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Resource partioning between sympatric congeners: A case study of river rays (*Potamotrygon* spp.) in the Amazon estuary

Partição de recursos entre congeners simpátricos: Um estudo de caso de raias de água doce (Potamotrygon spp.) no estuário amazônico

Cecile de Souza Gama[1], Ricardo de Souza Rosa[2]

*[1]Biologist, PhD in Biological Sciences (Zoology). Researcher at the Institute of Scientific and Technological Research of the State of Amapá – IEPA. Macapá-AP Brasil. E-mail: cecilegama@hotmail.com *Autor para correspondência*
[2]Biologist, PhD in Marine Science. Federal University of Paraiba. João Pessoa - PB Brazil. E-mail: rsrosa@dse.ufpb.br

Palavras-chave

Potamotrygon
Niche overlap
Stingrays

The syntopic occurrence of different species of freshwater stingray on a small fluvial island at the mouth of the Amazon River led to the investigation of the factors that underpin this coexistence. Stingrays were collected every two months from March 2012 to January 2013 and their exact sampling location was recorded and their stomach contents preserved and analyzed. Data were used to calculate the Levins' index of niche breadth and Pianka's index of niche overlap. The combined analysis of these two indices revealed four distinct scenarios, with only one of them favoring interaction between species, when feeding resources were scarce and patchily distributed. The latter conditions were found at two distinct moments during the study period – the peak of the flood and the peak of low water – whereas in other periods, the prevailing conditions were not conducive to resource sharing.

Keywords

Partição de recurso
Sobreposição de nicho
Raias de água doce

A ocorrência sintópica de diferentes espécies de arraia de água doce em uma pequena ilha fluvial na foz do rio Amazonas levou à investigação dos fatores que sustentam essa coexistência. As arraias foram coletadas a cada dois meses, de março de 2012 a janeiro de 2013, e o local exato da amostragem foi registrado e o conteúdo estomacal preservado e analisado. Os dados foram usados para calcular o índice de largura de nicho de Levins e o índice de sobreposição de nicho de Pianka. A análise combinada desses dois índices revelou quatro cenários distintos, com apenas um deles favorecendo a interação entre espécies, quando os recursos alimentares eram escassos e distribuídos de maneira irregular. As últimas condições foram encontradas em dois momentos distintos durante o período do estudo - o pico da enchente e o pico da maré baixa - enquanto em outros períodos as condições prevalecentes não foram propícias ao compartilhamento de recursos.

INTRODUCTION

Measures of niche overlap are widely used to infer trophic competition and resource sharing among sympatric fish species. The principle of competitive exclusion, which states that coexisting species cannot share a niche, has been challenged by field data collected over the past few decades. Those data have shown that the coexistence of potentially competing species is a frequent phenomenon in natural environments (e.g., LABROPOULOU; ELEFTHERIOU, 1997; GIACOMINI, 2007; BARRET et al., 2016) and places more emphasis to the principle of resource partitioning (SCHOENER, 1974). Resource partitioning stresses the different ways by which species in the same community utilize resources, and promotes the coexistence of species using the same resource. The theoretical analysis of the empirical evidence indicates that the principle of competitive exclusion may be substituted by a principle of "coexistence", based on differences in growth rates and patterns of spatial and temporal distribution (BASTOLLA et al., 2008). In this case, sympatry between closely related organisms, such as congeners, would lead to systematic differentiation in the exploitation of resources to avoid competitive interactions, especially when resources are scarce (GAUSE, 1934; MacARTHUR, 1972; MATTHEWS, 1998; PIANKA, 2000). On the other hand, a marked overlap in the diet at other times, when feeding resources are relatively abundant, may not necessarily result in competition (LONARDONI et al., 2006).

Species that exploit the same abiotic or biotic resources are not rare in nature. In such cases, the degree of overlap of geographic ranges depends on the ecological tolerance of the sympatric species in relation to shared resources, and their relative competitiveness (PINHEIRO et al., 1997). As two or more morphologically and ecologically similar species often occur in sympatry, it is important to understand the mechanisms that favor their co-occurrence (DURÉ et al., 2009).

Differences in the composition of the diet may indicate that some species are more specialized than others. The degree of specialization may vary between sites, communities and environmental conditions, and can be quantified by indices of niche size and breadth or amplitude. Niche size is a one-dimensional parameter and can be measured by observing the distribution of individuals in relation to the consumption or exploitation of a given set of resources (KREBS, 1989).

Five species of freshwater stingrays in the genus *Potamotrygon* Garman 1877 are found in the Parazinho Biological Reserve, a fluvial island at the mouth of the Amazon River (GAMA; ROSA, 2015a). The present study investigated the feeding aspects of these species, *Potamotrygon motoro* (MÜLLER; HENLE, 1841), *P. orbignyi* (CASTELNAU 1855), *P. scobina Garman*, 1913, *P. constellata* (VAILLANT, 1880) and *Potamotrygon marquesi* SILVA e LOBODA, 2019, to evaluate dietary overlap, and to understand how environmental conditions influence the community structure.

MATERIAL AND METHODS

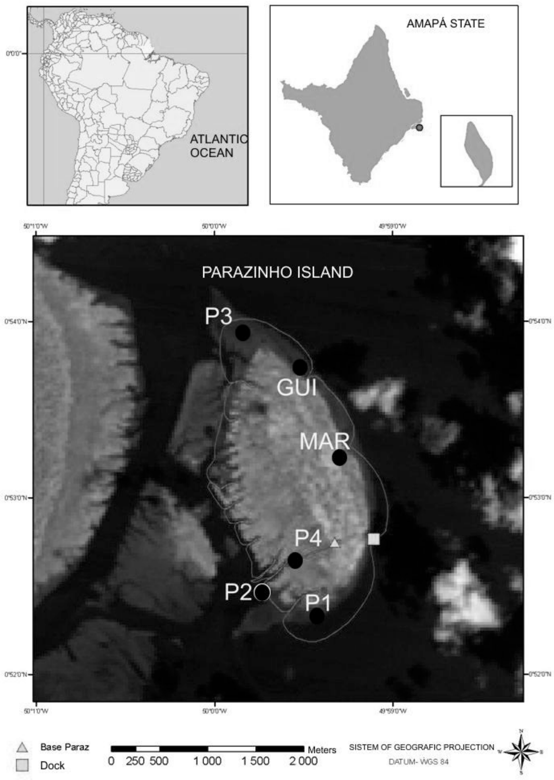
Study area

Parazinho Island (00°52'41.14 "N, 49°59'28.22" W), part of the Bailique Archipelago, is one of the outermost fluvial islands of the northern mouth of the Amazon River, and located in the municipality of Macapá, capital of the state of Amapá, Brazil. With an area of approximately 112 hectares (Figure 1), Parazinho Island was declared a state Biological Reserve (strictly protected conservation unit) by state decree number 005 of January 21st, 1985.

The island's hydrography is made up of drainage channels formed by tidal flooding. These channels are arranged radially, especially in the western portion of the island. The western channels are deep and well defined, resembling rivers during the flood tide, but dry out almost completely during the low tide. In the more open eastern shore of the island, the channels are not so sharply defined, probably due to their greater exposure to waves and erosive processes. The six points sampled in the present study were distributed in distinct portions throughout the perimeter of Parazinho Island (Figure1).

Specimens of Potamotrygon (river rays) were collected during six 7-day expeditions between March 2012 and January 2013: March 2012 (sample 1), May 2012 (sample 2), July 2012 (sample 3), September 2012 (sample 4), November 2012 (sample 5), and January 2013 (sample 6). During each expedition, stingrays were collected at six points around the perimeter of the island (Figure 1). Bottom longlines were installed at all six sampling points and inspected at each low tide. Other capture techniques included cast-nets, harpoons, and the blocking of flooded tidal channels with nets. All captured specimens were anesthetized with Eugenol, sacrificed and dissected for the removal of the stomach, which was fixed in 10% formalin neutralized with calcium carbonate. Each specimen was then fixed in 10% formalin. After a minimum period of seven days, the specimens were washed under running water and transferred to 70% alcohol for long-term preservation in the ichthyological collection of Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (IEPA), Macapá.

Figure 1. Satellite image of Parazinho Island, Amapá, Brazil, showing the six sampling points surveyed during the present study: Points P1-4, MAR = Maruins point and GUI = Guilherme Point.



(Source: SEMA-AP).

The stomach contents of all the specimens were documented and analyzed previously by Gama e Rosa (2015b). Those data are used herein for a new analysis of dietary diversity based on Levins' (1968) index of niche breadth.

The works published by Gama e Rosa (2015b) and Gama (2013) mentioned here showed 6 species found during the study. According to Silva e Carvalho (2015) two of these species were considered synonymous, with *Potamotrygon* *orbignyi* prevailing over *P. dumerilli*. The calculations of the indexes were then corrected by joining the data of the two species.

From the data of stomach content analysis, the niche width (B) and the niche overlap index (Ijk) of Pianka (KREBS, 1989), Schoener (1968) and Colwell e Futuyma (1971) were calculated. Those values were used to evaluate species overlap in the use of the trophic resources.

The trophic and spatial overlap between the five species of Potamotrygon analyzed in the present study was estimated using Pianka's (1973) index of niche overlap:

$$O_{\mathrm{jk}} = O_{\mathrm{kj}} = \frac{\sum_{\mathrm{i}}^{n} p_{\mathrm{ij}} \cdot p_{\mathrm{ik}}}{\sqrt{\sum_{\mathrm{i}}^{n} p_{\mathrm{ij}}^{2} \sum_{i}^{n} p_{\mathrm{ik}}^{2}}}$$

where: $O_{jk} = O_{kj}$ indicates that the index is symmetric, and p_{ij} = the proportion of the resources used by species *j* and p_{ik} = proportions of the resources used by species k.

Here resources were considered in two ways. the locations used by species to define spatial overlap and food items consumed for measuring trophic overlap. This index was calculated in the EcoSim Professional 2012 program (GOTELLI; ENTSMINGER, 2005), with the retention of niche breadth and re-sampling of zeros.

The amplitude of the niche can be measured by the distribution of a given set of resources among the individuals of a species (KREBS, 1989). In the present study, each of the six sampling points was defined as a distinct resource based on its physico-chemical characteristics (KREBS, 1989; Gama; Rosa, 2015a). These data were used to establish a resource matrix, with species arranged in rows and resources in columns (Colwell; Futuyma, 1971). Based on this matrix, the amplitude of the spatial niche of each species was calculated by the standardized Levins' measure (BA) and the percentage overlap between them (KREBS, 1989), as follows:

$$B_{\mathrm{j}} = \frac{1}{\Sigma p_{\mathrm{i}}^{2}}$$

where: B = niche amplitude and pj = the proportion of individuals using resource j.

This index measures the uniformity of the distribution of individuals among resources. It is often useful to standardize niche breadth to a proportion, varying from 0 to 1. This is done by dividing B by the total number of resources:

$$B_{\mathrm{A}} = \frac{B - 1}{N - 1}$$

Where: BA = Levins'standardized niche amplitude, B = Levins'niche amplitude, and N = total number of items.

Here, values < 0.6 indicate a diet dominated by only a few items, consistent with a specialist predator. Values > 0.6 indicate more generalist species (LABROPOULOU; ELEFTHERIOU, 1997).

RESULTS AND DISCUSSION

Three species, *Potamotrygon marquesi*, *P. motoro*, *P. orbignyi*, were recorded throughout the study period; *P. scobina* was recorded during four of the six expeditions; and *P. constellata* was captured only during the first expedition (Table 1). In general, the niche amplitude index recorded for the study species was lower than 0.6, both during the study period as a whole, and in each month. In fact, values higher than 0.6 were recorded only in *P. motoro*, and then, only in two months (May and November). Based on the values of Pianka's index, niche overlap varied considerably among months (Table 2) in terms of both spatial and dietary overlap, as previously reported by Gama (2013).

The combined analysis of the indices of spatial and dietary overlap provided an overview of the potential ecological relationships among the different ray species, indicating possible conditions of competitive stress, with four distinct scenarios of niche overlap and resource partioning (Table 3, Figure 2).

Feeding ecology involves the partitioning of resources with varying levels of interaction among species, especially in

Table 1. Standardized niche amplitude (Levins) recorded for the five species of *Potamotrygon* (river rays) collected during the study period. (# 1 = only one specimen collected, with a single item in the stomach).

	Levins' standardized index (B_A) recorded during each expedition (1–6):						
Potamotrygon species	1 Mar/12	2 May/12	3 Jul/12	4 Sep/12	5 Nov/12	6 Jan/13	Total
P. orbignyi	0.36	0.24	0.32	0.6	0.54	0.27	0.42
P. constellata	0.19	-	-	-	-	-	0.15
P. marquesi	0.30	0.42	0.50	0.52	0.49	0.48	0.30
P. motoro	0.28	0.62	0.42	#1	0.63	0.39	0.33
P. scobina	0.13	-	0.25	-	0.14	0.11	0.32

Table 2. Values of Pianka's index for spatial and dietary overlap among the five species of *Potamotrygon* (river rays) of Parazinho Island along the samples, Amapá, Brazil.

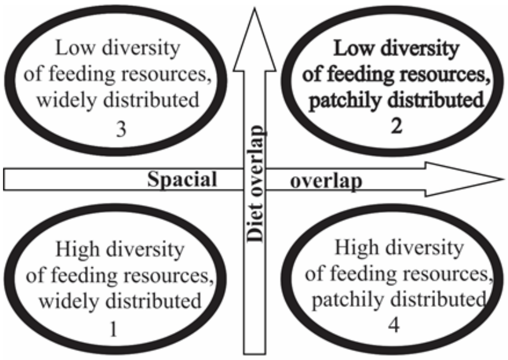
Sample	Number of species	Pianka's overlap index: Spatial	Dietary
1 (March 2012)	5	0.61980	0.46953
2 (May 2012)	4	0.38139	0.79322
3 (July 2012)	4	0.43393	0.17863
4 (September 2012)	4	0.28898	0.30157
5 (November 2012)	4	0.71308	0.54805
6 (January 2013)	4	0.57021	0.32965

Table 3. Combined analysis of the dietary and spatial overlap among the five species of *Potamotrygon* (river rays) studied at Parazinho Island, Amapá, Brazil, and the months during which each proposed scenario was found.

Scenario	Overlap: Dietary	Spatial	Condition	Expected level of resource sharing	Months
1	Low	Low	High diversity of feeding resources, widely distributed	Low	July/September 2012
2	High	High	Low diversity of feeding resources, patchily distributed	High	March/November 2012
3	High	Low	Low diversity of feeding resources, widely distributed	Low	May 2012
4	Low	High	High diversity of feeding resources, patchily distributed	Low	January 2013

environments with high biodiversity. While species of Potamotrygon are anatomically similar and coexist in many water systems, each population may have its own micro-habitat and distinct feeding habits (ALMEIDA et al., 2009). For example, while young Potamotrygon motoro occur in tributaries of both margins of the Negro River, the young of *Paratrygon aiereba* are found only at the mouths of these tributaries, and at nearby sandy beaches; adults of both species occur in the main channel of the river (ARAÚJO, 1998). The same study reported adults and young of *Potamotrygon orbignyi* to be associated with sandy beaches, and more often observed *P. wallacei* (reported as *Potamotrygon* sp.) in "igapós" (blackwater swamp forests) (ARAÚJO, 1998). Such findings indicated that these sympatric species exploit different habitats, feeding grounds, and types of prey, which may contribute to the reduction of competitive interactions.

Figure 2. Diagram of the different scenarios of spatial and dietary overlap among the five species of Potamotrygon (river rays) studied at Parazinho Island, Amapá, Brazil.



Based on Levins' index (Table 1), all of the five species studied have relatively narrow niches (Table I), indicating that they are specialists. *Potamotrygon orbignyi* was the least specialized by having the highest Levin's index (0.42) over the course of the entire study. The variation in the indices between months may reflect fluctuations in the environmental conditions that determine the availability of feeding resources for the river rays.

Samples 2 (May) and 5 (November), respectively, had the highest degrees of dietary overlap. Gama e Rosa (2015b) verified that the dietary overlap in sample 2 was due to the high consumption of shrimp. Shrimp is a resource found throughout the study area. This results in a reduced spatial overlap whereby species can feed at different locations and do not compete directly for the same space (Table 2). In the case of sample 5, the high indices may also be related to the availability of shrimp. But, in this case, the absence of shrimp on the island observed by Gama e Rosa (2015b) may have induced the rays to forage in other places. The site at which the most non-shrimp items were consumed during sample 5 was P4 (Figure 1), the tidal channel on the southwest portion of the island that leads to the headquarters of Biological Reserve. This channel is characterized by an abundance of apple snails (*Pomacea* sp.) and crabs that are present throughout the year. This may at least partially account for the large number of river rays collected at this point (GAMA; ROSA, 2015b), which may also contribute to the spatial overlap among species (Table 2).

The traditional interpretation of patterns of this type is that a significantly small overlap is due to interspecific competition and resource partitioning, whereas a significantly large overlap may indicate shared resource utilization and reduced competition (GOTELLI; GRAVES, 1996). However, high overlap may also reflect strong competition that has not yet resulted in a divergence in resource use. As each scenario is potentially possible, additional data on resource availability and interspecific interactions would be required to provide more definitive insights (SALE, 1974; CONNELL, 1980).

Santos et al. (2004) studied the feeding ecology of sympatric freshwater fish predators *Cichla monoculus* and *Oligosarcus hepsetus*. They found that the trophic niches of these species overlapped considerably (Ojk = 70%), indicating competition for similar feeding resources. Lonardoni et al. (2006) analyzed the diet of sympatric river rays *Potamotrygon motoro* and *P. falkneri* in the Paraná basin. They verified a high degree of niche overlap during the flood period, when feeding resources were abundant, and low overlap during low water, when resources became scarce and species differentiated their diets to avoid competition. Morphologically and/or ecologically similar species can only coexist when they are able to adopt strategies to minimize competition between them, such as the exploitation of distinct dietary items (PIANKA, 1973).

In natural environments where ecologically similar species are sympatric, high spatial and low dietary overlap would be expected, especially when preferred items become scarce. This is because ecologically similar species tend to prefer similar foods, which will increase the potential for interspecific competition, excluding those species less adapted for the exploitation of a given resource. However, competitive interactions normally tend to be avoided (GAUSE, 1934; MacARTHUR, 1972; MATTHEWS, 1998; PIANKA, 2000), allowing the coexistence of species.

When there is low spatial overlap, by contrast, dietary overlap may be expected to be high, given that species in different places are able to exploit the same preferred items. This spatial differentiation can occur in the dimension of the microhabitat, as observed in the present study. A number of different ray species are found on Parazinho Island, although low levels of spatial overlap were recorded during most samples (Table 2), indicating low levels of interspecific co-occurrence at the sampling points. While competition cannot be confirmed by the overlap indices alone, it is possible to confirm that the river ray species present at Parazinho Island share the food resources available in the environment.

Scenario 2 (Table 3), which corresponds to situations in which high levels of interaction are expected, was observed in March and November, which represent the peaks of the flood and dry seasons, respectively. These extreme conditions may influence the availability of resources in the environment, which in turn influences the distribution of the different ray species, resulting in increased spatial and dietary overlap and a greater potential for interspecific interaction.

CONCLUSION

The study of the sharing of food and space resources, when combined, made it possible to understand the degree of interaction between the 5 species of freshwater rays coexisting in REBIO do Parazinho. The observation of the shared use of these resources generated a way to predict the degree of interaction between syntopic species according to their availability in the environment.

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