N}$, has become popular providing a more integrated view of an organism's TP in an ecosystem (Layman et al. 2012). The more recent approaches to calculate fish TP with stable isotopes are improving our understanding of organisms' ecological roles within ecosystems (Bradley et al. 2015, Quezada-Romegialli et al. 2018).

Another indicator that can be useful in describing a species' ecological characteristics using stable isotopes is the isotopic niche. Newsome et al. (2007), defined this indicator as an area in δ -space with isotopic values as coordinates (typically $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Layman et al. (2007) extended the isotopic niche concept by adding additional measures to describe niche structures from individuals to communities, including the total area of Convex Hull (TA). TA describes the niche width of an organism or a community (Layman et al. 2007). When TA is used to describe the isotopic niche of a community, the mean of isotopic values for each group within the community is calculated and used as a point estimate for generating the TA of the community. More recently, Jackson et al. (2011) developed a Bayesian method to propagate uncertainty in the calculated mean of TA, allowing for more robust comparisons between systems. Trophic relationships in mangrove ecosystems are often difficult to reveal, due to the presence of multiple basal resources and different trophic pathways (Lee et al. 2014). Therefore, TP and measures of trophic niche width, like TA, are complementary tools to investigate fish communities in mangrove habitats by using information

about the primary resources ($\delta^{13}\text{C}$) as well as the position in the food web ($\delta^{15}\text{N}$; e.g., Abrantes et al. 2014, Sepúlveda-Lozada et al. 2015, López-Rasgado et al. 2016).

Most mangrove-associated fishes are small-bodied individuals in part for the obvious limitation of space (water) that these shallow coastal habitats present (Laegdsgaard and Johnson 2001). Nonresident fishes in mangroves are often juveniles of species that are later found in deeper habitats as adults (Aburto-Oropeza et al. 2009). This observation has helped reinforce the now widely recognized nursery function of mangroves for fishes (Sheaves 2017). Fish ontogenetic habitat shifts are also accompanied by changes in diet and therefore changes in fish TPs (Cocheret de la Morinière et al. 2003, Hammerschlag-Peyer et al. 2011). TP has been recognized to scale with body size (e.g., Romanuk et al. 2011), indicating that juvenile fishes inhabiting mangroves might have lower TPs than those of the same species inhabiting deeper habitats as adults. However, in diverse tropical aquatic food webs, differences in this relationship between guilds and species have been found (Layman et al. 2005, Ou et al. 2017).

Here we evaluate whether TP and TA differ in fish assemblages inhabiting mangrove ecosystems with different environmental settings in Panama (Caribbean Sea vs eastern Pacific mangroves). We also compared our estimates of TP against those commonly used in FishBase to identify potential biases when using this database in studies of functional and food web ecology. We hypothesized that mangrove fish communities in the Caribbean would have larger TAs compared to the fish communities in the Pacific, given the close proximity that the former fish communities may have to food sources from adjacent ecosystems such as coral reefs and seagrass beds (ecosystems that are generally lacking in the eastern Pacific). Since our samples consisted of mostly juvenile fishes, we also hypothesized that our TP estimates would be generally lower than those in FishBase, which normally uses information from adult and larger fishes, believed to have higher TPs.

MATERIALS AND METHODS

SAMPLING AREA.—The sampling took place along the eastern Pacific and Caribbean coasts of Panama in Central America (Fig. 1). The rise of the Isthmus of Panama between the Miocene and Pliocene (Montes et al. 2015, O’Dea et al. 2016) produced two environmentally distinct coasts where previously related marine biota started to follow different evolutionary trajectories (Lessios 2008). Mangrove ecosystems along both Panamanian coasts were the experimental grounds for the present study. In the Pacific, fish samplings took place at the Gulf of Montijo ($7^{\circ}46' \text{N}$, $81^{\circ}7' \text{W}$) whereas in the Caribbean Sea, fish samplings took place in Almirante Bay at Isla Colón and Isla San Cristóbal in the Archipelago de Bocas del Toro ($9^{\circ}21' \text{N}$, $82^{\circ}15' \text{W}$; Fig. 1).

More than 90% of the approximately 170,000 ha of mangroves in Panama are located along the Pacific coast. The Gulf of Montijo is an estuarine mangrove system that contains 12.7% of the country’s mangrove forest in the Pacific (Recio et al. 2016), which is dominated by *Rhizophora mangle* (Gross et al. 2014). This system is shaped by a semidiurnal tidal regime with amplitudes of approximately 4 m. Salinities fluctuate due to heavy rainfalls and the freshwater discharge of various rivers from about 8.2 in the wet season to up to 33.8 in the dry season (Gross et al. 2014). On the other Panamanian coast in the Caribbean Sea, mangroves of the Bocas del Toro province account for >30% of the Caribbean mangroves in Panama (ONU-REDD 2015). The

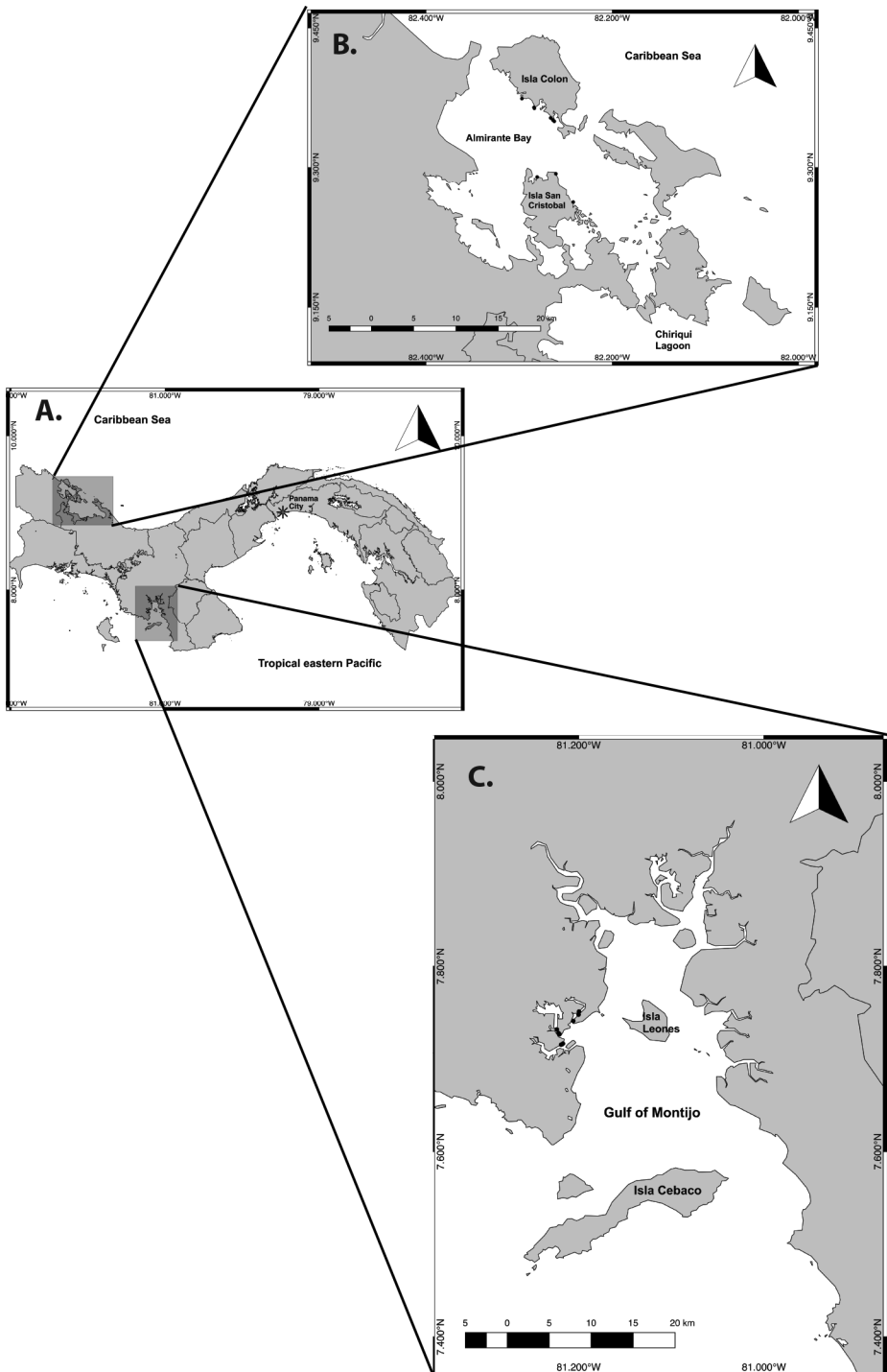


Figure 1. Map of (A) Panama with indicated sampling areas in (B) the Caribbean Sea (Bocas del Toro) and (C) the eastern Pacific coast (Gulf of Montijo). Black dots in (B) and (C) indicate sampling locations.

mangroves are mostly fringing mangroves with *R. mangle* as the dominant species (Guzmán et al. 2005). Coral reefs and seagrass beds occur at the edge of these mangroves, which are mostly permanently inundated in a microtidal regime with maximum amplitudes of 40 cm.

BIOLOGICAL SAMPLING.—The biological material for the study was collected from November 2016 to February 2017 during monthly samplings at the two locations in the Pacific and Caribbean coasts of Panama. Each sampling took place over three days during daytime. On the Pacific coast, block nets (15 mm stretched mesh size) were set in small intertidal mangrove creeks in a way that fishes migrating with the tide into the mangroves were captured on their way out of the creek at ebb-low tide (see detailed methodology in Castellanos-Galindo and Krumme 2014). Clove oil, an effective fish anesthetic (see Robertson and Smith-Vaniz 2010), was used to facilitate fish collection in case creeks were not fully drained at low tide. On the Caribbean coast, mangrove stands located approximately 1 m from the main mangrove fringe areas were encircled with a net (15 mm stretched mesh size) to capture the fishes associated with these mangrove stands. To facilitate fish collection, clove oil was also used inside the sampled area. On both coasts, clove oil was administered from the nozzle of a plastic bottle that contained a mixture of clove oil and alcohol in a 1:9 ratio.

The selection of baseline organisms for the calculation of TP followed Post (2002). Due to their low metabolic rate, long-living snails and mussels were used. In order to keep consistency across the two study areas, we used closely related species of the genus *Littoraria* [Pacific: *Littoraria zebra* (Donovan, 1825), Caribbean: *Littoraria angulifera* (Lamarck, 1822)] as a benthic baseline and filter-feeding oysters of the genus *Crassostrea* [Pacific: *Crassostrea columbiensis* (Hanley, 1846), Caribbean: *Crassostrea rhizophorae* (Guilding, 1828)] as a pelagic baseline. All baseline organisms were collected in February 2017 from mangrove trees at the fish sampling points or in close proximity to them.

SAMPLE PROCESSING.—All samples were stored on ice and frozen prior to further processing. For the stable isotope analysis, we used the species most representative in biomass and abundance in each studied system. Sample processing took place at the Smithsonian Tropical Research Station in Bocas del Toro, Panama. The fishes were identified and standard length (SL, cm) and weight (g) were recorded. Based on the species contribution to the total weight of the community, eight species in the Pacific and five in the Caribbean were selected as the dominant species for the stable isotope analyses (see Data Analyses below). When possible, 10 individuals with similar sizes from each species were used for the analysis. For isotope analysis, fish meat from under the dorsal fin was removed and for individuals <5 cm SL, the whole organism was used. This process followed the assumption that muscle samples of larger fishes (approximately >9 cm) give a good estimation of the isotopic value by introducing only some variability in $\delta^{13}\text{C}$. However, smaller fishes should be ground whole, as the use of only small plugs biases in this case the nitrogen isotopic values of the whole fish (Schielke and Post 2010). The samples were dried for at least 48 hrs at 60 °C, ground to a fine powder with mortar and pestle, and stored at room temperature until further analysis. Samples taken from the whole organisms were treated with acid to remove inorganic carbon. Stable isotope ratios of ($^{13}\text{C}/^{12}\text{C}$) and ($^{15}\text{N}/^{14}\text{N}$) were

measured at the Leibniz Centre for Tropical Marine Research (ZMT) in Bremen, Germany with a mass spectrometer (Delta Plus Analyser) coupled with an elemental analyser (Flash EA 1112, Thermo Finnigan). The standards for carbon and nitrogen were Pee Dee Belemnite (PDB) and atmospheric nitrogen. Stable isotope ratios were expressed in delta (δ) notation in units per mil (‰) based on the following formula (where R was $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$):

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

DATA ANALYSES.—The relative biomass of each fish species within the communities was calculated based on the total catch mass (biomass) from all fish samplings. As biomass measurements of the very abundant small pelagic species *Anchoa walkeri* (Baldwin and Chang, 1970) in the Pacific and *Jenkinsia stolifera* (Jordan and Gilbert, 1884) in the Caribbean were not taken, small pelagic biomass estimations from previous field studies in neighboring mangrove locations were used to derive a rough estimate of their relative abundance in our study areas (see Vaslet et al. 2010, Castellanos-Galindo and Krumme 2013). The feeding guilds of the captured fishes were obtained from FishBase (Froese and Pauly 2018).

Based on the obtained isotopic values, the TP of the mangrove fish communities was calculated using the Bayesian framework-based R package tRophicPosition version 0.7.5 (Quezada-Romegialli et al. 2018). The model “twoBaselinesFull” was used because it recognizes the heterogeneity of ecosystems by including two different baselines (e.g., pelagic and benthic). A mixing model calculates the importance of the two $\delta^{15}\text{N}$ sources for the consumer by incorporating the $\delta^{13}\text{C}$ values of consumers and baselines. The contribution of $\delta^{15}\text{N}$ sources is weighted accordingly for the different consumers in the calculation of TP. The model was run with 2000 iterations and 5 chains and as a prior a normal distribution with mean 4 (SD 0,1) [dnorm(4,0.1)] and trophic level of baselines (lambda) of 2 was chosen. *Littoraria zebra* (Pacific) and *L. angulifera* (Caribbean) were selected as benthic baselines for the Pacific and Caribbean, respectively, and *C. columbiensis* (Pacific) and *C. rhizophorae* (Caribbean) were chosen as pelagic baselines. The trophic enrichment factors (TEF) calculated by Post (2002), namely for $\delta^{13}\text{C}$ 0.4 ‰ (SD 1.3) and for $\delta^{15}\text{N}$ 3.4 ‰ (SD 1.0), were used in the model. Carbon and nitrogen observations of baselines, consumers, and TEFs are modeled in tRophicPosition as random variables having prior normal distributions on their means and uniform prior distribution on their standard deviations. TP is also modeled as having a uniform prior distribution. In order to check statistically for differences between the consumer TPs, the function “PairwiseComparison” in the package tRophicPosition was used. The posterior TP of a consumer was checked for a higher or equal TP against all other consumers. A probability for each pair and rank was given. Even though the function was provided in tRophicPosition, this pairwise comparison was based on Bayesian statistics and the method was run in the R package SIAR (Stable Isotope Analysis in R; Parnell and Jackson 2013). The variance of the species TPs within each consumer community was tested for significant differences with an F test for equality of variances in R (R Core Team 2018).

The TPs from all 13 fish species analyzed were also taken from FishBase (Froese and Pauly 2018) and compared to the TPs obtained using the stable isotope analysis. The data were tested for normal distribution with a Shapiro–Wilk normality test and the correlation coefficient was calculated using a Pearson correlation test in R (R

Core Team 2018). The difference in values was calculated in percentage based on the FishBase TP values in reference to the isotopic TP values.

To compare the TA of both mangrove fish communities, a SIBER (Stable Isotope Ellipses in R; Jackson et al. 2011) routine of SIAR (Parnell and Jackson 2013) was used. The package SIBER provides a model to compare entire communities using the Layman metrics (Layman et al. 2007). It recognizes that convex hulls based on the centroids of each species are subject to uncertainty in the place of the centroid. The model calculates the distribution of the convex hull areas based on the posterior distribution of the means of each species. As an initial step, the Bayesian multivariate normal distributions are fitted to each group in the data set using the JAGS software run. This model was run with 10,000 iterations and 2 chains. The posterior means were extracted and the distribution was plotted in box plots to visualize the credible intervals (Jackson et al. 2011, Jackson 2019).

RESULTS

COMPOSITION OF THE FISH COMMUNITIES.—All fishes caught were comparatively small and most were juveniles (Table 1). The dominant mangrove fish community in the Caribbean was composed of five species which accounted for 68% of the biomass of the community. In the Pacific, eight species accounted for 94% of the community biomass. The fish communities had only one family in common (Haemulidae), but encompassed fishes with similar feeding guilds, namely zoobenthivores, planktivores, and piscivores. Only one herbivore was found in the Caribbean [*Scarus iseri* (Bloch, 1789)]. More than half of the relative biomass in the Pacific was represented by the armed snook, *Centropomus armatus* (Gill, 1863). All other species represented 12% or less of the total biomass. The biomass in the Caribbean community was more evenly distributed with *Lutjanus apodus* (Walbaum, 1792) and *Haemulon flavolineatum* (Desmarest, 1823) being the most abundant species (45% and 29% in biomass, respectively).

MEASURED $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ VALUES.—The $\delta^{13}\text{C}$ values of the consumers in the Pacific were lower (-17.87‰ to -21.54‰) and had less variation (range = 3.7‰) compared to the community in the Caribbean (-13.05‰ to -18.27‰ ; range = 5.2‰). The $\delta^{15}\text{N}$ values however were higher in the Pacific (9.83‰ to 12.3‰), but with less variation (range = 2.5‰) than in the Caribbean (6.13‰ to 9.46‰ ; range = 3.3‰ ; Table 1). The baseline organisms from the Pacific had around 2‰–3‰ higher $\delta^{15}\text{N}$ values than their Caribbean counterparts [*C. columbiensis* $\delta^{15}\text{N}$ = 6.97‰ (SD 0.55) vs *C. rhizophorae* $\delta^{15}\text{N}$ = 4.5‰ (SD 0.37); *L. zebra* $\delta^{15}\text{N}$ = 4.67‰ (SD 0.78) vs *L. angulifera* $\delta^{15}\text{N}$ = 1.66‰ (SD 0.71)], but similar $\delta^{13}\text{C}$ values [*C. columbiensis* $\delta^{13}\text{C}$ = -18.89‰ (SD 0.67) vs *C. rhizophorae* $\delta^{13}\text{C}$ = -18.04‰ (SD 0.96); *L. zebra* $\delta^{13}\text{C}$ = -23.09‰ (SD 0.24) vs *L. angulifera* $\delta^{13}\text{C}$ = -23.13‰ (SD 0.79)].

TROPHIC POSITION AND ISOTOPIC NICHE OF FISH COMMUNITIES.—The TP of the species in the Pacific community ranged from 3.1 to 3.6 with *C. armatus* (3.6) and *A. walkeri* (3.6) showing the highest TP, followed by *Bairdiella armata* (Gill, 1863) (3.5), *Ariopsis seemanni* (Günther, 1864) (3.5), *Pomadasys macracanthus* (Günther, 1864) (3.3), *Diapterus peruvianus* (Cuvier, 1830) (3.3), *Oxyzygonectes dovii* (Günther, 1866) (3.2), and *Sphoeroides rosenblatti* Bussing, 1996 (3.1; Fig. 2, Table 2). The species in

Table 1. Families, species, and common names of the fish communities in Panamanian Caribbean and Pacific mangroves. Mean total length (SD) and relative biomass of analyzed species in the communities and reported maximal length for the Caribbean (Robertson and van Tassell 2015) and the Pacific (Robertson and Allen 2015) species and feeding guilds (Froese and Pauly 2018).

Family	Species	Common name	Total length (cm)	Maximal length (cm)	Relative biomass (%)	Feeding guild
Caribbean Sea—Bocas del Toro						
Haemulidae	<i>Haemulon flavolineatum</i>	French grunt	15.5 (0.7)	30.0	28.64	Zoobenthivore
	<i>Haemulon plumieri</i>	White grunt	12.0 (5.7)	53.0	8.98	Zoobenthivore
Clupeidae	<i>Jenkinsia stolifera</i>	Florida round herring	---	7.5	2.35	Planktivore
Lutjanidae	<i>Lutjanus apodus</i>	Schoolmaster snapper	14.2 (1.6)	67.5	45.14	Zoobenthivore, piscivore
Scaridae	<i>Scarus iseri</i>	Striped parrotfish	8.5 (1.1)	27.0	14.89	Herbivore
Eastern Pacific—Gulf of Montijo						
Engraulidae	<i>Anchoa walkeri</i>	Persistent anchovy	---	14.5	5.43	Planktivore
Sciaenidae	<i>Bairdiella armata</i>	Armed croaker	12.8 (6.1)	30.0	12.27	Zoobenthivore
Tetraodontidae	<i>Sphoeroides rosenblatti</i>	Oval puffer	23.0 (2.7)	30.0	4.52	Zoobenthivore
Gerreidae	<i>Diapterus peruvianus</i>	Peruvian mojarra	5.0 (0.0)	38.0	2.76	Zoobenthivore
Centropomidae	<i>Centropomus armatus</i>	Armed snook	22.1 (1.6)	37.0	58.37	Zoobenthivore
Anablepidae	<i>Oxyzygonectes dovii</i>	White-eye	14.2 (0.4)	35.0	4.98	Detritus, algae, insects
Haemulidae	<i>Pomadasys macracanthus</i>	Longspine grunt	8.0 (1.0)	35.0	9.51	Zoobenthivore
Ariidae	<i>Ariopsis seemanni</i>	Tete sea catfish	23.8 (3.4)	35.0	2.16	Zoobenthivore

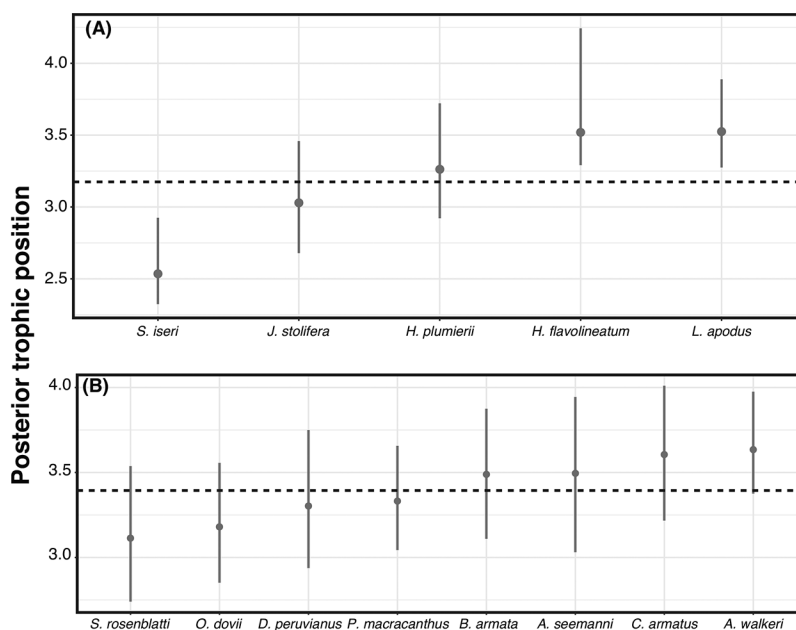


Figure 2. Trophic positions of the mangrove fish assemblage from (A) the Caribbean (Bocas del Toro) and (B) the Pacific (Gulf of Montijo) calculated with the R package tRophicPosition and expressed as posterior trophic position for each species. The dotted line marks the mean trophic position of the community independent from biomass. The grey bars show the 95% credibility interval of each posterior trophic position.

the Caribbean assemblage had TPs ranging from 2.5 to 3.5. The snapper *L. apodus* (3.5) and the grunt *H. flavolineatum* (3.5) had the highest TP in the community, followed by *Haemulon plumierii* (Lacépède, 1801) (3.3) and the schooling herring *J. stolifera* (3.0). All species had higher TPs (probability > 0.7) than the parrotfish *S. iseri* (2.5) based on the probability of similar or higher TPs, indicated in Table 1 as pairwise comparison between the species.

The mean community TP was slightly higher in the Pacific [3.4 (SD 0.2)] than in the Caribbean [3.2 (SD 0.4)], but no significant differences were found. However, the variation (SD) in the Caribbean community was significantly higher than the variation in the Pacific community ($F_{4,7} = 5.009$, $P = 0.03$). Similarly, the mangrove fish community of the Caribbean occupied a larger (9.8‰²) TA than the community in the Pacific (3.4‰²; Fig. 3).

COMPARISON WITH FISHBASE TROPHIC POSITIONS.—TP estimates from FishBase and those obtained with the stable isotope data showed a significant ($P > 0.05$) positive relationship (correlation coefficient = 0.759; Fig. 4). The mean TP was higher in FishBase than the stable isotope data in the Caribbean mangrove fish assemblage [3.4 (SD 0.9) and 3.2 (SD 0.4), respectively], whereas the overall TP for the mangrove fish community in the Pacific was the same for FishBase and the stable isotope data [3.4 (SD 0.4) and 3.4 (SD 0.2), respectively]. However, the estimates of the individual species differed in most cases: FishBase TPs were higher for 8 of the 13 species. For *L. apodus*, the calculated TP was 18% higher than the value in FishBase (Table 2). In 4 out of 13 species, the TP was lower when using FishBase, especially the TPs of the omnivore *O. dovii* from the Pacific and the Caribbean herbivore *S. iseri* (26.5% and 27.1% higher, respectively, than the values provided in FishBase).

Table 2. Mean stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic positions (TPs) of fish species representative of Pacific and Caribbean mangrove fish communities and organisms used as isotopic baselines. Number of replicates per species (n) are presented. TPs were calculated using stable isotopes (SI) and values reported in FishBase (Froese and Pauly 2018). Results of pairwise comparison test for \geq between each species TPs (SI). Parentheses show probability that the posterior TP of the indicated species is \geq the TP of the other species indicated. Only probabilities ≥ 0.7 are shown. Difference TPs (%) indicate the over (positive) or under (negative) estimation of TP FishBase values compared to TP (SI).

Family	Species	n	$\delta^{13}\text{C}$ (‰) (SD)	$\delta^{15}\text{N}$ (‰) (SD)	TP (SI)	TP (FishBase)	Pairwise comparison (probability)	Difference TPs (%)
Caribbean Sea—Bocas del Toro								
Haemulidae	<i>Haemulon flavolineatum</i>	10	-13.05 (1.41)	9.4 (0.44)	3.5	3.5	a a: b (0.872); c (0.976); e (1)	0.0
	<i>Haemulon plumieri</i>	10	-14.81 (1.97)	8.51 (1.01)	3.3	3.8	b b: c (0.838); e (0.998)	14.4
Clupeidae	<i>Jenkinsia stolifera</i>	5	-18.27 (0.14)	7.57 (0.58)	3.0	3.4	c c: e (0.975)	11.0
	<i>Lutjanus apodus</i>	10	-16.22 (1.86)	9.46 (0.51)	3.5	4.3	d d: b (0.872); c (0.977); e (1)	18.0
Scaridae	<i>Scarus iseri</i>	10	-15.01 (1.47)	6.13 (0.21)	2.5	2.0	e	-27.1
Baseline—Ostreidae	<i>Crassostrea rhizophorae</i>	5	-18.04 (0.96)	4.5 (0.37)				
Baseline—Littorinidae	<i>Littoraria angulifera</i>	5	-23.13 (0.79)	1.66 (0.71)				
Eastern Pacific—Gulf of Montijo								
Engraulidae	<i>Anchoa walkeri</i>	10	-17.87 (0.35)	12.3 (0.26)	3.6	3.4	a a: b (0.737); c (0.979); d (0.903); f (0.975); g (0.931); h (0.716)	-6.8
	<i>Bairdiella armata</i>	10	-18.55 (1.22)	11.68 (0.94)	3.5	3.3	b b: c (0.914); d (0.748); f (0.895); g (0.753)	-5.4
Tetraodontidae	<i>Sphoeroides rosenblatti</i>	6	-19.48 (0.74)	10.23 (0.67)	3.1	3.2	c c: -	2.1
	<i>Diapterus peruvianus</i>	3	-18.51 (0.08)	11.2 (0.09)	3.3	3.7	d d: c (0.784); f (0.738)	10.6
Centropomidae	<i>Centropomus armatus</i>	10	-21.54 (0.93)	10.67 (0.69)	3.6	3.9	e e: c (0.952); d (0.856); g (0.862); f (0.94)	7.6
	<i>Oxyzygonectes dowii</i>	8	-20.59 (0.82)	9.83 (0.44)	3.2	2.5	f f: -	-26.5
Haemulidae	<i>Pomadasys macracanthus</i>	9	-18.82 (0.63)	11.17 (0.35)	3.3	3.5	g g: c (0.805); f (0.762)	4.8
	<i>Ariopsis seemanni</i>	10	-21.41 (1.65)	10.42 (0.94)	3.5	3.6	h c (0.889); d (0.72); g (0.729); f (0.87)	3.1
Baseline—Ostreidae	<i>Crassostrea columbientis</i>	5	-18.89 (0.67)	6.97 (0.55)				
Baseline—Littorinidae	<i>Littoraria zebra</i>	5	-23.09 (0.24)	4.67 (0.78)				

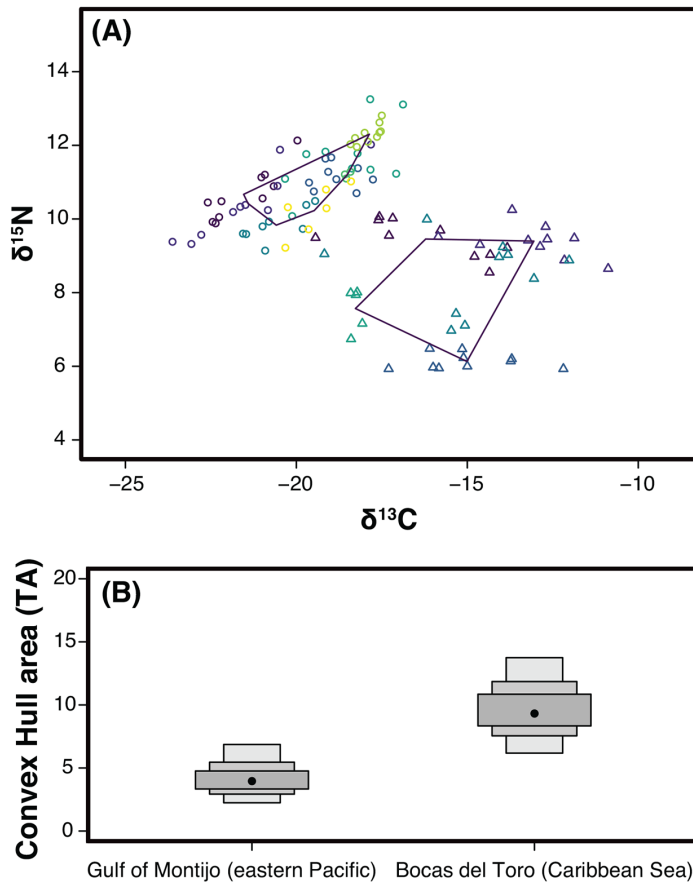


Figure 3. (A) TA of the communities in the Pacific (left polygon, circles) and the Caribbean (right polygon, triangles) in the isotopic biplot; each color represents individuals from a different species. (B) TA (black dots) of Pacific and Caribbean community with credible intervals in different grey shades (50%, 75%, and 95% from dark to light).

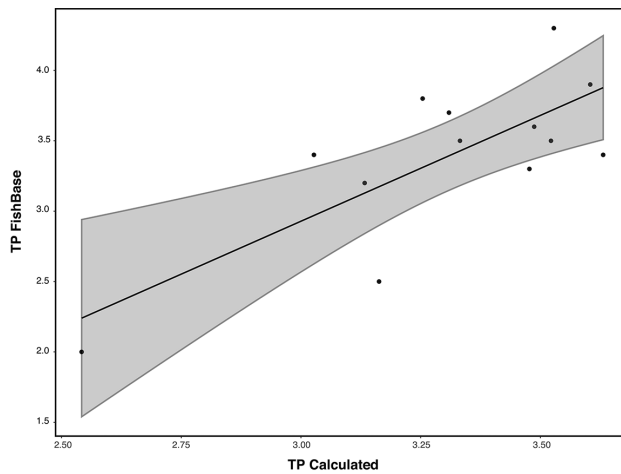


Figure 4. Correlation of the FishBase TPs (y-axis) vs the isotope-based TPs (x-axis) with a regression curve (black line) and a 95% confidence interval (grey area).

DISCUSSION

We found the mean TP values of mangrove fish communities to be similar between the Caribbean and Pacific coasts of Panama. However, the variation in TPs and TAs was greater in the Caribbean mangrove fish community than in the Pacific mangrove fish community, indicating differences in the trophic structure of both communities.

COMMUNITY STRUCTURE.—The species composition caught in the mangrove systems in the Caribbean Sea and the eastern Pacific of Panama are characteristic for tropical mangrove habitats in these regions [eastern Pacific: Castellanos-Galindo and Krumme 2013 (Colombia); Caribbean Sea: Vaslet et al. 2010 (Guadeloupe), Nagelkerken et al. 2000 (Curaçao)], having different trophic guilds, with zoobenthivory being the dominant feeding mode in both regions. Based on the size of the captured fishes, the communities consisted mostly of juveniles of species that are found later in their ontogeny in deeper habitats.

MEASURED $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ VALUES.—The isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of baseline organisms and consumers were in the range found in other studies in nearby areas of both Caribbean and Pacific regions [eastern Pacific: Viana et al. 2015 (Soná Peninsula in Pacific Panama); Caribbean Sea: Vaslet et al. 2012 (Belize and Florida), Cocheret de la Morinière et al. 2003 (Curaçao)]. The choice of baseline organisms in this study followed the experience that primary consumers, like filter feeders and scrapers, provide the best isotopic baseline not only in freshwater (Cabana and Rasmussen 1996), but also in marine systems (Mancinelli et al. 2013). We used filter feeders as a pelagic baseline (oysters) and scrapers as a benthic baseline (periwinkles) in both mangrove systems in order to provide a valid comparison (Table 2). The $\delta^{15}\text{N}$ values were higher by 2‰–3‰ in the organisms from the mangrove system in the eastern Pacific. This might be due to differences in global marine nitrogen fixation and denitrification patterns (Gruber and Sarmiento 1997) and the different fractionation of $\delta^{15}\text{N}$ in these processes (Sigman et al. 2009).

TROPHIC POSITION.—The mangrove fish communities in the Pacific and the Caribbean had similar mean TP, despite having different environmental settings and different isotopic baselines. Both systems were dominated by fish species with TPs between 3 and 4 (secondary to tertiary consumers). In both communities, the TP of the zoobenthivores varied between 3.1 and 3.6, being, as expected, higher than those of herbivores and planktivores. However, in the Pacific, the small pelagic *A. walkeri* and *C. armatus* shared the same TP value (3.6), which was also the highest observed in this community. The TP of *A. walkeri* was relatively high compared to other stable isotope studies where TP of anchovies (e.g., *Engraulis mordax*) was smaller (Miller et al. 2010). However, more recent studies indicate that TPs of anchovies (e.g., *Engraulis ringens* in Peru) could be higher than normally assumed, reaching values of 3.5 (Espinoza et al. 2017, Pizarro et al. 2019). We assume that the high TP could be due to underestimated isotopic baseline values for *A. walkeri* in the presented model. High $\delta^{15}\text{N}$ values are typical for areas influenced by upwelling. Newly upwelled nitrogen tends to be heavier than recycled nitrogen from excretions of consumers (e.g., O'Reilly et al. 2002). Therefore, in upwelling areas, organisms at the base of the food

web tend to show higher $\delta^{15}\text{N}$ values (Reddin et al. 2015). Upwelling occurs seasonally on the Pacific coast of Panama (O'Dea et al. 2004). Even though the upwelling effects are stronger in the Bay of Panama than in the more western basin of the country (O'Dea et al. 2004), Valiela et al. (2014) found higher ammonia followed by newly nitrified nitrate in the southern estuaries of the Soná Peninsula, close to our study sites, which indicates that upwelling can eventually reach this area of the Pacific coast of Panama. Small pelagics like *A. walkeri* may regularly migrate from estuarine mangrove areas like the Gulf of Montijo to offshore areas and feed on plankton with higher $\delta^{15}\text{N}$ values in areas influenced by upwelling. The consumption of plankton with relatively higher $\delta^{15}\text{N}$ values from upwelling areas may lead to a high TP of *A. walkeri* in the presented model. The baseline organisms used in the present model represent the studied system in the Gulf of Montijo, but do not account for baselines in other adjacent areas where anchovies could migrate.

In a study on mangrove food webs on the Pacific coast of Colombia using stable isotope analyses, the nitrogen baseline value calculated for the oyster *C. columbiensis* was approximately 1‰ higher than our calculated value in the Panamanian Pacific, whereas the value for the periwinkle *L. zebra* was similar between the two studies. Higher consumers showed slightly higher nitrogen values in the Colombian system (Medina Contreras et al. 2018), compared to the Panamanian system examined in the Pacific coast. The carbon values of the consumers were in the same range in both the Colombian and Panamanian Pacific systems, which suggests the use of similar primary producers. Calculated TPs of fish species were higher in Medina Contreras et al. (2018) with a mean community TL of 3.6. Similarly, the same fish species in the Colombian Pacific had higher TPs compared to the TPs found in the Pacific coast of Panama, i.e., *S. rosenblatti* (3.9), *A. seemanni* (4.2), and *Bairdiella ensifera* (Jordan and Gilbert, 1882) (4.1). Differences in TPs between studies may be due to differences in the TP calculation techniques. Even though the same fractionation values were used (Post 2002), Medina Contreras et al. (2018) based their calculation on primary producers, namely *R. mangle* as baseline, which can be inaccurate due to higher interspecific variabilities of $\delta^{15}\text{N}$ values of primary producers compared to primary consumers (Mancinelli et al. 2013). Additionally, we used a new Bayesian estimation of TPs using stable isotopes for the TP calculations, which has several advantages over previous methods. tRophicPosition (Quezada-Romegialli et al. 2018) recognizes the heterogeneity of ecosystems. Two baselines and $\delta^{13}\text{C}$ values of consumers and baseline organisms are considered and a mixing model calculates the importance of the two sources for the consumers and adjusts the $\delta^{15}\text{N}$ baseline accordingly. Another advantage of this method is the inclusion of variance for TEF and isotopic baselines based on Bayesian frequency. In contrast, traditional methods (i.e., Post 2002) are based on only one baseline and use point estimates for TEF and isotope values.

ISOTOPIC NICHE.—The TA (Layman et al. 2007) gives an indication of the niche widths of a community. Whereas the TA from Layman et al. (2007) was based on mean isotopic values of each species within the community, Jackson et al. (2011) developed a Bayesian method to include uncertainty in the mean, arising from the natural sampling process when calculating TA. The TA of the mangrove fish community in the Caribbean Sea was nearly three times (2.9) larger than the one from the Pacific. These results support our hypothesis that the Caribbean community occupies a larger isotopic niche than the Pacific community. The wider range

of carbon and nitrogen values in the fish species of the Caribbean mangrove site explains this difference. Stable isotopes, in this context, provide a measure of the dietary resources; therefore, a larger TA of the community suggests a broader use of different resources by fishes. The concept of the isotopic niche width can be used on the community as well as on the species level. Vaslet et al. (2015) studied the niche space of four fishes using standard ellipse areas, including the schoolmaster snapper, *L. apodus* and the French grunt, *H. favolineatum*, at offshore mangrove inlets of the Caribbean Sea and found only a small to moderate overlap of their isotopic niches. Thus, the higher differentiation of ecological niches of fish species inhabiting mangroves in the Caribbean can explain the overall larger isotopic niche width of this community when compared to mangrove fish communities in the eastern Pacific. The shallow-water systems in the Caribbean Sea provide a higher variability of primary carbon sources. Seagrasses, mangroves, and coral reefs are in close proximity to each other and due to the small tidal regime, these habitats are accessible to fishes all the time. The TA in the Pacific was smaller which suggests a higher trophic redundancy in this mangrove fish community. In this system, the fishes feed on a smaller range of food sources suggesting an overlap in their primary food sources. In meso- and macrotidal areas, like the study area in the Pacific, fish migration patterns across coastal habitats are associated with the tidal cycles (Krumme 2004). Fishes access the mangroves at high tide for food and shelter (Krumme 2009) and recede at low tide to adjacent subtidal areas. Contrary to the setting in many Caribbean Sea areas, mangroves in the eastern Pacific generally lack coral reefs and seagrass habitats and are surrounded by mudflats, subtidal creeks, and sandflats. In summary, TAs reflected that the trophic structure and functioning of mangrove fish communities could significantly vary depending on the characteristics of the adjacent habitats and the accessibility to the mangrove areas.

COMPARISON WITH FISHBASE TPs.—It is a common practice among the scientific community to use species traits (i.e., TP from information platforms like FishBase) in ecological studies when primary data is not available. FishBase values are mostly based on stomach content analyses (Mancinelli et al. 2013), which generally give a snapshot of a fish's diet. The comparison of the isotope-based TPs with FishBase values revealed a positive strong correlation. This was also found for fishes in a Mediterranean lagoon (Mancinelli et al. 2013). Even though there were no significant differences in the calculated mean TPs and the FishBase estimates, TPs of the individual species diverged from the FishBase values. Zoobenthivorous species had similar or higher TPs. The TP of the herbivorous parrotfish *S. iseri* and the omnivore *O. dovii* were, however, lower. The correlation between fish size and TP in tropical aquatic systems seems to be more complex with variations between different guilds and species (Layman et al. 2005, Ou et al. 2017) than the predicted more straightforward positive correlation between size and TP (e.g., Romanuk et al. 2011). FishBase estimates are normally calculated for adult fishes, whereas the mangrove fish communities contain usually small-sized juveniles of species that later migrate to deeper habitats as adults. Ontogenetic changes in fish feeding behavior over their ontogeny are common. For example, Haemulidae as well as Lutjanidae species (Cocheret de la Morinière et al. 2003) shift their diet from small crustaceans to fishes and decapods together with a change of habitats and life stage. This can explain the much higher TPs of *L. apodous* and *H. plumieri* in FishBase. *Scarus iseri* was the only herbivorous

fish analyzed, and the calculated TP is 26% higher in the present study compared to the FishBase estimates. The ontogenetic diet shift, which is very common for Haemulidae and Lutjanidae, is not reported for *S. iseri* (Cocheret de la Morinière et al. 2003). However, the evaluation of stomach contents of *S. iseri* is difficult (Cocheret de la Morinière et al. 2003, Dromard et al. 2015) and only a few studies on the feeding behavior of the juvenile stage of this parrotfish have been conducted (Dromard et al. 2017). Therefore, an underrepresentation of juvenile stomach content data in FishBase may be responsible for the observed differences between the two TP calculations. Species within the family Anablepidae feed on a variety of foods originating from different sources showing an omnivore-feeding pattern (Table 1). Omnivores can show high between-individual variances in their trophic position (Svanbäck et al. 2015), depending on the available food items. Therefore, the diet of *O. dovii* varies most likely between ecosystems and environmental settings and is hard to predict.

FishBase is a very useful platform and has many advantages in providing manifold information for global comparisons and meta-analyses. However, TPs of fishes in mangrove ecosystems differ from the FishBase estimates due to the characteristic fish life-stages found in mangroves. Therefore, these values should be taken with care and, when possible, directly calculated for the studied systems.

CONCLUSION

We found that fish communities inhabiting two strikingly different mangrove systems had similar average trophic positions (TPs). However, the broader range of available food sources in the Caribbean led to a higher differentiation in fish feeding strategies, expressed in higher variations of TPs and TAs compared to the fish community in the eastern Pacific, which showed a higher redundancy in feeding strategies. Our results support the idea that mangroves may provide different functions for fishes depending on the environmental settings where they occur.

ACKNOWLEDGMENTS

The authors would like to thank the Smithsonian Tropical Research Institute (STRI) and its field station in Bocas del Toro, the Universidad de Panamá (Veraguas Campus), and the Kellner & Stoll Stiftung for providing funding and logistic support. DR Robertson at STRI and AJ Vega and K Quintero at the Universidad de Panamá provided essential support during the course of this project. We would like to thank Victor, our guide and fish local expert in the Gulf of Montijo, for sharing his expertise and hospitality. This research was conducted with scientific permits issued under SC/A-32-16 and SC/A-52-16. GC-G was supported by the Alexander von Humboldt Foundation and a Senior Latin-American Fellowship provided by STRI. Two anonymous reviewers and the editor provided useful advice to improve previous versions of this manuscript.

LITERATURE CITED

- Abrantes KG, Barnett A, Bouillon S. 2014. Stable isotope-based community metrics as a tool to identify patterns in food web structure in east African estuaries. *Funct Ecol.* 28(1):270–282. <https://doi.org/10.1111/1365-2435.12155>
- Aburto-Oropeza O, Dominguez-Guerrero I, Cota-Nieto J, Plomozo-Lugo T. 2009. Recruitment and ontogenetic habitat shifts of the yellow snapper (*Lutjanus argentiventris*) in the Gulf of California. *Mar Biol.* 156(12):2461–2472. <https://doi.org/10.1007/s00227-009-1271-5>

- Baker R, Sheaves M, Johnston R. 2015. Geographic variation in mangrove flooding and accessibility for fishes and nektonic crustaceans. *Hydrobiologia*. 762(1):1–14. <https://doi.org/10.1007/s10750-015-2329-7>
- Bradley CJ, Wallsgrove NJ, Choy CA, Drazen JC, Hetherington ED, Hoen DK, Popp BN. 2015. Trophic position estimates of marine teleosts using amino acid compound specific isotopic analysis. *Limnol Oceanogr Methods*. 13(9):476–493. <https://doi.org/10.1002/lom3.10041>
- Cabana G, Rasmussen JB. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proc Natl Acad Sci USA*. 93(20):10844–10847. <https://doi.org/10.1073/pnas.93.20.10844>
- Castellanos-Galindo G, Krumme U. 2013. Tidal, diel and seasonal effects on intertidal mangrove fish in a high-rainfall area of the Tropical Eastern Pacific. *Mar Ecol Prog Ser*. 494:249–265. <https://doi.org/10.3354/meps10512>
- Castellanos-Galindo GA, Krumme U. 2014. Long-term stability of tidal and diel-related patterns in mangrove creek fish assemblages in North Brazil. *Estuar Coast Shelf Sci*. 149:264–272. <https://doi.org/10.1016/j.ecss.2014.08.016>
- Castellanos-Galindo GA, Krumme U. 2015. Tides, salinity, and biogeography affect fish assemblage structure and function in macrotidal mangroves of the neotropics. *Ecosystems*. 18(7):1165–1178. <https://doi.org/10.1007/s10021-015-9887-4>
- Cocheret de la Morinière E, Pollux B, Nagelkerken I, Hemminga M, Huiskes A, van der Velde G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Mar Ecol Prog Ser*. 246:279–289. <https://doi.org/10.3354/meps246279>
- Dromard CR, Bouchon-Navaro Y, Harmelin-Vivien M, Bouchon C. 2015. Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *J Sea Res*. 95:124–131. <https://doi.org/10.1016/j.seares.2014.07.014>
- Dromard CR, Vaslet A, Gautier F, Bouchon-Navaro Y, Harmelin-Vivien M, Bouchon C. 2017. Resource use by three juvenile scarids (*Cryptotomus roseus*, *Scarus iseri*, *Sparisoma radians*) in Caribbean seagrass beds. *Aquat Bot*. 136:1–8. <https://doi.org/10.1016/j.aquabot.2016.08.003>
- Espinoza P, Lorrain A, Ménard F, Chérel Y, Tremblay-Boyer L, Argüelles J, Tafur R, Bertrand S, Tremblay Y, Ayón P, et al. 2017. Trophic structure in the northern Humboldt Current system: new perspectives from stable isotope analysis. *Mar Biol*. 164:86. <https://doi.org/10.1007/s00227-017-3119-8>
- Ewel KC, Twilley RR, Ong JE. 1998. Different kinds of mangrove forests provide different goods and services. *Glob Ecol Biogeogr Lett*. 7(1):83. <https://doi.org/10.2307/2997700>
- Froese R, Pauly D, editors. 2018. FishBase. World Wide Web electronic publication. Accessed 15 December, 2018. Available from: www.fishbase.org
- Gross J, Flores Eric E, Schwendenmann L. 2014. Stand structure and aboveground biomass of a *Pelliciera rhizophorae* mangrove forest, Gulf of Montijo Ramsar Site, Pacific Coast, Panama. *Wetlands*. 34(1):55–65. <https://doi.org/10.1007/s13157-013-0482-1>
- Gruber N, Sarmiento JL. 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochem Cycles*. 11(2):235–266. <https://doi.org/10.1029/97GB00077>
- Guzmán HM, Barnes PAG, Lovelock CE, Feller IC. 2005. A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. *Caribb J Sci*. 41(3):430–440. <http://dx.doi.org/10.1186/s13287-016-0351-y>
- Hammerschlag-Peyer CM, Yeager LA, Araújo MS, Layman CA. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLOS ONE*. 6(11):e27104. <https://doi.org/10.1371/journal.pone.0027104>
- Hyslop EJ. 1980. Stomach contents analysis—a review of methods and their application. *J Fish Biol*. 17(4):411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>
- Igulu MM, Nagelkerken I, Dorenbosch M, Grol MGG, Harborne AR, Kimirei IA, Mumby PJ, Olds AD, Mgaya YD. 2014. Mangrove habitat use by juvenile reef fish: meta-analysis reveals

- that tidal regime matters more than biogeographic region. *PLOS ONE*. 9(12):e114715. <https://doi.org/10.1371/journal.pone.0114715>
- Jackson AL. 2019. Introduction to SIBER. Accessed 23 June, 2019. Available from: <https://cran.r-project.org/web/packages/SIBER/vignettes/Introduction-to-SIBER.html>
- Jackson AL, Inger R, Parnell AC, Bearhop S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J Anim Ecol*. 80(3):595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Krumme U. 2004. Patterns in tidal migration of fish in a Brazilian mangrove channel as revealed by a split-beam echosounder. *Fish Res*. 70(1):1–15. <https://doi.org/10.1016/j.fishres.2004.07.004>
- Krumme U. 2009. Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. *In*: Nagelkerken I, editor. *Ecological connectivity among tropical coastal ecosystems*. Dordrecht: Springer Netherlands. p. 271–324. https://doi.org/10.1007/978-90-481-2406-0_8
- Laegdsgaard P, Johnson C. 2001. Why do juvenile fish utilise mangrove habitats? *J Exp Mar Biol Ecol*. 257(2):229–253. [https://doi.org/10.1016/S0022-0981\(00\)00331-2](https://doi.org/10.1016/S0022-0981(00)00331-2)
- Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA, et al. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev Camb Philos Soc*. 87(3):545–562. <https://doi.org/10.1111/j.1469-185X.2011.00208.x>
- Layman CA, Arrington DA, Montaña CG, Post DM. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*. 88(1):42–48. <https://doi.org/10.1890/0012-9658>
- Layman CA, Winemiller KO, Arrington DA, Jepsen DB. 2005. Body size and trophic position in a diverse tropical food web. *Ecol*. 86(9):2530–2535. <https://doi.org/10.1890/04-1098>
- Lee SY, Primavera JH, Dahdouh-Guebas F, McKee K, Bosire JO, Cannicci S, Diele K, Fromard F, Koedam N, Marchand C, et al. 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. *Glob Ecol Biogeogr*. 23(7):726–743. <https://doi.org/10.1111/geb.12155>
- Leigh EG, O’Dea A, Vermeij GJ. 2014. Historical biogeography of the Isthmus of Panama. *Biol Rev*. 89(1):148–172. <https://doi.org/10.1111/brv.12048>
- Lessios HA. 2008. The great American schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annu Rev Ecol Evol Syst*. 39(1):63–91. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095815>
- López-Rasgado FJ, Lluch-Cota SE, Balart EF, Herzka SZ. 2016. Variation in isotopic trophic structure and fish diversity in mangrove systems subject to different levels of habitat modification in the Gulf of California, Mexico. *Bull Mar Sci*. 92(4):399–422. <https://doi.org/10.5343/bms.2015.1100>
- Mancinelli G, Vizzini S, Mazzola A, Maci S, Basset A. 2013. Cross-validation of $\delta^{15}\text{N}$ and FishBase estimates of fish trophic position in a Mediterranean lagoon: the importance of the isotopic baseline. *Estuar Coast Shelf Sci*. 135:77–85. <https://doi.org/10.1016/j.ecss.2013.04.004>
- Medina Contreras D, Cantera Kintz J, Sánchez González A, Mancera E. 2018. Food web structure and trophic relations in a riverine mangrove system of the tropical Eastern Pacific, Central Coast of Colombia. *Estuar Coasts*. 41(5):1511–1521. <https://doi.org/10.1007/s12237-017-0350-y>
- Miller T, Brodeur R, Rau G, Omori K. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. *Mar Ecol Prog Ser*. 420:15–26. <https://doi.org/10.3354/meps08876>
- Montes C, Cardona A, Jaramillo C, Pardo A, Silva JC, Valencia V, Ayala C, Perez-Angel LC, Rodriguez-Parra LA, Ramirez V, et al. 2015. Middle Miocene closure of the Central American Seaway. *Science*. 348(6231):226–229. <https://doi.org/10.1126/science.aaa2815>

- Nagelkerken I, Sheaves M, Baker R, Connolly RM. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish Fish.* 16(2):362–371. <https://doi.org/10.1111/faf.12057>
- Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, den Hartog C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar Coast Shelf Sci.* 51(1):31–44. <https://doi.org/10.1006/ecss.2000.0617>
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL. 2007. A niche for isotopic ecology. *Front Ecol Environ.* 5(8):429–436. [https://doi.org/10.1890/1540-9295\(2007\)5\[429:ANFIE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[429:ANFIE]2.0.CO;2)
- O'Dea A, Herrera-Cubilla A, Fortunato H, Jackson J. 2004. Life history variation in cupuladriid bryozoans from either side of the Isthmus of Panama. *Mar Ecol Prog Ser.* 280:145–161. <https://doi.org/10.3354/meps280145>
- O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, Collins LS, de Queiroz A, Farris DW, Norris RD, et al. 2016. Formation of the Isthmus of Panama. *Sci Adv.* 2(8):e1600883. <https://doi.org/10.1126/sciadv.1600883>
- O'Reilly CM, Hecky RE, Cohen AS, Plisnier P-D. 2002. Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. *Limnol Oceanogr.* 47(1):306–309. <https://doi.org/10.4319/lo.2002.47.1.0306>
- ONU-REDD. 2015. La superficie boscosa y la tasa de deforestación en Panamá Insumos para establecer datos oficiales a ser utilizados en las estadísticas nacionales, y para informar a convenciones y procesos internacionales. Panama City. Available from: https://unredd.net/index.php?view=download&alias=14899-superficie-boscosa-y-tasa-de-deforestacion-en-panama&category_slug=sistema-satelital-monitoreo&option=com_docman&Itemid=134
- Ou C, Montaña CG, Winemiller KO. 2017. Body size–trophic position relationships among fishes of the lower Mekong basin. *R Soc Open Sci.* 4(1):160645. <https://doi.org/10.1098/rsos.160645>
- Parnell A, Jackson A. 2013. SIAR: Stable Isotope Analysis in R. R package version 4.2. Accessed 23 March, 2014. Available from: <https://CRAN.R-project.org/package=siar>
- Pizarro J, Docmac F, Harrod C. 2019. Clarifying a trophic black box: stable isotope analysis reveals unexpected dietary variation in the Peruvian anchovy *Engraulis ringens*. *PeerJ.* 7:e6968. <https://doi.org/10.7717/peerj.6968>
- Post DM. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology.* 83(3):703. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- Quezada-Romegialli C, Jackson AL, Hayden B, Kahilainen KK, Lopes C, Harrod C. 2018. tRophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods Ecol Evol.* 9(6):1592–1599. <https://doi.org/10.1111/2041-210X.13009>
- R Core Team. 2018. R: A Language and Environment for Statistical Computing. Vienna. Available from: <https://www.r-project.org>
- Recio ME, Kuper J, Vallejo M, Sommerville M, Nayna J. 2016. Central America mangroves, tenure, and Redd+ assessment. Washington, DC: USAID Tenure and Global Climate Change Program.
- Reddin CJ, Docmac F, O'Connor NE, Bothwell JH, Harrod C. 2015. Coastal upwelling drives intertidal assemblage structure and trophic ecology. *PLOS ONE.* 10(7):e0130789. <https://doi.org/10.1371/journal.pone.0130789>
- Robertson DR, Allen G. 2015. Shorefishes of the Tropical Eastern Pacific online information system. Version 2.0 Smithsonian Tropical Research Institute, Balboa, Panama. Accessed 15 January, 2019. Available from: www.stri.org/sfstep
- Robertson DR, Smith-Vaniz WF. 2010. Use of clove oil in collecting coral reef fishes for research. *Mar Ecol Prog Ser.* 401:295–302. <https://doi.org/10.3354/meps08374>

- Robertson DR, van Tassell J. 2015. Shorefishes of the Greater Caribbean online information system. Version 1.0 Smithsonian Tropical Research Institute, Balboa, Panama. Accessed 15 January, 2019. Available from: www.stri.org/sfgc
- Romanuk TN, Hayward A, Hutchings JA. 2011. Trophic level scales positively with body size in fishes. *Glob Ecol Biogeogr*. 20(2):231–240. <https://doi.org/10.1111/j.1466-8238.2010.00579.x>
- Schielke EG, Post DM. 2010. Size matters: comparing stable isotope ratios of tissue plugs and whole organisms. *Limnol Oceanogr Methods*. 8(7):348–351. <https://doi.org/10.4319/lom.2010.8.348>
- 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 Ecol Manage*. 23(2):293–314. <https://doi.org/10.1007/s11273-014-9382-2>
- Sheaves M. 2017. How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept. *Fish Fish*. 18(4):778–789. <https://doi.org/10.1111/faf.12213>
- Sigman DM, Karsh KL, Casciotti KL. 2009. Nitrogen isotopes in the ocean. *In*: Steele J, Thorpe S, Turekian K, editors. *Encyclopedia of ocean sciences*. 2nd ed. Elsevier Ltd. p. 40–54. <https://doi.org/10.1016/B978-012374473-9.00632-9>
- Svanbäck R, Quevedo M, Olsson J, Eklöv P. 2015. Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia*. 178(1):103–114. <https://doi.org/10.1007/s00442-014-3203-4>
- Twilley RR, Rovai AS, Riul P. 2018. Coastal morphology explains global blue carbon distributions. *Front Ecol Environ*. 16(9):503–508. <https://doi.org/10.1002/fee.1937>
- Valiela I, Bartholomew M, Giblin A, Tucker J, Harris C, Martinetto P, Otter M, Camilli L, Stone T. 2014. Watershed deforestation and down-estuary transformations alter sources, transport, and export of suspended particles in Panamanian mangrove estuaries. *Ecosystems*. 17(1):96–111. <https://doi.org/10.1007/s10021-013-9709-5>
- Vaslet A, Bouchon-Navaro Y, Charrier G, Louis M, Bouchon C. 2010. Spatial patterns of mangrove shoreline fish communities in relation with environmental variables in Caribbean lagoons. *Estuaries Coasts*. 33(1):195–210. <https://doi.org/10.1007/s12237-009-9225-1>
- Vaslet A, Phillips DL, France C, Feller IC, Baldwin CC. 2012. The relative importance of mangroves and seagrass beds as feeding areas for resident and transient fishes among different mangrove habitats in Florida and Belize: evidence from dietary and stable-isotope analyses. *J Exp Mar Biol Ecol*. 434–435:81–93. <https://doi.org/10.1016/j.jembe.2012.07.024>
- Vaslet A, Phillips DL, France CAM, Feller IC, Baldwin CC. 2015. Trophic behaviour of juvenile reef fishes inhabiting interlinked mangrove-seagrass habitats in offshore mangrove islets. *J Fish Biol*. 87(2):256–273. <https://doi.org/10.1111/jfb.12715>
- Vander Zanden MJ, Rasmussen JB. 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology*. 80(4):1395–1404. [https://doi.org/10.1890/0012-9658\(1999\)080\[1395:PCCANA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1395:PCCANA]2.0.CO;2)
- Viana IG, Valiela I, Martinetto P, Monteiro Pierce R, Fox SE. 2015. Isotopic studies in Pacific Panama mangrove estuaries reveal lack of effect of watershed deforestation on food webs. *Mar Environ Res*. 103:95–102. <https://doi.org/10.1016/j.marenvres.2014.10.003>



