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The isotopic niche of the macrobenthos in a major mangrove area of the southern Caribbean Sea

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ABSTRACT: Trophic organization of the mangrove macrobenthos communities is poorly known. Using nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope analysis, and Bayesian models, this paper assesses the isotopic niche size and overlap between the trophic guilds of the macrobenthos in the Atrato River Delta estuary (Colombia). A total of 10 species encompassed four trophic guilds. A compact food web supports the macrobenthos, where the isotopic niche size of the community was 3.3‰^{2}. The isotopic niche size was larger for deposit feeders (4.3‰^{2}) than omnivores (3.3‰^{2}), followed by herbivores (1.9‰^{2}) and carnivores (1.3‰^{2}). Considerable overlap of isotopic niche space was found between herbivores (crabs of the Sesarmidae family) and deposit feeders (crabs of the Ocypodidae family). Both former trophic guilds constituted the first consumers within the trophic structure of the system. There also was considerable overlap between the highest trophic levels (omnivores and carnivores). These results can potentially be useful to understanding and monitoring changes in this community.
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KEY WORDS: stable isotopes, mangroves, macrobenthos, Bayesian mixing models, Gulf of Urabá, Atrato River Delta, Colombia.

Изотопная ниша макробентоса крупного мангрового района южной части Карибского моря

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РЕЗЮМЕ: Исследована трофическая организация сообществ макробентоса мангровых лесов эстуария реки Атрато (Колумбия). Используя анализ стабильных изотопов азота ($\delta^{15}N$) и углерода ($\delta^{13}C$), а также байесовские модели, были оценены размеры изотопных ниш и их перекрывание между трофическими гильдиями 10 массовых видов макробентоса. Всего выделено четыре трофические гильдии. Размер изотопной ниши сообщества составлял 3,3‰^{2}, что указывает на относительно компактную пищевую сеть. Размер изотопной ниши был больше у детритофагов (4,3‰^{2}), чем у всеядных (3,3‰^{2}), за которыми следовали фитофаги (1,9‰^{2}) и хищники (1,3‰^{2}). Значительное перекрытие пространства изотопных ниш обнаружено между фитофагами (крабы сем. Sesarmidae) и детритофагами (крабы сем. Ocypodidae), а также между гильдиями высших трофических уровней — всеядными и хищниками. В тоже время, существует относительная сегрегация ниш между трофическими гильдиями низкого (фитофаги и детритофаги) и высокого (всеядные и хищники) трофических уровней. Полученные результаты важны для понимания изменений, происходящих на обширных территориях мангровых сообществ юга Карибского бассейна и их мониторинга.

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КЛЮЧЕВЫЕ СЛОВА: стабильные изотопы, мангры, макробентос, Байесова модель, Залив Ураба, дельта реки Атрато, Колумбия.

Introduction

The ecological niche is originally defined as the multidimensional space comprising the resources used by an organism (Hutchinson, 1957); it is fundamental in ecology, but difficult to measure in practice (Leibold, 1995). However, the ecological niche can be analyzed using different approaches, including stable isotope analyses (SIA), which is known as the isotopic niche. (Newsome *et al*., 2007; Jackson *et al*., 2011). The isotopic niche is defined as the hypervolume of the isotopic space (n-dimensional), where the axes are the isotopic compositions that represent the bionomic and scenopoetic components of the niche (Newsome *et al*., 2007; Marques *et al*., 2017).

Mangroves are important habitats for fish and invertebrates (Lee, 1995; Sheaves, Molony, 2000). Several studies using SIA have described the trophic structure and habitat use of organisms in mangrove ecosystems (e.g. Abrantes, Sheaves, 2009; Medina-Contreras *et al*., 2020; Sandoval *et al*., 2022b). For instance, the isotopic niche has been used as a tool to describe the structure and trophic dynamics of mangrove macrobenthos communities (Medina-Contreras *et al*., 2023). In addition, isotopic niches have been useful to compare the trophic structure of fish communities across habitats and seasons (Shahraki *et al*., 2014; Sepulveda-Lozada *et al*., 2017; Stuthmann, Castellanos-Galindo, 2020), and to assess ontogenetic shifts of fish predators (e.g. Sandoval *et al*., 2020b; Jiao *et al*., 2022). Recently, Medina-Contreras and Arenas (2022) have highlighted that the isotopic niche is also useful for tracking the effect of anthropogenic activities in mangrove ecosystems, where the largest isotopic niches would be related to systems with greater anthropogenic intervention.

Benthic macrofaunal communities are ecologically important components of mangrove ecosystems, shaping the structure and function of mangrove forests through activities such as bioturbation, organic matter processing, and propagule predation (Werry, Lee, 2005; Lee, 2008; Cannicci *et al*., 2021). However, their trophic organization is relatively poorly known compared to fish communities. Mangrove systems in the Gulf of Urabá, Colombia, are under threat due to illegal logging (Blanco *et al*., 2012) and urban development, such as for building three mega-ports (Sandoval, 2019). Recent research in the Gulf using SIA has revealed aspects of the trophic pathways of mangrove systems, which is useful to protect extensive mangrove areas (Sandoval *et al*., 2022b). In the present brief communication, the objective was to assess the isotopic niche size and overlap between trophic guilds of the most abundant species of the macrobenthos community in the Atrato River Delta estuary (ARD).

Material and methods

The Urabá Gulf, located near the western border of northern Colombia next to Panama, has extensive mangrove forests (*ca*. 5690 ha). About 78% of the total mangrove extent in the Gulf is in the ARD (Blanco-Libreros, 2016). Macrobenthos were collected from La Paila Bay in the ARD during the rainy season (September–October) of 2016 (Fig. 1). Each biological sample consisted of a pool of several specimens of the same species of about the same size. Epibenthos was collected manually from inside the mangroves. Carnivorous shrimp and swimming crab

Fig. 1. Study area at La Paila Bay in the Atrato River Delta of the Gulf Urabá, Caribbean Sea. The projected coordinate system is MAGNA-SIR-GAS Colombia Oeste.
Рис. 1. Район исследований: бухта Ла Пайла в дельте реки Атрато залива Ураба Карибского моря.

species were collected using a gill net close to the mangroves.

For shrimp, a sample of abdomen muscle tissue was taken after exoskeleton and digestive tract removal. For crabs and mollusks, the chelae and foot muscles, respectively, were removed to form individual or composite samples according to the size of the specimens. At least 3 individuals of each species were analyzed. All samples were dried at 60 °C for at least 48 h in Petri dishes. Dried samples were ground to a fine powder with a mortar and pestle and stored in clean glass vials. Between 0.7 and 1 mg of the sample was weighed on a micro-scale and deposited in a tin capsule for isotopic analysis. Analyses were carried out in Laboratorio de Biogeoquímica de Isotopos Estables at Instituto Andaluz de Ciencias de la Tierra (Granada, Spain). Laboratory isotopic analysis details are described in Sandoval *et al*. (2022b). Because the variation of lipid content in tissues affects $\delta^{13}C$ values and ecological interpretations, a mathematical normalization method was used to standardize lipid content for samples (Post *et al*., 2007), as described by Sandoval *et al*. (2022b).

The trophic guilds of the most abundant macrobenthos species were assessed based on cluster analysis using the trophic level values and the percent of

Table 1. Mean ± SD carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values, trophic guilds, trophic position, and percent of primary producer's contributions (median) for the most abundant macrobenthos consumers collected in the ARD, Colombian Caribbean.

Таблица 1. Среднее ± SD значений стабильных изотопов углерода ($\delta^{13}C$) и азота ($\delta^{15}N$), трофические гильдии, трофическое положение и относительный вклад продуцентов (медиана) для наиболее многочисленных потребителей макробентоса, собранных в эстуарии реки Атрато, Карибское море, Колумбия.

Species/Taxon	n(N)	$\delta^{13}C$(‰)			$\delta^{15}N$(‰)			TG	TP	PP's contributions (Median %)			
										Mang	Balg	Mphy	Malg
EPIBENTHOS													
Gastropoda													
Thaisella coronata trinitatensis	3	–24.5	±	0.2	8	±	0.1	CAR	3.1	7	29	11	50
Neritina virginea	9(6)	–25.7	±	1.1	5.8	±	0.7	OMN		13	21	22	41
Grapsidea													
Aratus pisonii	9(5)	–25.6	±	0.8	3.9	±	0.7	HER	1.8	75	2	10	9
Pachygrapsus transversus	3(3)	–25.4	±	0.3	4.8	±	0.1	HER	2	60	2	10	25
Ocypodidae													
Uca spp.*	9(3)	–27.8	±	0.8	3.6	±	0.9	DEP	1.6	28	2	38	29
Panopeidae													
Panopeus rugosus	3	–25.6	±	0.8	7.7	±	0.8	CAR	3	11	22	9	55
Eurytium limosum	3	–25.3	±	0.3	6.8	±	0.3	OMN	2.7	13	16	35	33
SHRIMP AND SWIMMING CRAB													
Penaeidae													
Litopenaesu schmitii	3(2)	–23.7	±	0.2	7.3	±	0.1	OMN	2.9	9	32	24	31
Portunidae													
Callinectes bocourti	3	–26	±	0.3	7.1	±	0.3	OMN	2.8	14	16	22	46

* Two unidentified species.

TP and PP's contributions (Median %) by Sandoval *et al.*, 2022b.

Abbreviations: Balg — benthic algae; CAR — carnivores; DEP — deposit feeders; HER — herbivores; Malg — macroalgae (Chlorophytes; *Rhizoclonium* sp.); Mang — mangrove; Mphy — macrophytes (cattail *Typha* sp.); n — number of samples; N — number of pooled individuals in each sample; OMN — omnivores; PP — primary producer; TG — trophic guild; TP — estimated trophic position.

primary producers' contribution estimated by Sandoval *et al*. (2022b) (Table 1). Former authors used the mathematical formula proposed by Post (2002) to calculate trophic level and MixSIAR (Bayesian stable isotope mixing models) to estimate the proportional contribution of different primary producers to macrobenthos consumers (Stock, Semmens, 2016). For cluster analysis, each variable was log-transformed to reduce skewness of data, and it used the Bray-Curtis index and the Unweighted Pair Group Mean Average algorithm. The trophic guilds were assigned following the separation of trophic groups and the species' trophic level. Results were corroborated according to literature information (Palomares *et al*., 2022).

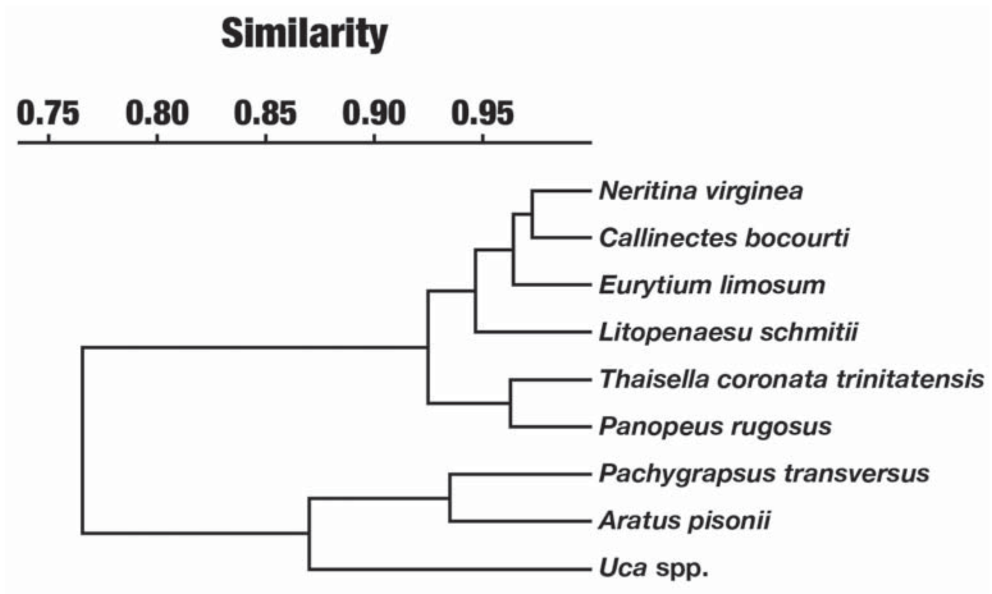
To compare the isotopic niche size and overlap between trophic guilds a Stable Isotope Bayesian Ellipses (SIBER) routine was used (Jackson *et al*., 2011) in R (R Core Team, 2022). The total area (TA) was used to describe the isotopic niche of the community. The standard ellipse area corrected for small sample sizes (SEAc, containing approximately 40% of data) was used as the measure of isotopic niche. The SEAc based on the maximum likelihood was used to calculate the overlap between groups. The Bayesian standard ellipse area (SEA_B) was used to compare the probability that distributions are smaller between trophic guilds. The Bayesian approximation model was generated through 10,000 Monte Carlo simulations and Markov chains. The distribution values were plotted in box plots to visualize the credible intervals (Jackson *et al*., 2011).

Results and discussion

A total of 10 the most abundant species that could be found in all seasons of the year were caught and analyzed (Table 1). Mangrove habitats have generally lower species richness of macrobenthos (e.g. 17 species) than adjoining habitats such as seagrass meadows and open sand/mudflat, but they are dominated by large populations of few species (Lee, 2008). Salinity has been identified as influencing assemblage structure and abundance of macrobenthic communities (Lui *et al*., 2002; Lee, 2008). Macroinvertebrates' richness in the Urabá Gulf mangroves is lower than in other Caribbean systems, this could be due to the large freshwater discharge of the Atrato River (Blanco-Libreros, Ortiz-Acevedo, 2016). Despite the lower species richness, the abundance of brachyuran crab species of the Sesarmidae and Ocypodidae families is relatively high in the region (personal observations), as in other mangrove ecosystems (Lee, 2008). Here, it is studied the trophic organization of the most abundant benthonic species in the ARD, which would be crucial to understanding and monitoring changes in this community. However, the composition and abundance of mangrove macrobenthos should also be scrutinized.

The cluster analysis indicated the separation of four major trophic groups at a 0.94 similarity level, specifically deposit feeders (*Uca* spp.), herbivores (*Aratus pisonii* (H. Milne Edwards, 1837) and *Pachygrapsus transversus* (Gibbes, 1850)), carnivores (*Panopeus rugosus* A. Milne-Edwards, 1880 and *Thaisella trinitatensis* (Guppy, 1869)) and omnivores (*Litopenaes schmitii* (Burkenroad, 1936), *Eurytium limosum* (Say, 1818), *Callinectes bocourti* A. Milne-Edwards, 1879, and *Neritina virginea* (Linnaeus, 1758)) (Fig. 2). In contrast, Medina-Contreras *et al*. (2020) (Tropical Eastern Pacific system) and Medina-Contreras *et al*. (2023) (Subtropical Eastern Pacific system) identified six trophic guilds, finding filter-feeder bivalves and filter feeders, which were not found in this study. The lower number of trophic guilds in the ARD would be related to the low macroinvertebrate richness in the region caused by the large freshwater discharge. For instance, filter-feeder bivalves in the Urabá Gulf, such as the mangrove cupped oyster (*Crassostrea rhizophorae* (Guilding, 1828)), are related to estuarine habitats with relatively higher salinity, such as Rionegro Cove on the northeastern coast of the Gulf (Blanco-Libreros, Ortiz-Acevedo, 2016).

Mean $\delta^{13}C$ values ranged between –27.8‰ (*Uca* spp.) and –23.7‰ (*L. schmitii*). Mean $\delta^{15}N$ values oscillated between 3.6‰ (*Uca* spp.) and 8‰ (*T. trinitatensis*) (Table 1). The isotopic niche size of the community (TA) was 3.3‰^{2} suggesting a relatively compact food web. Medina-Contreras *et al*. (2023) found a larger TA (14.1‰^{2}) in a semi-arid mangrove system (Gulf of California, Mexico), where there was a larger species number (18) and a diversity of food sources (mangrove, microphytobenthos, macroalgae, sedimentary organic carbon, and plankton), which had a large separation along the $\delta^{13}C$ axis (~14‰). The relative lower TA in ARD would be explained because mangrove and macroalgae ($\delta^{13}C$ depleted sources: –31 ± 1.5‰ and –30.8 ± 0.0, respectively) are the main sources supporting macroinvertebrates consum-



ig. 2. Hierarchical clustering of macrobenthos' feeding guilds based on trophic level values and the percentage of primary producer contributions. Deposit feeders (*Uca* spp.), herbivores (*Aratus pisonii* and *Pachygrapsus transversus*), carnivores (*Panopeus rugosus* and *Thaisella trinitatensis*) and omnivores (*Litopenaesu schmitii*, *Eurytium limosum*, *Callinectes bocourti*, and *Neritina virginea*).
Рис. 2. Иерархическая кластеризация трофических гильдий макробентоса на основе значений трофического уровня и доли вклада первичных продуцентов. Детритофаги (*Uca* spp.), фитофаги (*Aratus pisonii* и *Pachygrapsus transversus*), хищники (*Panopeus rugosus* и *Thaisella trinitatensis*) и всеядные (*Litopenaesu schmitii*, *Eurytium limosum*, *Callinectes bocourti* и *Neritina virginea*).

ers (Sandoval *et al.*, 2022b), and because there is a strong stratification in ARD (Montoya *et al.*, 2017), which would not allow macroinvertebrate's access to other sources, such as planktonic sources, as have been showed in macrotidal and mesotidal mangrove systems (Medina-Contreras *et al.*, 2020; Medina-Contreras *et al.*, 2023).

The isotopic niche size was larger for deposit feeders (SEAc 4.3‰^{2}) and omnivores (SEAc 3.3‰^{2}), followed by herbivores (SEAc 1.9‰^{2}) and carnivores (SEAc 1.3‰^{2}) (Fig. 3). As a result, the probability that the SEA_B of deposit feeders is greater than those of the herbivore and carnivores was 98%, while the probability that the SEA_B of omnivores is greater than those of the herbivore and carnivores was 94–95% (Fig. 4). Deposit feeders' largest isotopic niche size would be explained because they feed mainly on mangroves and macrophytes, sources that have a relatively large separation along the δ^{13}C axis (–31 ± 1.5‰ and –27.3 ± 0.1‰, respectively) (Sandoval *et al.*, 2022b). While the small isotopic niche of herbivores and carnivores would be due to their dependency on mangrove leaves and omnivores invertebrates, respectively (Sandoval *et al.*, 2022b). Omnivores' large isotopic niche size would be explained because they can feed on primary producers such as microphytobenthos and macroalgae, but also on micro and macrozoobenthos (Sandoval *et al.*, 2022b). Which showed a relatively larger width in the δ^{15}N axis for these consumers, since the δ^{15}N of micro and macrozoobenthos would be enriched by 3–4‰ relative to their diet primary producers (Post *et al.*, 2002) (Fig. 3).

Considerable overlap of isotopic niche space was found between herbivores and deposit feeders (Fig 3), the isotopic niche space of herbivores overlapped 40% of the niche space of deposit feeders, while the isotopic niche space of deposit feeders overlapped 91% of the niche space of herbivores. Both trophic guilds were closer to δ^{13}C depleted sources (mangroves: –31 ± 1.5‰) since herbivores feed mainly on man-

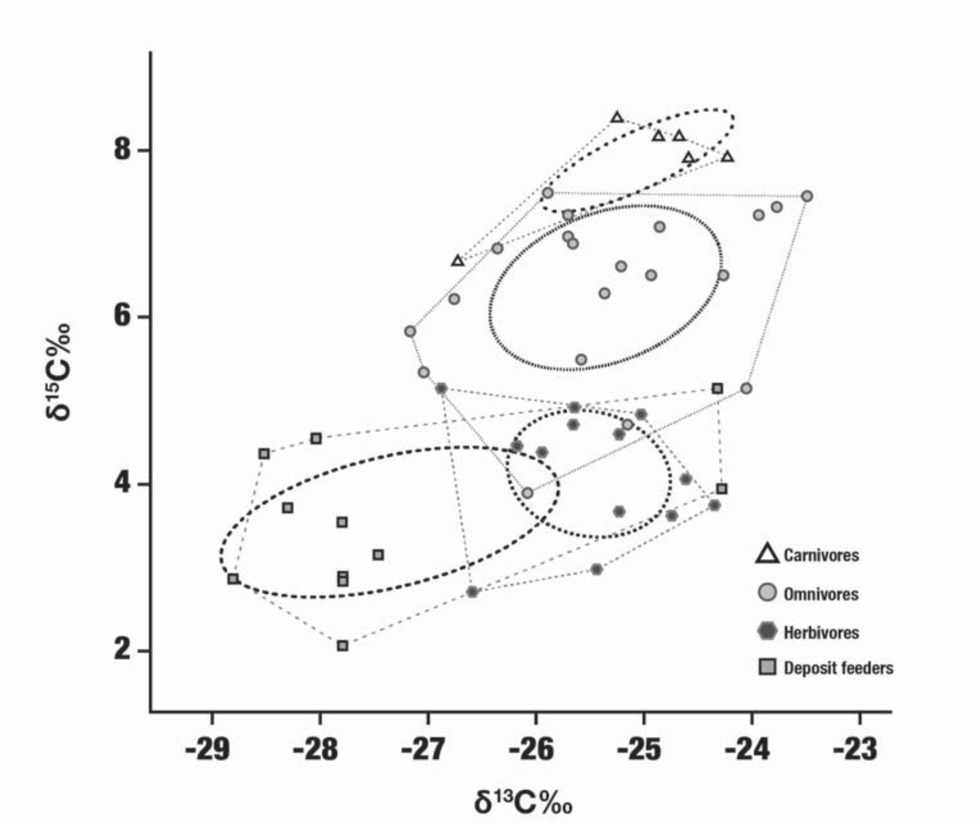


Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of macrobenthos belonging to different trophic guilds. Thick lines enclose the standard ellipses area (SEAc), containing *c*. 40% of the data, showing the isotopic niche of the trophic guilds. Thin lines are the convex hull areas of each trophic guild, corresponding to the area including all individuals of that group.

Рис. 3. Значения δ13C и δ15N макробентоса, относящегося к разным трофическим гильдиям. Толстые цветные линии (эллипсы — SEAc) ограничивают область, содержащую примерно 40% данных, показывающих изотопную нишу трофических гильдий.

groves, while deposit feeders feed on mangroves and macrophytes (Sandoval *et al*., 2022b). The importance of mangrove leaf in the herbivores' diet in the ARD has also been exhibited experimentally (Sandoval *et al*., 2022a). Thus, herbivores (crabs of the Sesarmidae and Grapsidae families) and deposit feeders (crabs of the Ocypodidae family) constituted the first consumers within the trophic structure of the system (Fig. 3a), evidencing their importance on trophic dynamics, where they would mediate the transfer of mangrove primary production to other consumers (e.g. Kristensen *et al*., 2017; Cannicci *et al*., 2021).

The isotopic niche of omnivores overlapped the niche space of deposit feeders by 26%, the niche of herbivores by 50%, and the niche of predators by 80%. In this way, there was also a considerable overlap in the space of isotopic niches between the highest trophic levels (omnivores and carnivores) (Fig. 3). This functional redundancy at higher trophic levels has been found in other mangrove systems (Abrantes, Sheaves, 2009; Medina-Contreras *et al*., 2023). This would explain because some omnivores species (such as *E. limosum* and *C. bocourti*) feed on a variety of invertebrates (as carnivores), but they also feed on detritus (Palomares *et al*., 2022).

Overall, a compact food web supports the macroinvertebrates community in the ARD where herbivores and deposit feeders are the

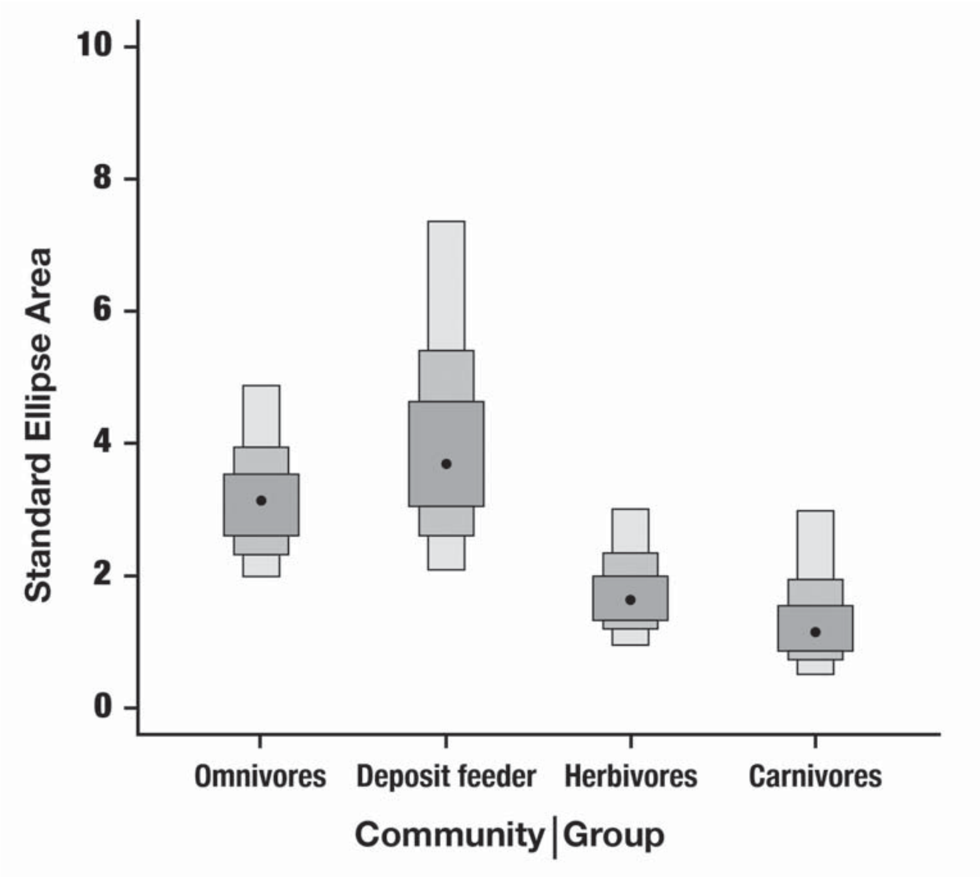


Fig. 4. Density plot of the Bayesian standard ellipse areas (SEA_B). Black points: modes; Boxes: 50, 75, and 95% BCI (Bayesian credible interval) from dark gray to light gray for every trophic guild.
Рис. 4. График плотности областей байесовского стандартного эллипса (SEAB) для каждой трофической гильдии. Черные точки — моды; ящики — 50, 75 и 95% (доверительный интервал) от темно-серого до светло-серого.

first consumers. There is a considerable overlap between herbivores and deposit feeders, and between omnivores and carnivores. However, there is relative niche segregation between trophic guilds at the lowest (herbivores and deposit feeders) and highest trophic levels (omnivores and carnivores). These results can potentially be useful to monitoring changes in this community in the extensive mangrove areas in the southern Caribbean.

Compliance with ethical standards

CONFLICTS OF INTEREST: The author declares that he has no conflicts of interest.

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